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ARTICLE

Bycatch in a Commercial Lobster Fishery: Effects on Two Benthic Predators, Sea Raven and Longhorn Sculpin

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Abstract

Studying the species-specific responses to fishing capture is critical for effective management and conservation of bycatch species given that acute stress incurred from capture and handling may ultimately lead to mortality. While species of low commercial value are often overlooked, having accurate information on the effects of capture on *all* species is necessary for ecosystem-based management. Sea Raven (SR) *Hemitripterus americanus* and Longhorn Sculpin (LHS) *Myoxocephalus octodecemspinosus* are routinely captured in the commercial American lobster *Homarus americanus* fishery in the Gulf of Maine, and they are discarded due to low commercial value. Despite a lack of economic value, these predatory species play important roles in shaping the benthic communities that they inhabit, highlighting the need to study their stress and mortality due to capture and handling. To help understand the effects of the lobster fishery on these species, the current study evaluated the physical, behavioral, and physiological stress responses of SR and LHS to capture in the state of Maine Zone G commercial lobster fishery. Collectively, our results suggest that although these species appeared to be resilient to capture based on an overt injury assessment, stress responses occurred based on reflex impairment and physiological perturbations, and these responses were species-specific. Given the prevalence of behavioral and physiological stress in this study, further research into the survival outcomes of SR and LHS following release in the commercial lobster fishery is warranted.

Commercial fisheries of the United States discarded an average of approximately 11.4% (296 million kg) of total catch as fish bycatch annually from 2010 to 2013 (NMFS 2013, 2016). Among other issues, discards of this magnitude may be considered a significant waste of natural resources, particularly when the mortality of such bycatch

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is high (Harrington et al. 2005). Given the scope of this problem, substantial amounts of time and funding have been dedicated to assessing the condition, stress, and survival of discarded fish (e.g., Barkley et al. 2017; Talwar et al. 2017; Sulikowski et al. 2018; Weissman et al. 2018). While the vast majority of studies to date have focused on commercially important species (Ryer 2002; Davis and Parker 2004; Danylchuk et al. 2007; Capizzano et al. 2016), species of low commercial value are frequently overlooked. However, concerns for animal welfare that are associated with fisheries capture should not be limited to commercially or socially valuable species; equal consideration should be given to underappreciated species (Huntingford et al. 2006; Iwama 2007). Additionally, having accurate information regarding the effects of capture on *all* species that are subject to fishing pressures, regardless of economic importance, is necessary for ecosystem-based management (Hall 1996; Link et al. 2002).

Given that acute stress due to fishing capture and handling may ultimately lead to mortality, understanding organismal responses to capture and handling is critical for the effective management and conservation of bycatch species (Davis 2002, 2005; Raby et al. 2012; Baker et al. 2013). To help meet this need, various indicators of physical, behavioral, and physiological stress have been developed and validated for use with fish (Barton 2002; Davis 2010; Sopinka et al. 2016). For instance, injury conditions and reflex responses have become increasingly popular indicators of fishing stress (Davis and Ottmar 2006; Davis 2010; Sopinka et al. 2016). These measures of external trauma and behavioral impairment have been applied to both teleost and elasmobranch species in the Northwest Atlantic including Yellowtail Flounder *Limanda ferruginea* (Barkley and Cadrin 2012), Monkfish *Lophius americanus* (Weissman et al. 2018), Atlantic Cod *Gadus morhua* (Humborstad et al. 2009; Capizzano et al. 2016), and several skate species (Knotek et al. 2018). In addition to quantifying the physical and behavioral stress that is related to capture and handling, numerous biochemical markers including plasma cortisol, glucose, lactate, and other hematological parameters have been used (Barton 2002; Sopinka et al. 2016). Interpreting these indicators may be challenging given the species- and gear-specific nature of fishing stress (Davis et al. 2001; Barton 2002; Raby et al. 2013). For example, benthic teleosts with low metabolic rates (e.g., Sea Raven *Hemitripterus americanus*) are thought to have reduced or delayed physiological stress responses (Vijayan and Moon 1994; Vijayan et al. 1996; Lays et al. 2009) relative to more active species (Pankhurst 2011). Further, the severity and type of injury may vary by gear type, with scraping common in trawls or traps and barotrauma common in gear that is deployed at depth (Davis 2002). Given these complexities, species- and gear-specific stress and injury investigations are imperative to effective fisheries management.

The American lobster *Homarus americanus* supports one of the most lucrative commercial fishing industries of New England, with an estimated ex-vessel value of over US\$540 million in 2016 (Maine DMR 2018) and over 3.5 million actively fished traps (ASMFC 2015). Based on observer data, numerous nontargeted species (e.g., sculpins, Sea Raven, Cunner *Tautoglabrus adspersus*, Cusk *Brosme brosme*, and others) are captured as bycatch and likely discarded in the American lobster fishery (MSC 2013), yet no published studies to date have investigated the effects of lobster trap capture on any of these species. The two most frequently bycaught teleost species in the fishery, Longhorn Sculpin (LHS) *Myoxocephalus octodecemspinosus* and Sea Raven (SR), are unregulated due to their low commercial value (MSC 2013), and their responses to fishing capture stress are currently unknown. However, LHS and SR are becoming increasingly dominant benthivore (LHS) and piscivore (SR) species in the Gulf of Maine, and their distribution range (LHS) and relative abundance (SR) have expanded in recent years (Link and Garrison 2002; Link 2007). Because the feeding ecology of these predatory fish species plays a critical role in shaping the benthic communities that they inhabit (Ojeda and Dearborn 1991; Link and Garrison 2002; Link 2007), understanding the effects of capture in lobster gear on LHS and SR will be important to maintaining trophic dynamics and ecosystem status in the Gulf of Maine (Link et al. 2002).

The current study characterized the extent of physical injury, reflex impairment, and physiological stress in LHS and SR that were captured in the state of Maine Zone G commercial lobster fishery. We examined the effects of key abiotic (i.e., soak time, air exposure duration, air and water temperature, fishing depth) and biotic (fish size) factors on the observed stress indicators, as it was hypothesized that the severity of stress would be directly related to the degree of capture stressors. Additionally, we examined the correspondence between stress indicators (injury conditions, reflex impairment, and physiological stress parameters) to determine the ability of each indicator to accurately represent capture stress in these species. Finally, we observed the species-specific nature of stress following capture in the commercial lobster fishery.

METHODS

Sampling techniques.—Sea Raven and LHS were opportunistically sampled from May 29 to October 5, 2016, and June 26 to September 26, 2017, aboard the F/V *Christina Mae* during a directed study of postrelease mortality in Atlantic Cod (see Swezey et al. 2018). The fishing operations were conducted off Kennebunk, Maine, following management regulations of the state of Maine Zone G, including the use of commercial lobster traps (121.92 ×

TABLE 1. Descriptions of the vitality indices used to represent the extent of overt physical trauma and reflex impairment in Sea Raven and Longhorn Sculpin captured in the commercial lobster fishery.

| Vitality indicator | Description |
|--------------------|--|
| Injury code | |
| (1) Uninjured | No observable injuries |
| (2) Minor damage | Torn fins, scrapes, mucus damage, minor barotrauma (i.e., stomach expansion) |
| (3) Severe trauma | Large lacerations, exposed internal organs, major barotrauma (i.e., everted stomach) |
| (4) Dead | Unresponsive |
| Reflex | |
| (1) Body flexion | Body flex stimulated by handling |
| (2) Head complex | Alternated mouth gaping and operculum flaring, as if gasping for air |
| (3) Swim | Actively swam away upon release |

53.34 × 34.29 cm) that were supplied with standard bait (Atlantic Herring *Clupea harengus*, Atlantic Menhaden *Brevoortia tyrannus*, and/or cowhite; Krouse 1989; Lehuta et al. 2014). Along the coast of Maine, commercial lobster traps are typically set in depths up to 100 m, although most are located in <50 m (Incze et al. 2010). Therefore, to encompass standard practices within the region, traps were deployed at various depths (38.7–64.6 m) and were hauled as is typical in the fishery, every 4–14 d. Upon capture, SR and LHS were removed from the traps and placed on an air-exposed sorting table (along with landed lobsters) until individual assessment began. All of the fish were measured for total length (TL) and abiotic factors such as geographic location, depth (mean ± SD = 50.2 ± 5.3 m, range = 38.7–64.6 m), soak time (days from trap deployment to trap retrieval; mean ± SD = 6.2 ± 2.3 d, range = 4–14 d), bottom (Hobo Water Temp Pro v2, Onset Computer Corporation, Bourne, Massachusetts; mean ± SD = 8.4 ± 1.2°C, range = 5.3–12.5°C) and air (Traceable Waterproof Mini Thermometer, Ben Meadows; mean ± SD = 23.6 ± 4.3°C, range = 16.2–36.4°C) temperature, difference between air and bottom temperature (mean ± SD = 16.3 ± 4.8°C, range = 6.8–28.0°C), and air exposure duration (minutes from removal from water to release; mean ± SD = 4.8 ± 2.3 min; range = 1–11 min) were recorded upon the capture of an individual. Additionally, each fish was affixed with a Floy T-bar tag (model FD-94, MARK III Regular Pistol Grip, 1.96 mm outer diameter) prior to release to opportunistically observe the survival of any recaptured individuals; however, no individuals were recaptured. Following all of the assessments, fish were released at the surface and monitored for their ability to swim to depth as part of a vitality assessment (as described below).

Vitality indicators.—All of the SR and LHS were assessed for vitality—a protocol that evaluated both overt physical trauma and reflex impairment (Table 1). A physical condition index that was developed by Weissman et al. (2018) was used to document the extent of external injuries

(Figure 1). For reflex impairment, three generalized reflexes that are related to survival (e.g., Humborstad et al. 2009; Davis 2010) were evaluated for presence or absence. These reflexes were selected because they have been used previously with other benthic teleost species (Humborstad et al. 2009; Barkley and Cadrin 2012; Methling et al. 2017) and permitted the rapid (<30 s) assessment of each individual.

Physiological stress exams.—To quantify the physiological stress markers that are associated with capture in lobster gear, 1 mL of blood was collected from a subset of SR and LHS. Following the assessment of vitality indicators, blood was extracted from the caudal vein by using a heparinized syringe and 22-gauge needle. Handheld meters that were validated for use with teleost blood (Clark et al. 2008; Stoot et al. 2014; Collins et al. 2016) were used in situ to measure glucose (Glucose Max Plus, Nova Biomedical, Waltham, Massachusetts), lactate (Lactate Plus, Nova Biomedical, Waltham, Massachusetts), and hemoglobin (HemoCue Hb 201+, HemoCue America, Brea, California) concentrations. When glucose or lactate concentrations were below the detection limits of the meters, the minimum detection values (20 mg/dL and 0.3 mmol/L for glucose and lactate, respectively) were assigned. Hematocrit (packed erythrocyte volume, %) was determined following ≈5 min of centrifugation (International Equipment Company, Needham Heights, Massachusetts) of the small blood samples in microcapillary tubes. The mean corpuscular hemoglobin concentration (MCHC) was calculated from the hemoglobin to hematocrit ratio (e.g., Sulikowski et al. 2003). The remainder of whole blood was centrifuged to separate the plasma from the red blood cells, and the plasma was removed and stored frozen until the cortisol analyses were conducted. The plasma cortisol concentrations were quantified at the University of New England following a standard radioimmunoassay technique that is outlined in Weissman et al. (2018), and antibodies were used in a final dilution of 1:2,100. The average hormone extraction recoveries were calculated as 83.2% and 83.3% for SR and LHS,



FIGURE 1. Representative examples of injury codes observed in Sea Raven and Longhorn Sculpin that were captured in the commercial lobster fishery. The top photograph represents an injury 1 fish, the middle photograph represents an injury 2 fish, and the bottom photograph represents an injury 4 fish. Note: no photo is available for the single injury 3 fish that was captured in this study.

respectively. Inter-assay and average intra-assay variances were calculated as 5.7% and 3.5%, respectively.

Statistical analysis.— Descriptions of the statistical analyses that were used in this study can be found in the Supplementary Materials Table S1 available separately online. For all of the statistical analyses in this study, nonparametric tests were used when assumptions of parametric tests were violated. A Kruskal–Wallis test (SR) and a Mann–Whitney *U*-test (LHS) were used to determine whether there were significant differences in the number of reflexes that were present among injury conditions for each species. Proportional odds models were used to

evaluate the effect of each abiotic and biotic factor (air exposure duration, air temperature, bottom temperature, temperature difference, TL, depth, and soak time) on injury condition and reflex responses, respectively. Linear regressions were used to evaluate the effect of each abiotic and biotic factor (air exposure duration, air temperature, bottom temperature, temperature difference, TL, depth, and soak time) on the biochemical markers (plasma cortisol, glucose, lactate, hemoglobin, hematocrit, and MCHC) for each species. The biochemical marker concentrations were log transformed when evidence of nonnormality was present. Additionally, *t*-tests and one-way ANOVAs were used to determine whether any of the physiological stress parameters (plasma cortisol, glucose, lactate, hemoglobin, hematocrit, or MCHC) were significantly different between injury conditions and among the number of reflex responses present. To minimize the likelihood of obtaining a type I error, a sequential Bonferroni procedure (Rice 1989) was used to adjust the probability values for all of the statistical tests that were performed for each species. In addition, *t*-tests were used to determine significant differences in physiological stress parameters between SR and LHS. Due to limited sample sizes, interactive models could not be included in this study. Statistical significance was set at $\alpha = 0.05$ and all of the statistical analyses were completed in RStudio (R Foundation). The results of each statistical test that was used for SR and LHS can be found in the Supplementary Materials (Table S2 and S3, respectively) while only relevant results will be presented herein.

RESULTS

Characterizing Injury Condition, Reflex Impairment, and Physiological Stress

A total of 86 SR (ranging in size from 21 to 52.5 cm TL) and 33 LHS (ranging in size from 18.9–31 cm TL) were sampled for injury condition and reflex responses over the course of this study. The descriptive results (% and *n*) for the injury conditions that were observed for each species are presented in Table 2. Capture in the commercial lobster fishery resulted in reflex impairment (<3 reflexes present) in 62.2% and 53.5% of SR and LHS, respectively. The reflex that was impaired most frequently in both species was the swim response. The descriptive results (means \pm standard error of the mean, range, and *n*) of the physiological stress parameters that were quantified for each species are presented in the Supplementary Materials (Table S4).

Effect of Abiotic and Biotic Factors on Stress Indicators

The proportional odds models revealed that larger SR displayed significantly more reflex responses than their smaller conspecifics that were captured in the commercial

TABLE 2. Descriptive results (% , *n*) of each injury condition for Sea Raven and Longhorn Sculpin collected in commercial lobster traps over the duration of the study.

| Species | % Injury 1 (<i>n</i>) | % Injury 2 (<i>n</i>) | % Injury 3 (<i>n</i>) | % Injury 4 (<i>n</i>) |
|------------------|-------------------------|-------------------------|-------------------------|-------------------------|
| Sea Raven | 62.8 (54) | 23.3 (20) | 1.2 (1) | 12.8 (11) |
| Longhorn Sculpin | 75.8 (25) | 15.2 (5) | 0.0 (0) | 9.1 (3) |

lobster fishery did ($\chi^2 = 17.93$, $P < 0.01$; Figure 2). No other abiotic or biotic factor affected the degree of reflex impairment in SR or LHS ($P > 0.05$), and injury condition was not affected by any abiotic or biotic factor in either species ($P > 0.05$). Additionally, linear regressions indicated that the physiological stress markers were also unaffected by abiotic and biotic factors in SR and LHS ($P > 0.05$).

Correspondence between Stress Indicators

Collectively, the average number of reflex responses that was present decreased as injury condition increased (worsened) in both SR (Kruskal–Wallis test, $\chi^2 = 5.10$, $df = 2$, $P > 0.05$) and LHS (Mann–Whitney *U*-test, $W = 90$, $P > 0.05$) but these relationships were not statistically significant (Figure 3). According to the *t*-tests, the physiological stress markers were unrelated to injury condition in

SR and LHS ($P > 0.05$; Figure 4). Similarly, the physiological stress markers were not significantly related to reflex responses in SR or LHS ($P > 0.05$; Figure 5).

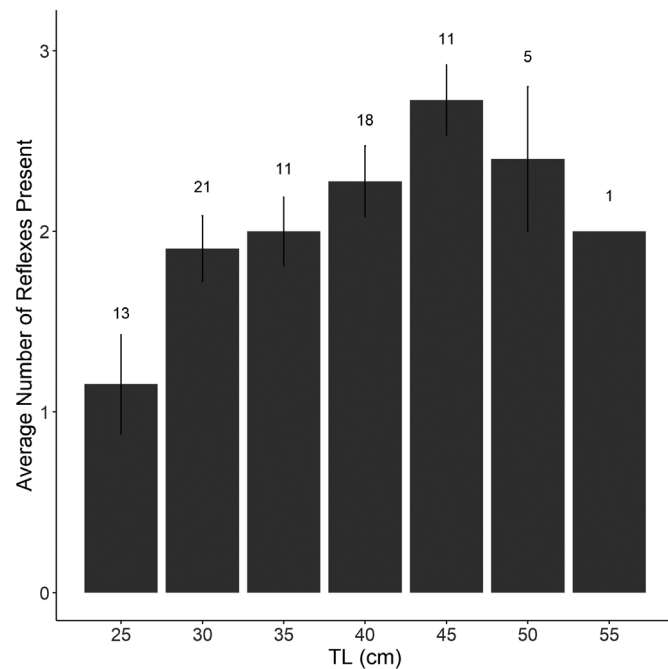


FIGURE 2. Relationship between total length (TL) and the number of reflex responses present in Sea Raven that were captured in the commercial lobster fishery. The data are mean reflexes present, binned by 5-cm TL intervals. The error bars represent \pm SE and the numbers above the error bars represent the sample size. The number of reflexes present significantly increased as TL increased (proportional odds model; $\chi^2 = 17.93$, $P < 0.01$).

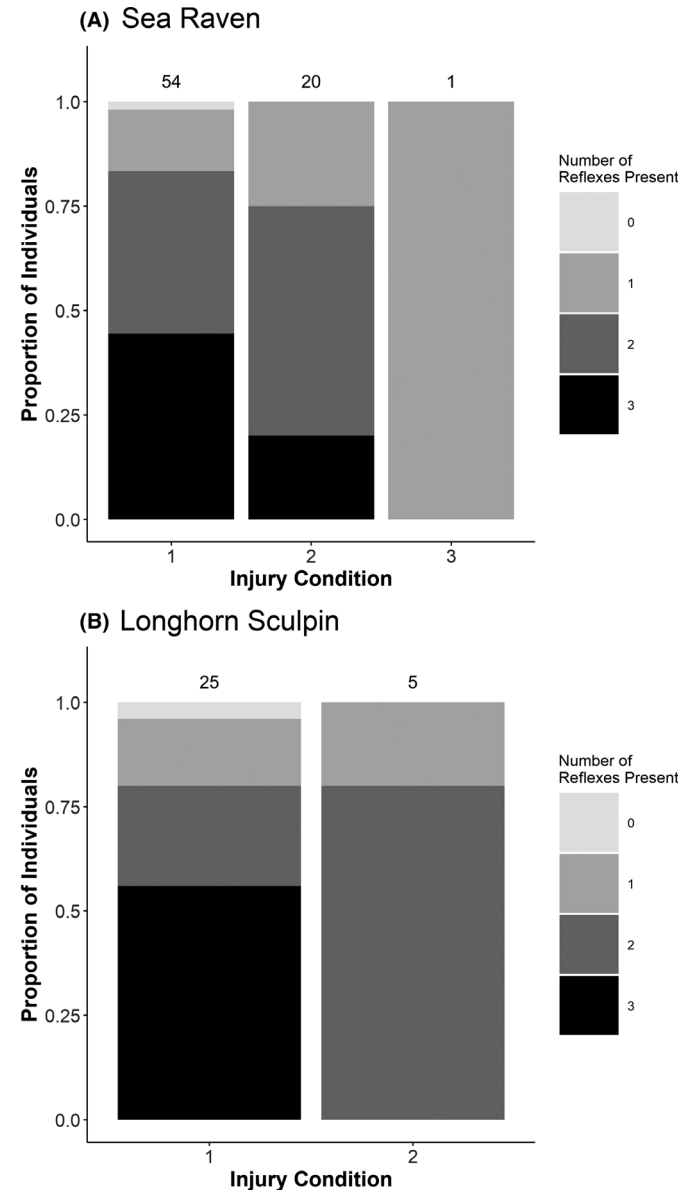


FIGURE 3. The number of reflexes present as a function of injury condition for (A) Sea Raven and (B) Longhorn Sculpin that were captured in the commercial lobster fishery. The numbers above bars represent sample size.

Species Comparison

There were significant differences in plasma cortisol, glucose, lactate, and hemoglobin concentrations as well as hematocrit between SR and LHS (see the Supplementary Materials Table S4). Particularly, SR expressed

significantly higher plasma cortisol concentrations (t -test, $t = -3.9333$, $df = 58$, $P < 0.001$) and significantly lower glucose (Mann-Whitney U -test, $W = 660$, $P < 0.001$), lactate (Mann-Whitney U -test, $W = 588.5$, $P < 0.001$), hemoglobin (Mann-Whitney U -test, $W = 686$, $P < 0.01$), and

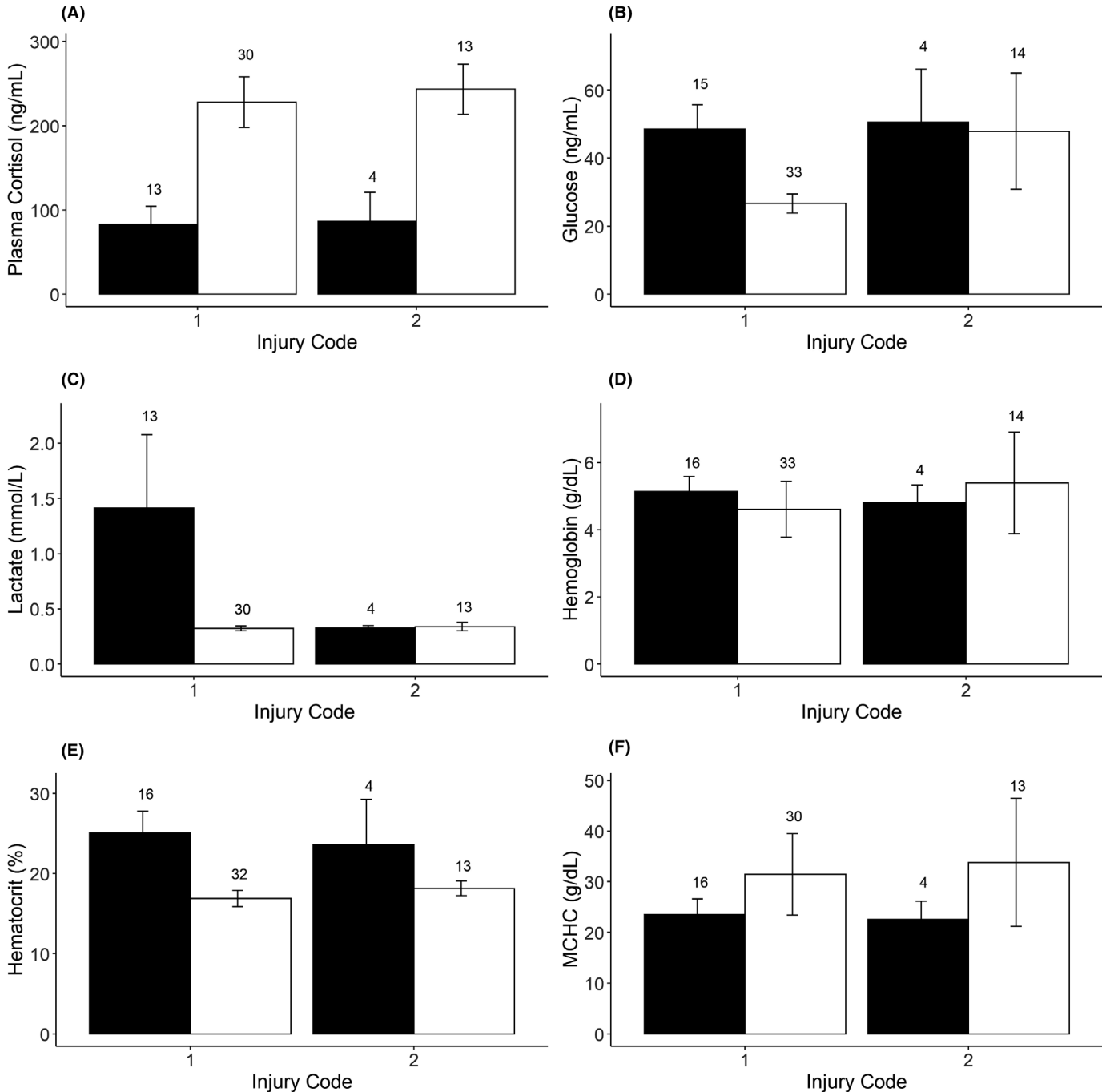


FIGURE 4. Relationships between the injury condition and (A) plasma cortisol concentrations (ng/mL), (B) glucose concentrations (mg/dL), (C) lactate concentrations (mmol/L), (D) hemoglobin concentrations (g/dL), (E) hematocrit (%), and (F) MCHC (g/dL) in Longhorn Sculpin (black bars) and Sea Raven (white bars) that were captured in the commercial lobster fishery. The data are mean concentrations, the error bars represent \pm SE, and the numbers above the error bars represent sample size.

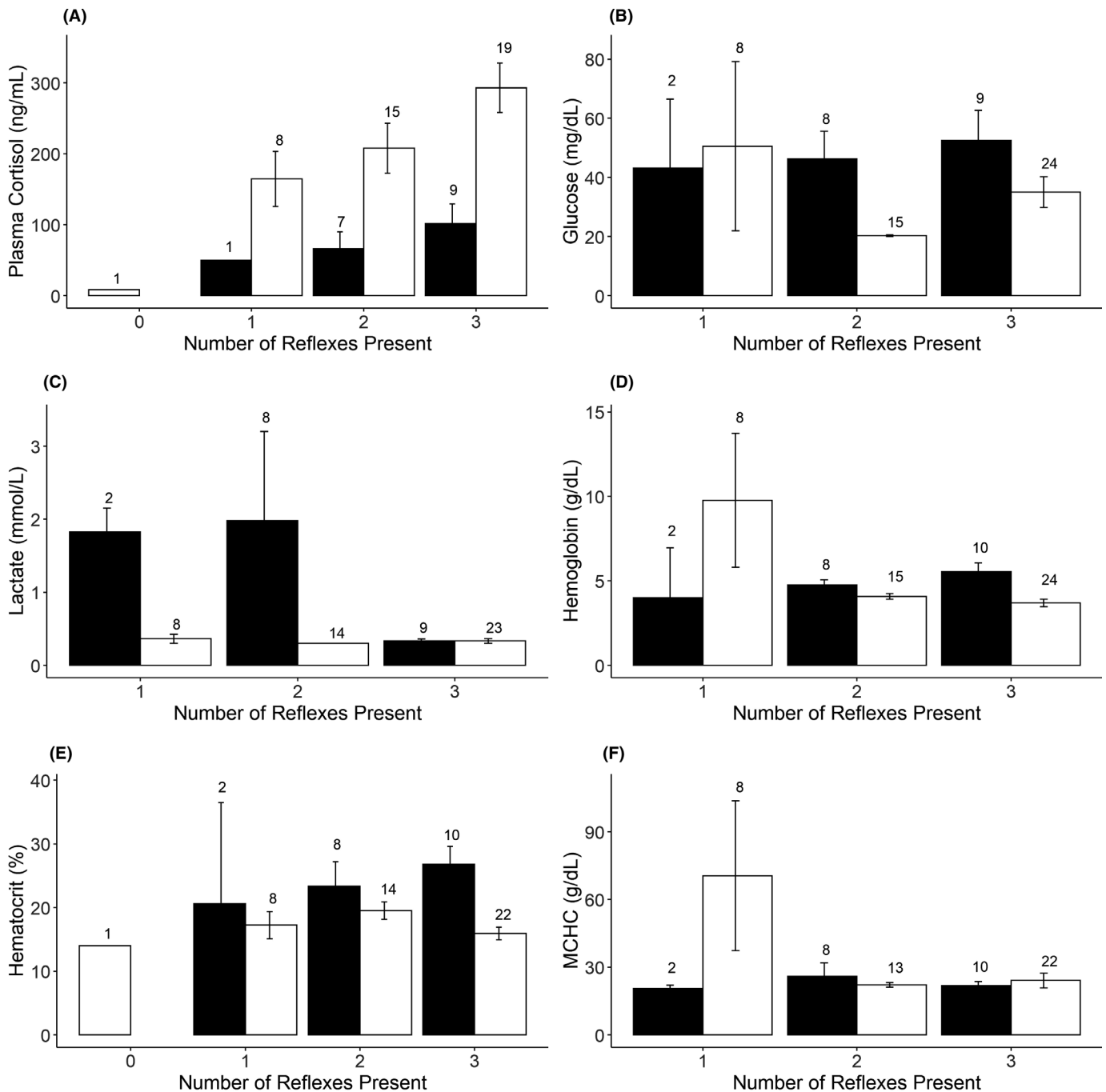


FIGURE 5. Relationships between the number of reflexes present and (A) plasma cortisol concentrations (ng/mL), (B) glucose concentrations (mg/dL), (C) lactate concentrations (mmol/L), (D) hemoglobin concentrations (g/dL), (E) hematocrit (%), and (F) MCHC (g/dL) in Longhorn Sculpin (black bars) and Sea Raven (white bars) that were captured in the commercial lobster fishery. The data are mean concentrations, the error bars represent \pm SE, and the numbers above the error bars represent sample size.

hematocrit (Mann-Whitney U -test, $W = 651.5$, $P < 0.01$) than LHS did. Additionally, although the relationships between reflex responses and physiological parameters were not statistically significant in either species (as described above; $P > 0.05$), the overall trends in these

relationships appeared to be species-specific (Figure 5). In particular, plasma cortisol concentrations were generally lower and glucose, hemoglobin, and MCHC were generally higher in reflex-impaired SR than in conspecifics that were less impaired. In comparison, plasma cortisol

concentrations appeared to be lower while lactate concentrations appeared to be higher in reflex-impaired LHS than in conspecifics that were less impaired.

DISCUSSION

The vast majority of SR and LHS suffered no or minimal overt physical trauma from capture in lobster traps; 85.9% and 91.0% of the sampled individuals were categorized as injury 1 and injury 2 (combined) for SR and LHS, respectively. While direct comparisons are limited, these findings differ from previous studies that have observed fish to suffer physical abrasions, wounds, and fungal infections due to capture in various other configurations of fish traps (Munro et al. 1971; Cooke et al. 1998; Cleary et al. 2000). Differences in the degree of physical trauma may be a result of fishing practices such as trap construction, soak time, and/or water temperatures. For example, the plastic or rubber coating on standard commercial lobster traps (Miller and Rodger 1996) may smooth sites of abrasion and reduce physical injury and associated infections, as compared with the wire mesh fish traps that were used in previous studies (Munro et al. 1971; Cooke et al. 1998). The shorter trap soak times that are used in the commercial lobster fishery (an average of approximately 6 d in the current study) may also minimize the occurrence of injuries (i.e., predation wounds, skin abrasions, or secondary fungal infections) that are often associated with extended soak times (up to 2 weeks) that were used in previous studies of fish traps (Munro et al. 1971). Additionally, the warmer water conditions (approximately 18–22°C) in previous studies (Cooke et al. 1998; Cleary et al. 2000) may have led to a greater occurrence of skin infections (Cooke et al. 1998) compared with the water conditions in the current study (average of 8.4°C). Collectively, these comparisons suggest that capture in the commercial lobster fishery may inflict less overt physical trauma than capture in other types of fish traps does and that the studied groundfish species appear to be physically resilient to capture in the state of Maine Zone G lobster fishery.

While physical trauma was generally minimal in this study, some degree of reflex impairment (<3 reflexes present) was observed in the majority of SR (62.2%) and LHS (53.5%). Given that the loss of reflex behaviors is often an indicator of stress and postrelease mortality in fish (e.g., Davis 2005, 2007, 2010), the prevalence of behavioral impairment in this study suggests possible physiological compromise or even eventual mortality (although we did not examine mortality directly). For example, the most commonly impaired reflex in the current study was the swim response; the response was absent in 57.3% of SR and 48.4% of LHS. In SR, this impairment often accompanied stomach expansion (i.e., from seawater or air), which prevented individuals from

returning to depth. In contrast to SR, signs of stomach expansion (or barotrauma) were uncommon in LHS, which suggests that impaired swimming was associated with other factors (i.e., unobserved internal injuries, physiological stress) in this species. Nevertheless, the frequency of swimming impairment in this study raises concern for the survival of discarded SR and LHS, as the inability to return to depth may increase the probability of mortality (i.e., Feathers and Knable 1983; Hannah et al. 2008). Indeed, sea bird predation on floating discarded SR was occasionally observed in this study. However, observations of predation in the current study were opportunistic in nature and more directed research would be needed to determine the prevalence of predation on discarded SR and LHS in the commercial lobster fishery.

In SR, the degree of reflex impairment was influenced by fish size such that larger individuals were less impaired due to capture than smaller conspecifics were. This result was similar to those of other studies where size has been found to influence vitality and survival in several benthic teleost species. For example, improved vitality and/or survival have been observed in larger Atlantic Cod (Milliken et al. 1999), Lingcod *Ophiodon elongatus* (Davis and Olla 2002), Sablefish *Anoplopoma fimbria* (Davis and Parker 2004), and European Plaice *Pleuronectes platessa* (Uhlmann et al. 2016) following various capture stressors. Although the exact mechanism underlying this relationship is uncertain, it is possible that the reduced reflex impairment in larger SR may be attributed to greater aerobic and/or anaerobic capacity as well as a greater resilience to physiological stress compared with smaller conspecifics (Uhlmann et al. 2016). Interestingly, no other factors were found to influence the degree of physical injury, reflex impairment, or physiological stress in SR or LHS in this study. These findings contradict our prediction that the degree of stress in these species would be directly related to the degree of capture stressors in the commercial lobster fishery. It is likely that multiple interactive and confounding factors influence the degree of observable stress in captured fish (e.g., Davis 2002; Gingerich et al. 2007), and this may have inhibited the detection of independent relationships between individual factors and stress indicators in this study. However, the limited sample sizes in our opportunistic study precluded the use of multivariate models. It is also important to consider the likelihood of additional stressors that went unaccounted for in our analyses (i.e., water temperature gradient and catch biomass) and the uncontrolled nature of this fishery-dependent study. For example, it is important to note that individuals may enter and escape trap gears at will (e.g., Jury et al. 2001; Cole et al. 2004), so soak time may not be an accurate measure of the duration of time that the individuals were confined in traps.

When attempting to understand the effects of fishing and the mechanisms underlying fish vitality, it is important to evaluate numerous measures of stress to establish an accurate profile (i.e., cortisol, glucose, reflexes, wounding, etc.; Martinez-Porchas et al. 2009; McLean et al. 2016). In the current study, the stress indicators (injury condition, physiological stress markers, and reflex responses) were not significantly related in either species. For example, although physical trauma was absent or minimal in the majority of SR and LHS that were captured in lobster gear, it was clear that many of the individuals were behaviorally impaired and/or physiologically compromised based on their reflex responses and biochemical stress markers. Moreover, although there is typically an underlying association between physiological stress and behavioral impairment in fish (i.e., physiological stress may manifest into behavioral impairment; McLean et al. 2016) and there appeared to be trends between biochemical stress markers and reflex responses in this study, these relationships were not statistically significant in SR or LHS. It is important to consider that the lack of significant relationships between stress indicators in this study may be attributed, in part, to the uncontrolled and opportunistic nature of our study. However, collectively, these findings demonstrate that the use of a single stress indicator (i.e., injury, reflexes, or physiological stress) is not fully representative of SR and LHS condition and the assessment of multiple indicators is necessary to understand the true health of these species following capture. Additionally, the majority of biochemical marker concentrations were significantly different between SR and LHS, and trends in the relationships between reflex responses and physiological parameters, albeit not statistically significant, also appeared to be species specific. These findings corroborate previous conclusions that stress responses vary among species (e.g., Wendelaar Bonga 1997; Mommsen et al. 1999; Barton 2002; Sopinka et al. 2016) and further support the importance of evaluating multiple biochemical stress markers to understand the true effects of capture and handling on individual species. Given that stress often cannot be generalized (even within a given fishery), these findings also highlight the need to evaluate the stress responses of other bycatch species (i.e., Cunner and Cusk) to gain a better understanding of the broader effects of the commercial lobster fishery and to support more comprehensive ecosystem-based management.

Conclusions

This study provides the first insight into the physical, behavioral, and physiological responses of SR and LHS to fishing capture. Collectively, our results suggest that while SR and LHS appear resilient to capture in the commercial lobster fishery based on overt injury assessment, behavioral and physiological analyses suggest that stress responses are occurring and are species specific. Given that such sublethal

effects may alter behavior, growth, reproduction, and ultimately survival, understanding organismal responses to capture is critical when evaluating the population- and ecosystem-level effects of fisheries (Wilson et al. 2014). Although the current study provides insight into the stress responses of SR and LHS that are discarded in the commercial lobster fishery, further research into the survival outcomes of these species is warranted. Of particular concern is the prevalence of swimming impairment in discarded SR and LHS, which may increase predation risk and negatively affect the survivability of these species. If postrelease mortality is high, undocumented population- and ecosystem-level consequences may occur. Therefore, to minimize the aforementioned sublethal consequences and potential mortality that are incurred due to capture in the commercial lobster fishery, avoidance tactics are recommended. If avoidance tactics are unsuccessful or unrealistic to implement, modified release practices which assist SR and LHS in returning to depth (i.e., descending devices) may have the potential to reduce short-term postrelease mortality (i.e., Bellquist et al. 2019).

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.