The use of external electronic tags on fish: an evaluation of tag retention and tagging effects

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The use of external electronic tags on fish: an evaluation of tag retention and tagging effects

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Abstract

External tagging of fish with electronic tags has been used for decades for a wide range of marine and freshwater species. In the early years of fish telemetry research, it was the most commonly used attachment method, but later internal implants became preferred. Recently, the number of telemetry studies using external tagging has increased, especially with the development of archival tags (data storage tags, DSTs), pop-up satellite archival tags (PSATs) and other environment-sensing tags. Scientific evaluations of the tagging method are rather scarce for most species. We identified 89 publications, reporting effects of external tagging for 80 different fish species, which constitute the main basis for this review. External attachment holds certain benefits compared to other tagging methods, for example, speed of application, and it may be the only option for fishes with a body shape unsuitable for surgical implantation, or when using tags with sensors recording the external environment. The most commonly reported problems with external tags are tissue damage, premature tag loss, and decreased swimming capacity, but the effects are highly context dependent and species specific. Reduced growth and survival have also been recorded, but direct mortality caused by external tagging seems rare. Most of the studies reviewed evaluate tag retention, survival, and tissue reactions. There is a general need for more research on the effects of external tagging of fish with electronic tags, but particularly there are few studies on predation risk, social interactions, and studies distinguishing capture and handling effects from tagging effects. For PSATs, especially those that are large relative to fish size, there are particular problems with a high proportion of premature tag losses, reduced swimming capacity, and likely increased predation, but there remains a paucity of tag effect studies related to the use of PSATs. Before embarking on a field study employing external tagging with electronic tags, we recommend the use of appropriate pilot studies, controlled where possible, to quantify potential impacts of tagging.

Keywords: Telemetry, Tag attachment, Archival tag, PSAT, Survival, Tissue damage, Tag retention, Growth, Swimming, Drag, Entanglement, Biofouling, Predation

Background

More than four decades ago, Bruce Shepherd [1] wrote: "Although many researchers have looked in a cursory fashion at transmitter attachment and its effect on fish behavior, none have done so in detail. Results from a study of fish activity have convinced me of the need for careful examination of this problem". This statement is still valid. In general, the combined effect of capture, handling and tagging may change an animal's behavior, and lead to flawed results in telemetry studies.

Electronic tagging (referred to as telemetry and bio-logging) of free-ranging animals is widely used to study fish spatial ecology, survival, and responses to the environment [2–4]. The main methods for attaching electronic tags to fish are surgical implantation in the body cavity, gastric insertion, and external attachment [5, 6]. External attachment was the most common telemetry tag attachment method for fish studied in the first two decades (1956–1975) of application [2], but was overtaken in popularity

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in the 1980s by surgical implantation in the body cavity, largely due to tag miniaturization and extended battery life [2]. While surgical implantation remains the most commonly used method for electronic tag attachment to fish [3], external attachment is widely used, especially, but certainly not only, with the increased use of archival (data storage tags, DSTs) and satellite tags [3], particularly pop-up satellite archival tags (PSATs, or PATs) [7].

While there are several review papers focusing on surgical implantation of tags and of their effects [8, 9], or wider comparison of tag attachment methodologies [5], there are relatively few studies on the effects of externally attached tags and no papers summarizing the experiences with, and evaluations of, external tagging of fish, across the breadth of taxa and habitats. Over 20 years ago, Baras [10] reviewed more than 1000 papers from studies using aquatic telemetry and found only 14 to evaluate the effects of external attachment of electronic tags on fish. In 2012, Drenner et al. [11], reviewed tagging studies of salmonids in marine environments and commented on the lack of evaluations of tagging/handling effects. A generic problem in such evaluations is to disentangle the various effects of capture, handling, tagging, holding, and transporting wild fish. When studies try to estimate the effect of tagging it is often the combination of effects that is measured. This makes it difficult to directly compare different tagging methods in terms of adverse effects and the critical reader should bear this in mind.

In this paper, our aim is to summarize and evaluate experiences with external tagging of fish with electronic tags, based on published studies and the authors' own experiences. We do not provide a comparison of the main tagging methods, which is available elsewhere [3–6]. Instead, we provide a detailed overview of the utility and problems associated with external attachment of electronic tags, with the aim of helping researchers to determine the suitability of this method for planned studies, and to be able to interpret data collected by using such methods and draw appropriate conclusions from the studies done. We also highlight key advantages and disadvantages of external tagging with electronic tags and suggest some important research areas that need to be addressed for the better evaluation of external tag effects. The following sections examine the important issue of tag retention and appraise evidence for the extent and nature of impacts of external tags on key attributes of fish health. The main sections cover tag retention and effects of tagging on swimming performance, growth, social interactions, and survival.

Review

Literature searches for this review were made through the Thomson Reuters Web of Science database and ProQuest Biological Sciences database with different combinations of the key words: extern*, tag*, effect*, fish, telemetry, transmit*. In addition, the authors have undertaken research on tagging effects and performed tagging studies for many years, and their collections of scientific literature were used, as well as searching through reference lists of previous publications. The aim was to cover publications on effects of external tagging as extensively as possible. Thus, we identified 89 publications describing various effects of externally attached electronic tags, ranging from detailed experimental evaluations to more descriptive, but in our opinion relevant, reports of observed effects. A body of literature exists reporting the effects of external conventional tags [e.g. 12], but here we focus only on externally attached electronic tags. Many of the same issues apply for attachment of conventional tags, but fundamental differences are the larger size of electronic tags and that they usually, but not always, take longer to attach than conventional tags and often involve induction of general anesthesia as part of the tag attachment procedure [3, 6]. In the 89 papers (Table 1), information on 80 species, representing 20 orders is presented (Fig. 1), giving a total of 122 "species studies" (several papers cover multiple species). Of these, 45 % were carried out in marine/brackish environments and 55 % in freshwater. For marine/brackish environments, 38 % of the studies were wholly or partially conducted in controlled laboratory/mesocosm conditions, while in freshwater, this applied to 64 % of cases. Of 24 studies examining tag effects (including tag retention) on elasmobranchs, coelacanth, tarpon, tunas, and billfishes, only three were under controlled conditions. Most of the publications concern tag retention (44), survival (38), tissue reaction to tag presence (31), general behavior (27), swimming performance (21), growth (17), and feeding (17). Few papers reported effects regarding physiology (6), predation (5), catchability (3), and social interactions (3) (Fig. 2).

A variety of attachment methods have been used for external tags (Table 2) often optimized/tailored for the species and study in question, and refined over time. Early studies often used external attachment methods based on easily available materials, including fish hooks [13], alligator clips [14] and pull ties [15], and included descriptive evaluation of the most effective tagging methods and body locations under semi-controlled conditions, but without detailed evaluation of effects by comparison to controls [16]. This lack of detailed studies was also because early electronic tags were short-lived and so only the most obvious acute impact effects were considered. For fusiform and laterally compressed species, electronic tags are often fixed with steel wires or nylon filaments through the muscle at the base of the dorsal fin (Fig. 3),

Table 1 Summary table of studies that incorporate an evaluation of one or more effects of external tagging

Species	General behaviour/activity	Buoyancy	Catch-ability	Migra-tion	Equilib-rium	Feeding	Growth	Infections, wounds, tissue reactions, healing	Physi-ological effects	Preda-tion	Repro-duction	Response to transmit-ter output	Retention/expulsion	Social interac-tions	Survival	Swimming performance	Refer-ences
Sea lamprey (*Petromyzon marinus*)	X			X													[99]
Basking shark (*Cetorhinus maximus*)													X				[17]
Basking shark (*Cetorhinus maximus*)													X				[58]
Bigeye thresher shark (*Alopias superciliosus*)													X		X		[7]
Great white shark (*Carcharodon carcharias*)													X		X		[7]
Shortfin mako shark (*Isurus oxyrinchus*)													X		X		[7]
Blacktip reef shark (*Carcharhinus melanopterus*)													X				[100]
Blue shark (*Prionace glauca*)													X		X		[7]
Lemon shark (*Negaprion brevi-rostris*)																X	[73]
Oceanic whitetip shark (*Car-charhinus longimanus*)													X		X		[7]
School shark (*Galeorhinus galeus*)	X																[101]
Silky shark (*Carcharhinus falciformis*)													X		X		[7]
Cownose ray (*Rhinoptera bonasus*)																X	[102]
Cownose ray (*Rhinoptera bonasus*)									X							X	[55]
Cowtail stingray (*Pastinachus atrus*)													X				[100]
Porcupine ray (*Urogymnus asper-rimus*)													X				[100]
Southern stingray (*Dasyatis americana*)						X											[103]
West Indian ocean coelacanth (*Latimeria chalumnae*)	X							X					X				[59]
Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*)													X				[29]
Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*)													X				[104]
Lake sturgeon (*Acipenser fulvescens*)							X						X				[31]

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Table 1 continued

Species	General behaviour/activity	Buoyancy	Catch-ability	Migra-tion	Equilib-rium	Feeding	Growth	Infections, wounds, tissue reactions, healing	Physi-ological effects	Preda-tion	Repro-duction	Response to transmit-ter output	Retention/expulsion	Social interac-tions	Survival	Swimming performance	Refer-ences
Lake sturgeon (*Acienser fulvescens*)								×					×		×		[32]
Shortnose sturgeon (*Acipenser brevirostrum*)													×				[29]
Shortnose sturgeon (*Acipenser brevirostrum*)								×					×		×		[30]
White sturgeon (*Acipenser transmontanus*)													×		×	×	[33]
Tarpon (*Megalops atlanticus*)													×		×		[7]
American eel (*Anguilla rostrata*)							×	×					×		×	×	[38]
American eel (*Anguilla rostrata*)										×					×		[91]
European eel (*Anguilla anguilla*)																×	[69]
European eel (*Anguilla anguilla*)																×	[70]
European eel (*Anguilla anguilla*)	×						×	×					×		×		[19]
European eel (*Anguilla anguilla*)																×	[71]
Longfin eel (*Anguilla dieffenbachia*)													×				[54]
Barbel (*Barbus barbus*)							×										[75]
Common bream (*Abramis brama*)	×													×			[78]
Common carp (*Cyprinus carpio*)	×												×				[105]
Common carp (*Cyprinus carpio*)													×		×		[82]
Dace (*Leuciscus leuciscus*)							×							×	×		[77]
Tench (*Tinca tinca*)	×					×		×					×		×		[85]
Tigerfish (*Hydrocynus vittatus*)				×									×				[106]
Blue catfish (*Ictalurus furcatus*)								×					×		×		[34]
Mekong giant catfish (*Pangasianodon gigas*)							×	×					×		×		[36]
Chinook salmon (*Oncorhynchus tshawytscha*)								×							×		[81]
Chinook salmon (*Oncorhynchus tshawytscha*)													×		×		[40]
Chinook salmon (*Oncorhynchus tshawytscha*)							×	×					×		×		[41]
Chinook salmon (*Oncorhynchus tshawytscha*)								×					×		×		[23]
Chinook salmon (*Oncorhynchus tshawytscha*)																×	[72]
Chinook salmon (*Oncorhynchus tshawytscha*)										×						×	[67]

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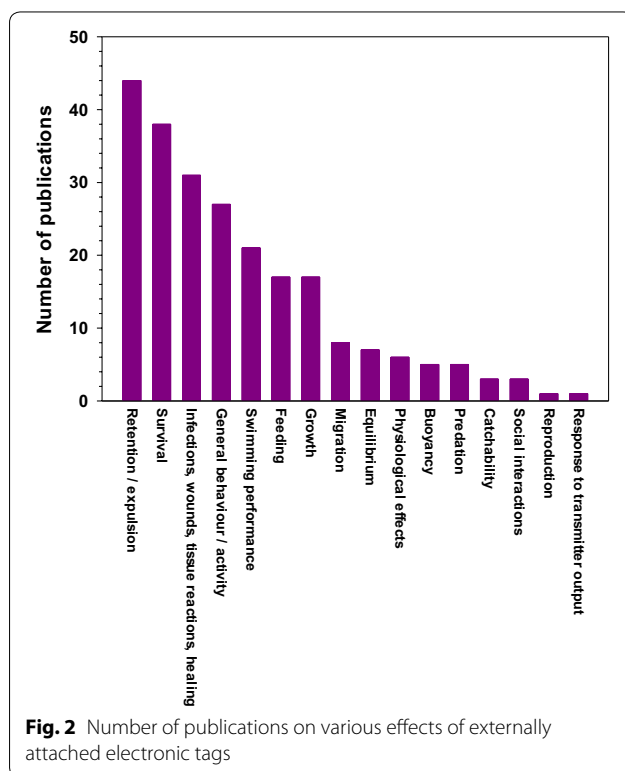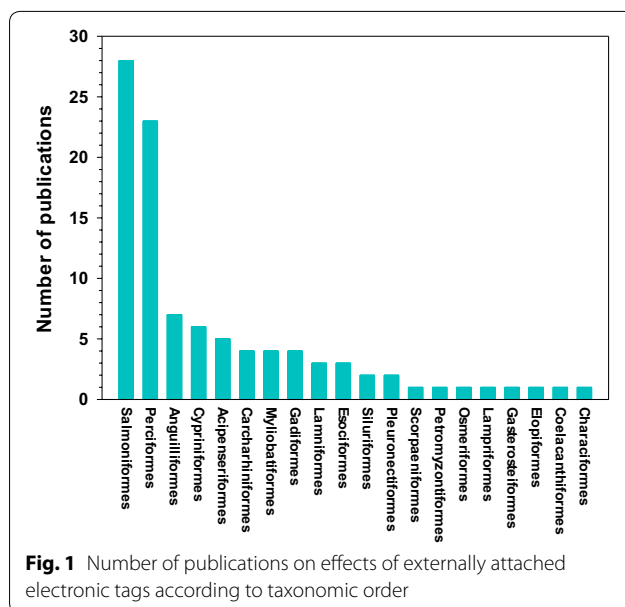
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Table 1 continued

Species	General behaviour/activity	Buoyancy	Catch-ability	Migra-tion	Equilib-rium	Feeding	Growth	Infections, wounds, tissue reactions, healing	Physi-ological effects	Preda-tion	Repro-duction	Response to transmit-ter output	Retention/expulsion	Social interac-tions	Survival	Swimming performance	Refer-ences
Masu salmon (*Oncorhynchus masou*)							×	×	×				×		×	×	[68]
Rainbow trout (*Oncorhynchus mykiss*)	×																[1]
Rainbow trout (*Oncorhynchus mykiss*)															×	×	[63]
Rainbow trout (*Oncorhynchus mykiss*)														×		×	[64]
Atlantic salmon (*Salmo salar*)					×		×								×		[74]
Atlantic salmon (*Salmo salar*)												×					[107]
Atlantic salmon (*Salmo salar*)				×													[108]
Atlantic salmon (*Salmo salar*)															×	×	[65]
Atlantic salmon (*Salmo salar*)																×	[66]
Atlantic salmon (*Salmo salar*)	×			×		×		×								×	[109]
Atlantic salmon (*Salmo salar*)						×	×	×					×		×		[76]
Atlantic salmon (*Salmo salar*)								×	×							×	[27]
Brown trout (*Salmo trutta*)	×					×											[46]
Brown trout (*Salmo trutta*)	×																[110]
Brown trout (*Salmo trutta*)	×					×											[111]
Brown trout (*Salmo trutta*)						×											[112]
Brown trout (*Salmo trutta*)				×									×		×		[26]
Brown trout (*Salmo trutta*)			×					×							×		[93]
Brown trout (*Salmo trutta*)			×	×											×	×	[28]
Cutthroat trout (*Salmo clarki*)																×	[1]
Arctic char (*Salvelinus alpinus*)	×			×									×				[25]
Arctic char (*Salvelinus alpinus*)			×					×									[93]
Lake whitefish (*Coregonus clupeaformis*)	×					×	×						×		×		[42]
Inconnu (*Stenodus nelma*)				×									×		×		[44]
Muskellunge (*Esox masquinongy*)							×	×							×		[113]
Northern pike (*Esox ucius*)	×				×								×				[24]
Northern pike (*Esox lucius*)	×												×				[48]
Northern pike (*Esox lucius*)									×						×		[113]
Eulachon (*Thaleichthys pacificus*)		×						×	×						×		[86]
Opah (*Lampris guttatus*)										×					×		[88]
Atlantic cod (*Gadus morhua*)							×	×					×		×		[50]
Atlantic cod (*Gadus morhua*)		×						×	×						×	×	[62]

Table 1 continued

Species	General behaviour/ activity	Buoyancy	Catch-ability	Migration	Equilibrium	Feeding	Growth	Infections, wounds, tissue reactions, healing	Physiological effects	Predation	Reproduction	Response to transmitter output	Retention/ expulsion	Social interactions	Survival	Swimming performance	References
Atlantic cod (*Gadus morhua*)	×	×						×									[114]
Atlantic cod (*Gadus morhua*)			×					×					×				[49]
Long-snouted seahorse (*Hippocampus guttulatus*)	×						×										[115]
European plaice (*Pleuronectes platessa*)			×					×					×				[49]
Sole (*Solea solea*)							×	×					×		×		[53]
Copper rockfish (*Sebastes caurinus*)	×				×	×		×									[116]
Quillback rockfish (*Sebastes maliger*)	×				×	×		×									[116]
Bluegill (*Lepomis macrochirus*)							×	×					×		×		[47]
Largemouth bass (*Micropterus salmoides*)						×	×										[80]
Smallmouth bass (*Micropterus dolmieui*)					×	×											[117]
Rock bass (*Ambloplites rupestris*)					×	×											[117]
Rock bass (*Ambloplites rupestris*)	×										×						[79]
Yellowtail (*Seriola quinqueradiata*)	×															×	[16]
European seabass (*Dicentrarchus labrax*)		×											×				[118]
European seabass (*Dicentrarchus labrax*)	×	×						×					×				[114]
European sea bass (*Dicentrarchus labrax*)					×	×	×	×					×		×		[53]
White perch (*Morone americana*)								×		×							[64]
River blackfish (*Gadopsis marmoratus*)	×				×			×					×		×		[119]
Two-spined blackfish (*Gadopsis bispinosus*)						×		×					×		×		[20]
Yellow perch (*Perca flavescens*)					×	×											[117]
Yellow perch (*Perca flavescens*)					×	×	×								×		[80]
Yellow perch (*Perca flavescens*)							×	×					×		×		[47]
Mulloway (*Argyrosomus japonicus*)						×	×						×		×		[43]
Salema porgy (*Sarpa salpa*)	×	×				×		×					×		×		[52]
Yellowfin bream (*Acanthopagrus australis*)	×					×							×		×		[43]
Silver perch (*Bidyanus bidyanus*)													×		×		[22]

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Table 1 continued

Species	General behaviour/activity	Buoyancy	Catch-ability	Migra-tion	Equilib-rium	Feeding	Growth	Infections, wounds, tissue reactions, healing	Physi-ological effects	Preda-tion	Repro-duction	Response to transmitter output	Retention/expulsion	Social interac-tions	Survival	Swimming performance	Refer-ences
Golden perch (*Macquaria ambigua*)	×							×					×				[105]
Macquarie perch (*Macquaria australasica*)						×		×					×		×		[21]
Pink happy (*Sargochromis giardia*)													×				[60]
Three spot tilapia (*Oreochromis andersonii*)													×				[60]
Monkeyface prickleback (*Cebidichthys violaceus*)	×					×											[120]
Black cod (*Paranototothenia angustata*)	×					×		×	×								[121]
Bigeye tuna (*Thunnus obesus*)	×												×				[122]
Bluefin tuna (*Thunnus thynnus*)													×		×		[7]
Yellowfin tuna (*Thunnus albacares*)	×												×				[122]
Yellowfin tuna (*Thunnus albacares*)													×		×		[7]
Swordfish (*Xiphias gladius*)													×		×		[7]
Black marlin (*Istiompax indica*)													×		×		[7]
Blue marlin (*Makaira nigricans*)													×		×		[7]
Striped marlin (*Kajikia audax*)													×		×		[7]
White marlin (*Tetrapturus albidus*)										×					×		[88]
White marlin (*Tetrapturus albidus*)													×		×		[90]

Ranked in taxonomic order

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Fig. 1 Number of publications on effects of externally attached electronic tags according to taxonomic order

Fig. 2 Number of publications on various effects of externally attached electronic tags

but many variations of this method are used. For tagging larger, marine fish, much development has recently been carried out to refine methods of pole- and spear gun-deployed dart attachments and tethers associated with PSATs. The high cost of these tags and the high

proportion of premature releases in many studies have been strong drivers for improved attachment reliability [7, 17].

Tag retention

Given the substantial cost of electronic tags, it is no surprise that studies have frequently evaluated rates and duration of tag retention, in some cases under laboratory or mesocosm conditions, but often under field conditions. The use of laboratory or mesocosm environments enables easy recording of tag loss, but may not be representative of the natural conditions, particularly in terms of snagging and fouling risks, which may increase the loss rate of external tags under natural compared to laboratory conditions [e.g. 4, 11, 25]. In the field, retention of electronic tags is most often demonstrated by recapture, which can be habitat- and sampling efficiency dependent. Alternatively, tag loss may be demonstrated by premature release and reporting of pop-up tags [7, 18, 19]. Double tagging, where a conventional tag or PIT tag is used in combination with the main telemetry tag, can provide estimates of tag retention for recaptured fish. A marked change in movement patterns (most commonly an absence of movement as most tags are heavier than water and sink to the bottom), depth or temperature, can be indicative of electronic tag loss, although it can also indicate mortality [3]. Thus definitive records of external electronic tag retention, gained from recapture or direct observation, are most easily recorded in shallow, accessible environments, notably freshwater and clear inshore, marine environments.

The recent, rapid development and application of pop-up tags has encouraged greater attention to effective attachment methods due to the high proportion of premature (before the pre-set time) releases when the attachment fails [7, 19]. However, problems with retention of radio, acoustic, and data storage tags may be just as evident across many species in freshwater habitats. Broadhurst et al. [20] tagged wild two-spined blackfish (*Gadopsis bispinosus*) with external transmitters and kept them in aquaria and found that all (100 %) of the tags were shed within 8 days after tagging. In contrast, they found no loss of external tags on Macquarie perch (*Macquaria australasica*) after 28 days in a similar study [21]. The two species were tagged the same way, but with very different results, demonstrating the importance of not uncritically transferring results from one species to others. For wild silver perch (*Bidyanus bidyanus*) equipped with external tags, more than 50 % of the fish had rejected their external tags within 146 days in tanks or sea-cages [22]. Corbett et al. [23] also reported 100 % tag loss during a 50-day laboratory experiment with adult Chinook salmon (*Oncorhynchus tshawytscha*).

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Table 2 Examples of the range of methods used to externally attach electronic tags to fish, several of which are suited to the specific morphology or taxa involved

Method	Example taxon	Reference
Fishing hook at base of dorsal fin attached by nylon tether to transmitter	*Roccus chrysops* white bass	[13]
Small fishing hook at base of dorsal fin, attached by stiff nylon tether to PIT tag (highly temporary, minimal handling)	*Alosa sapidissima* American shad	[97]
Dorsal fin attachment using miniature alligator clip	*Oncorhynchus clarki* cutthroat trout	[14]
Three nylon T-bar tags anchored on pterygiophores used to mount an H-shaped rubber saddle housing the transmitter	*Paranotothenia angustata* black cod	[121]
Pop-up satellite transmitter on monofilament tether with medical grade nylon dart harpoon attached at base of dorsal fin (other studies have used stainless steel/titanium darts)	*Thunnus thynnus* bluefin tuna	[123]
Steel dart attached to transmitter deployed by pneumatic gun; dart aimed at lateral surface of fish, posterior to second dorsal fin (no internal organs)	*Latimeria chalumnae* coelacanth	[59]
Archival tag attached to a barbed nylon pin passed through pre-punched hole in dorsal fin and secured by female half of cattle ear tag	*Galeorhinus galeus* school shark	[101]
Pull tie covered in soft tubing attached around caudal peduncle, tag attached to main pull tie	*Sciaenops ocellata* red drum	[15]
Absorbable suture attachment through caudal peduncle, tag on one side, soft plate on other	*Esox lucius* northern pike	[24]
Ventral attachment at base of anal fin	*Seriola quinqueradiata* yellowtail	[16]
Ventral attachment in mid-section of abdomen	*Gadus morhua* Atlantic cod	[114]
Pannier (dorsal saddle) attachment with tag and battery components on either side of the dorsal fin	*Salmo trutta* brown trout	[46]
Side mount attachment on one side of dorsal musculature, below dorsal fin, with a flexible backing plate on the other side, wire/monofilament through muscle section	*Oncorhynchus mykiss* rainbow trout	[64]
Side mount attachment with neoprene pad	*Leuciscus leuciscus* dace	[77]
Side mount attachment with soft, spacing mounds	*Cyprinus carpio* Common carp	[105]
Anterior-dorsal soft saddle attached superficially	*Esox lucius* northern pike	[95]
Posterior dorso-lateral soft saddle harness attached through musculature	*Esox lucius* northern pike	[48]
Flattened tag attached to inside of operculum using two lengths of monofilament, fastened outside with washer and crimp	*Cebidichthys violaceus*	[120]
Tag attached to bony appendages on back of fish with polyfilament Dacron tether	*Phycodurus eques* Leafy seadragon	[124]

Tag loss is not necessarily a negative outcome, because shedding of a tag that becomes snagged in such a way that it would immobilize the fish prevents suffering of the animal [24]. This may be achieved if, for example, weak links or absorbable sutures are used. However, it can be difficult to do this in such a way that premature tag losses do not occur before appropriate data have been gathered and while ensuring that such tag losses can be identified. McCubbing et al. [25] used a single absorbable suture through the dorsal muscle to attach radio tags to pre-spawning adults of a threatened Arctic char (*Salvelinus alpinus*) population to ensure that tag attachment was temporary, but found in preliminary observations that upon release in the stream, fish sought refuge under boulders and most tags were rapidly shed. The premature shedding (determined by locating and recovering shed tags during mobile tracking) was reduced by releasing fish in the lake from which they had migrated, several hundred meters downstream, but still a 25 % (5/20 fish) tag loss occurred from within a few days after tagging. More conventional, and more invasive, dorsal musculature tag attachments (body-tight, by use of stainless steel wires) in salmonids such as adult Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in rivers have much higher retention rates [26–28] than those observed for char by McCubbing et al. [25].

Generally, external tag attachment in fishes using benthic habitats causes difficulties in achieving adequate

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Fig. 3 Example of typical external transmitter placement on a fusiform-bodied fish (Atlantic salmon, *Salmo salar*). This radio tag has a flattened section that lies close to the body surface and is held in place by stainless steel wires through the musculature. Note that these tags have conspicuous return information, which is not problematic for adult salmon, but could be an issue for smaller fish that may be susceptible to increased predation risk

tag retention. Tags must be attached snugly to the body to minimize the risk of entanglement/snagging, biofouling and to minimize drag. Several studies have reported problems with external tagging of sturgeon and catfish species. Collins et al. [29] used external radio tagging on shortnose (*Acipenser brevirostrum*) and Atlantic (*A. oxyrinchus*) sturgeons in a field study and found poor retention for both species. In a subsequent tank experiment, only one of 12 individuals retained the tag after 40 days [30]. They judged external tagging unsuitable for these species. However, Sutton et al. [31] tested different attachment methods on juvenile lake sturgeon (*A. fulvescens*) kept in tanks and reported that heavier suture material decreased transmitter loss, but the retention was still poor (75 % loss after 26 days). A subsequent test of different shapes of external tags resulted in loss of over

30 % of the tags in juvenile lake sturgeon after 8 weeks [32]. In contrast, Counihan and Frost [33] tagged juvenile, hatchery-reared white sturgeon (*A. transmontanus*) using external tags (two tagging methods/locations) and observed no tag-loss during the short laboratory study (7–20 days). Like sturgeon, catfishes are known to exhibit low tag retention [e.g. 34]. Bodine and Fleming [35] attempted an alternative tag attachment method for blue catfish (*Ictalurus furcatus*) by using the skeletal structure (supraoccipital bone). In their 2-month laboratory/pond study, tag retention was 100 %, but in the subsequent field study in a lake, tag retention was 40 % at 6 months and 19 % at 12 months. Mitamura et al. [36] attached dummy (acoustic) tags to the pectoral fin of juveniles Mekong catfish (*Pangasianodon gigas*) kept in a pond for 2 months. All tagged fish survived and were retrieved, but all had lost their tags. The reason why catfish and sturgeon are shedding both internal and external tags at a higher rate than most other fishes remains to be understood, but generally they seem to have very active tissue reactions to foreign bodies [37].

Adult anguillid eels represent a particularly difficult group for achieving a high retention rate of external tags. This is not only because of their benthic habits (except during migrations in the open sea), but also because of their body shape and flexibility, enabling them to bite at tag attachments midway along the body, and facilitating tag shedding by 'knotting' their body or passing through narrow crevices. In a thorough laboratory study of the effects of tagging American eel (*Anguilla rostrata*), Cottril et al. [38] found poor retention (9 %) of external tags after a 12-week period. Most eels lost the tags within the first 3–4 weeks after tagging. Furthermore, considerable tissue erosion was evident around the stainless steel wire holding the external tags in place, and major scarring on eels that shed tags was observed. However, in a similar study with smaller (18×7.3 mm) external tags, European eels, kept in a perforated tank in a river, showed 100 % retention after 30 days (M. Lowry, pers. comm.).

Reduction of electronic tag size to a degree suitable for small fish includes reduction of battery size, and hence results in a short battery life. Thus, since the life of small electronic tags is usually low (but see [39]), external tagging can be preferred due to lower acute health effects compared to surgical implantation, where a longer recovery period may be evident. In a field study on Chinook salmon smolts, Brown et al. [40] observed 10 % tag loss 9–17 days after tagging, as well as a high proportion of tags that were loose or displaced. In another laboratory study on Chinook smolts, only 5 % of the fish lost the external tags within 2 weeks [41], but tearing and loosening of the sutures holding the tags were also observed. In lake whitefish (*Coregonus clupeaformis*), Bégout Anras

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et al. [42] observed tag loss for 92 % of the fish within 20 days in tanks. Pursche et al. [43] observed 100 % retention of external miniature acoustic tags (5 days battery life) on mulloway (*Argyrosomus japonicus*) and yellowfin bream (*Acanthopagrus australis*) kept in an aquarium, after a study period of 7 days. Brown and Eiler [44] externally tagged gravid female inconnu (*Stenodus nelma*) and found no evidence of tag loss or mortality in a 2-week field tracking study.

Some studies have sought to divide mass and volume between two elements of a tag on either side of the fish, attached in a pannier-mount, assuming that this should reduce disequilibrium, and especially in cases of high tag to body mass ratio [3, 45]. In general, use of this method [e.g. 46] is less frequent today due not only to technical advances in reducing tag size, but also because saddle type tags, straddling the dorsal surface, are often associated with reduced tag retention rates and because of greater tissue reaction effects (see below). In a laboratory-based comparison of single-side mounted and pannier type transmitters on bluegill (*Lepomis macrochirus*) and yellow perch (*Perca flavescens*), Weimer et al. [47] found that 40 % of the perch and 14 % of the bluegill held in tanks shed their pannier type tags within 40 days. None of the fish tagged with single-side mounts lost these. Herke and Moring [48] tested a novel "harness-fixed-tag" to attach large radio-tags to pike (*Esox lucius*) and concluded that the method gave a high retention rate, but two of six fish shed their tags during the 115-day field study. One pike was recaptured after 54 days with the tag still in place, but some abrasion and tissue tearing were evident.

A variety of marine-based studies have used modifications of conventional tagging methods (Floy, T-bar, Carlin, Peterson disc, etc.), to attach acoustic tags and DSTs. A common method has been to attach a loose-hanging tether from the electronic tag to a wire saddle through the dorso-lateral musculature, secured by a Peterson disc on the other side, for species such as Atlantic cod (*Gadus morhua*) and plaice (*Pleuronectes platessa*) [49, 50] or through fin musculature for thornback ray (*Raja clavata*) [51]. The purpose of the Peterson tag is to spread the tension and reduce cutting of the wire through the skin and muscle. Righton et al. [50] tagged Atlantic cod in the laboratory with external DSTs in this way and observed 100 % retention of tags over a 6-month period. Arnold and Holford [49] reported recaptures of a 'significant proportion' of plaice with acoustic tags (attached to Petersen discs with a loose tether) and cod from the North Sea that had lost acoustic tags, but did not quantify this.

In a comparison of tagging methods for sea bream (*Sarpa salpa*) in experimental tanks, all fish with externally mounted acoustic transmitters retained their tag over a 14-day period, but on all fish some abrasion, injuries, and fouling occurred [52]. In a study of the effects of tagging on growth of juvenile European seabass (*Dicentrarchus labrax*) and juvenile sole (*Solea solea*) in saltmarsh ponds, Bégout Anras et al. [53] observed a tag-loss of 60 % after 47 days in sea bass, but reported 100 % retention of tags by sole during 72 days.

When using PSATs, tag retention until the planned release date is a crucial element of experimental planning and has been difficult to achieve across a wide variety of taxa [7, 19, 54]. This is particularly so for migrating eels, which in the early stages of sea migration inhabit highly structured environments. PSAT tagging of longfin eel (*Anguilla dieffenbachii*) revealed a high rate of tag loss, with only three of 10 tags providing data [54]. Results from 275 silver European eel (*A. anguilla*) released on European coasts equipped with PSATs to study the ocean spawning migration indicated a large premature tag release [19]. This was partly related to mechanical tag loss, but also to a high predation rate (>20 % confirmed predation of eels with PSATs). The natural predation rate is unknown, so it is unclear to what extent the tag contributed to an increased predation risk. Mean time from tagging to premature tag release was 14–21 days (maximum 9 months). In a laboratory test of four different attachment methods for PSATs on European eel, Økland et al. [19] observed an overall tag retention after 6 months of 54 %. Retention varied from 0 to 100 % among the attachment methods, but the method that achieved no tag loss was regarded as less suitable because of a strong negative reaction (the tagged fish were struggling to try to shed the tag and did not swim normally) in the first 2 days after tagging and showed consequent damage to the swimming musculature.

PSAT attachment for inshore and demersal fish is most commonly achieved under sedation or anesthetization by harness attachment to the fish while in a tagging trough, in a manner similar to tagging with radio or acoustic transmitters. However, for large pelagic species, tagging with a pole-mounted dart placed at the base of the dorsal fin, usually with the fish still in the water, is the most common method. Onboard tagging is routinely performed with large bluefin tuna (*Thunnus thynnus*) in Nova Scotia, with no apparent problems for the fish or tag retention (M. Stokesbury, pers. comm.). However, a meta-analysis demonstrated that onboard tagging did not improve tag retention for tunas and billfishes, while for sharks it reduced tag retention duration [7] and suggests that unless landing is needed (e.g. for insertion of sensors), in situ tag attachment may be more effective. A wide range of dart heads and associated attachment elements have been designed and used to try to maximize retention. Musyl et al. [7] emphasized the importance of

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a small entry wound to minimize tissue damage and aid healing. While 'umbrella' and 'flopper' dart head types, with retaining elements that open after dart entry, are often employed to improve retention, a meta-analysis demonstrated nylon tag heads to have lower retention characteristics than all other dart head designs [7].

Key factors likely contributing to PSAT loss in field studies are the relatively high drag and buoyancy of these devices, causing local pressure at the attachment point [55], increased by biofouling [7, 18]. Biofouling has also been reported for standard telemetry tags [56]. Most PSAT tags in large, pelagic species are lost from tens to a few hundred days after attachment, while conventional tag losses in tunas, for example, are typically 2–5 % per year [57]. Witt et al. [58] reported high premature loss rates of PAT (pop-up archival transmitting) tags attached to basking shark (*Cetorhinus maximus*) at the base of the dorsal fin. Eight of nine tags released prematurely, and four of these were lost after just 2 months. They found that nine of 12 smaller PAT tags attached the same way were retained after 7 months. This supports a causal relationship between tag-size, drag, and tag loss in this species. As tag size continues to shrink with technological advances, this should give improved retention in most species when dart-head deployments of PSATs are used. In deep-water environments, darting may be more effective than other external tagging methods, since other methods than darting require the fish's ascent to the surface for tagging. Shauer et al. [59] used in situ darting to tag 11 coelacanths (*Latimeria chalumnae*) with large (30 g) transmitters. Despite the hard ganoid scales of the coelacanth, the dart was shot into the fish using a pneumatic gun from a manned submersible. Tracking records demonstrated that the tags stayed in place for "at least 3–4 weeks". After a period, the tags eventually came off and apparently caused minimal harm to the fish.

As evident from the above-referred studies, tag retention is a major problem in many studies using external tagging. Even for short-term studies this problem can occur. It can be difficult to mount a tag so that it stays in place without injuring the fish or resulting in premature tag-loss. External tagging is particularly problematic for fish that live in close contact with sediment, vegetation or that take shelter in hard structures (roots, woody debris, rocks or crevices). In general, the best success with external tagging has been with large, robust free-swimming fish like adult Atlantic salmon, brown trout; large, open-ocean fishes, or bottom dwelling flatfishes that live on flat sediments. Likewise, experience with external tags for large cichlids has been good [60, 61]. For fusiform and laterally compressed fishes tagged ex situ, a tag flattened on one side, mounted close to the body, below the dorsal fin and affixed by wire or nylon

through the musculature, seems to be the best method, whereas most pannier-saddle-type mounts have been problematic. For many large marine pelagic and deep-water species, external tags may best be applied in situ by darting.

Swimming performance

Reduced swimming performance is one of the expected effects of attaching external tags to fish because of the additional drag exerted by the tag as the fish moves through the water. External tags will change the streamlined body shape that many fish species possess, disturb balance and, at worst, cause loss of equilibrium if the tag is too heavy compared to the mass of the fish. Predatory species that rely on speed to catch prey may be less successful and suffer reduced growth. For prey species dependent on escaping predators, the additional drag and weight of a tag (tag burden) may skew the balance between life and death. The most commonly used metric of tag burden is the ratio of tag mass to fish body mass in air, though for external tags it may not be the most relevant, since tag shape and volume strongly influence drag imparted and may influence swimming, especially at higher speeds, since drag increases as the square of velocity. For migrating species, changes in swimming performance may delay or reduce migration success. Such indirect effects of tagging are difficult to assess, but we identified 21 studies that have used different methods to evaluate effects on swimming performance by externally tagged fish.

In an early study, Shepherd [1] reported a swim trial where the oxygen consumption rate of externally tagged wild cutthroat trout (*Salmo clarki*) was compared with control fish. The study demonstrated a higher oxygen demand of tagged fish. A similar approach with small numbers of tagged and untagged cod showed a higher mass-specific oxygen consumption rate of tagged fish during swimming, indicating that there is a measurable drag effect from the tag [62], as predicted by Arnold and Holford [49]. In a study of the effect of external tagging on juvenile rainbow trout (*Oncorhynchus mykiss*), Lewis and Muntz [63] used tail beat frequency, opercular beat rate, and drag measurements as indicators of swimming performance. All three indicators were elevated in tagged fish compared to controls, and a pannier-saddle-mounted tag, generating more drag than a single-side mount, caused a greater impact. Tests with a dorsal saddle-type tag on the same species showed that time to exhaustion was shorter for externally tagged fish than for surgically implanted and control fish [64]. The same test with white perch (*Morone americana*) showed large individual variation, but no difference was found between treatments [64].

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A common approach to determine tagging impacts on the swimming performance of fishes is to measure the critical swimming speed (*Ucrit*), which is based on incremental increases in water velocity, and hence swimming velocity, in a flume. Peake et al. [65] detected a difference in *Ucrit* between tagged and untagged wild Atlantic salmon smolts, both for surgically implanted and externally tagged fish. This difference was not found in hatchery fish. In a similar study of hatchery smolts, McCleave and Stred [66] found external tags to reduce the critical swimming speed in comparison with untagged control fish and intragastrically tagged fish. In a recent, comprehensive study by Janak et al. [67] on hatchery-reared Chinook smolts, the mean *Ucrit* for control fish was 11 and 22 % higher than the mean for fish tagged with small and large external transmitters, respectively. For juvenile masu salmon (*Oncorhynchus masou*), the *Ucrit* of externally tagged fish was lower than that of surgically implanted and sham-tagged (surgical procedure without a tag inserted) groups [68]. Externally tagged juvenile white sturgeon also exhibited lower *Ucrit* than control fish [33].

Cottril et al. [38] did not find any differences in swimming performance between American eels tagged with dummy acoustic tags (0.5 % tag/bm ratio) by external, surgically implanted, and gastric methods and untagged fish. However, for larger PSAT tags (2–3 % tag/bm), several studies have reported strong effects on swimming performance of eels, including up to three-fold increases in energy cost of transport [69–71]. Using spherical PSAT dummies of varying sizes, in a series of respirometry measurements and kinematic analyses, Tudorache et al. [71] suggested that the optimal location for single point attachment of PSAT tags is more anterior than at the middle of the body length in eels.

For adult Atlantic salmon, Thorstad et al. [27] compared swimming endurance between fish with large external tags, small external tags, surgically implanted tags, and control fish, and found no differences among groups in endurance, nor in values of plasma glucose, haematocrit and plasma chloride. In a field evaluation, Gray and Haynes [72] compared rates of upstream movement of adult Chinook salmon tagged externally and with gastric implanted tags in a field study in the Columbia River, and found no difference in upstream movements between the groups. Sundström and Gruber [73] attached large speed sensing tags to seven juvenile lemon sharks (*Negaprion brevirostris*) in the field and observed "elevated swimming speed" during the first 24 h after tagging, but after that "normal" behaviour was observed.

In general, these studies document a measurable effect on oxygen demand and swimming performance from fishes carrying an external electronic tag. This effect is most pronounced in relatively small fish, or when large buoyant tags have been applied, as in the case of PSATs and related devices. No marked effect was observed for adult Atlantic salmon and lemon sharks with closely attached traditional telemetry tags of less than 3 % tag mass to body mass ratio [72, 73].

Growth

External tags may affect feeding and thus growth, because movement can be impaired by the presence of the tag. Furthermore, capture, handling, holding, and tagging may compromise the health of a fish, affecting the motivation and physical capability for feeding. External tags also involve additional mass and drag, which may result in increased energy expenditure and reduced growth, even if the fish is feeding normally. Thus, growth integrates a range of effects into one measurable parameter, because reduced performance will likely result in a reduced growth. Growth rate can, therefore, be a good indicator of long-term effects by tagging and a useful metric of impact. Field experiments where a tagged fish must compete with untagged conspecifics for food and habitat provide the best test, but most evaluations of tag effects on growth are based on laboratory/mesocosm studies. The challenges of doing field-based growth experiments on identifiable individual fish (from which individual growth rates can be measured) are significant and it is both costly and risky for data capture to move from laboratory to field, thus limiting the number of studies.

For hatchery-reared juvenile Atlantic salmon, Greenstreet and Morgan [74] observed a negative effect of dorsal saddle-type external tags on growth (in tanks) for all size classes, with the smallest fish losing weight during a 17-day period. Weimer et al. [47] found a similar negative effect on growth in yellow perch and bluegill in tanks carrying a saddle-type tag. These species tagged with a single-side mounted external tag also showed reduced growth during the 40-day period, but the effect was less pronounced than for the fish with saddle-type tags [47]. A similar pattern was also observed in hatchery-reared juvenile Chinook salmon, tested for three tagging methods, with reduced growth evident after 2 weeks, and the most pronounced negative effect seen in the saddle-tagged group [41]. Tank-reared barbel (*Barbus barbus*) with side-mounted external dummy tags (2 % of body mass) lost an average of 10 % of their body mass in the 60 days post tagging, compared to controls that gained 2 % of body mass. Externally tagged barbel had a significantly lower growth rate than surgically tagged fish [75]. Externally tagged sub-adult farmed Atlantic salmon exhibited normal activity and feeding in tanks the day after intervention (unlike surgically implanted fish), but

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after 6 weeks, their growth rate was still only half that of controls [76].

In a study of wild Atlantic cod, the use of externally attached data-storage tags was tested both in the laboratory and in a large field experiment [49]. The laboratory results showed that growth of tagged cod did not differ from untagged control fish. In the field experiment, growth of recaptured cod was compared to the growth of wild untagged cod and a slightly (but not significantly) lower growth rate (length) was observed for the tagged cod. Cottrill et al. [38] compared length and weight of European eels in a laboratory study (control, gastric, surgically implanted, external) 8–10 weeks after treatment and found no effect of tagging. Likewise, Økland et al. [19] found no difference in growth (weight loss) between tagged and untagged silver eels after 4 weeks. In the case of silver eel, growth is not a strong indicator of tagging effects because silver eels, like many other semelparous fish species, are known not to feed after they start their seaward migration. However, during migration, energy use and weight loss of eels with large external tags may be elevated due to increased drag. Beaumont et al. [77] observed externally tagged dace (*Leuciscus leuciscus*) in a glass-sided fluviarium tank and compared the condition-factor (*K*) between tagged and untagged fish after a 10-week period, and no significant difference was recorded.

As most studies using external tagging with electronic tags are relatively short-term, potential impacts on growth have not been of deep concern, but the studies above show negative effects on growth or body condition in Atlantic salmon juveniles, yellow perch, bluegill, and barbel, but not in cod, eel, and dace. The negative effect on growth was stronger for dorsal-mounted pannier-saddle-type tags than for single-sided tags.

Social interactions

Movement and habitat use is partly determined by social interactions in many fish species. Stress caused by capture, handling, and tagging may change aggression, position in dominance hierarchies, competition, parental care, shoaling, and other types of social behavior, and thus, lead to biased results in telemetry studies. Further, features such as bright colors, specific color patterns, body size and shape, or size and shape of other morphological attributes (for instance adipose fin size in reproductively mature male salmonids, degree of asymmetry) have evolved in many fishes through sexual selection either to increase attractiveness to the opposite sex or related to competition with rivals of the same sex, with the ultimate aim to maximize reproductive success. The presence of an external tag on a fish may, due to the size, shape or color of the tag, interfere with such signals.

External tags may also increase the visibility of the fish to such an extent that the predation risk is increased (see "Survival" section below). Such effects may be reduced by dying the tag to blend with fish color, thus camouflaging the tag [67]. Bright tag labels with return-information should be kept on the side of the tag towards the fish to reduce the visibility.

Only a few studies have been carried out to evaluate the effects of external tagging on social interactions in fish (Fig. 2), and the existing studies have not revealed severe impacts. In a study of rainbow trout, dominance rank of individual fish only changed marginally after tagging [64]. Externally tagged dace were observed to integrate into a shoal after tagging [77]. When externally radio tagged bream (*Abramis brama*) were located and recaptured by seine netting, they were always part of a bream shoal, demonstrating that after tagging they had reintegrated [78]. Using field observational methods, Cooke [79] found no evidence that externally attached radio transmitters affect parental care by rock bass (*Ambloplites rupestris*). Studies of social interactions may be more sensitive to subtle but chronic effects by external tagging than studies of other type tagging effects, but are difficult to carry out in a controlled way. There is clearly a need for more studies on social interactions. The lack of documented effects is not indicative of a lack of real effects, because the number of existing studies is so low.

Survival

Survival is not a sufficient indicator of the suitability of a tagging method, but low survival is often a good indicator for a problematic method. In most telemetry studies, survival rates of externally tagged fish have been high, but with species, habitat, and methodological variations. Thus, half of the studies where survival of externally tagged fish was reported found no increased mortality [compared to control fish (laboratory) or expected levels (field)]. Mortalities reported in laboratory/mesocosm studies are rarely predation related, as relatively few such tests have been done (but see, for example, Ross and McCormick [80] who quantified such effects), whereas, in the field, mortalities represent a composite of disease, stress, physiological insult, and predation effects, but these impacts are often difficult to disentangle. In the laboratory, Greenstreet and Morgan [74] observed relatively high mortality of the smallest Atlantic salmon juveniles tagged with a "saddle-pack" dummy transmitter, but no mortality for larger individuals (18–20 cm). Tests of single-side and saddle type transmitters on wild bluegill and yellow perch, kept in tanks, showed up to 50 % mortality, mainly for perch, and highest with the saddle mounted tags [47]. Testing of an external attachment method, as an alternative to surgical implantation,

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on wild blue catfish kept in ponds, revealed mortality of 13 % over 6 months, possibly related to tagging. However, the authors also state that this may be attributed to elevated stress and subsequent infection associated with confinement in the hatchery pond [35]. Brown et al. [81] compared survival of externally tagged hatchery-reared Chinook salmon juveniles during simulated turbine passage (laboratory) and found no difference in mortality between tagged and control fish. A further (field) comparison between surgically implanted (PIT-tags) and externally tagged hatchery-reared Chinook smolts during passage of hydropower stations and along river reaches showed that external tags were suitable for short-term migration studies, but not for longer periods than 10 days due to tag loss and mortality [40]. In masu salmon (*Oncorhynchus masou*) juveniles, kept in an outdoor tank, 83 % of externally tagged and 42 % of surgically implanted fish died within 68 days [68]. By contrast, Broadhurst et al. [21] found high mortality (and tag expulsion) in the surgically implanted group, but no mortality or tag loss in the externally tagged group in wild Macquarie perch kept in aquaria. The same result was found in a study of common carp (*Cyprinus carpio*), kept in concrete ponds in Africa, where all fish in the surgically implanted group died and all externally tagged fish survived [82].

Corbett et al. [23] compared external tagging with gastric implant for adult Chinook in a 50-day laboratory experiment. Only one of 10 externally tagged salmon died, whereas there was high mortality (19/20) of fish with gastric implants. In the field, Thorstad et al. [28] found little mortality (1 out of 39 fish did not migrate upstream) in externally tagged sea trout (anadromous *S. trutta*). A similar outcome for this species was recorded by Økland et al. [26]. Likewise, in a lowland Danish river, Aarestrup and Jepsen [83] used externally attached radio tags to study wild sea-trout pre- and post-spawning movements. They observed some mortality (<20 %) of tagged fish, but ascribed this to natural post-spawning mortality. Some tagged fish left the river after the spawning period, but 10 of 25 tagged fish were retrieved by electrofishing with the tags still in place and only minor abrasions. No tag loss was observed [83]. Similar results were recorded for externally tagged Atlantic salmon in the same river [84]. However, in a similar study of sea trout spawning migration, in a smaller stream with abundant vegetation, the external tagging method had to be abandoned due to tag loss, mortality, and observation of wounds at the tag position, most likely caused by entanglement in vegetation (N. Jepsen, unpublished). By contrast, for externally tagged tench (*Tinca tinca*) in a weedy lake after 1 month at liberty, nine of 15 fish were recovered with tags [85]. While some of the tags in this study were shown to have loosened, the method was judged as

successful even with fish living in a weedy environment. The "tilt-tags" employed in this study also indicated that tench exhibited the head-down feeding behaviors expected [85], suggesting normal behavior.

Low mortality levels have been reported for mulloway and yellowfin bream externally tagged with miniature acoustic tags in controlled studies of short (7 days) duration [43]. However, over a longer timescale and for larger silver perch with external tags, elevated mortality occurred for tagged fish (40 %) compared to control fish (10 %) after 257 days, and all surviving fish had shed their tags [22]. Hanson and Ostrand [86] tested different electronic tagging methods on small anadromous eulachon (*Thaleichthys pacificus*) and found high mortality (50 %) after only 5 days, of all groups, including non-tagged control fish, indicating that this species is sensitive to capture, handling, and holding (in aquaria). For yellow perch tagged with externally attached transmitters, Ross and McCormick [80] found low survival (7 %) after 86 days in a pond with low oxygen levels in summer, compared to 82 % of control fish from the same pond, suggesting a chronic impact of external tagging, combined with poor water quality. In another experiment, they found that externally tagged yellow perch, in a small pond with good water quality and a small number of predatory northern pike, exhibited 41 % survival, compared to 94 % for controls [80]. Several tagged perch were found in pike stomachs at the end of the experiment, and the authors inferred different susceptibility to predation to be a key cause of mortality.

In the case of PSATs, it is possible to identify mortality in pelagic species because a static depth record over several days is indicative of mortality, with the tagged fish lying on the bottom, as opposed to normal changes in depth through the water column. When released from the fish, PSATs will float to the surface, due to their positive buoyancy. Most PSATs will automatically release in response to a preset time threshold at a stable depth (typically when on the bottom) and hence data can be used to determine mortality rates [87], but may be unreliable in some species, such as basking shark, which may spend protracted periods at a stable depth. Since mortality may also occur over deep-ocean areas, a failsafe release is deployed at a specific depth to prevent pressure damage to the PSAT, which can also be used to estimate mortality rates [87]. Mortality through predation can be identified on occasion, due to the tag's light sensor recording darkness (in the predator's gut) over an extended period, and thermistor and depth log information can help to identify the predator type (e.g. persistent elevated temperatures, with temperatures characteristic of endothermic tunas and sharks, or marine mammals) [88, 89]. While such mortality estimates are possible, they were not

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included in Musyl et al.'s detailed meta-analytical study [7], perhaps because interpretation of mortality in such instances is an inexact science. Holland and Braun [17] identified a discussion-based reticence to report mortalities, as this could jeopardize some PSAT-based research. We consider it likely that many PSAT-recorded mortalities of large oceanic fish [e.g. 87] reflect capture and handling effects more than direct effect of tagging. Indeed, many of those studies are actually directed at assessing survival of released large pelagic species from unwanted by-catch in commercial operations [e.g. 87, 90]. As smaller fishes are being tagged with miniaturized PSATs, predation is increasingly likely (large carnivores eat smaller animals), but to distinguish the effects of natural mortality from the increase due to PSAT tagging is difficult. The high mortality rates of PSAT-tagged American eel [91], attributed most likely to predation by porbeagle shark (*Lamna nasus*), may have been facilitated at least in part by the relatively large and buoyant tag, perhaps making the eel more conspicuous than normal. Undoubtedly, migrating eels can provide reliable food sources for top predators, but identifying the additional effect of tagging with large, positively buoyant tags in such an environment is difficult.

From the published studies, it appears that direct mortality caused by external tagging is usually low, but that tagging may be contributory. Particularly, when tagging fishes of relatively small size compared to the large buoyant PSAT tags, there seem to be an extra risk of mortality due to predation. Hence, one should be cautious to draw conclusions on natural mortality levels of relatively small fishes, and causes for this mortality, based on results from PSAT tagged fish. The combined effect of capture, handling, tagging, and holding fish for observation can cause significant mortality, and it is difficult to separate between the effects of the tag and tagging itself, and the effects of capture and handling. It is therefore important to include untagged control fish in studies, whenever possible (laboratory/tanks/ponds), or, for instance, by comparing with less invasive tagging methods like dye-marking, coded wire tagging, or PIT-tagging in field studies. In general, it seems that external tagging of juvenile salmonids can be done, but the experiences are not as good as they are for the surgical implant or tag injection [39] techniques. Also perciforms (including Percidae, Teraponidae, Centrarchidae) can be vulnerable to external tagging, but here the results vary among species and studies. Overall, there is large variation in survival rates among studies. In few cases, increased mortality rate can be directly linked to the tagging procedure, but usually acute mortality is caused by the combined effect of being captured, held, handled, and/or carrying the tag, whereas the carrying of the tag is manifested principally

as a chronic effect on growth, though in some cases with increased incidence of mortality, linked to disease and/or predation.

Discussion

A vital element of telemetry studies is that the tag should not alter animal behavior or performance, and if it does, that the effect can be measured and accounted for and thus does not interfere with the conclusions of the study [3]. Based on the information covered in this review, it is clear that while external tagging can be a valuable method to attach electronic tags to fish, substantial tag loss and adverse effects to the fish can occur. In this context, it is important to distinguish between acute and chronic impacts of external tagging on fish behavior and health. External attachment of standard electronic tags can be achieved more quickly and less invasively than by surgical implantation employing suture closure, and may, particularly through dart-deployment in the field, require no anesthesia or handling of the fish [9]. Therefore, recovery and subsequent change in behavior from external tagging may be minimal and involve no immediate risk of pathogen entry to the body cavity. However, while incision and closure (by suturing) of the body wall in surgical implantation is invasive, once healed, long-term impacts are often low, while increased tissue abrasion, tag visibility to predators, and long-term elevated drag effects have the potential to generate marked chronic impacts in external telemetry tagging applications [4, 8]. This is the main reason for generally recommending surgical implants for long-term studies.

Some of the subtle effects of tagging and release into the natural environment, such as predation risk, are among the best indicators of impact [92], but are increasingly difficult to evaluate under controlled conditions because of complexities in obtaining ethical/welfare committee decisions to do so. One of the few examples of studying increased predation risk resulting from external electronic tagging [80] is more than 30 years old. Control fish (handled and individually identifiable but not telemetry-tagged) cannot easily be recaptured from many natural environments, so this inhibits or biases assessment of their survival, by comparison to telemetry tagged fish, the known locations of which facilitate recapture, at least in shallow water. Also, under field conditions, without direct observation or tag recovery, it can be difficult to distinguish telemetry tag loss from mortality of the tagged fish, and to determine the cause of mortality (whether from disease or predation, for example), in many aquatic habitats. The best options for quantifying effects may be in experiments using semi-natural closed systems that can be drained down and efficiently sampled, and where densities of predators and prey, including instrumented/

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treated fish, can be manipulated. However, there can be problems with obtaining animal welfare permission to establish such systems where the prime objective is to expose tagged, sham-treated, and control animals to predation risk. Animal welfare committees can perceive this as unnecessarily stressful to the experimental prey fish, but demonstration of no impact (and hence bias) under nature-like conditions for telemetry studies needs exactly this type of experiment and evidence base.

Advantages and disadvantages of external tagging

Advantages of external tagging include (1) the attachment can be easy and fast and requires less training than some other tagging methods; (2) the method can be used for fishes with a body shape not suitable for surgical implantation, for instance, in laterally or dorso-ventrally compressed fish with little space available in the body cavity; (3) external tag position is an advantage if sensors are used to record external variables (e.g. water temperature, light, acceleration, salinity and oxygen concentration); (4) anesthetization is not always required or desirable (e.g. for many large, marine, pelagic species, or for large freshwater fishes like sturgeon); (5) tagging fish like adult salmon, that may be used for consumption, without using anesthesia, makes it possible to release these immediately after tagging without a withdrawal period [89]. Such a period is often required to prevent human consumption of 'narcotics', and (6) if recovery of tags is essential, external tags can easily be identified by fishers at recapture and there is no need for a conventional external tag to identify tagged fish (which is especially important for data storage tags that need to be returned to download stored data). Further, externally tagged fish can be more easily recaptured, because the external tags can be entangled in gillnets [93]. This may be regarded as a disadvantage, but it is sometimes an advantage if the tags need to be retrieved (e.g. data storage tags [93]). External attachment is the only option for PSATs that must be released from the fish and float to the surface to be able to transmit data to satellites. A last advantage of external tagging is that it can be applied to female fish close to the spawning period. Using surgical implants on gravid females may be problematic due to the presence of large gonads (lack of room) and the concern that a tag may block the passage of eggs and thus interfere with spawning.

The most commonly reported problems with external tags are tissue damage, tag loss and decreased swimming capacity. In summary, the disadvantages of external tagging are that (1) the tag interferes with the streamlined body shape of the fish and increases drag, disequilibrium and energy expenditure, and reduces swimming performance, (2) algae and sessile animals may grow on the tag and antenna (fouling, especially in coastal areas) and increase the drag, which may further reduce swimming performance, (3) the tag or antenna can be entangled in aquatic vegetation, roots, between rocks or in fishing nets, (4) the visible tag may affect predation risk, competition and other interactions with conspecifics, (5) the method is not well-suited in the long term for fast-growing or non-feeding fish, (6) attachment wires may, in the long term, cause extensive damage to muscle and integument, (7) there is potential for substantial tag loss in long term studies (size/shape/species dependent), and (8) the method is not usually suitable for measuring internal, physiological variables in the long-term. In many cases researchers can test for these disadvantages in preparation for or during the study. Knowledge about the species in question, the habitat the tagged fish will be in and of the current literature on tagging effects, will aid the decision of tagging method.

There is no perfect tagging method: which method to choose?

There is no method for attaching electronic tags without some degree of negative impact on the fish, though in many cases the effects may be minimal and may not be detectable in comparisons with controls. The lack of a perfect tagging method and the diversity of taxa and system-specific effects make it difficult to choose which tagging method to use. Choice of method should be based on careful evaluation of advantages and disadvantages of the different tagging methods, dependent on fish species, size, and life stage to be studied and the habitat, duration, and aim of the study. Information and advice to aid the decision can be found in the literature, and particularly from studies of tagging effects in the same or similar species and habitats, but in many cases pilot experiments are necessary.

Our own experiences with tagging adult Atlantic salmon and brown trout with radio transmitters can serve as an example of considerations and compromises made when selecting the tagging method. In general, we commonly use surgical implantation for tagging fishes with electronic tags, but have often used external attachment, for example, for adult salmonids during the riverine upstream migration. The reason is that surgical incisions may not heal easily in fish that are in periods of high physical activity, and incisions may open up when fish are jumping and swimming in waterfalls and strong currents (own observations in Atlantic salmon, [27]). An alternative could be to tag fish with surgically implanted tags and hold them for some weeks after tagging in a pen to let the incision heal before release. However, the risk that keeping wild fish in captivity during the migration stage might affect their post-release behavior is too large [e.g. 94]. Laboratory studies in a swim speed chamber

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have shown that even relatively large external tags (1–3 % tag to body mass ratio) do not affect the swimming performance of Atlantic salmon compared to fish with surgically implanted tags and untagged control fish [27]. However, large external tags (2–5 % tag to body mass ratio) have been shown to reduce the total migration distance of the fish in rivers with strong currents and waterfalls, and increase the duration of delay below waterfalls compared to fish tagged with smaller (0.5–1 % tag to body mass ratio) external or surgically implanted tags in both sea trout and Atlantic salmon ([27] and unpublished results). Hence, it seems that large external tags may affect burst activity and jumping ability more than sustainable swim speeds [27] as would be expected from drag vs swimming velocity relationships. A comparison between fish with small external tags and untagged fish has not been possible in these field studies. In summary, we have concluded that both surgically implanted and external tags may negatively affect upstream-migrating salmonids in high-gradient rivers with strong flows and obstructions to passage, but that external tags overall have less negative impact than implants in such cases. We use the smallest tags possible in fast-flowing rivers, even though this reduces the duration of the study period, and when we draw conclusions from the results we have to consider that a tagged fish might migrate a shorter distance and at a slower speed than an untagged fish in some cases.

The best success in studies using external tag attachment for fusiform or laterally compressed fish has often been achieved with the simplest methods; a tag flattened on the side facing the fish, fixed closely to the body on one side of the fish, usually close to the dorsal fin, with two wires through the dorsal muscles. However, as an example of how it is possible to adjust and modify tagging methods to achieve better retention, Beaumont and Masters [24], Armstrong et al. [95], and Herke and Moring [48] all tagged pike externally with different methods for different purposes and perspectives. Each of the methods had specific advantages and limitations.

For researchers not entirely sure about the choice of tagging method, controlled tag effect studies will be useful to carry out. If resources are small and such studies not possible, it can still be useful to tag a few fish and observe them in the laboratory for shorter or longer time-periods. This can be cost-effective by reducing the risk of performing large field studies that result in little or heavily biased data because of a large tag loss rate or mortality. Useful information can also be collected by recapture of some of the tagged fish towards the end of field studies to evaluate tagging effects. This is particularly feasible in smaller freshwater systems, but recaptures by fishers in larger systems, and also in some marine systems, can also help to evaluate the tagging methods.

Fish and tag size

Despite considerable emphasis on limits of tag mass to fish body mass (e.g. the so-called 2 % rule, [45]), there is no generally applicable rule for how large the tag can be in relation to fish body size [96]. The appropriate maximum relationship between tag size and fish body size is determined by the specific study objectives, the tagging method, the species/life stage involved, and evidence from pilot studies and related insights. In some cases, tag effects are demonstrated with tags weighing less than 2 % of the body mass of the fish, and in other cases larger tags can be used without any significant tagging effects [96]. For potential tagging effects, tag size (volume) can be as important as tag mass. If tags must be large, it is possible to produce them so they are neutrally buoyant in water to reduce the effects of extra weight, but the larger size of the tag may increase drag and risk of entanglement in aquatic vegetation. For PSATs, which are slightly positively buoyant and are attached by a tether, two forces act on the tagged animal: the lift from the tag's buoyancy and drag as the tag is moved through the water column. Hence, the attachment of PSATs is more challenging than of external tags that can be attached against the fish body. Nevertheless, we would also be very cautious in applying external telemetry tags for studies concentrating on measuring peak swimming performance such as in fishway trials, due to drag effects, though it should be noted that some studies have applied small external PIT tags (0.6 g, <0.5 % tag to body mass ratio), with minimal fish handling, for such evaluations with good outcomes (e.g. [97]).

For small fish (<15 cm body length), the authors generally prefer to use surgical implantation instead of external attachment methods. This is because a similar sized tag can be carried inside the body cavity better than externally, because the tag is nearer the fish's center of mass and there is no drag. However, the recent advent of radio- and acoustic 'picotags' (<1 g in weight) now allow the tracking of smaller individuals, albeit over shorter time periods (7–21 days), and may in some instances be well-suited for external attachment as some of the cited papers have shown. Equally, Deng et al's [39] demonstration of an injectable acoustic tag, 0.22 g mass in air and 3.4 mm in diameter with a life of 100 days provides a long-life, rapid tagging option that may herald a new generation of picotag with low tagging impact.

There is no clear tag/fish size threshold, so we recommend using as small tags as possible to safeguard against negative effects, even though this may compromise the duration of the study period. If the goal is to study fish

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behavior over several seasons, an option is to tag new fish each season instead of studying the same fish over longer term. Several studies have shown that tag effects are less severe for smaller tags when compared to larger tag sizes (e.g. [28, 58]). For example, a larger proportion of fish with large external tags had signs of wounds at the tag attachments than those tagged with smaller tags [27].

Tag shape

External tags are often attached with stainless steel wires or nylon filaments through the muscle at the dorsal fin, with the tag resting at the skin below the fin. Tags with a flat shape facing the body are better suited for such external attachment than cylindrical tags because they interfere less with a streamlined body shape, rest closer to the fish, and are, therefore, less likely to loosen and cause long-term negative impacts. However, due to the components of acoustic tags, they are usually produced with a cylindrical shape and are, therefore, less suitable for external tagging than radio transmitters and archival tags, which are available in both cylindrical and flat shapes. An exception to this may be for sturgeon, which seems to have better tag retention for cylindrical tags than flat tags when using external attachment, likely because of their concave body shape beneath the bone plates (scutes) [31].

The way forward

The large variation in results, even from the same tags attached to the same species and size of fish, makes it difficult to generalize tagging advice, and the best advice is to test the specific method as thoroughly as possible before using it in the field. There is a need for more tag effect studies (including externally mounted electronic tags) in both field and laboratory environments, particularly studies including control groups of untagged fish, studies evaluating effects of different tag/fish sizes, and studies with larger sample sizes. Also, inclusion of sham tagged groups could be useful to separate possible effects of the tagging process from the effects of carrying a tag. In studies of surgical implanting, sham-tagged control groups are often included, but this has not been the case in external tagging studies.

Although potentially relevant, subtle effects like social interactions and predation are the least studied impacts. Studies of predation risk related to tagging may be among the best bioassays of impact (e.g. [98]) and are important to evaluate how well tagged fish represent natural mortality in different ecosystems. There is, however, still a need for studies of tag loss, swimming performance, and growth for many species, as well as studies that can be used to refine tagging methods.

For large PSATs, published tagging effect studies have demonstrated particular problems related to tag loss, reduced swim capacity, and likely increased predation. However, there is still a paucity of tag effect studies related to the use of PSATs and a large need for studies quantifying tagging effects and studies that can be used to refine tagging methods and reduce possible effects.

In all tagging experiences, it is crucial that the experimental fish are captured (if wild) and handled in the most careful way. Most experienced fish researchers agree that acquiring the right fish, at the right time, in the right condition, is often the most challenging part of a telemetry study, especially when using wild fish. There is much focus in the literature and by ethical committees on tag effects, but often the combined effects of capture and handling may be even more important for the welfare of the fish and the outcome of the study than tagging itself. We would, therefore, like to emphasize the particular need for more studies on effects of capture and handling, by comparison to tagging, on subsequent performance in the short and longer term.

Authors' contributions
All authors contributed to the collection of the literature and drafting of the manuscript. All authors read and approved the final manuscript.

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