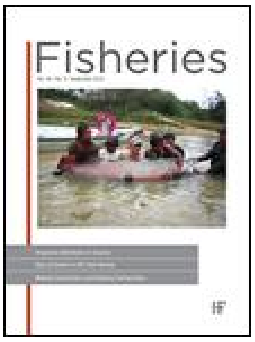

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FISH Out of WATER: How Much Air is Too Much?

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FISH Out of WATER

How Much Air Is Too Much?

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Exposing fish to air following capture influences postrelease survival and behavior. Air exposure causes acute hypoxia and physical damage to the gill lamellae, resulting in physiological stress and physical damage that increases with air exposure duration. Air exposure duration is a relevant and easily quantified metric for both fishers and managers and can therefore provide a definitive benchmark for improving postrelease survival. Yet, fishers are rarely provided with specific recommendations other than simply to “minimize” air exposure. This is a subjective recommendation, potentially causing confusion and noncompliance. Here we discuss and summarize the literature regarding air exposure thresholds in both commercial and recreational fisheries, the factors influencing these thresholds, and identify knowledge gaps limiting our understanding of tolerance to air exposure in captured fish.

Pez fuera del agua: ¿cuánto es mucho aire?

Exponer a los peces al aire tras ser capturados influencia su supervivencia y comportamiento a la hora de liberarlos. La exposición al aire causa hipoxia aguda y maltrata las lamelas de las branquias, lo que resulta en estrés fisiológico y daño físico, el cual se incrementa a medida que se expone el pez al aire por más tiempo. La duración de la exposición al aire es una medida relevante y fácil de cuantificar tanto para los pescadores como para los manejadores y, por lo tanto, brinda un punto de referencia para mejorar la supervivencia tras la liberación. Aun así, a los pescadores rara vez se les dan recomendaciones específicas que van más allá de “minimizar” la exposición de los peces. Esta es una recomendación subjetiva que potencialmente causa confusión y no se acata. Aquí se discute y resume la literatura referente a los límites de exposición al aire tanto en pesquerías comerciales como recreativas, los factores que afectan esos límites y se identifican huecos del conocimiento que limitan el entendimiento de la tolerancia de los peces capturados cuando se les expone al aire.

Un poisson hors de l’eau : Quelle est la quantité d’air maximale admissible?

Exposer les poissons à l’air après leur capture influe sur la survie et le comportement après remise à l’eau. L’exposition à l’air provoque une hypoxie aiguë et des dommages physiques aux lamelles des branchies, ce qui entraîne un stress physiologique et des dommages physiques qui augmentent avec la durée d’exposition à l’air. La durée d’exposition à l’air est une mesure pertinente et facilement quantifiée pour les pêcheurs et les gestionnaires et peut donc constituer une référence définitive pour l’amélioration de la survie après remise à l’eau. Pourtant, les pêcheurs reçoivent rarement des recommandations spécifiques autres que de simplement « minimiser » l’exposition à l’air. Cette recommandation est subjective, et peut semer la confusion et conduire à la non-conformité. Ici, nous discutons et faisons le point sur la documentation concernant les seuils d’exposition à l’air à la fois pour la pêche commerciale et la pêche récréative, les facteurs influençant ces seuils, et identifions les lacunes dans les connaissances qui limitent notre compréhension de la tolérance à l’exposition de l’air chez les poissons capturés.

External variables such as environmental conditions, species, or life history stage can all factor into air exposure tolerance; therefore, there is no universal threshold applicable to all fish-capture events.

INTRODUCTION

The primary objective of both commercial and recreational fisheries is to capture fish, but for a variety of reasons (e.g., regulations, individual conservation ethic, lack of commercial market), many are released (Cooke and Cowx 2006). Although it is often assumed that released fish will experience negligible consequences to lifetime fitness and will survive to return to the common population (Wydoski 1977; Wilson et al. 2014), a capture event and the associated handling can cause sublethal disturbances or mortality. Consequently, there have been increasing efforts to evaluate the relative importance of factors that may contribute to mortality among released fish, including the extent of air exposure.

Recreational anglers may remove fish from water for measuring, admiration, or photography prior to release (Pelletier et al. 2007), and in commercial fisheries, nontarget “bycatch” species are typically exposed to air during sorting. Air exposure durations are variable in commercial fisheries, ranging from a few minutes for small catches to over an hour with larger catches (Davis 2002). Given a fish’s ability, and need, to extract oxygen from aqueous environments, with the unique exception of air-breathing fish, it has long been recognized that removing fish from water is harmful.

Most fisheries lack explicit recommendations regarding exactly how much air exposure is tolerable. Pelletier et al. (2007) reviewed existing best handling guidelines for anglers and found that although 90% of the evaluated guidelines incorporated recommendations regarding air exposure, these recommendations were inconsistent and vague; only in one case was a discrete threshold identified (Maine; 15 s). External variables such as environmental conditions, species, or life history stage can all factor into air exposure tolerance; therefore, there is no universal threshold applicable to all fish-capture events. As such, both scientists and managers tend to avoid endorsing specific air exposure thresholds, favoring a cautious recommendation that air exposure be simply minimized or eliminated wherever possible. Though this is certainly valid, without specific recommendations fishers can take a subjective approach in interpreting what constitutes “appropriate” air exposure.

Air exposure duration can provide a proximate estimate of the likelihood of mortality and is an easily quantifiable metric for both the fisher and the fishery observer in recreational and commercial fisheries. Explicit air exposure thresholds could provide a measuring stick for fisher behavior whereby specific guidelines, through formal regulation or educational programs, would facilitate compliance by fishers and enable enforcement by management and conservation officers. Educating fishers about the requirements of their focal species is an important component of ensuring compliance or simply instilling conservation-oriented behaviors (Cooke et al. 2013). Therefore, where specific guidelines are unavailable, improved education regarding the effects of air exposure can act to transfer responsibility for fish welfare to the fisher.

Experimental research quantifying the effects of air exposure commonly includes simulations that incorporate variable air exposure durations, often in combination with exhaustive exercise to mimic the synergistic effects of a capture event. There is a growing body of literature documenting the effects of air exposure on a variety of fish. Here we examine this literature and review the factors influencing the susceptibility of fish to the effects of air exposure. This synthesis aims to provide managers and fishers with clear information to consider when developing and applying fish handling guidelines.

EFFECTS OF AIR EXPOSURE

Air exposure can be considered acute hypoxia for fish, and when a fish is removed from water, a cascade of physical and physiological disturbances supervene (Figure 1). Gill filaments adhere to one another, and the gill lamellae, the respiratory organs responsible for gas exchange, collapse (Ferguson and Tufts 1992). Gas exchange normally occurring via capillaries in the gill lamella therefore stops, ceasing aerobic respiration (Ferguson and Tufts 1992). The individual develops an oxygen debt, and acidic carbon dioxide accumulates, which combined with the lactic acid released during anaerobic exercise, decreases blood pH (i.e., extracellular acidosis; Ferguson and Tufts 1992; Suski et al. 2004). The heart rate slows (i.e., bradycardia) until the fish is returned to water, at which point the heart action becomes tachycardic (i.e., beyond the normal range; Cooke et al. 2001). The longer the air exposure duration, the longer these cardiac disturbances take to recover (Cooke et al. 2001).

Asphyxia due to air exposure is an acute stressor, activating the hypothalamic–pituitary–interrenal axis and triggering a physiological stress response that results in increased circulating lactate, glucose, and cortisol (Arends et al. 1999). The duration of disturbance as a result of capture is proportional to the magnitude of physiological response (e.g., Chopin et al. 1996) and greater stress responsiveness (i.e., the change from baseline to stress-induced concentrations of cortisol) as a result of air exposure has been previously linked to mortality in Sockeye Salmon *Oncorhynchus nerka* (Cook et al. 2014). However, the stress history of the individual is also important. Stress responses can be cumulative (Barton et al. 1986); therefore, stress due to air exposure can be influenced by preceding events such as chase, injury due to capture, and environmental conditions. In fisheries where fish "fight" to exhaustion, burst swimming and the resulting power output from locomotory muscles, fueled by anaerobic metabolism, depletes tissue energy stores and initiates a stress response (Kieffer 2000). When the exhausted individual is removed from the water, additional lactate accumulates, extracellular acidosis is increased, and osmoregulatory disruption is exacerbated (Cooke and Suski 2005). Similarly, behavior during air exposure can influence the magnitude of homeostatic disruption. In Rainbow Trout *O. mykiss*, mortality during air exposure was highest in the individuals that struggled to escape, whereas survivors remained comparatively calm (Van Raaij et al. 1996).

RECOMMENDATIONS FROM THE LITERATURE: HOW MUCH AIR EXPOSURE IS TOO MUCH?

Recreational Fisheries

Air exposure durations in recreational fisheries are typically short and unlikely to cause immediate mortality. However, numerous studies have observed sublethal impairments due to air exposure following angling. For example, neither Thompson et al. (2008) nor White et al. (2008) observed mortality in black

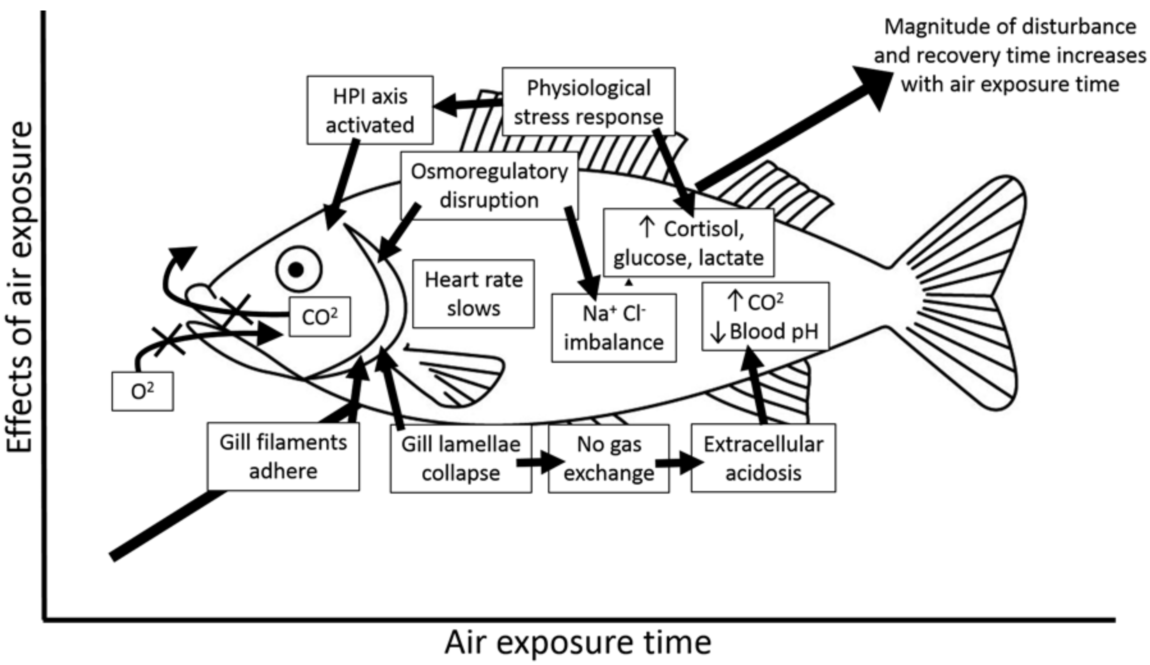

Figure 1. Physiological responses occurring when fish are removed from water. Effects of air exposure increase with the duration of air exposure.

bass *Micropterus* spp. following air exposure for up to 10 min in 23°C water and up to 15 min in 21°C water, respectively, but both studies observed latent recovery (i.e., failure to maintain equilibrium), and Thompson et al. (2008) observed elevated blood glucose. Additionally, following just 2–3 min of air exposure, Schreer et al. (2005) identified disturbed swimming behavior in Brook Trout *Salvelinus fontinalis* during a 3-month observation period, and Hanson et al. (2007) observed angled and air exposed Smallmouth Bass *M. dolomieu* and Largemouth Bass *M. salmoides* abandon their nest guarding charges more frequently than fish angled but not air exposed. In an extreme example, just 10 s of air exposure was determined to affect the fecundity of Atlantic Salmon *Salmo salar*; genetic analyses indicated that fish not air exposed produced twice as many offspring as those air exposed for up to 10 s and three times as many as those exposed for more than 10 s (Richard et al. 2013).

Observations of delayed recovery in air-exposed fish have inspired questions about the effects of angling on postrelease predation (Bartholomew and Bohnsack 2005). Dallas et al. (2010) found that lactate, ammonia, and urea were excreted by Bonefish *Albula vulpes* after capture, and 1 min of air exposure, which disrupts the resting behavior of Lemon Sharks *Negaprion brevirostrus*, a prominent predator of Bonefish in coastal flats habitats. Although air exposure did not directly influence postrelease predation of Bonefish in a study by Danylchuk et al. (2007), fish exposed to longer air exposure durations lost equilibrium more often and individuals losing equilibrium encountered six times the predation than those able to maintain equilibrium.

Commercial Fisheries

Nontarget species and/or fish outside of size restrictions (i.e., bycatch) are captured along with target individuals in commercial fisheries, sometimes in large numbers. The whole catch is often deposited onto the deck of the vessel for sorting, and bycatch is discarded. Due to the propensity with which large-scale commercial fisheries may interact with nontarget species and the high mortality of released fish (Cooke and Cowx 2006), there is increasing interest in identifying factors causing mortality among bycatch species (Davis 2002). Given the necessity of efficiency in commercial operations, the release of bycatch is often not prioritized, leading to extensive air exposure. Some research has suggested that many common bycatch species can tolerate such protracted air exposures. For example, no mortality occurred during 10 days in Pacific Halibut *Hippoglossus stenolepis* exposed to simulated trawl capture followed by 30 min of air exposure (Haukenes and Buck 2006), and Davis and Olla (2002) observed no immediate mortality after 45 min air exposure in adult Lingcod *Ophiodon elongatus*.

As with recreational fisheries, the sublethal effects of capture are also very important to consider but are less frequently evaluated in commercial fisheries (Wilson et al. 2014). In one example, survival was high in Atlantic Sturgeon *Acipenser oxyrinchus* captured and released from otter trawls, but blood lactate concentrations increased with air exposure duration (up to 5 min; Beardsdall et al. 2013). In laboratory studies of Sablefish *Anoplopoma fimbria*, 15 min of air exposure resulted in immunosuppression (i.e., diminished in vitro–stimulated proliferation of leukocytes; Lupes et al. 2006). Understanding the effects of air exposure in commercial fisheries would benefit from further assessments of sublethal disturbances.

Specific air exposure threshold recommendations for commercial bycatch species are rare. Davis and Parker (2004) suggested that discarded demersal fish (e.g., Sablefish) captured with fixed gear suffer no measurable effects of air exposure if they are released within 10 min of air exposure. The authors caution, however, that this would not be the case in trawl fisheries. Davis and Olla (2002) made a very specific recommendation for a Lingcod fishery with slot limits that at temperatures greater than 16°C and with air exposure for greater than 30 min, mortality is sufficiently high for released fish that high grading is no longer an effective management strategy.

FACTORS AFFECTING RESPONSES TO AIR EXPOSURE

Quantifying effects of air exposure among released or discarded fish is difficult because of the complex interactions between stress, the environment, and the capture process. Air exposure is just one factor among several that can contribute to postrelease fate. Severity of injuries, exercise duration, and environmental conditions can all induce a stress response, which is exacerbated by air exposure. Additionally, traits such as size, sex, life stage, and condition can alter an individual's response to capture and require consideration when exploring sensitivity to air exposure.

Study Methods

Specific methodologies chosen for the study (e.g., laboratory versus field investigations) can considerably impact the interpretation of results. Laboratory methods can introduce handling effects and confinement, potentially producing results that are not representative or applicable to management. For example, in the seminal study of air exposure tolerance in fish, Ferguson and Tufts (1992) observed high mortality after just 30–60 s among Rainbow Trout exercised to exhaustion. However, study fish were cannulated (i.e., anesthetized to insert a small plastic tube into the dorsal aorta via the roof of the mouth), an invasive procedure, which could have resulted in increased sensitivity to air exposure stress (e.g., thrashing fish during air exposure could dislodge the cannulae).

Whether the study was conducted in a laboratory setting or in the field can influence the applicability of results and can produce conflicting results. For example, Davis and Schreck (2005) identified 40–60 min as the air exposure limit of Pacific Halibut in a laboratory study, whereas 20–40 min was identified as a threshold range in field studies (Oddsson et al. 1994). Conversely, effects of air exposure have shown to be more pronounced in laboratory assessments where confinement stress may be an issue. Mortality of wild-caught Coho Salmon *O. kisutch* bycatch from commercial purse seine fisheries was higher for fish held in a net-pen than those tagged and released (Raby et al., in press), and Common Carp *Cyprinus carpio* showed greater physiological disturbances following 10 min of air exposure in a laboratory study than in field settings (Rapp et al. 2014).

Temperature

As ectotherms, fish have a relatively restricted scope of temperature optima and outside of this range exhibit abnormal bursts of activity, rapid ventilation, and decreases in aerobic scope and cardiac function (Farrell 1997). A suboptimal thermal environment elicits stress, which increases vulnerability during capture. Temperature is therefore extremely important to consider when generating recommendations with respect to fish handling and welfare.

Water temperature has to be considered as well as temperature changes that may be experienced during capture. For example, when captured fish are forced to rapidly ascend through warmer water strata, thermal shock can occur. Thermal shock is especially harmful to demersal fishes that are caught below 100 m and can experience dramatic temperature changes (e.g., 6–17°C; Olla et al. 1998). Mortality due to an abrupt temperature change increases with the magnitude of change (e.g., in Sablefish subjected to simulated net towing and thermal shock; Olla et al. 1998). Likewise, when Little Skates *Leucoraja erinacea* were exposed to 50 min of air exposure in both the winter and summer, Cicia et al. (2011) suggested that the resulting metabolic and ionic imbalances were predominantly due to thermal shock because mortality was 27% in the winter but 100% in the summer. Ideally, regulatory actions will consider temperature effects. For example, in the presence of acute thermal change, a lower threshold for air exposure is expected, and simply accounting for seasonal effects in handling protocols could improve the survival of released fish.

In freshwater recreational fisheries, summer water temperatures regularly approach critical temperature thresholds, beyond which only passive, anaerobic metabolism is possible, a phenomenon that will increase as the climate warms (Pörtner and Farrell 2008). Gingerich et al. (2007) demonstrated that air exposure up to 16 min resulted in minimal mortality of Bluegill *Lepomis macrochirus* at low and moderate water temperatures (18.2°C, 22.8°C), but the same treatment after removal from warm water (27.4 °C) resulted in much higher mortality. Similarly, Gale et al. (2011) simulated recreational angling practices (i.e., exhaustive exercise and one-minute air) on Sockeye Salmon and found that when temperatures were warmer than historical norms, abilities to properly ventilate and maintain equilibrium were compromised.

Species

Survival of released fish could be greatly improved if regulations explicitly state that fishers prioritize the return of sensitive species. Research on common marine bycatch species has revealed greater resiliency to air exposure among some species. For example, mortality was not observed in Winter Flounder *Pleuronectes americanus*, Lingcod, or Sablefish with up to 30–45 min of air exposure following simulated commercial capture (Ross and Hokenson 1997; Parker et al. 2003; Davis and Parker 2004). Conversely, mortality resulted after only 15 min of air exposure in Witch Flounder *Glyptocephalus cynoglossus*, American Plaice *Hippoglossoides platessoides*, and Pollock *Pollachius virens* (Ross and Hokenson 1997) and just 7 min of air exposure in Walleye Pollock *Theragra chalcogramma* (Olla et al. 1997).

Resiliency has been observed in some species of recreationally targeted species, though air exposure durations are considerably less than those observed in commercial fisheries. It has been suggested that Common Carp have a high resiliency to air exposure. Rapp et al. (2014) observed no measurable physiological disturbances after 10 min of air exposure at different temperatures. Conversely, Bonefish, prized for fighting to exhaustion during capture, are often in poor condition upon landing and particularly susceptible to the effects of air exposure; increments of just 35 s of air exposure were enough to detect increasing behavioral impairment (Danylchuk et al. 2007).

In Pacific salmon *Oncorhynchus* spp., there are species-specific differences with respect to tolerance to capture stressors as well as population-specific differences (Donaldson et al. 2012). Within a species, returning Pacific salmon adults have high fidelity to natal spawning areas, which has resulted in hundreds of genetically distinct populations with specific physiological adaptations. Managing individual populations is especially challenging because species and populations often comigrate. For example, Coho Salmon bycatch is a concern in commercial purse seine fisheries in southern British Columbia, Canada, because a population listed as endangered is known to comigrate with other, more abundant Coho Salmon populations, and postrelease survival differs among released populations (Raby et al., in press; K.V. Cook, University of British Columbia, unpublished data).

Life Stage: Size and Maturity

Many fisheries are regulated by fish size; therefore, it is important to understand how body size influences susceptibility to air exposure. Though younger and smaller fish have been observed to be more sensitive to capture stress (Davis 2002), environmental and anthropogenic perturbations can select for smaller fish (Daufresene et al. 2009). An inverse relationship between core body temperature and fish size suggests that elevated air temperatures are more detrimental for small fish (Haukenes and Buck 2006); however, smaller fish suffer less physiological disturbance and recover faster following exposure to exercise and air exposure (Clark et al. 2012; Gingerich and Suski 2012). Conversely, a number of experiments conducted on commercial bycatch species have found that smaller fish are more sensitive. Significant mortality occurred in Pacific Halibut after exposure to 40 min in air for age-1 fish but not until 60 min for age-2 fish (Davis and Schreck 2005). Similarly, 100% mortality was observed in small Lingcod after 60 min of air exposure but not until after 75 min in larger Lingcod (Davis and Olla 2002), and age-1 Sablefish have higher mortality than age-2 Sablefish following air exposure (Davis and Parker 2004; Davis 2005). Behavioral impairment as a result of air exposure can also differ with fish size; after 10 min of air exposure, depressed responses to stimuli were most pronounced in small Lingcod after 24 h (Davis and Parker 2004).

Reproductive maturity or physiological status at certain life stages can also influence vulnerability to capture stress. Semelparous Pacific salmon are an excellent model to study these relationships because they are angled throughout their anadromous spawning migrations and hence at varying levels of maturity. Donaldson et al. (2012) exposed two populations of comigrating Sockeye Salmon with differing spawning times to various capture simulations involving air exposure and found reduced survival in the later spawning (less mature) stock. On spawning grounds, Raby et al. (2013) concluded that Pink and Chum salmon *O. keta* may be resilient to certain forms of capture stress and be capable of recovering from substantial physiological disturbance. Both species were exposed to up to 16 min of air exposure, and although behavioral impairment responses increased with air exposure duration, prespawn mortality rates did not differ among air exposure treatments and were similar to those naturally occurring during the study year (Raby et al. 2013). It could therefore be hypothesized that Pacific salmon become more physiologically equipped to endure acute stress the closer they are to spawning. In Atlantic Salmon, although the effects of air exposure were not specifically addressed, Brobbel et al. (1996) supported this hypothesis: postrelease survival following angling was greater for postspawn (i.e., kelt) compared to prespawn (i.e., bright) salmon.

CONCLUSIONS

Air exposure appears to be universally stressful for fish—that is, under few, if any circumstances, is air exposure benefi-

Figure 2. Although air exposure should be avoided, there are certain handling practices and tools that can be adopted to improve fish welfare and reduce air exposure. In recreational angling, unhooking and measuring can happen underwater, and if a photo must be taken, the angler should secure and support the fish's body with wet hands and barely lift the individual out of the water in time for an instant photograph. Photo by Vivian Nguyen.

Figure 3. (A) In commercial fisheries, reducing or eliminating air exposure requires gear-specific or methodological changes. Fish can be brailed right into water-filled totes in some fisheries to eliminate air exposure. Photo by Graham Raby. (B) Alternatively, sorting small batches of fish at a time on a sorting table, rather than on deck, with a chute to release fish overboard reduces air exposure duration, handling time, and probability of injury. Photo by Katrina Cook. (C) Finally, giving incidentally captured fish recovery time in a tote with flow-through water can reduce stress and mortality. Photo by Graham Raby.

SIDEBAR: GUIDELINES FOR REDUCING AIR EXPOSURE IN CAPTURED FISH

Recreational Fisheries

With responsible fishing practices and the appropriate tools, there is rarely a need for air exposure durations to exceed 10 s. Lack of investment in the stewardship of fishery resources can be major contributors to mortality and poor handling in recreational fisheries. Thus, education plays an important role. Fish capture resulting in limited handling and no air exposure require that fish are hooked superficially (i.e., in the jaw), played for appropriate lengths of time (i.e., not to or beyond exhaustion), and unhooked while submerged in water. For the general welfare of the fish and to reduce air exposure, anglers should always use lines of appropriate breaking strength that will not extend fight durations and excessively exhaust fish (Landsman et al. 2011). Extensive air exposure can occur when removing deeply lodged hooks (Fobert et al. 2009), which can be avoided if appropriate tackle is used (Bartholomew and Bohnsack 2005) and hooks are set in a timely manner (Schisler and Bergeson 1996). The appropriate bait and hook types depend on the target species, but single barbless circle hooks (if using organic bait) and artificial lures, especially artificial flies, typically result in superficial hooking, short handling times, and limited tissue damage (Bartholomew and Bohnsack 2005). When landing a fish, although nets can cause damage and abrasion, cradles or knotless mesh nets are necessary for some fish and enable unhooking to occur while the fish is in water (Barthel et al. 2003). When fishers wish to photograph or measure their catch, underwater cameras and measuring tapes are essential tools. If these are not available, air exposure should still not exceed 10 s. After hook removal underwater, anglers can secure and support a fish's body with wet hands and gently lift the individual out of the water in time for an instant photograph, as shown in Figure 2A.

Commercial Fisheries

Excessive air exposure occurs in commercial fisheries when catches are very large or when removal of nontarget species is not prioritized. Releasing nontarget species immediately or sorting small batches of fish at a time could substantially improve survival of bycatch. Additionally, changes could be made to certain vessels to reduce air exposure such as incorporating sorting decks with water to prevent desiccation and having chutes overboard that allow fish to be discarded rapidly with minimal handling, as seen in Figure 2B. Stressors extend beyond those experienced during air exposure, however, and any change that minimizes handling and gear encounter times would reduce stress and mortality (Davis 2002). It may be possible to adjust fishing practices to reduce catch size (e.g., trawl or soak times), thereby reducing numbers of nontarget species as well as handling time on deck, without decreasing catch per unit effort (Davis 2002). High air temperatures or large temperature changes during capture can also play a significant role in bycatch mortality. Adjusting fishing effort to cooler seasons, altering deck conditions to provide shade, or misting seawater would improve survival (Davis 2002). For severely impaired fish, certain fish revival techniques have proven effective (e.g., recovery boxes that provide assisted gill ventilation; Farrell et al. 2001) and allowing for recovery time onboard with recirculating water may improve survival for some fishes. However, these methods may only be useful if the fish is severely impaired (e.g., cannot maintain equilibrium; see Robinson et al. 2013). Although fish welfare issues should be considered in commercial fisheries and air exposure reduced as much as possible, it will take education, willingness, and potentially regulatory change to implement alternative handling methods. However, it is prudent that research regarding release of bycatch in commercial fisheries moves beyond simply characterizing composition and mortality rates to examining methods that reduce mortality.

cial for fish, no matter how short the duration. Nonetheless, air exposure is common in many fish capture scenarios and is sometimes protracted. There are numerous interacting factors at play during capture and handling; therefore, quantifying responses to air exposure without including other relevant stressors (e.g., exercise) provides a conservative estimate of the overall effects of capture. Because air exposure can be easily monitored, identifying species-specific threshold air exposure durations is nonetheless important for the development of fisheries management regulations and voluntary "best practices" guidelines. Fishers should be provided with information regarding air exposure that is more explicit than simply to "minimize," which is both subjective and confusing. Although thresholds have been determined for some fisheries and species, continued research and education will be central to this issue. Unfortunately, there will never be a silver bullet or "one-size-fits-all" recommendation, and scientific results will be inevitably context specific.

The consequences of air exposure for fish in terms of survival and reproductive capacity can violate the core assumptions upholding the management strategy of releasing fish. Given currently available literature, we recommend less than 10 s of cumulative air exposure for captured fish to be released as a cautious target. As detailed previously, a difference of just 10 s air exposure was indeed sufficient to reduce fecundity in Atlantic Salmon (Richard et al. 2013). Although other research has found resiliency to longer durations in some species, in the interest of fish welfare, the goal should be to reduce air exposure as much as possible, thus aiming for no more than 10 s. In fisheries where this is not possible, a similarly cautious target needs to be set. A 10 s limit is attainable in recreational fisheries, where with access to appropriate tools there is little need for air exposure for unhooking, measuring, or photographing fish (appropriate photographing technique shown in Figure 2). Extreme care should especially be taken to reduce air exposure when the landed fish is exhausted, water temperatures are beyond the normal range, or with known sensitive species. The same principles apply to commercial fisheries, but managing air exposure duration is much more difficult, often gear dependent, and very few species/fisheries have been examined. For those species that have been assessed, little information exists pertaining to the sublethal or long-term effects of air exposure to released fish. This is an area that could greatly benefit from more research. In many commercial fisheries, reducing air exposure duration to less than 10 s would require changing methods (e.g., depositing fish directly into water-filled totes; Figure 3A) or gear (e.g., sorting tables with water to prevent desiccation or chutes to rapidly discard fish; Figure 3B). A further consideration with large commercial catches is that oxygen depletion of water in crowded conditions can also cause asphyxia and have many of the same effects of air exposure (Raby et al. 2012). Solutions to reduce air exposure would have to be fishery specific. Where air exposure cannot be minimized, regulatory agencies should consider the argument of whether it is ethical to release captured fish. If a fish suffers physiological or physical trauma from which recovery is unlikely, harvesting the fish may be the more appropriate action.

Many knowledge gaps still exist on this topic, and there is much potential for research that will directly benefit management and fish welfare. Threshold studies, where fish are exposed to varying durations of air exposure and postrelease survival is monitored, would greatly increase the ability to provide accurate species-specific recommendations and use air exposure duration as a definitive benchmark to manage fisheries. With threshold studies, however, it is imperative to assess not only immediate mortality and/or postrelease survival but also sublethal effects such as physiological impairments. These investigations are lacking in species that are targeted commercially. Additionally, the interspecific and among-population mechanistic differences supporting resiliency to air exposure remain unclear. There is a need to conduct research to identify the most sensitive species, understand the factors causing this sensitivity, and use this information to propose regulations regarding air exposure accordingly. Such research requires consideration of covariates and other confounding factors that may contribute synergistically to mortality. Research into different means of recovering incidentally captured fish (e.g., artificially ram ventilating fish prior to release in an attempt to provide increased oxygen; Farrell et al. 2001) has shown promise with some species and fisheries and also deserves further attention as a tool for use in both recreational and commercial fisheries.

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