

Tag use to monitor fish behaviour in aquaculture: a review of benefits, problems and solutions

Macaulay G ^{*1}, Warren-Myers F ¹, Barrett LT ¹, Oppedal F ², Føre M³, Dempster T ¹

¹ Sustainable Aquaculture Laboratory –Temperate and Tropical (SALTT), School of BioSciences, University of Melbourne, Victoria 3010, Australia

² Institute of Marine Research, Matre Aquaculture Research Station, 5984 Matredal, Norway

³ NTNU Department of Engineering Cybernetics, 7491 Trondheim, Norway

*Corresponding author gmacaulay@student.unimelb.edu.au

Keywords: Telemetry, Remote sensing, DST, PIT, Survival, Fish welfare

Abstract

A variety of tagging techniques are now available to monitor fish behaviour, physiology, and their environmental experience. Tagging is frequently used in aquaculture research to monitor free-swimming individuals within farmed populations. However, for information gathered from tagged fish to be representative of farmed populations, tagging must not fundamentally affect fish behaviour, physiology, or survival. Here, we systematically review studies that used tags to monitor farmed fish behaviour and test factors that affect tag retrieval and tag-related mortality. Most studies using tags assessed movement and

swimming behaviour in salmonids, predominantly in Europe and North America. Mortality of tagged fish was 10 times higher in sea-cages (mean = 25%, range = 0-61.5%, n = 22 studies) than in tanks (mean = 2.5%, range = 0-17%, n = 23 studies), while mortality of tagged fish in sea-cages was markedly higher in longer trials (from 4% in single day trials to 36% after 100 days). Higher-than-usual mortality rates among tagged fish, together with largely unknown sub-lethal effects on behaviour, should caution against using tagging studies to make decisions related to farm management. Moreover, key metrics such as mortality rates of tagged and untagged fish or evidence of sublethal effects are often unreported. We make several recommendations to improve future tagging studies and increase transparency in reporting. A greater insight into the causes of tagged fish mortality in sea-cages is required to secure animal welfare and data validity in studies that use tags to assess fish behaviour in aquaculture.

Introduction

Tagging technology has revolutionised the way researchers study animal behaviour. Now, with the miniaturisation of tags, data storage capability with efficient flash memory, satellite detectability, extended battery life and the capacity for telemetry tags to relay environmental, behavioural, and physiological data in real-time, information about individual animal behaviour has never been so easily accessible (Hussey *et al.* 2015). For fish especially, the use of tags has been essential in gleaning information about these otherwise difficult to observe animals (Lucas & Baras 2000). Tags developed for studying wild fish behaviour are largely created with the purpose of long-term monitoring of free-swimming fish, with the goal of conservation or fisheries management (Crossin *et al.* 2017). For instance, tags have

revealed important insights into mortality rates of wild fish (Paulik 1963; Linard & Matley 2020) and the migration and movement behaviour of bluefin tuna (Block *et al.* 2005), basking sharks (Dewar *et al.* 2018), manta rays (Braun *et al.* 2015) and saithe (Uglem *et al.* 2009). These tags, originally designed for studying wild fish ecology, have now transitioned into the world of farmed fish. Wild fish tagging studies can provide valuable information regarding tagging fish in aquaculture, for instance, many researchers discount the first several days of data post-tagging in the wild to allow time for fish behaviour to return to normal. While wild fish studies can inform tagging practices in aquaculture, the environments of wild and farmed fish differ substantially.

The finfish aquaculture industry has grown significantly over the past three decades. The 'more farmed than captured' milestone was reached for freshwater fish in 1986, diadromous fish in 1997, and the production of marine fishes continues to approach wild capture (FAO 2020). In 2014, fish for consumption raised in aquaculture surpassed wild fisheries (FAO, 2020) and by 2030 aquaculture is predicted to account for two thirds of all fish consumed (WorldBank, 2020). Despite the industry's swift expansion and immense production output, much is still unknown about the behaviour of many farmed fish species. Industrial aquaculture is still in its infancy compared to industrial terrestrial livestock farming, with many more fish species being farmed (Huntingford *et al.* 2011) and many of these being not fully domesticated (Teletchea & Fontaine 2014). As such, there is considerable room for improvement in management and animal husbandry to ensure finfish production is environmentally sustainable and ethically sound. Both public and industry concern for farmed fish welfare is increasing (Noble *et al.* 2018; Bovenkerk & Meijboom 2020). Securing fish welfare can benefit both fish and farmer; as healthy fish have better growth (Huntingford &

Kadri 2014), farmers will spend less on treatments or stock loss associated with fish in poor condition and the shelf life of the final product is longer in less stressed fish. Fish behaviour and welfare are inextricably linked, and changes in behavioural patterns such as feeding, responses to environmental conditions or movement inside the production environment are often indicative of the welfare status of fish. Therefore, improving aquaculture management requires a detailed knowledge of how farmed fish behave.

With hundreds of thousands to millions of individuals cultured at high stocking densities in one farm, effectively tracking fish behaviour in aquaculture is inherently difficult (Føre *et al.* 2018). Typically, farmers will use their own personal experience and visual assessment of fish from the surface or subsurface cameras to monitor how a portion of their stock behave (Skøien 2017). Using data from environmental sensors as a surrogate for behavioural monitoring is also common (Andrewartha *et al.* 2015), with the view that if environmental conditions are typical, so should be the behaviour and welfare of the animals. In addition to traditional methods, different technologies for monitoring group behaviour in aquaculture exist. For instance, sonar can be used in tandem with environmental sensors to provide an instantaneous view of how Atlantic salmon (*Salmo salar*) distribute themselves vertically within sea-cages in response to changes in the cage environment (Oppedal *et al.* 2011a). Other approaches based on optics coupled with machine vision techniques can also provide insight into cage dynamics such as feeding activity (Måløy *et al.* 2019). While such technology is available, it is not commonly used in the industry to monitor general behaviour but is gaining pace as a tool in salmon farming to control and monitor feeding (e.g. www.cageeye.com). However, recent advancements in tagging technology could transform

the way behaviour is monitored in aquaculture as it enables acquiring data histories on the individual level, something optical and hydroacoustic methods cannot do.

Individual based behavioural monitoring has been explored in terrestrial animal agriculture as part of the 'Precision Livestock Farming' (PLF) framework. Farmers implementing PLF use various technologies to continuously monitor the behaviour of individual animals in real-time, so they can take swift action when an animal welfare issue occurs (Berckmans 2014). For example, accelerometers attached to dairy cows monitor the amount of time cows spend lying down; too much time spent lying down indicates lameness and has significant consequences for welfare (Darr & Epperson 2009). This 'smart-farming' approach has recently been adapted to aquaculture (Føre *et al.* 2018). For instance, farmed oysters have been equipped with tags that monitor their cardiac activity (Andrewartha *et al.* 2015). These tagged individuals act as 'sentinels', much like canaries in a coal-mine, with their activity levels representing those of the rest of the population. A similar approach has been advocated for finfish aquaculture (Føre *et al.* 2018) with behavioural monitoring of individuals to inform farm management. Sampling individual fish using tags permits the observation of how individuals behave in their environment within the greater population (Føre *et al.* 2017). Tagging individual 'sentinel fish', could provide welfare related information useful to monitor and manage feeding, parasites and disease, and environmental conditions. However, while using tags can provide useful information, there are challenges.

A primary assumption of this approach is that the behaviour of tagged individuals is representative of untagged individuals. To ensure that this assumption is not compromised, tags must not alter the behaviour or physiology of the tagged individuals to the extent that they no longer represent those of the whole population (Perry *et al.* 2001). Tagging a fish also

requires catching, handling, anaesthesia, tag attachment, and recovery, all of which may change behaviours after release leading to erroneous data (Jepsen *et al.* 2015). In aquaculture, incorrect data could lead to flawed management decisions that negatively impact fish welfare and ultimately production. Furthermore, a tag or tagging procedure that leads to negative sublethal effects creates poor fish welfare. Hence, the effects of tags and tagging on farmed fish should be first understood, and then minimised wherever possible. The 3Rs guidelines for the human use of animals for scientific research include the following: (1) *Replacement*, which encourages removing the use of animals entirely when possible, (2) *Reduction*, which limits the number of animals used for experimentation to a minimum, and (3) *Refinement* which ensures that experimental methods are sophisticated enough so that experimental animals undergo the least amount of suffering possible (Russell & Burch 1959). If tags cause suffering, they should be replaced with other technologies to monitor behaviour. If different methodologies are not appropriate, then the number of tagged fish used should be reduced to the minimum number that still provides relevant results. Finally, tagging methodologies should be *refined* to minimise potential suffering.

There is a broad body of literature on the methods and challenges of tagging wild fish (see reviews by Cooke *et al.* (2011), Thorstad *et al.* (2013) and Brownscombe *et al.* (2019)) which can partly inform best use practices in aquaculture. However, challenges associated with tagging fish in the wild differ to those on a farm. As farmed fish are typically stocked at high densities (Fernö *et al.* 2006), rates of external tag loss may be higher due to interactions with conspecifics or the cage structure. High population densities in spatially static enclosures also promote the swift spread of disease and parasites (Murray & Peeler 2005). Infection of tagging-induced wounds may therefore be more likely to occur in a high-density environment

and may lead to altered behaviour in the tagged fish, rendering it unrepresentative of the farmed population. In addition, common husbandry processes or environmental conditions on farms can induce stress that can suppress the immune system and cause altered behaviour or elevated mortality of tagged individuals if they are already under additional stress from tagging (Sykes *et al.* 2012; Stehfest *et al.* 2017). Aquaculture also forces spatially and seasonally restricted environments on fish, of which may include extreme experiences that normally would be avoided in the wild.

Retrieving tags in aquaculture seems simpler than retrieving tags from the wild, as farmed fish are in confinement. However, if only a few individuals are tagged out of potentially hundreds of thousands of fish in an enclosure, recovering these tags during harvest can be difficult as hundreds of tons of fish must be checked manually or via sensing methods at harvest point or in processing facilities (Føre *et al.* 2017). This is especially true for sea-cage aquaculture, which is conducted in floating cages attached to moorings in the sea that are open to the wider marine environment and the farmer has little control over environmental conditions. In tank aquaculture, which is conducted on-land in closed containment, the farmer can heavily control environmental conditions and may be more likely to retrieve lost tags as they will not fall out of net cages as they might in sea-cage aquaculture.

Tag recovery is arguably more important in aquaculture than in wild fish studies, as an unaccounted-for tag could render an entire batch of fish unsellable, to avoid customers potentially encountering tag components (plastic, metal, fibreglass) in their food. Furthermore, deploying many tagged individuals in one production unit may be unfeasible depending on tag type. Because acoustic telemetry tags (originally designed for wild fish), were not designed to be used in restricted spaces, a concern with using these tags in

aquaculture is that too many acoustic tags using the same frequency may cause signal interference or 'tag clashes' (Kolarevic *et al.* 2016; Martos-Sitcha *et al.* 2019). However, this potential issue can be partly remedied through more advanced signal processing in the receiver unit, optimising receiver deployment and designating unique acoustic frequencies for each cage or tank (Føre *et al.* 2017). Irrespective of these challenges, tags are powerful tools that are becoming more commonly used in aquaculture research to obtain important information about individual farmed fish behaviour.

The unique possibilities and challenges of using fish tags to deliver information on behavioural attributes important for production in aquaculture have received little attention since an early review by Baras and Lagardère (1995). Here, we summarise the different types of tags used to investigate behaviours of fish in farming contexts, assess trends in reporting of data, and analyse factors that affect tagged fish mortality and tag retrieval in fish farms. Building upon our results, we make recommendations about the use of tags as an information gathering tool in aquaculture.

Methods

We searched the *Web of Science* database in May 2020 for publications (from all years) that used tags to study fish behaviour in aquaculture using the following search terms: (aquaculture OR fish farm) AND fish AND behav* AND (tag* OR telemetry OR bio-telemetry OR biotelemetry OR satellite OR bio-log* OR biolog* OR PIT OR remote sensing OR acoustic telemetry OR depth OR movement OR swimming depth OR vertical distribution OR thermoregulation OR habituation). This initial search returned 573 results. These papers were manually checked by title and abstract and eliminated if the subject matter was clearly

unrelated to the search terms, or otherwise after reading the full text. Additional publications missed by our initial search were discovered by examining reference lists of appropriate articles and through additional investigative searches using *Google Scholar* and *Scopus* databases up until August 2020.

Several papers included multiple tagging studies (e.g. multiple species, tag types, cage/tank sizes, cage/tank designs and stocking densities). The data in these papers was split accordingly into separate studies, so the effect of these different aspects of the study on fish mortality could be evaluated (**Table S1**). Studies that gave the number of untagged fish, density, biomass or mentioned the presence of untagged fish were classed as studies where tagged fish were co-located with untagged conspecifics.

Statistics

Beta regression models (betareg package: Cribari-Neto & Zeileis (2009)) in R (version 4.0.2, R Core Team, 2020) were used to test the relationship between two response variables (TagMortality: the mortality rate of tagged fish; TagRetrieval: the proportion of tags retrieved) and predictor variables (see Table 1 for list). Both responses were initially calculated at the level of experimental units (tanks or cages), and then aggregated to study level by computing the mean of all comparable experimental units. Beta regression models were selected after examination of response variable distributions and residuals using the DHARMA package (Hartig 2016). Beta regression models cannot fit proportions of exactly 0 or 1, so where these occurred, we assigned dummy values of 0.0001 or 0.9999, respectively. Where values were reported as a range (e.g. 'stocking density was 22-25 kg/m³') the midpoint of the range was used for the analysis. Studies were proportionally weighted within the model according to the number of experimental units that contributed to the study mean value (i.e. number of tanks

or cages). Many potentially important predictor variables were not ubiquitously reported by tagging studies. We did not include the following variables due to these being under-reported and decreasing the model sample size: fish weight, tag weight, tag volume, tag length.

Predictor variables included in models are listed in **Table 1**. We fitted a set of models for each response variable, each designed to maximise the sample size for a given predictor variable of interest. Final model specifications are outlined in **Table 2**. Analysis of Deviance (Type II Wald X^2 test) was used to test the significance of predictor variables (Anova function, car package: Fox & Weisberg 2019). To test the sensitivity of the findings to particularly influential studies, we fitted models without 2 studies that were outliers in their long duration (Sykes *et al.* (2012) ~1100 days; Jurajda *et al.* (2016) ~730 days). We also fitted models with and without 2 studies that used submerged cages (and reported on tagged fish mortality) (Korsøen *et al.* 2012; Wright *et al.* 2019) to test the sensitivity of findings to submerged cages, which can have high levels of mortality. The final models excluded the two long studies and the two submerged cage studies due to the model being sensitive to their influence. Tanks studies were also excluded in the final models due to the low mortality rates in these environments. Duration of tank and sea-cage studies were of similar length.

The `ggeffects` package (Lüdtke, 2018) was used to predict tagged fish mortality with marginal effects from sea-cage volume.

1. Results

The literature search yielded a total of 83 studies (from 49 research articles) that used tags to monitor behaviour of fish in aquaculture environments, with the first study that used tags to monitor farmed fish behaviour being conducted in 1989 (Gusar *et al.* 1989).

1.1 Study location, species, and experimental units

Most studies were conducted in Europe and North America (Norway (43%), USA (12%), Canada (10%), Fig 1). Sea-cages (of varying sizes) were the most common study environment (61%) followed by tanks (33%) and ponds (6%). Atlantic salmon (*Salmo salar*) was the most studied species, followed by rainbow trout (*Oncorhynchus mykiss*) and Atlantic cod (*Gadus morhua*) (Fig. 2). It was most common for all tagged fish to be monitored in a single cage, tank, or pond (59% of all studies in a single experimental unit, 12% in 2 experimental units, 29% in 3 or more experimental units).

1.2 Study focus

Assessments of movement and swimming behaviour (3D spatial location of fish) were the most common study focus. Response to increasing stocking density and measuring responses to various types of stress were the second and third most prevalent study focuses, respectively. Other areas of focus, addressed by a smaller number of studies, included: feeding behaviour, respiration and swimming activity (e.g. acceleration, tail beat frequency), response to cage designs, parasites, aggression, environmental conditions, surface activity and coping styles (Fig. 3).

1.3 Tag types

Transmitter tags were the most widely used to study behaviour in aquaculture. These transmitter tags provided the following types of data: location of fish in 3-dimensions, swimming trajectory, acceleration, pressure, or muscular activity (Fig. 3). DSTs (Data Storage Tags) were the second most widely used tag, recording a variety of types of data including swimming depth, body temperature, heart rate, gastro-intestinal blood flow and acceleration. 24% of studies that internally implanted telemetry, DST or PIT tags also externally attached non-electronic external marker tags (*External marker tags = coloured tag, Floy, T-bar,

numbered Peterson's discs + opercular loop tag FT4) to the same fish to allow researchers to identify tagged individuals for the purpose of tag retrieval or monitoring tagged individuals via video or direct observation. Three studies used only external marker tags as a method to observe individuals for data collection and did not use an accompanying electronic recording tag (Laursen *et al.* 2011; Bui *et al.* 2013; Staven *et al.* 2019). PIT tags were used for identification of individuals, but also used in combination with PIT antennae to register activity of individuals relating to a behaviour (e.g. surface activity, size-dependent swimming).

1.4 Tag attachment

60% of studies internally attached electronic tags with surgical with surgical implantation into the abdominal cavity (Wright *et al.* 2019), or the dorsal musculature behind the head (Kristiansen *et al.* 2004; Nilsson *et al.* 2013). 19% of studies had internally attached tags with a non-electronic external marker tag also (e.g. Macaulay *et al.* 2020). 20% of studies externally attached tags to the musculature adjacent to the dorsal fin. In final models, tag attachment was not a significant predictor of either tagged fish mortality or tag retrieval (Table 2).

1.5 Fish

1.5.1 Untagged conspecifics

Of the 52 studies that mentioned tagged fish being co-located with untagged conspecifics only 4 reported a measure of mortality of the untagged fish (e.g. Føre *et al.* (2017) reported "less than 5%"; Wright *et al.* (2018) reported "less than 1%"; Leclercq *et al.* (2018) reported "no significant mortalities occurred"; Macaulay *et al.* (2020a) reported only total mortality). This means a baseline mortality rate for untagged (control) fish was lacking throughout majority of studies, making it impossible to compare mortality rates of tagged and untagged fish.

For the studies that presented data on untagged conspecifics (and reported sample sizes per replicate), mean percentage of the entire population that were tagged per unit replicate was 4.9%, with a median of 0.58%. This large difference between the mean and median values reflects the influence of relatively few studies that had a high percentage of tagged fish, where most or all fish were tagged due to the small number of fish used.

1.6 Tagging effects

1.6.1 Sublethal effects

Reporting on the physical effects of tags (e.g. skin/scale loss, necrosis, bacterial infection, fouling) was uncommon and brief when done so. Examples of how these effects were reported in externally tagged fish include: Sykes *et al.* (2012), who reported cases of ripped opercula and chronic skin lesions around the tag attachment site in FT4 opercular loop tagged fish, and reduced growth rates in externally tagged fish compared to PIT tagged fish. Ferrer *et al.* (2020) reported no signs of haemorrhaging or tissue damage in their externally tagged fish. Examples of how physical effects were reported in internally tagged fish include: Bauer and Schlott (2004) reported inflammation surrounding the incision in tagged carp but no 'severe' tissue necrosis after 121 days. Conversely, Rillahan *et al.* (2009) reported no incidences of infection, Føre *et al.* (2017) found no obvious visual signs of impaired health in tagged individuals and Svendsen *et al.* (2020) found no signs of poor wound healing or infection after inspection of tagged fish at the end of the study duration.

Behavioural effects of the tag, such as tag influence on swimming performance (McFarlane *et al.* 2004), were more commonly reported on than physical sublethal effects, but were not reported in great detail when done so. Pilot trials conducted in tanks were used in some studies to determine whether the tag had an effect of fish behaviour (e.g. Rillahan *et al.* (2009)

internal attachment; Stehfest *et al.* (2017) external attachment), while others kept the fish in small containers for longer recovery times prior to deployment in larger sea-cages or ponds to monitor behaviour post-tagging (e.g. Jurajda *et al.* (2016) internal attachment). Some studies reported normal tagged fish growth or food consumption to indicate that tagging had no significant effect on the fish or results; e.g. Rillahan *et al.* (2009) compared behaviour and feeding of cod before and after internal tag implantation in tanks; Kolarevic *et al.* (2016) stated all individuals increased their body weight during this study (after being internally tagged with transmitters and externally tagged with marker tags); Føre *et al.* (2017) found no obvious visual signs of impaired health or lowered growth on the internally tagged individuals identified at slaughter. Korsøen *et al.* (2012), however, reported that internally DST tagged salmon had significantly lower growth in submerged cages compared to control cages with surface access, and that submerged tagged fish exhibited irregular swimming patterns for several days.

16% of studies mentioned the 'tag weight to fish body weight ratio' rule of thumb that states tags should not weigh more than 2% of the fish's weight in air. Of these studies, tag weights ranged from 0.2 – 3 % of the fish's weight in air (Table S1). Recovery time from tag attachment varied widely, from no recovery period (fish placed straight back into experimental cage/tank after tag attachment) to up to 7 days in a recovery area (Table S1).

1.6.2 Mortality

Mean tagged fish mortality across a range of trial durations was 10 times higher in sea-cages (mean \pm SE = 25% \pm 4.07, range = 0-61.5%, n = 22 studies), compared to tank studies (mean \pm SE = 2.5% \pm 1.15, range = 0-17%, n= 23 studies). While mortality was variable in sea cages there was a clear positive correlation between study duration and tagged fish mortality; the

longer the study, the greater the mortality (Fig. 4). Model predictions (TagMortProp ~ UnitVol_m3 + StudyDays, weights = No.treatrep) forecast 3% mortality on day 1 increasing to a predicted 28% mortality on day 100 in for a sea-cage volume of 2000 m³ and up to a predicted 36% mortality on day 100 in a 5000 m³ sea-cage..

33 % of studies did not explicitly report mortality of tagged fish, or only stated there was 'some mortality' but did not give numbers. Only studies that clearly indicated mortality were included in the analyses.

We found no correlation between tag volume, tag weight, or tag:body weight ratio on fish mortality. However, as these tag attributes were not widely reported throughout the studies, the sample size we assessed was small.

1.7 Tag retrieval

Tank data was left out of the final model for tag retrieval, as there was 100% tag retrieval in tank studies. Study duration was the only significant predictor of number of tags retrieved in sea-cages (Table 2). There was a negative relationship between tags retrieved and study duration in sea-cages; the longer the study the less tags were successfully recaptured.

2. Discussion

Our analysis revealed significantly higher rates of tagging-related mortality occurred in sea-cages compared to tanks, and that this effect increased with study duration (Fig. 4). Fewer tags were successfully retrieved at the completion of longer-term studies in sea-cages. These relationships did not occur in tank environments, and therefore reveal a disparity in outcomes when tags are used to record fish behaviour in tanks versus sea-cages. This has clear implications for studies aiming to obtain industry-relevant data on fish behaviour. Few studies

compared tagged fish mortality to untagged fish mortality. Deprived of baseline mortality rates, we cannot truly determine to what extent tagging influences survival.

2.1 Tagging effects

2.1.1 Mortality

The discovery that mortality rates were 10× higher for tagged fish in sea-cages compared to tanks highlights fundamentally different outcomes for fish in these two study environments. This result has several implications for researchers, including: 1) results obtained in tanks may not be generalisable to sea-cage environments, 2) high mortality rates in sea cages experiments calls into question how representative tagged fish are of untagged fish, and 3) with such high mortality rates in sea-cages, tagging in this environment creates significant animal welfare issues. Why such high rates of mortality of tagged fish occur in sea-cage studies, and why it differs from tank studies is unclear. However, experiments conducted in small tanks are typically done under more controlled culture conditions, where researchers can largely prevent poor water quality and adverse events. In comparison, experiments conducted in extensive outdoor systems, such as sea-cages, create exposure to depth and seasonally variable and potentially unfavourable environmental conditions (temperature, salinity, dissolved oxygen, current, pollutants and pathogens, all of which can affect fish behaviour, welfare, and survival). Data first obtained from controlled tank experiments must be ground-truthed at industrial scale if it is to have commercial relevance.

Though mortality was variable in sea-cages between different studies, more tagged fish died as study length increased; the model fit indicated that 36% of tagged fish died by trial day 100 in sea-cage with a volume of 2000 m³. This mortality rate is likely an order of magnitude higher than the average mortality rate experienced by fish in sea cages across 100 days. As an

example, Atlantic salmon mortality over a three-month period would be approximately 3% (Stien *et al.* 2019). Ideally, tagged fish mortality should be within the bounds of the normal mortality rates of untagged fish in the cages. Beyond that, representativeness of the data delivered from tagged fish is questionable. However, it may be argued that the surviving fish have coped after surgery and represent normal behaviour, while the mortalities were not. This is demonstrated in a recent DST heart rate study fish with moribund fish displaying deviating results (Hvas *et al.* 2020b).

Mortality on untagged fish in tagging studies was largely underreported; only 2 of the 49 research articles we reviewed reported the percentage of untagged fish that died over the duration of their studies. Føre *et al.* (2017) reported less than 5% mortality of the untagged fish population, while average tagged fish mortality across both cages and all tag types (acoustic transmitters and DSTs) was 19%. Clearly, there is a large difference between untagged and tagged fish mortality in this study. Wright *et al.* (2019) reported mean mortality of untagged fish was 0.4% in standard cages and 0% of tagged fish. However, mean untagged fish mortality across both fresh and seawater snorkels was 0.5%, while mean tagged fish mortality in these submerged cages was 30%. This stark difference between tagged fish and untagged fish mortality in submerged cages highlights the risks of submerging tagged physostomous fish and indicates that adding additional stressors to tagged fish should be avoided, unless measuring stress responses is the purpose of the study. Without a baseline mortality for untagged fish, it is impossible to compare mortality rates of tagged and untagged fish. These results highlight an urgent need to better understand tag-related mortality in sea cage environments through specific testing of all aspects that could contribute to poor outcomes.

While tags at present have only been used as research tools, the ambition to use them for 'sentinel fish' for real-time monitoring of behaviour to inform management decisions in commercial environments remains (e.g. Føre *et al.* 2018). The high rate of mortality in sea-cage studies challenges the achievability of this concept given the present technology level, both from a welfare and data accuracy/ representativity perspective. Currently, there are issues of an ethical and welfare nature when it comes to tag use in sea-cage finfish aquaculture. An experience that causes elevated rates of mortality is also an experience that causes elevated levels of stress and suffering that ends in mortality. Tagging methods in aquaculture therefore must improve the survival rates of tagged fish to minimise the issue of animal welfare. Future use of data from tagged sub-populations of fish in management decisions related to farm management requires that we first know and understand the causes of mortality and sub-lethal effects of tags on fish behaviour.

2.1.2 Sublethal physical effects

Although reports of sublethal physical effects were uncommon, this does not necessarily mean these effects were not present, but rather may be untested or under-reported. There has been extensive research into wound closure methods following tag insertion for internal attachment in wild fish telemetry. Common sublethal physical effects of following tag insertion include necrosis and inflammation (Lowartz *et al.* 1999; Wagner *et al.* 2000; Wagner & Cooke 2005). Despite Sykes *et al.* (2012) detailing cases of ripped opercular and chronic skin lesions around the tag attachment site in FT4 opercular loop tagged fish, the focus of this study was to explicitly test tagging effects for this tag type. Researchers that are using tags to get answers on behavioural questions may not be as concerned with necrosis or inflammation at the tagging site if the fish's behaviour appears normal throughout the study. Nevertheless,

because an injured or stressed fish may behave differently in the long term and can be more vulnerable to infection due to suppressed immune function (Wagner & Cooke 2005), any sublethal physical effects found on tagged fish should be stated plainly. Tagging technology is continually evolving to increase the capacity for gathering data, whilst simultaneously reducing the burden tags have on their individual bearer. Using smaller tags for future tagging trials will probably contribute to reduce the invasiveness of the procedure, and recent experiments have demonstrated the application of tags weighing as little as 600 mg (Martos-Sitcha *et al.* 2019).

2.1.3 Sublethal behavioural effects

If tags alter the behaviour of tagged fish, then the validity of any data provided by the tag is compromised as is the welfare of the tagged fish. Both Korsøen *et al.* (2012) and Wright *et al.* (2019) studied the behaviour of salmon in surface modified cages using DSTs. Korsøen *et al.* (2012) reported that submerged tagged salmon swam irregularly for several days, while Wright *et al.* (2019) found that DST tagged salmon in depth-modified snorkel cages experienced a 38% mortality rate compared to 0% for tagged individuals in a standard sea-cage. Salmon are a physostomous fish, meaning they require surface access to refill their swim bladder and regulate buoyancy (Fänge 1953). In both studies, the added weight of the tag would reduce the salmon's maximum neutral buoyancy depth, reducing the capacity of the tagged fish to cope in these deep cages with restricted surface access (Macaulay *et al.* 2020b). Similarly, Perry *et al.* (2001) found that tagged Chinook salmon (*Oncorhynchus tshawytscha*) swam shallower than untagged conspecifics. In studies on wild salmonid smolts, concerns around tag weight negatively affecting fish lead to the largest individuals being chosen for tagging (Newton *et al.* 2016). Because fish size influences smolt survival, initially choosing only

the largest fish for tagging biases results and leads to erroneous representations of true behaviour and survival (Deng *et al.* 2015). Stehfest *et al.* (2017) asserted that 'only tagged fish that fully regained balance and responded to manual agitation after recovery were released back into the cage' in their study, although they did not report how many fish were unable to regain balance fully, or comment on whether the fish that regained balance were truly representative of the untagged population. Clearly, tags can influence buoyancy in fish, and so affect their behaviour and survival rate, which has inherent consequences for the validity of the data derived from tags as well as the welfare status of the tagged fish.

2.1.4 Tag:fish weight rule

Through our literature search, 9 research articles mentioned the tag:fish weight ratio. This general rule-of-thumb, originating from wild fish telemetry studies in the 1980s (Winter 1983), states that a tag should not weigh more than 2% of the fish's weight in air, to reduce negative impacts of tag weight on buoyancy, balance and swimming ability (Adams *et al.* 1998). Researchers often state this rule to imply that the tagging procedure did not affect the findings of their study. However, there are arguments against widely employing this rule across fish taxa (Jepsen *et al.* 2005; Cooke *et al.* 2011). For instance, tags weighing up to 12.7-14 % of Atlantic salmon smolt and post-smolt weight have been used for migration studies, with no reported negative effects on survival (Lefèvre *et al.* 2013; Newton *et al.* 2016). However, other studies indicate that higher tag weight to body weight ratios reduce fish growth (juvenile Atlantic salmon: Larsen *et al.* (2013); lake sturgeon *Acipenser fulvescens*: Sutton and Benson (2003)). Nonetheless, tag weight alone is a poor scale on which to base expectations of the effect of tags on fish behaviour and physiology, as two tags that have identical weights in air can have very different densities, affecting tagged fish buoyancy

accordingly (Brown *et al.* 1999). Of the studies found through our systematic review, 40% reported tag weight in air, 17% reported tag weight in water, and 56% reported tag length and diameter, such that tag volume could be calculated (Table S1). Tag volume is also important. An internally implanted tag that is neutrally buoyant but has a large volume will take up more space in the body cavity, pressing on vital organs, potentially also sutures, and could reduce swim bladder capacity (Macaulay *et al.* 2020b). A large neutrally buoyant tag that is externally attached could cause significant drag or epidermal damage (Brown *et al.* 1999; Jepsen *et al.* 2015). In addition, measuring fish weight in water (or fish body density) is important. As fish weigh much less in water, basing tag weight on fish weight in air may still cause negative effects on fish buoyancy (Macaulay *et al.* 2020b). Evidently, the tag:fish weight rule should be used with caution. Other more relevant tag and fish measurements discussed above will likely give a better indication of the effects of the tag's physical characteristics on fish physiology and behaviour.

2.2 Study focus

Because tagging is a rather invasive means to gather behavioural data, other methods should be considered before tagging is chosen, if they can deliver suitable data to answer the research question. The first principle of the 3Rs guidelines for the human use of animals for scientific research, is Replacement, which encourages removing the use of animals entirely when possible (Russell & Burch 1959). This principle should be the foundation of tag use, especially in aquaculture where tagged fish mortality rates are presently too high (Fig. 3). As Brownscombe *et al.* (2019) states, 'studies that involve tagging animals simply for the sake of tagging' should be avoided. Most studies used telemetry tags to study movement and swimming behaviour, highlighting that tags are frequently used to track how fish use space in

fish farms. Many of these studies simply used tags to track the swimming depth of individual tagged fish (e.g. Johansson *et al.* 2009; Korsøen *et al.* 2012; Stehfest *et al.* 2017; Wright *et al.* 2019). Combining this individual-based data to explain behaviour of a group of animals is not the best use of tags when less intrusive technologies are available to measure group-based behaviours, such as depth distribution or biomass measurements. For example, echo-sounder technology has been used effectively in several studies to study the swimming depth distribution of salmon in sea-cages (for review see Oppedal *et al.* (2011b)). Although the echosounders used so far cannot deliver fine-scale measurements of parameters such as swimming speed, acceleration or movement in the horizontal plane, many studies do not require this type of data to answer questions about vertical distributions or swimming densities in production units. Camera systems can be of great value in gathering data on behaviours that echo-sounders cannot. Furthermore, setting up a tagging experiment can be more logistically challenging than using alternative technologies. An example of an unused technology in aquaculture is the split-beam technology used in fisheries, which can track individuals within schools over short time periods and give representative measures of individual behaviours in the 3D plane (e.g. Handegard 2007) and even tail-beat frequency (Handegard *et al.* 2009).

When other less-invasive technologies cannot provide the fine-scale individual data needed to answer a research question, applying tagging technology using more innovative and rigorous approaches can yield deeper insights. For example, Nilsson *et al.* (2013) tagged different sized salmon with PIT tags and deployed PIT registering antennae at different depths. To discover previously unknown size-dependent vertical distribution of farmed salmon, with larger fish generally swimming deeper. These results have direct consequences

for size sampling at farms, as sampling fish from one depth only, will likely mean one size class is over-represented (Folkedal *et al.* 2012). Deciding whether a study would really benefit from tag data is an important consideration for aquaculture behavioural research.

2.3 Tag types

Different tag types each come with their own advantages and limitations. Tag type selection will largely depend on research question, type of data required and the study species and environment. Telemetry tags were used more often than DSTs, indicating the benefits of obtaining data wirelessly via transmission. Real-time relay of behavioural or physiological data means that farmers could monitor behaviour and make immediate management decisions (Berckmans 2014). This type of tag use relates back to the concept of ‘sentinel’ animals in livestock farming, where individuals act as representatives for the wider population (Andrewartha *et al.* 2015). However, since this concept is yet to be applied in the aquaculture industry, the advantage of not necessarily having to recapture tagged fish to gather data is likely what resulted in the preference for this tag type. In comparison, data from DSTs cannot be remotely collected so the tag must be retrieved to access the data. Despite this, DSTs can still provide valuable information, for instance in the form of high-resolution data that may shed light on fish recovery after surgery. Heart-rate DSTs have shown that the heart rate of tagged Atlantic salmon did not return to baseline levels for 4 days on average (up to 6 days) after surgery and anaesthesia (Føre *et al.* 2020). This has implications for interpretation of data from transmitters or other electronic tags, as for salmon at least, the first weeks of data may be unrepresentative of untagged fish. Similarly, in telemetry studies on wild fish, researchers often discount the first few days of data to allow fish to return to baseline behaviours. Heart rate patterns in moribund fish, caused by the surgery procedures, deviated

largely from normal fish and stresses the variable representativity of HR in following trials (Hvas *et al.* 2020b). Furthermore, DSTs can validate behavioural data gathered at the group level by other methods (e.g. echosounders), such as environmental preference seeking (Johansson *et al.* 2009).

While PIT tags technically fall under the telemetry tag category, they are more often used to simply identify individuals due to their small size and limited capacity to relay more complex data. However, their application to study behaviour is increasing. As PIT tags are quick to insert, do not require sutures and are generally small (24 mm max), negative physical effects of PIT tags are assumed to be less common than for larger electronic tags, however, dependent on fish and PIT tag size PIT tags can still have adverse outcomes for fish welfare (Vollset *et al.* 2020). Although PIT tags cannot provide information such as heart rate or muscular activity, using these lightweight tags in more creative ways can yield insight to individual fish behaviour. For example, counting registrations of individuals at PIT antennae has shed light on feeding habits and coping styles of halibut (Kristiansen & Fernö 2007), the learning ability of salmon to refill their swim bladder at underwater air domes (Macaulay *et al.* 2020a), and the spatial learning skills of mulloway (*Argyrosomus japonicus*). However, PIT tag use is limited by the short detection range (only a few cm), one tag occupying the detection range can block other tags from being detected, and that when tags approach antennae diagonally, identification of the tag's unique code may fail to be registered (Brännäs & Alanära 1993; Baras & Lagardère 1995) and their use in small fish can lead to increased mortality and tag loss (Vollset *et al.* 2020).

External non-electronic marker tags were commonly used in addition to the transmitter or DST to aid in the identification of tagged individuals (20% of studies). Non-electronic external

markers dimensions were not widely reported (Table S1) as coloured T-bar anchor tags are light and small and thus thought not to affect fish buoyancy greatly. T-bar tags that are inserted into the dorsal musculature require extra handling and on top of internal surgery. While we did not find that fish tagged with both external markers and internal surgery suffered higher rates of mortality (Table 2), it does not mean that external marker dimensions should not be reported on more thoroughly. Three studies used only physical marker tags to identify individuals and make behavioural observations directly. This method of tagging for behavioural studies relies on being able to see the tag clearly either directly or via video, and so is often conducted in lab conditions or with few other conspecifics, and therefore is inapplicable at commercial scale.

2.4 Tag attachment

Tag attachment method did not predict tagged fish mortality or tag retrieval. However, as most studies (83%) used internal attachment via surgical implantation, the sample size of studies using externally attached electronic tags was too small to provide robust insights on comparative effects of internal and external tags. In wild fish studies, tag retention is species specific, dependent on behaviour, physiology, and environment (Baras & Lagardère 1995; Bridger & Booth 2003). Regardless of species, both external and internal attachment methods have some general advantages and disadvantages. Arguably, surgical implantation is the most invasive method of tagging. Fish must endure complete anaesthesia, ventral cuts, insertion of a foreign body near vital organs, suturing, and a higher risk of infection compared to other attachment methods (Jepsen *et al.* 2002). Historically, the positives of internally tagging are that tags are often closer to the fish's centre of gravity, interfering less with balance, and largely have longer retention times compared to external tags (Baras & Lagardère 1995),

although we did not find longer retention times for internal tags in this review. Advantages of external tags include quicker attachment and handling times and tagged fish being easily visible (Bridger & Booth 2003). However, external tags can affect balance and cause drag (Thorpe *et al.* 1981; Jepsen *et al.* 2015), and in high velocity waters or with constantly high speed swimming species, extended periods of drag can erode dorsal muscles (Baras & Lagardère 1995). Moreover, external tags can cause irregular swimming and scraping behaviour and are more prone to being entangled in structures (Collins *et al.* 1999). Larger external tags influence the amount of inflammation and damage to the epidermis at the site of attachment (Thorstad *et al.* 2000). Furthermore, externally tagged fish may be more prone to stress during common husbandry practices that involve crowding, which could ultimately lead to death (e.g. Sykes *et al.* (2012)). It is likely that the perceived disadvantages of external electronic tags resulted in a preference for internal tagging for monitoring fish behaviour at farms.

2.5 Tag retrieval and data loss

As expected, tag retrieval decreased with study duration in open sea cages compared to tanks where 100% retrieval is possible. We did not include tags that malfunctioned or provided corrupt data in the 'lost' tags category, meaning that the number of useable tags is often even smaller than the total number retrieved. Mortality also results in loss of useable data in many studies. A combination of tag loss, tag malfunction and mortality can lead to studies having a very low data capture success rate. For example, Johansson *et al.* (2009) implanted 58 salmon with DSTs to measure the effect of different stocking densities on how salmon respond to thermal stratification in sea-cages. A total of 30 out of 58 DST tagged salmon were retrieved (15 were dead or undiscovered, 13 fish with tag loss). However, only 12 retrieved tags were

useable in the normal-density group, and a total of 11 tags were useable in the high-density group, across replicates. This means that only 23 of the original 58 tagged fish (~40%) were retrieved with useable data. Similarly, Solstorm *et al.* (2018) used only 50% of tag data in final analyses. Bauer and Schlott (2004) reported that 3 out of 4 tags stopped working during one trial period intended to observe overwintering behaviour of carp in a pond. Given the amount of useable data that long-term tagging studies can provide, together with higher instances of mortality as study length increases, the present application of tags in commercial aquaculture as a monitoring tool should be limited to short-term use, with the caveat that study length must be greater than recovery time.

2.6 Recommendations for future research to improve tagging in farm environments

Our results reveal a significant knowledge gap regarding tagging protocols for aquaculture which consistently lead to low mortality rates. This needs to be remedied to secure the welfare of tagged fish and reliability of data produced from tagging in production settings. A first step toward this should be targeted research around the effects of (1) characteristics of the tag itself, (2) various aspects of the tag attachment procedure; and (3), how this interacts with a variety of biotic aspects of fish in production environments. In Table 3 we make a series of recommendations for more accurate and transparent reporting of tag use and outcomes for behavioural studies in aquaculture environments that should enable more robust assessments of data quality.

Studies that compare physical condition, growth, behaviour, and morphology between tagged and untagged conspecifics, as well as sham fish (that undergo a 'tagging procedure' without the insertion/attachment of the tag), are required. An additional handling treatment with no surgery (just handling and anaesthetic) would also be of value to determine the

impact of handling and anaesthesia only. Contrasting the effect of biotic factors (such as life-stage, sex and source of fish) on the severity of negative tagging effects is also vital (Bridger & Booth 2003). Additionally, investigating the effects of common events unique to the farm environment, such as various husbandry and farm operations, on physiology and behaviour should shed light if it is appropriate to carry out these routine procedures with tagged fish present. Aside from comparing the adverse effects of tagging between tagged, sham and untagged fish, testing different features of the tagging procedure will be important, including anaesthesia, attachment methods, incision sites, wound closures, sterility, antibiotic use, surgeon experience, recovery time and tag coatings (Bridger & Booth 2003; Cooke *et al.* 2011). Furthermore, understanding the effects of essential abiotic factors such as dissolved oxygen levels, pH, salinity, and temperature of water on the outcome of surgery is important (Cooke *et al.* 2011).

A better understanding of the factors that contribute to sublethal or lethal tagging effects in an industrial setting will help to reduce adverse consequences of tagging. Based on our findings, tagged fish in sea-cage culture environments had worse outcomes. This is a challenging result for the use of these tags to monitor behaviour in industrial aquaculture settings. Mariculture continues to use even larger cages (e.g. Oldham *et al.* (2018)), with interest growing in placing these cages in more exposed locations, further away from populated coastlines to increase production and reduce adverse ecological impacts associated with nearshore farms, such as disease and parasites (Froehlich *et al.* 2017). Thus, further research is required if the approach of using tags to aid behavioural monitoring is to succeed in these future farming environments.

2.6.1 Experimental design

When planning a tagging study in aquaculture, a clear research question is essential. What do you want to know about farmed fish behaviour? Will the data that a tag provides be suitable (and necessary) to answer that question? Wasted time, effort and resources can result from inadequately planned studies that do not have clear aims and that simply use tags for the sake of using tags (Koehn 2012; Brownscombe *et al.* 2019). While wasting time and money can be costly for research, it is also costly for the fish.. The ethical and welfare issues associated with putting fish through the stressful event of tagging that increases their likelihood of experiencing sublethal and lethal effects to provide data that might be unusable is unacceptable. Replacing the use of tagged fish when possible with alternative technologies (e.g. with cameras, echosounders) must be considered before tags are employed in aquaculture settings.

We found that 59% of studies had all tagged fish in a single cage, tank, or pond. Not all work in a single experimental unit is designed poorly, especially if the authors are not generalising their results to situations outside of that unit, such as for proof-of-concept work. However, it is inappropriate to make generalisations about fish behaviour in many cages or many farms using data from just one cage. Increased replication of experimental units (sea-cages, tanks, ponds) is then needed and we caution against using multiple individual tagged fish in one production unit as pseudo-replicates. A minimum of three replicates per treatment is advised, with more being desirable. For example, Føre *et al.* (2017) used two sea-cages within close proximity of each other, with comparable stocking densities, environment conditions and farm management in their study testing the concept of using acoustic tagged fish as ‘sentinels’ for commercial salmon aquaculture. They found that individual behaviour and vertical distribution of tagged fish differed between the two similar and co-located replicate cages.

On average, tagged fish represented 4.9% (median 0.6%) of the entire population per unit replicate (among studies that reported numbers of untagged conspecifics). Increasing the number of tagged fish per unit replicate would increase sample size and representativeness, but this must be balanced against the animal welfare and research costs of tagging unnecessarily large numbers of fish. Furthermore, looking at the correlation between tag retrieval and study duration, more research is needed to ensure there is less tag loss over time, opposed to simply adding more tagged fish to compensate for tag loss.

2.6.2 Reporting on tagging effects

Transparency is necessary when reporting on mortality in tagging studies (Klinard & Matley 2020). In Table 3, we make a series of recommendations for what study aspects to report on for research using tags to monitor farmed fish behaviour in aquaculture environments. Firstly, if there was no mortality of tagged fish, this should be stated clearly. Secondly, if there is mortality during the tagging procedure, the number of individuals that died should be stated to highlight the potential negative effects of the tag, tagging method or combination of both. Only considering fish that survived may lead to bias, as these survivors could exhibit tag related morbidity and thus might not be representative of the whole untagged population. Reporting on the mortality rate of untagged fish is also crucial. Without knowledge of standard mortality among untagged individuals, we cannot know how much tagging influences survival. This unique opportunity exists in aquaculture, as mortality is recorded frequently at fish farms (it is much more difficult to estimate mortality of untagged wild fish). Any sublethal physical effects found on tagged fish should also be stated plainly, because an injured or stressed fish may behave differently in the long term, and sublethal behavioural effects (e.g. scraping, swimming behaviour) should be reported for the same reason.

Tagging technology is becoming increasingly more available, affordable, and more sophisticated. Simultaneously, the negative effects of these tags should decrease as tags evolve and become more miniaturised and attachment methods less invasive in the future. Currently, tagging is still a stressful experience for fish. Researchers using tags should be aware of the potential lethal and sublethal effects of tags on fish behaviour in aquaculture and how these deviations from normal behaviour can bias results and create poor welfare. Through a better understanding of the negative effects of tags, a best practice for tagging in production environments can be established, leading to the improved welfare and data validity of tagged fish.

Acknowledgments

This study was funded by the University of Melbourne, and the Norwegian Research Council through the Centre for Research-based Innovation in Aquaculture Technology, EXPOSED (237790) and project Future Welfare (267800). We thank members of the SALTT lab for comments on the manuscript.

References

- Adams NS, Rondorf DW, Evans SD, Kelly JE (1998) Effects of surgically and gastrically implanted radio transmitters on growth and feeding behavior of juvenile Chinook salmon. *Transactions of the American Fisheries Society* **127**: 128-136.
- Andrewartha S, Elliott N, McCulloch J, Frappell P (2015) Aquaculture sentinels: smart-farming with biosensor equipped stock. *Journal of Aquaculture Research & Development* **7**: 1-4.
- Baras E, Lagardère J-P (1995) Fish telemetry in aquaculture: review and perspectives. *Aquaculture International* **3**:77-102.
- Bauer C, Schlott G (2004) Overwintering of farmed common carp (*Cyprinus carpio* L.) in the ponds of a central European aquaculture facility—measurement of activity by radio telemetry. *Aquaculture* **241**:301-317.
- Berckmans D (2014) Precision livestock farming technologies for welfare management in intensive livestock systems. *Rev. Sci. Tech* **33**: 189-196.
- Block BA, Teo SL, Walli A, Boustany A, Stokesbury MJ, Farwell CJ *et al.* (2005) Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* **434**: 1121-1127.
- Bovenkerk B, Meijboom F (2020) *Ethics and the Welfare of Fish*. Pages 19-42 in Kristiansen TS, Fernö A, Pavlidis MA, and van de Vis H, editors. *The Welfare of Fish*. Springer International Publishing, Cham.
- Brännäs E, Alanärä A (1993) Monitoring the feeding activity of individual fish with a demand feeding system. *Journal of Fish Biology* **42**: 209-215.

Braun CD, Skomal GB, Thorrold SR, Berumen ML (2015) Movements of the reef manta ray (*Manta alfredi*) in the Red Sea using satellite and acoustic telemetry. *Marine Biology* **162**: 2351-2362.

Bridger CJ, Booth RK (2003) The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. *Reviews in Fisheries Science* **11**: 13-34.

Brown RS, Cooke SJ, Anderson WG, McKinley RS (1999) Evidence to challenge the “2% rule” for biotelemetry. *North American Journal of Fisheries Management* **19**:867-871.

Brownscombe JW, Lédée EJ, Raby GD, Struthers DP, Gutowsky LF, Nguyen VM *et al.* (2019) Conducting and interpreting fish telemetry studies: considerations for researchers and resource managers. *Reviews in Fish Biology and Fisheries* **29**:369-400.

Bui S, Oppedal F, Korsøen ØJ, Dempster T (2013) Modifying Atlantic salmon behaviour with light or feed stimuli may improve parasite control techniques. *Aquaculture Environment Interactions* **3**:125-133.

CageEye (2020) (web archive link, 29 August 2020). Available from URL: <https://www.cageeye.com> [Cited 29 August 2020].

Collins MR, Cooke DW, Smith TI (1999) Telemetry of shortnose and Atlantic sturgeons in the southeastern USA. Proceedings of the 15th International Symposium on Biotelemetry 1999 May 9 (pp. 145-53).

Cooke SJ, Woodley CM, Eppard MB, Brown RS, Nielsen JL (2011) Advancing the surgical implantation of electronic tags in fish: a gap analysis and research agenda based on a review of trends in intracoelomic tagging effects studies. *Reviews in Fish Biology and Fisheries* **21**:127-151.

Cribari-Neto F, Zeileis A (2009). "Beta Regression in R." *Journal of Statistical Software*, 34(2), 1–24. <http://www.jstatsoft.org/v34/i02/>.

Crossin GT, Heupel MR, Holbrook CM, Hussey NE, Lowerre-Barbieri SK, Nguyen VM *et al.* (2017) Acoustic telemetry and fisheries management. *Ecological Applications* **27**:1031-1049.

Darr M, Epperson W (2009) Embedded sensor technology for real time determination of animal lying time. *Computers and Electronics in Agriculture* **66**:106-111.

Deng Z, Carlson TJ, Li H, Xiao J, Myjak MJ, Lu J *et al.* (2015) An injectable acoustic transmitter for juvenile salmon. *Scientific Reports* **5**:1-6.

Dewar H, Wilson SG, Hyde JR, Snodgrass OE, Leising A, Lam CH *et al.* (2018) Basking Shark (*Cetorhinus maximus*) Movements in the Eastern North Pacific Determined Using Satellite Telemetry. *Frontiers in Marine Science* **5**:163.

Fänge R (1953) The mechanisms of gas transport in the euphysoclist swimbladder. *Acta physiologica Scandinavica. Supplementum* 30:1-133.

FAO (2020) *The State of World Fisheries and Aquaculture 2020. Sustainability in action.* Rome. <https://doi.org/10.4060/ca9229en>

Fernö A, Huse G, Jakobsen P, Kristiansen T 2006. *The Role of Fish Learning Skills in Fisheries and Aquaculture.* Blackwell Publishing, Oxford.

Ferrer MA, Calduch-Giner JA, Díaz M, Sosa J, Rosell-Moll E, Abril JS (2020) From operculum and body tail movements to different coupling of physical activity and respiratory frequency in farmed gilthead sea bream and European sea bass. Insights on aquaculture biosensing. *Computers and Electronics in Agriculture* **175**:105531.

Folkedal O, Stien LH, Nilsson J, Torgersen T, Fosseidengen JE, Oppedal F (2012) Sea caged Atlantic salmon display size-dependent swimming depth. *Aquatic Living Resources* **25**:143-149.

Føre M, Frank K, Dempster T, Alfredsen JA, Høy E (2017) Biomonitoring using tagged sentinel fish and acoustic telemetry in commercial salmon aquaculture: A feasibility study. *Aquacultural Engineering* **78**:163-172.

Føre M, Frank K, Norton T, Svendsen E, Alfredsen JA, Dempster T *et al.* (2018) Precision fish farming: A new framework to improve production in aquaculture. *Biosystems Engineering* **173**:176-193.

Føre M, Svendsen E, Økland F, Gräns A, Alfredsen JA, Finstad B *et al.* (2020) Heart rate and swimming activity as indicators of post-surgical recovery time of Atlantic salmon (*Salmo salar*).

Fox J, Weisberg S (2019). An R Companion to Applied Regression, Third edition. Sage, Thousand Oaks CA. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.

Froehlich HE, Smith A, Gentry RR, Halpern BS (2017) Offshore aquaculture: I know it when I see it. *Frontiers in Marine Science* **4**:154.

Gusar A, Barus V, Pavlov D, Gajdusek J, Halacka K (1989) The results of ultrasonic telemetry of the carp, *Cyprinus carpio*, in a wintering pond during the winter period. *Folia zoologica (Brno)*, **38**, 87-95.

Handegard NO (2007) Observing individual fish behavior in fish aggregations: tracking in dense fish aggregations using a split-beam echosounder. *The Journal of the Acoustical Society of America*. **122**: 177-187.

Accepted paper, please cite as: Macaulay G, Warren-Myers F, Barrett LT, Oppedal F, Fore M, Dempster T. Tag use to monitor fish behaviour in aquaculture: a review of benefits, problems and solutions. *Reviews in Aquaculture*, 18. DOI: <https://doi.org/10.1111/raq.12534>

Handegard NO, Pedersen G, Brix O (2009) Estimating tail-beat frequency using split-beam echosounders. *ICES Journal of Marine Science*. **66**: 1252-1258.

Hartig F (2016). DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.1.1. <https://github.com/florianhartig/DHARMA>

Huntingford F, Jobling M, Kadri S (2011) *Aquaculture and Behavior*. John Wiley & Sons, Chichester, UK.

Huntingford F, Kadri S (2014) Defining, assessing and promoting the welfare of farmed fish. *Revue scientifique et technique* (International Office of Epizootics) **33**:233-244.

Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT *et al.* (2015) Aquatic animal telemetry: a panoramic window into the underwater world. *Science* **348**:1255642.

Hvas M, Folkedal O, Oppedal F (2020a) Heart rate bio-loggers as welfare indicators in Atlantic salmon (*Salmo salar*) aquaculture. *Aquaculture* **529**: 735630.

Hvas M, Folkedal O, Oppedal F (2020b) Heart rates of Atlantic salmon *Salmo salar* during a critical swim speed test and subsequent recovery. *Journal of Fish Biology* in press.

Jepsen N, Koed A, Thorstad EB, Baras E (2002) Surgical implantation of telemetry transmitters in fish: how much have we learned? *Aquatic Telemetry* (pp. 239-248). Springer, Dordrecht.

Jepsen N, Schreck C, Clements S, Thorstad E. 2005. A brief discussion on the 2% tag/bodymass rule of thumb. *Aquatic Telemetry: Advances and Applications*. **3**:255-259.

Jepsen N, Thorstad EB, Havn T, Lucas MC (2015) The use of external electronic tags on fish: an evaluation of tag retention and tagging effects. *Animal Biotelemetry* **3**:49.

Johansson D, Ruohonen K, Juell J-E, Oppedal F (2009) Swimming depth and thermal history of individual Atlantic salmon (*Salmo salar* L.) in production cages under different ambient temperature conditions. *Aquaculture* **290**:296-303.

Jurajda P, Adámek Z, Roche K, Mrkvová M, Štarhová D, Prášek V *et al.* (2016) Carp feeding activity and habitat utilisation in relation to supplementary feeding in a semi-intensive aquaculture pond. *Aquaculture International* **24**:1627-1640.

Klinard NV, Matley JK (2020) Living until proven dead: addressing mortality in acoustic telemetry research. *Reviews in Fish Biology and Fisheries*. **30**: 485–499.

Koehn JD (2012) Designing studies based on acoustic or radio telemetry. Telemetry techniques: a user guide for fisheries research. *Maryland: American Fisheries Society* pp. 45-87

Kolarevic J, Aas-Hansen Ø, Espmark Å, Baeverfjord G, Terjesen BF, Damsgård B (2016) The use of acoustic acceleration transmitter tags for monitoring of Atlantic salmon swimming activity in recirculating aquaculture systems (RAS). *Aquacultural Engineering* **72**:30-39.

Korsøen ØJ, Dempster T, Oppedal F, Kristiansen TS (2012) Individual variation in swimming depth and growth in Atlantic salmon (*Salmo salar* L.) subjected to submergence in sea-cages. *Aquaculture* **334**: 142-151.

Kristiansen TS, Fernö A (2007) Individual behaviour and growth of halibut (*Hippoglossus hippoglossus* L.) fed sinking and floating feed: evidence of different coping styles. *Applied Animal Behaviour Science* **104**:236-250.

Kristiansen TS, Fernö A, Holm JC, Privitera L, Bakke S, Fosseidengen JE (2004) Swimming behaviour as an indicator of low growth rate and impaired welfare in Atlantic halibut (*Hippoglossus hippoglossus* L.) reared at three stocking densities. *Aquaculture* **230**:137-151.

Larsen MH, Thorn AN, Skov C, Aarestrup K (2013) Effects of passive integrated transponder tags on survival and growth of juvenile Atlantic salmon *Salmo salar*. *Animal Biotelemetry* **1**:1-8.

Laursen DC, Olsén HL, de Lourdes Ruiz-Gomez M, Winberg S, Höglund E (2011) Behavioural responses to hypoxia provide a non-invasive method for distinguishing between stress coping styles in fish. *Applied Animal Behaviour Science* **132**:211-216.

Leclercq E, Zerafa B, Brooker AJ, Davie A, Migaud H (2018) Application of passive-acoustic telemetry to explore the behaviour of ballan wrasse (*Labrus bergylta*) and lumpfish (*Cyclopterus lumpus*) in commercial Scottish salmon sea-pens. *Aquaculture* **495**:1-12.

Lefèvre M, Stokesbury M, Whoriskey F, Dadswell M. 2013. Migration of Atlantic salmon smolts and post-smolts in the Rivière Saint-Jean, QC north shore from riverine to marine ecosystems. *Environmental biology of fishes* **96**:1017-1028.

Lowartz S, Holmberg D, Ferguson H, Beamish F (1999) Healing of abdominal incisions in sea lamprey larvae: a comparison of three wound-closure techniques. *Journal of Fish Biology* **54**:616-626.

Lucas MC, Baras E (2000) Methods for studying spatial behaviour of freshwater fishes in the natural environment. *Fish and Fisheries* **1**:283-316.

Lüdecke D (2018). "ggeffects: Tidy Data Frames of Marginal Effects from Regression Models." *Journal of Open Source Software*, **3**(26), 772. doi: [10.21105/joss.00772](https://doi.org/10.21105/joss.00772).

Macaulay G, Bui S, Oppedal F, Dempster T (2020a) Acclimating salmon as juveniles prepares them for a farmed life in sea-cages. *Aquaculture* 735227.

Macaulay G, Wright D, Oppedal F, Dempster T (2020b) Buoyancy matters: Establishing the maximum neutral buoyancy depth of Atlantic salmon. *Aquaculture* 734925.

Måløy H, Aamodt A, Misimi E (2019) A spatio-temporal recurrent network for salmon feeding action recognition from underwater videos in aquaculture. *Computers and Electronics in Agriculture* **167**:105087.

Martos-Sitcha JA, Sosa J, Ramos-Valido D, Bravo FJ, Carmona-Duarte C, Gomes HL *et al.* (2019) Ultra-low power sensor devices for monitoring physical activity and respiratory frequency in farmed fish. *Frontiers in Physiology* **10**: 667.

McFarlane W, Cubitt K, Williams H, Rowsell D, Moccia R, Gosine R *et al.* (2004) Can feeding status and stress level be assessed by analyzing patterns of muscle activity in free swimming rainbow trout (*Oncorhynchus mykiss Walbaum*)? *Aquaculture* **239**:467-484.

Murray AG, Peeler EJ (2005) A framework for understanding the potential for emerging diseases in aquaculture. *Preventive Veterinary Medicine* **67**:223-235.

Newton M, Barry J, Dodd J, Lucas M, Boylan P, Adams C (2016) Does size matter? A test of size-specific mortality in Atlantic salmon *Salmo salar* smolts tagged with acoustic transmitters. *Journal of Fish Biology* **89**:1641-1650.

Nilsson J, Folkedal O, Fosseidengen JE, Stien LH, Oppedal F (2013) PIT tagged individual Atlantic salmon registered at static depth positions in a sea cage: vertical size stratification and implications for fish sampling. *Aquacultural Engineering* **55**:32-36.

Noble C, Gismervik K, Iversen MH, Kolarevic J, Nilsson J, Stien LH *et al.* (Eds.) (2018) Welfare Indicators for farmed Atlantic salmon: tools for assessing fish welfare 351 pp

Oldham T, Oppedal F, Dempster T (2018) Cage size affects dissolved oxygen distribution in salmon aquaculture. *Aquaculture Environment Interactions* **10**:149-156.

Oppedal F, Dempster T, Stien LH (2011a) Environmental drivers of Atlantic salmon behaviour in sea-cages: a review. *Aquaculture* **311**:1-18.

Oppedal F, Vågseth T, Dempster T, Juell J-E, Johansson D (2011b) Fluctuating sea-cage environments modify the effects of stocking densities on production and welfare parameters of Atlantic salmon (*Salmo salar* L.). *Aquaculture* **315**:361-368.

Paulik G (1963) Estimates of mortality rates from tag recoveries. *Biometrics* 28-57.

Perry RW, Adams NS, Rondorf DW (2001) Buoyancy compensation of juvenile Chinook salmon implanted with two different size dummy transmitters. *Transactions of the American Fisheries Society* **130**:46-52.

Raoult V, Trompf L, Williamson JE, Brown C (2017) Stress profile influences learning approach in a marine fish. *PeerJ*, **5**, e3445.

Rillahan C, Chambers M, Howell WH, Watson III WH (2009) A self-contained system for observing and quantifying the behavior of Atlantic cod, *Gadus morhua*, in an offshore aquaculture cage. *Aquaculture* **293**:49-56.

Russell, W. M. & Burch, R. L. (1959). The principles of humane experimental technique.

London: Methuen & Co Ltd. Skøien KR (2017) Feed Distribution in Large Scale Sea Cage Aquaculture: Experiments, modelling and simulation. Norwegian University of Science and Technology (NTNU), Norway (2017) Doctoral dissertation.

Solstorm D, Oldham T, Solstorm F, Klebert P, Stien LH, Vågseth T *et al.* (2018) Dissolved oxygen variability in a commercial sea-cage exposes farmed Atlantic salmon to growth limiting conditions. *Aquaculture* **486**:122-129.

Staven FR, Nordeide JT, Imsland AK, Andersen P, Iversen NS, Kristensen T (2019) Is habituation measurable in Lumpfish *Cyclopterus lumpus* when used as cleaner fish in Atlantic salmon *Salmo salar* aquaculture? *Frontiers in Veterinary Science* **6**:227.

Stehfest KM, Carter CG, McAllister JD, Ross JD, Semmens JM (2017) Response of Atlantic salmon *Salmo salar* to temperature and dissolved oxygen extremes established using animal-borne environmental sensors. *Scientific Reports* **7**:4545.

Stien LH, Kristiansen T, Folkedal O, Mortensen S, Skiftesvik AB, Waagbø R *et al.* (2019) Welfare of salmon and cleaner fish in sea cages. In: Risk report Norwegian fish aquaculture. Fisken og havet 2019-5 (In Norwegian).

Sutton TM, Benson AC (2003) Influence of external transmitter shape and size on tag retention and growth of juvenile lake sturgeon. *Transactions of the American Fisheries Society* **132**:1257-1263.

Svendsen E, Føre M, Økland F, Gräns A, Hedger RD, Alfredsen JA *et al.* (2020) Heart rate and swimming activity as stress indicators for Atlantic salmon (*Salmo salar*). *Aquaculture*: 735804.

Sykes P, Stryhn H, McClure C, Brooking C, Hammell K (2012) Evaluation of external operculum loop tags to individually identify cage-cultured Atlantic halibut *Hippoglossus hippoglossus* in commercial research trials. *Journal of Fish Biology* **80**:2267-2280.

Teletchea F, Fontaine P (2014) Levels of domestication in fish: implications for the sustainable future of aquaculture. *Fish and Fisheries* **15**:181-195.

Thorpe J, Ross L, Struthers G, Watts W (1981) Tracking Atlantic salmon smolts, *Salmo salar* L., through Loch Voil, Scotland. *Journal of Fish Biology* **19**:519-537.

Thorstad E, Økland F, Finstad B (2000) Effects of telemetry transmitters on swimming performance of adult Atlantic salmon. *Journal of Fish Biology* **57**:531-535.

Thorstad EB, Rikardsen AH, Alp A, Økland F (2013) The use of electronic tags in fish research—an overview of fish telemetry methods. *Turkish Journal of Fisheries and Aquatic Sciences* **13**:881-896.

Uglem I, Dempster T, Bjørn P-A, Sanchez-Jerez P, Økland F (2009) High connectivity of salmon farms revealed by aggregation, residence and repeated movements of wild fish among farms. *Marine Ecology Progress Series* **384**:251-260.

Vollset KW, Lennox RJ, Thorstad EB, Auer S, Bär K, Larsen MH *et al.* (2020) Systematic review and meta-analysis of PIT tagging effects on mortality and growth of juvenile salmonids. *Reviews in Fish Biology and Fisheries*, 1-16.

Wagner GN, Cooke SJ (2005) Methodological approaches and opinions of researchers involved in the surgical implantation of telemetry transmitters in fish. *Journal of Aquatic Animal Health* **17**:160-169.

Wagner GN, Stevens ED, Byrne P (2000) Effects of suture type and patterns on surgical wound healing in rainbow trout. *Transactions of the American Fisheries Society* **129**:1196-1205.

Winter, J.D. 1983. Underwater biotelemetry. In Nielsen, L. A. & Johnsen, J. D. eds., *Fisheries Techniques*. 371-395 pp. Bethesda, Maryland, American Fisheries Society.

WorldBank (2020) (web archive link, 26 November 2020). Available from URL: <https://data.worldbank.org/indicator/ER.FSH.AQUA.MT> [Cited 26 November 2020].

Wright DW, Stien LH, Dempster T, Oppedal F (2019) Differential effects of internal tagging depending on depth treatment in Atlantic salmon: a cautionary tale for aquatic animal tag use. *Current Zoology* **65**:665-673.

Accepted paper, please cite as: Macaulay G, Warren-Myers F, Barrett LT, Oppedal F, Fore M, Dempster T. Tag use to monitor fish behaviour in aquaculture: a review of benefits, problems and solutions. *Reviews in Aquaculture*, 18. DOI: <https://doi.org/10.1111/raq.12534>

Table 1 – Names and description of predictor and response variables tested.

Predictor variables	Description	Type
StudyDays	Duration of trial (days).	Numeric
UnitVol_m3	Volume (m ³) of the tank/cage or pond the trial was conducted in in cubic metres.	Numeric
Attach	Method used to attach the tag to the fish (3 levels): Internal (tags surgically implanted); External (tags were externally attached to musculature or skin); Both (both internal and external tags used within the study).	Factor
Response variables	Description	Type
TagMortProp	Proportion of tagged fish that died per unit replicate. Only included in models if numbers of tagged fish were given.	Numeric proportion
TagsRetrvdProp	Proportion of tags retrieved per unit replicate. Only included in models if reported.	Numeric proportion

Table 2 – Results and description of beta-regression models (betareg package for R; Cribari-Neto & Zeileis (2009)) testing for an association between tagged fish mortality (Model 1) or proportion of tags retrieved (Model 2) and study characteristics in sea-cages. Associated pseudo-R² and sample size (n) of each model are included. Bold text indicates a significant change in the deviance of the model when the associated predictor variable is added to the model. Model terms were using the Anova function in the car package for R, using type II sums of squares (Fox & Weisberg 2019).

Response 1: TagMortProp sea-cage		<i>betareg(TagMortProp ~ UnitVol_m3 + Attach + StudyDays, weights = No.treatrep)</i>		
Model 1 n = 17				
Pseudo model R ² = 0.54				
Term	χ^2	Model df	P	
UnitVol_m3	0.86	1	0.3536	
Attach	0.46	2	0.7945	
StudyDays	14.20	1	0.0001	
Response 2: TagsRetrvdProp sea-cages		<i>betareg(TagsRetrvdProp ~ UnitVol_m3 + Attachment + StudyDays, weights = No.treatrep)</i>		
Model 2 n = 19				
Pseudo model R ² = 0.6				
Term	χ^2	Model df	P	
UnitVol_m3	0.53	1	0.4664	
Attach	0.76	3	0.8587	
StudyDays	28.79	1	<0.0001	

Accepted paper, please cite as: Macaulay G, Warren-Myers F, Barrett LT, Oppedal F, Fore M, Dempster T. Tag use to monitor fish behaviour in aquaculture: a review of benefits, problems and solutions. *Reviews in Aquaculture*, 18. DOI: <https://doi.org/10.1111/raq.12534>

Table 3 – Summary of recommendations for experimental design and reporting for tagging studies in aquaculture.

Experimental design recommendations

Considerations and suggestions	Description
Replacement	Are there alternative technologies available to use to monitor farmed fish behaviour that could answer the research question without the use of tags? For example, video cameras or echosounders?
Appropriate replication at the level of treatment	If possible, have at least three separate unit replicates (ponds/tanks/cages) and divide equal number of tagged individuals among these to avoid pseudo-replicates
Tagging effects	Compare the growth, behaviour, physiology of tagged fish to (a) untagged conspecifics, (b) 'sham' or procedural control fish and (c) fish that were handled and anaesthetised only.
Biotic factors	Compare the growth, behaviour and physiology of tagged fish of different life-stage, sex or source
Abiotic factors	Test how different abiotic factors such as temperature, pH, dissolved oxygen and salinity affect the outcome of surgery
Aspects of tagging procedures	Compare the growth, behaviour and physiology of tagged that have undergone different tagging procedures. For example, different recovery times, attachment methods/locations, anaesthesia, wound closures, surgeon experience.

Recommendations for reporting

Before tagging	Description
Tag dimensions	Record tag brand, length, width, volume, weight in air, weight in water. Ensure tag dimensions are reported for external marker tags also.
Tagged fish source	Where did the tagged fish come from?
Method of collecting fish	Were fish crowded? Was a net used?
Tagging procedure	Description
Weight and length	Record weight and length of both tagged and untagged fish prior to or immediately after tag attachment.
Anaesthetic	Type and amount of anaesthetic used, and mean time taken for anaesthesia to be achieved.
Attachment process	How was the tag attached (externally vs. internally)? Where was the location of attachment on the fish? Method of wound closure (e.g. suture, surgical glue, staples). Were prophylactic antibiotics used? What was the water temperature during tagging? How long on average did the tag attachment process take? Were external marker tags used in addition to electronic tags?
Recovery	Where did the fish recover? How long did the fish take to recover on average? What metric was used to determine a fish was recovered (e.g. balanced swimming, or response to agitation)? Record any abnormal behaviours or physical signs of damage on tagged fish during recovery.

Number of fish tagged	Record the total number of fish that underwent the tag attachment procedure.
Mortality	Record the total number of fish that did not recover or died after tag attachment.
<hr/>	
<i>During trial</i>	<i>Description</i>
Number of tagged and untagged fish per replicate	Record the total number of tagged and untagged fish placed in each unit replicate.
Behaviour and physical health	Record any behavioural abnormalities and physical signs of damage of tagged fish throughout the trial compared to untagged fish.
Mortality	Total number of both tagged and untagged fish that died throughout the trial in each unit replicate.
Farm procedures/experimental conditions	Note any farm or animal husbandry procedures that occurred during the trial (or any experimental manipulation).
Environmental conditions	Volume and depth of tank/cage/pond. Water temperature, dissolved oxygen levels and salinity over the trial period.
<hr/>	
<i>Post-trial</i>	<i>Description</i>
Tag retrieval	Total number of tagged fish successfully retrieved per unit replicate and number of tagged fish that were undiscovered.
Weight and length	Mean fish weight in air and length after trial for both tagged and untagged fish.
Useable tags	Total number of tags retrieved that provided complete and useable data sets per unit replicate.
Weight of fish in water	Weighing fish in water after euthanasia (with swim bladder deflated or removed) allows fish density and fish volume to be calculated.
Tagged fish condition	Inspection of the tag attachment site: is there any inflammation? Signs of necrosis, infection? Do the tagged fish's physical condition appear visibly different to the untagged fish?
<hr/>	

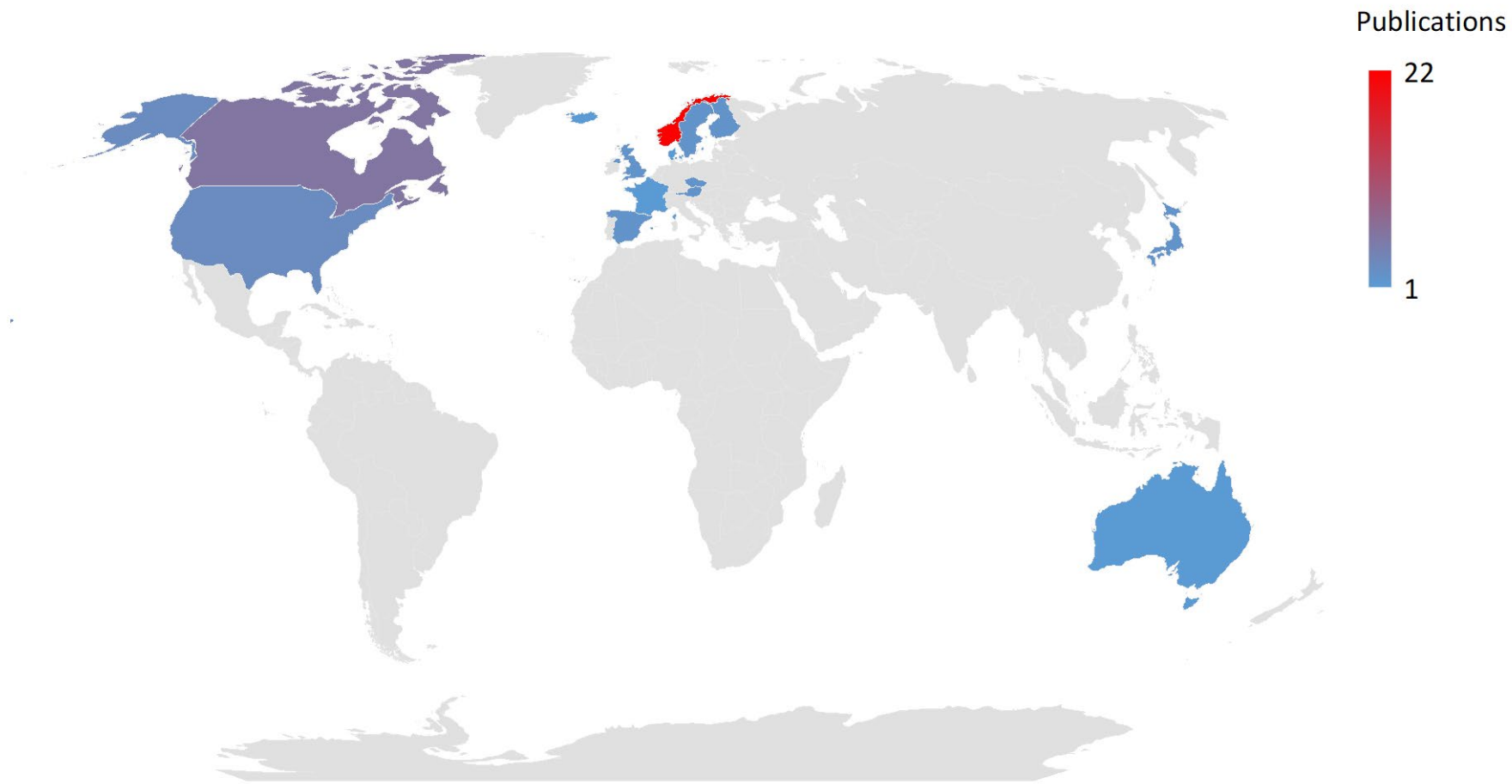


Figure 1 – Heat map of number of publications from different countries on monitoring behaviour in farmed fish using electronic tags.

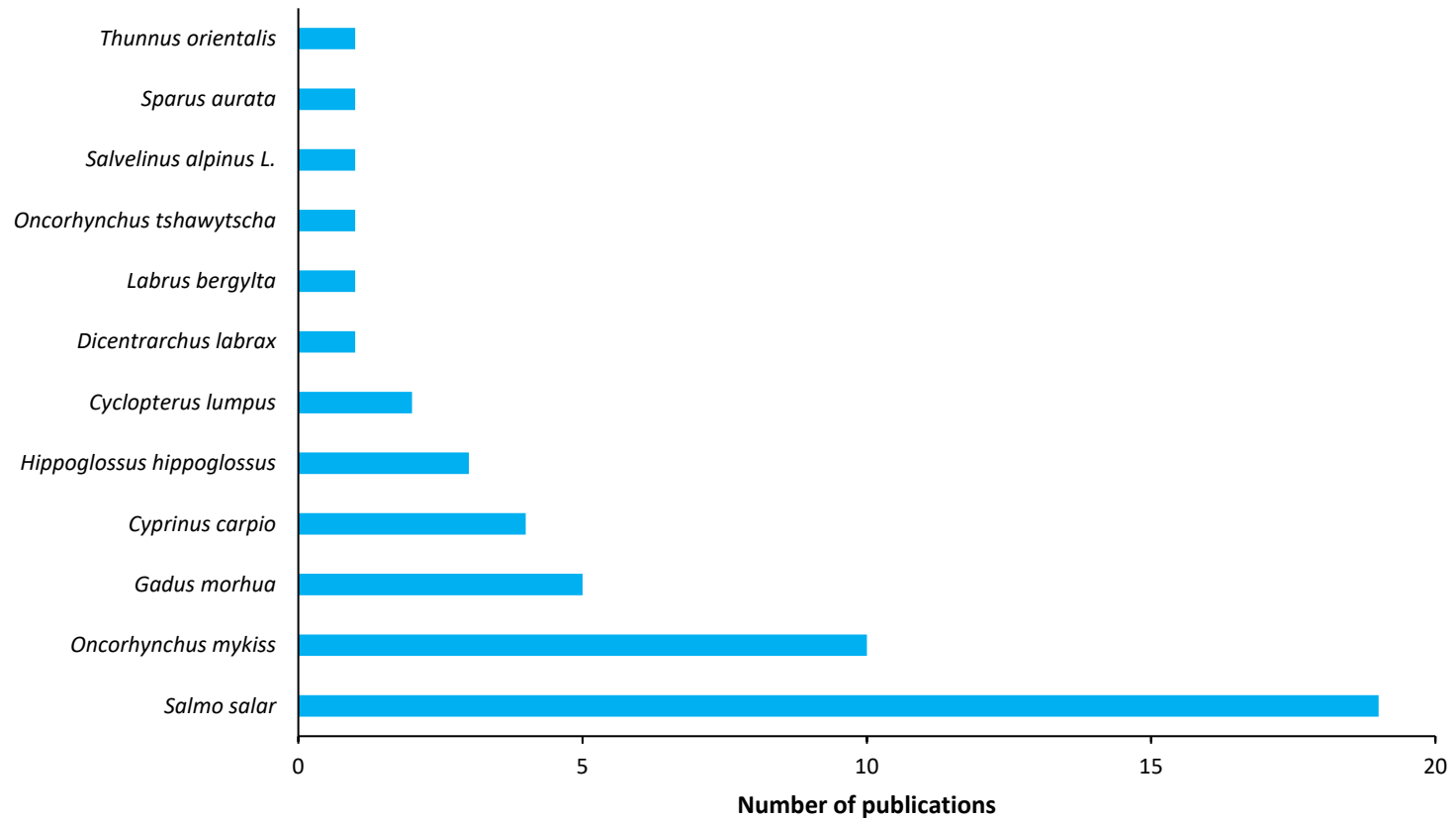


Figure 2 – Number of studies on monitoring behaviour using tags on different species of farmed fish.

Accepted paper, please cite as: Macaulay G, Warren-Myers F, Barrett LT, Oppedal F, Fore M, Dempster T. Tag use to monitor fish behaviour in aquaculture: a review of benefits, problems and solutions. *Reviews in Aquaculture*, 18. DOI: <https://doi.org/10.1111/raq.12534>

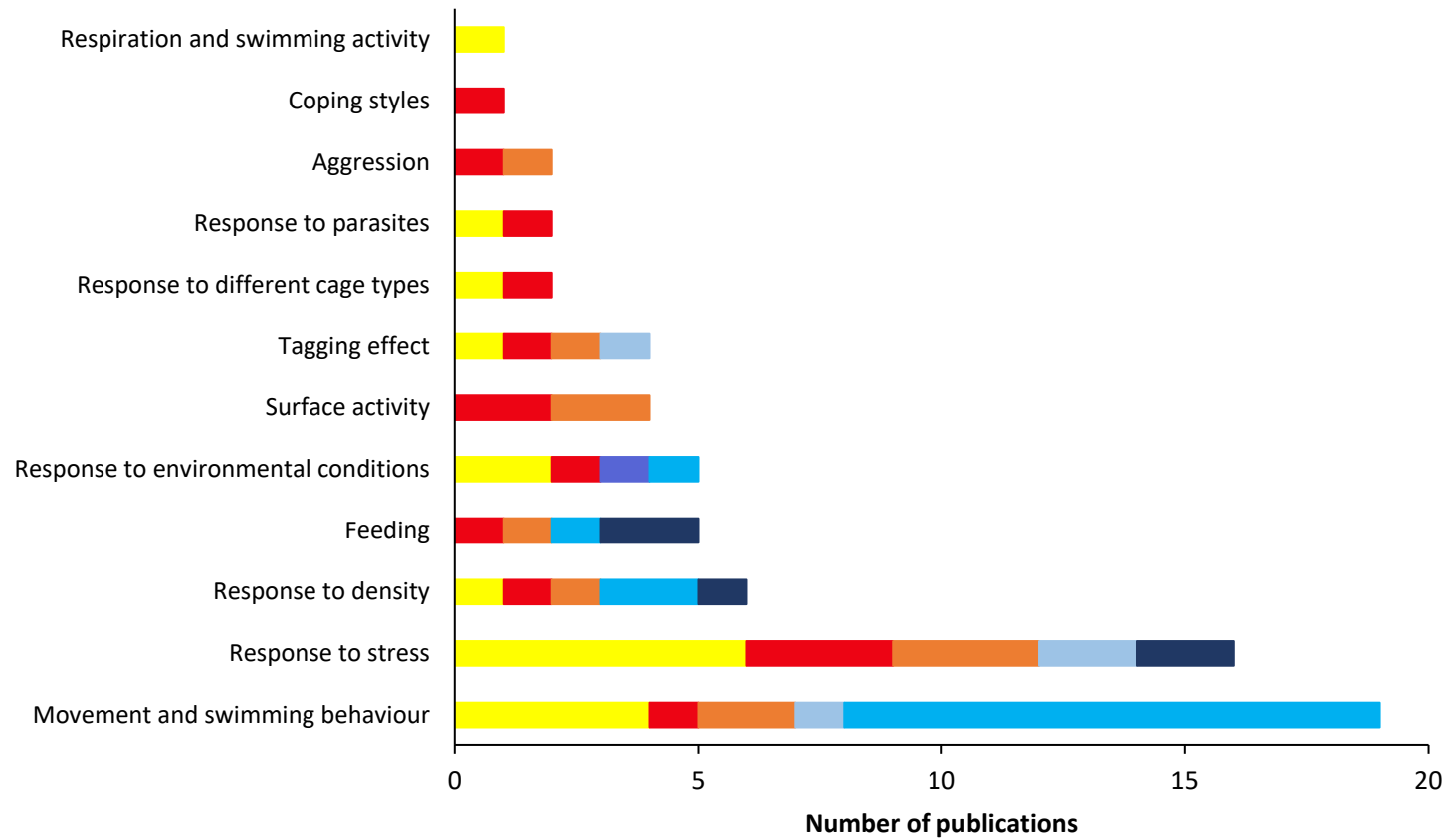


Figure 3 – Number of publications returned by the literature review, according to tag type and study focus. Publications that used multiple tag types appear multiple times. Note: Transmitter (movement) = 3D positioning, depth transmitters. Transmitter (activity) = acceleration, swim speed/angle, body angle transmitters. Transmitter (physiology) = electromyogram, opercular pressure transmitter. Transmitter (environment) = pressure, dissolved oxygen transmitter. DST = any kind of archival data tags (e.g. heart rate bio-loggers). External marker tags = coloured tags, floy and T-bar tags, and numbered Peterson’s discs.

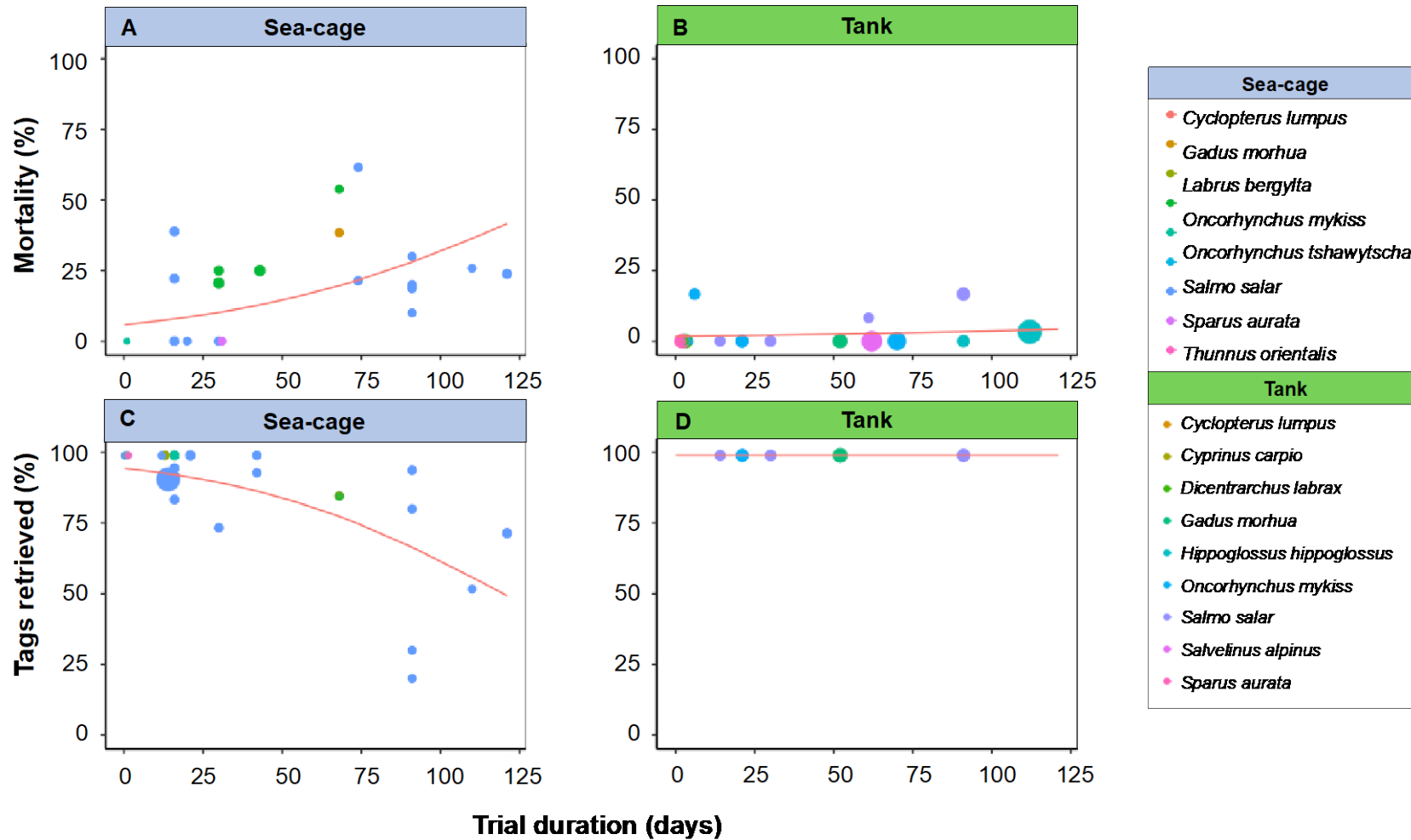


Figure 4 – Relationship between tagged fish mortality (%) and study duration in sea-cages (A) and tanks (B) and the relationship between tags successfully retrieved (%) and study duration in sea-cages (C) and tanks (D). Dot size is scaled for number of tagged fish per unit replicate and the graph is weighted by number of unit replicates. Fitted lines are predictions from a beta regression model fitted using the betareg package for R (Cribari-Neto & Zeileis (2009)) (model specification: Response ~ StudyDays).

Accepted paper, please cite as: Macaulay G, Warren-Myers F, Barrett LT, Oppedal F, Fore M, Dempster T. Tag use to monitor fish behaviour in aquaculture: a review of benefits, problems and solutions. *Reviews in Aquaculture*, 18. DOI: <https://doi.org/10.1111/raq.12534>