Physiological and behavioral effects of angling on california sheephead (*semicossychus pulcher*): response, recovery, and captivity stress of an important gamefish in Southern California.

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Abstract

California sheephead, Semic ossyphus pulcher, have experienced significant population declines in recent decades but have remained an important nearshore gamefish in southern California by hook and line anglers. Regulations in the recreational sector currently include a minimum size and bag limit; however, the resulting widespread catch and release practices have unknown physiological and behavioral impacts on *S. pulcher* individuals and population. The objective of this study was to evaluate the sublethal responses of *S. pulcher* to catch and release fishing, determine the potential impacts of current management strategies, and recommend best practices for anglers to minimize fish stress. Physiological responses were measured for known stress indicators (cortisol, glucose, lactate) in blood samples collected after varying angling and confinement treatments, while fish behavior was evaluated by active tracking of *S. pulcher* with acoustic transmitters. We found that baseline biomarker levels were comparable to other teleosts, although blood collected using a novel underwater sampling method exhibited lower levels than reported for other marine fish. It was also determined that biomarkers were significantly elevated the longer fish fought on the line up to 20 min ($p<0.001$) while concentrations continued to peak levels in fish held captive for up to 2 h post-capture. However, caught fish released back into their natural environment and subsequently resampled showed full recovery of cortisol to baseline levels even in fish resampled as early as 18 h post-hooking ($p>0.05$). By contrast, fish held in captivity after catching maintained elevated glucose and cortisol levels for 14 and 30 d, respectively ($p>0.01$). Behavioral evaluations indicated that caught and released males used significantly more area and had higher rates of movement, as compared with females in the first 24 h post-release; however, there were no discernable differences between angled and control fish. The results of this study indicate that catch and release angling results in physiological stress for *S. pulcher*, but this can be reduced by minimizing fight times and handling before returning the fish back into their home environment. Rapid recovery (in <18 hours) and the lack of behavioral impacts supports catch and release as a viable management strategy for this species.

Keywords: Catch and release, Angling stress, Acoustic tracking, Fish telemetry, Physiology, Fish stress, Recreational fishing, Sublethal.

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Introduction

For many fish species targeted by recreational anglers, daily bag and size limits are commonly used regulations to limit fishing mortality and mitigate angling pressures. In the recreational fishery for California sheephead (*Semicossyphus pulcher*) these regulations have resulted in widespread mandatory catch and release practices, yet the impacts of angling and handling on *S. pulcher* physiology, behavior, and survival are largely unknown [1-3]. Like many gamefish species, *S. pulcher* populations are increasingly threatened by loss of habitat, recreational and commercial fishing activity, and rapid climate change. Understanding the impacts of current fishing regulations and practices will support the sustainable management of this important fishery.

In recent years, significant decline in *S. pulcher* populations have prompted a need for better understanding of how catch and release fishing impacts this fishery. *S. pulcher* typically inhabit temperate rocky reef and kelp forest habitats from Cabo San Lucas, Mexico to Monterey Bay, California [4-6] and has historically supported a valuable commercial trap live-fish fishery, and steady growth (since the 1960s) in recreational hook and line and spearfishing activities [7-11]

Commercial fishing operations for the live-fish market have traditionally harvested plate-sized fish [12], while recreational anglers generally target the largest individuals in the population. Both of these size-selective pressures can impact size at maturity and sex ratios in populations of this protogynous hermaphroditic species and makes managing this fishery particularly challenging [8,13-15]. Noticeable stock declines beginning in the 1980s eventually prompted bag limits (5 fish/day) and size limits (>30 cm total length) to be implemented in the late 1990s; while the resulting catch and release practices reduced the total number of fish harvested annually, the short and long-term impacts of these regulations have never been investigated for this species[7-10]. As recreational fishing continues to be managed through bag and size limits in an attempt to rebuild stocks, with more fish being caught and released, it is increasingly important for management to account for the response and recovery of fish to angling and handling stressors, as well as the potential impacts of size-selective harvesting on population sex ratios, reproductive potential, and, ultimately, population dynamics.

In addition to mortality, capture-related stress can result in sublethal changes to fish physiology that may ultimately impact population growth or recovery. Fish may survive post-release yet still experience deleterious physiological effects from the stressors of angling (hooking and fighting the line), handling, barotrauma, and air exposure. Capture and handling related activities typically result in hormonal and biochemical changes affecting cardiovascular capacity, metabolic function, somatic growth, immune response, and reproduction [16-24]Measurement of the hormone cortisol is a preferred metric of physiological stress in fish given its role in facilitating adaptive biochemical and physiological changes, as well as its prolonged elevation in circulation that allows for precise sampling regimes throughout the response and recovery periods [17, 25-30]

When a perceived stress triggers the hypothalamus-pituitary-interrenal (HPI) axis, cortisol is synthesized by interrenal cells and released into the bloodstream [24,26,31]. Because it takes time for the neuroendocrine HPI axis to result in increasing cortisol levels, basal (non-stressed) states in fish can also be evaluated using rapid blood sampling protocols. Upon removal of a stressor(s), circulating cortisol levels may remain elevated for hours, or longer, until negative feedback on the HPI axis and other mechanisms lead to a return to basal status [17,27,28,31,32,].

A principal physiological effect of cortisol is the mobilization of energy reserves to meet the metabolic demands of behavioral and physiological responses during stress [16,26,33-37]. Cortisol directly activates glycogenolysis and gluconeogenesis, resulting in increased glucose production and release during stress responses, measurable as increased blood glucose concentrations [35,38,39]. Alongside cortisol-activated glucose level, the metabolite lactate is also often measured in evaluations of stress responses, serving as a useful metric of fish condition following the muscular exertion inherent in angling and handling [34,40-43]. Recent advances in the technology of portable meters supports accurate blood glucose and lactate measurements to be made immediately in the field, reducing time and cost of storage, transport, and traditional laboratory processing methods.

Behavior and physiology are inextricably connected in the well-being and survival of wild fish, thus physiological stress responses from catch and release occur simultaneously with behavioral responses, which can be monitored using fine-scale acoustic telemetry. In research on other gamefish species, behavioral responses to angling stressors have included reduced foraging and reproductive activities which have significant potential to impact individual and population level performance [18,27,44-48]. Home-ranging species, like *S. pulcher*, may retreat to their core range and exhibit less movement immediately following release, as a response to intense physiological stress and to reduce further physiological demands during the recovery phase [49,50]. However, this type of behavior has not been thoroughly investigated for *S. pulcher*, although such information could lend valuable insight into the vulnerabilities of released fish and their habitat preferences, and provide guidance for management in support of fish recovery and survival. Behavior of released fish can be closely monitored by either passive tracking, using an array of acoustic receivers to provide the location of multiple individuals, or active tracking and recording precise location of a single individual.

Correlating the physiological and behavioral stress responses in fish caught and released to recover in their natural habitat can provide valuable information for managing a fishery where catch and release is a widespread practice. Identifying and quantifying responses and recovery rates of physiological and behavioral metrics are particularly critical for gamefishes where small fluctuations in fitness or mortality may conceivably have significant effects at the population level, and this is especially true for long-lived species and populations that may experience repetitive stressors [51-53]. Surprisingly, relatively few studies have attempted to co-evaluate physiological and behavioral stress responses in fish, and no such studies have been done on *S. pulcher*, despite the potential for important biological and ecological insight into gamefish population dynamics. A better understanding of how physiological changes are associated with behaviors, and how behavior may facilitate physiological recovery, may also help to ensure appropriate regulation and to encourage anglers toward best capture and handling practices [48,54]. Most previous research in this area has been limited by using fish in captivity where physiological and behavioral responses are likely to be different from what they would experience in the wild, and therefore are potentially misleading to researchers and managers. Some teleost fishes experience chronic stress from confinement which prevents effective assessment of physiological recovery. Likewise, pelagic and gamefish fish behavior during stress and recovery in artificial environments is unlikely to be the same as that exhibited in their natural habitat. Given these considerations, evaluating the impacts of fishing related practices on *S. pulcher* and other gamefish would best be carried out, when possible, in wild individuals that are caught, released, and monitored in their natural environment. *S. pulcher* provides a special opportunity to carry out such studies since it is possible to recapture and blood sample fish under water in their natural environment.

The purpose of this study was provide new scientific information on the physiological and behavioral effects of currently mandated catch and release practices on wild *S. pulcher*, and on their post-release survival and recovery, in order to promote sustainable recreational fishing practices. The main objectives were to 1) determine physiological responses to different angling and handling practices using cortisol, glucose, and lactate as markers of stress and exertion, 2) evaluate behavioral responses (e.g. rate of movement, area use) in fish tracked post-release, and 3) compare recovery rates of captive fish versus individuals released back into the wild to demonstrate the importance of monitoring animals in their natural environment.

Methods

Study Site

All fishing activity occurred within the 130,000 m2 Catalina Island Marine Life Reserve (CIMLR), a no-take reserve on the lee-ward side of Santa Catalina Island, California (Figure 1), between 2001-2004. The CIMLR ranges in depth from 0 to 40 m and encompasses areas of rocky reef, sand/mud flats, and kelp forest (Macrocystis pyrifera). Vertical structure is naturally provided by kelp forest, cliff walls, and boulder riprap, as well as from anthropogenic structures like a pier, floating dock, and scattered mooring blocks. [11,55] determined that the home ranges of *S. pulcher* in the CIMLR rarely extend beyond the protection of the reserve, which provides some assurance that fish in this study were unlikely to have been recently caught and released by recreational anglers.

Figure 1. Satellite imagery of Santa Catalina Marine Life Reserve on Catalina Island, California. Reserve boundaries designated by dashed white line. Inset map shows the location of the CIMLR on Catalina Island its relation to the California coast.

Physiology

Cortisol and metabolite (glucose and lactate) concentrations were initially determined from blood samples collected by caudal vein puncture within <3 min of hooking the fish, using typical recreational hook and line fishing methods [41]. In addition to these surface-sampled control (SC) fish, which experienced rapid ascent and brief air exposure, a second group of under-water control (UW) fish included individuals caught on baited handline and sampled under water (within <3 min of first contact) never experiencing rapid ascent or air exposure.

The timing and magnitude of the endocrine response to capture stress was evaluated by comparing the SC and UW control groups to fish held in on-board holding tanks and sampled after varying periods up to 2 h; this type of extended period is common practice for recreational anglers. In addition, the effects of angling duration (time fighting the line) on stress responses were determined by allowing fish to fight for 5, 10, or 20 min, before landing and blood sampling. Recovery in captivity was evaluated in *S. pulcher* caught and placed into 2.0 m diam. x 0.8 m depth outdoor tanks for up to 30 d. Recovery rates of captive fish were compared with *S. pulcher* that were caught, initially blood-sampled, tagged, and then released back into their natural environment. Fish in the latter group were recaptured in the wild after varying times at liberty, ranging from 18 h to 80 d. All sampled fish were measured for total length (TL cm), weighed (g), sexed (Male/Female/Transitional) and tagged with an external identification number (Floy Tag, USA).

Upon collection, whole blood samples were centrifuged for 5 min at 3,000 rpm, plasma was then decanted and stored at -75°C for later analyses. Cortisol concentrations were measured in all plasma samples using a double antibody radioimmunoassay kit (RIA) from Diagnostic Systems Laboratories, Inc., Webster, TX. Dilutions of *S. pulcher* plasma produced a curve parallel to the standard curve of %B/Bo versus concentration of unlabeled ligand added at 0.01-1000 ng/ml. The lowest detectable cortisol concentration was 1.1 ng/ml; intraassay and interassay coefficients of variation were 6.0% and 2.9%, respectively. In addition, precision and repeatability were ensured by dividing up a set of plasma samples for measurement by the RIA used in the laboratory of Dr. Carl B. Schreck (Oregon State University, Corvallis, OR) and by a commercially available enzyme-linked immunosorbent assay (ELISA) from Cayman Chemical, Inc., Ann Arbor, MI; all sample measurements coincided [56].

Plasma concentrations of glucose and lactate were quantified using colorimetric assays obtained from Sigma Chemical Co., St. Louis, MO. Absorbances were read using a Synergy H1 Hybrid Multi-Mode Microplate Spectrophotometer (BioTek Instruments Inc., Winooski, VT). Standard curves were used to calculate the sample metabolite concentrations (mmol/L) using SPSS Inc. software.

Differences in mean plasma cortisol, glucose, and lactate concentrations between the SC and UW control groups were compared using Student's t-test. Treatment groups with increasing angling duration and time in confinement were compared using one-way or two-way ANOVA on log-transformed data, followed by Holm-Sidak multiple comparison test or Student's t-test, as appropriate, to identify which treatment exhibited significant responses. The importance of fish sex, or fish length, on biomarker response was evaluated using ANCOVA with sex, or length, as a co-variate. All statistical analyses were conducted using SPSS software, and figures were produced in R Studio. Mean differences were considered statistically significant when p<0.05.

Behavior

To provide a non-angled (NA) reference group for evaluating fish behavior, scuba divers handfed *S. pulcher* acoustic transmitters (Vemco Ltd, USA; V8SC-6L and -1L, 22 mm•8 mm diam. or 26 mm•8 mm diam., respectively) hidden inside squid bait to avoid causing stress from capture and handling. To assess the behavioral impacts of capture and handling stress, *S. pulcher* caught on hook and line were immediately anesthetized in MS-222 (Finquel 0.15 g 1-1) and surgically implanted with an acoustic transmitter in the peritoneal cavity using a 1 cm incision along the ventral line (between the pelvic fins and the anus). The incision was closed using 2-3 interrupted sutures (Ethicon ChromicGut 2-0) and fish were revived in saltwater holding tanks for 5 min prior to release back into their natural environment. Fish from both the NA group and the caught and released (CR) group were actively tracked for 24 h post-release from a 5 m Boston Whaler equipped with an acoustic receiver (VR100, Vemco Ltd.) and gunnel-mounted directional hydrophone (Vemco model VH110) with the geo-position of the tracked individual recorded at 15 min intervals using GPS (Garmin-48). To determine how movement behaviors of CR fish were modified from those of the NA fish, mean hourly rate of movement (ROM) and area utilization distributions were compared between groups. To evaluate how long impacts on behavior may persist in CR fish, some CR individuals were tracked for an additional 24 h period at 1-week and 1-month post-capture and compared with similarly tracked NA fish. When differences between CR fish and NA fish behavior were not significantly different, this was considered a full behavioral recovery.

Correspondance between physiological and behavioral changes in angled fish were determined by comparing recovery timelines. Mean hourly core range (50% UD, m2) and home range (90% UD, m2) were determined using Brownian Bridge movement models in the adeHabitate HR package in R Studio (R 3.2.4). Data were log transformed when necessary and generalized linear models were used to evaluate whether treatment, sex, and time post-release had a significant impact on *S. pulcher* behavior.

Results

The average time from hooking to blood collection for control groups were 1.83 ± 0.27 min (mean ± 1SE, n=26) and 2.32 ± 0.13 min (n=65) for UW and SC, respectively. Baseline plasma cortisol concentrations for fish in these groups were not significantly different from each other (Student's T test, p > 0.05, Table 1), but plasma glucose and lactate were slightly higher in the SC group (p < 0.001, Table 1). Fish size and sex were not significant factors affecting physiological parameters for either control group (p > 0.05), but plasma metabolite and cortisol concentrations were positively correlated with increased sampling time in both groups.

In response to increasing angling durations (Figure 2), plasma cortisol concentrations exhibited dramatic increases after 10 and 20 min (p <0.001), while at 5 min they had not yet increased (Figure 1). Plasma glucose concentration lagged behind that of cortisol, showing an increase only in the 20 min group (p<0.001, Figure 2). In contrast, plasma lactate increased in a linear manner, progressively increasing with increasing angling times (p<0.001; Figure 2).

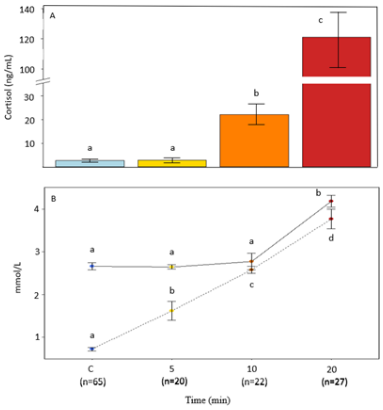

Figure 2. Plasma cortisol (A) and metabolite (B) concentrations in *S. pulcher* subject to increasing angling times. In panel B, solid line represents glucose levels and dotted line represents lactate. Control group, C, includes fish angled and sampled at the surface in <3 min. Superscripts (a-d) designate statistically significant differences between groups based on one-way ANOVA and Holm-Sidak multiple comparison test (p<0.001). Values presented are Mean ± 1SE.

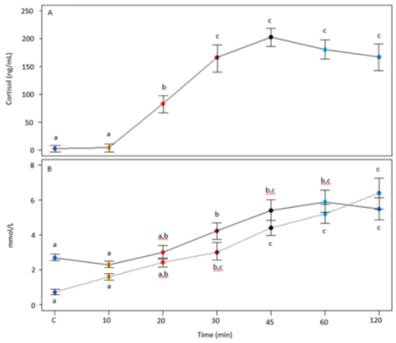

Figure 3. Plasma cortisol (A) and metabolite (B) concentrations of *S. pulcher* angled and kept for short-term confinement in on-board bait-tanks. In panel B, solid line represents glucose levels and dotted line represents lactate. Control fish, C, includes fish angled and sampled at the surface in <3 minutes. Superscripts designate statistically significant differences determined by one-way ANOVA and pairwise Holm-Sidak test (p<0.001). Values are Mean ± 1SE with n = 5-65.

Average plasma cortisol, glucose, and lactate levels after capture, handling, and confinement were significantly elevated throughout both short-term (Figure 3) and long-term (Figure 4) confinement periods. Plasma cortisol was significantly elevated after 20 min, similar to that observed in the 20 minutes angled group shown in Figure 2, but then continued to increase with confinement duration showing a peak of 203 ng/ml in the 45 min group (p < 0.001, Figure 3). Cortisol concentrations appeared to level off at concentrations between 150-200 ng/ml after 30 min of confinement, as there were no significant differences among the 30, 45, 60, and 120 min groups ($p > 0.05$, Figure 3).

Fish in long-term confinement maintained significantly elevated cortisol levels throughout the 30-d monitoring period as compared with SC controls ($p < 0.001$, Figure 4A). While fish confined for 1, 3, 5 and 7 d had cortisol concentrations ranging between 75-165 ng/ml, by day 14 cortisol levels had dropped to ~20 ng/ml ($p<0.001$ vs. earlier time-points). At 30 d, cortisol levels were similar to that seen at 14 d (~20 ng/ml); however, both the 14 d and 30 d groups still exhibited significantly higher cortisol than that in the control group ($p<0.001$).

Plasma glucose concentration exhibited a similar profile to that of cortisol in both short-term (Figure 3) and long-term (Figure 4) confinement. Glucose concentrations were significantly elevated above controls after 30 minutes in short-term confinement, peaked at 5.41 ± 0.52 mmol/L at 1 h, and exhibited a leveling off between 45 minutes to 2 hours (Figure 3). Plasma glucose concentrations in fish in long-term confinement were also significantly elevated throughout 14 d in captivity ($p < 0.001$; Figure 4), returning to baseline by the end of the 30-d monitoring period ($p > 0.05$ vs. control group).

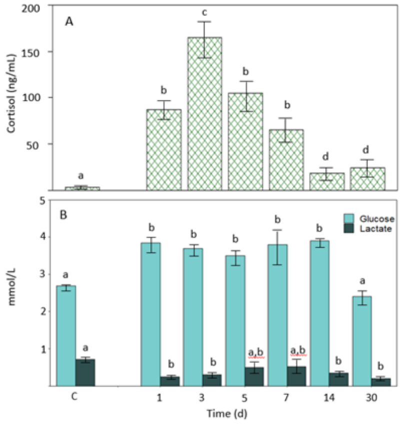

Figure 4. Plasma cortisol (A) and metabolite (B) concentrations of *S. pulcher* confined up to 30 d in 3,000 L outdoor holding tanks. Control group, C, includes fish angled and sampled at the surface in <3 minutes. Superscripts (a-d) designate statistically significant differences determined by one-way ANOVA and Holm-Sidak multiple comparison test ($p<0.001$). Values are Mean ± 1SE with n = 5-65.

Plasma lactate concentrations steadily increased throughout the 2-h short-term confinement period (Figure 3). However, by day 1 of confinement, and continuing to 30 days in the long-term confinement experiment, lactate had subsided to concentrations at or below baseline levels ($p > 0.005$, Figure 4).

Seventy-three *S. pulcher* were recaptured after initial tagging and release in the CIMLR, with time at liberty in their natural environment ranging from <1 d to 82 d. All recaptured individuals were free of any sign of infection due to tagging or blood sampling, and most appeared to be completely healed at the original site of blood sampling. Fish recaptured and rapidly sampled (within 3 minutes of hooking) all exhibited plasma cortisol concentrations comparable to baseline concentrations, including two individuals recaptured in less than 24 h ($p > 0.05$, Figure 5). Fish that were not rapidly resampled (i.e., >3 min from time hooked, ranging up to 10 min) showed variable but significantly elevated cortisol above baseline ($p < 0.05$, Figure 5). Plasma concentrations of glucose (Figure 5) and lactate (Figure 5) across all recaptured fish were more variable than cortisol and showed no distinct time-related patterns. As an overall group, however, both metabolites exhibited slightly, but significantly, elevated concentrations above their baselines ($p < 0.05$).

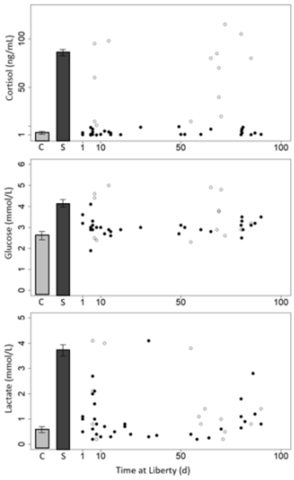

Figure 5. Plasma cortisol, glucose, and lactate concentrations in *S. pulcher* recaptured in the field after previous catch and release stress. Control group (C) consisted of fish angled and sampled at the surface in <3 min, Stress group (S) was composed of fish subject to 20 min angling. Solid symbols indicate samples were collected at the surface in <3 minutes, while open points indicate sample was collected in >3 min from time hooked.

A total of 32 *S. pulcher* (CR n=17; NA n=15) were actively tracked for 24 hour post-release; 15 of these comprised a non-angled (NA) reference group, which were fed with an acoustic transmitter, and compared with 17 that were caught and released (CR) after peritoneal insertion of an acoustic transmitter. Additional 24 hour tracks occurred at 1 week (n=11) and 1 month (n=8) after the initial tracking. Of the 17 CR fish, 10 were male (33.2 ± 0.83 cm SL) and 7 were female (28.8 ± 1.06 cm SL), while all of the NA individuals were male (34.8 ± 0.56 cm SL) due to inability to handfeed smaller females a transmitter. Survival of angled *S. pulcher* through 1 mo post-release was 100%. At night *S. pulcher* are typically quiescent in rock caves or similar refuge habitat and Topping et al. [55] found their movement in the CIMLR to be negligible during this period; therefore, only fish positions recorded during daylight hours (06:00-18:00) were included in behavioral analyses.

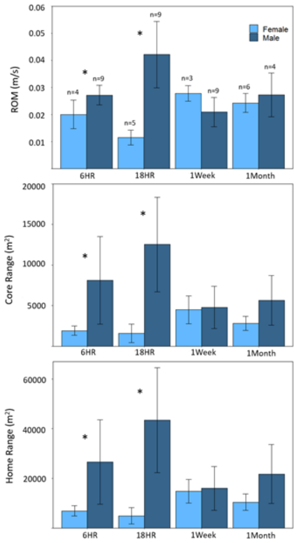

Figure 6. Rate of movement (ROM), core range, and home range of female (light blue) and male (dark blue) caught and released *S. pulcher*. ROM and area use metrics were averaged over 6 hour periods immediately after release (6HR), 18-24 hour post release (18HR), 1 week post-release (1Week), and 1 month post-release (1Month) at the same time of day as the 6HR tracks. Sample size varies because fish were not tracked at night. * indicate statistically significant differences between female and male S.pulcher determined by one-way ANOVA and post-hoc Tukey HSD test ($p<0.001$). Values Mean ± 1SE.

Area use (core range and home range) and rate of movement (ROM) were not significantly different between male *S. pulcher* in the CR and NA treatment groups ($p > 0.05$), although individual variation was high in both groups during the initial 24-hours tracking. There were, however, significant behavioral differences between the sexes with CR males exhibiting greater ROM and larger area use than females in the first 24 hours post-release ($p > 0.05$, Figure 6). On average, CR males increased their ROM and area use throughout the first 24 hours of tracking, while female ROM decreased and area use was similar between the first 2 tracking periods ($p > 0.05$, Figure 6).

Discussion

The rapid blood sampling methods used in the current study established that basal plasma cortisol concentrations in *S. pulcher* are ~2-3 ng/mL, which is consistent with the literature for other marine teleosts [26, 35,57]. Analyses by two laboratories (CSULB and Oregon State University) confirm that over 30% of the UW control group contained cortisol concentrations that were actually below the RIA detection limit of 1.1 ng/mL; therefore, true basal levels are likely less than the mean values determined for the SC and UW groups (2.27 and 2.93 ng/mL, respectively). These levels are relatively low compared to basal cortisol levels reported for most marine teleosts, which range from 1-10 ng/mL across species and environments [26,35,57] including freshwater [58,59], temperate [60,61], tropical [62,63], and Antarctic species [64]. Typically, blood collection within 5 min of a fish being hooked is considered sufficient for measuring basal cortisol levels. However, the low concentrations reported here are likely due to the novel approach of blood sampling undertaken in situ, in their environment under water, without hooking, angling, and air exposure. These results may provide the closest measure of the “unstressed state” in fish studies to date. We recommend this method be adopted in future studies when the behavior and temperament of the subject species allow, particularly for species susceptible to barotrauma. While the effects of rapid ascent have been investigated for other marine species, e.g. rockfishes [65,66], symptoms of barotrauma, including distended stomachs and prolapsed rectum/intestine, were observed for *S. pulcher* in this study and should be further investigated.

Significantly elevated blood cortisol and metabolite concentrations indicate that fight duration is a significant source of physiological stress for *S. pulcher*. Plasma cortisol and glucose were significantly elevated above their baseline levels after 10 and 20 minutes of angling, respectively. The evident time delay from initial hooking to elevated circulating cortisol (requiring around 10 minutes) reflects the complex response of the neuroendocrine HPI axis culminating in the synthesis and release of cortisol into the blood circulation. The lag between elevated plasma glucose (at 20 minutes) and elevated cortisol (at 10 minutes) reflects the time required for increased circulating cortisol to activate glucose production eventually leading to elevated circulating glucose levels [24,35].

In contrast to cortisol and glucose, plasma lactate concentrations increased steadily with prolonged fight time, indicative of exhaustive, anaerobic muscle activity during angling. During periods of anaerobic activity, lactate cannot be processed by oxidative tissues (e.g. red muscle, heart, gills, etc.) as rapidly as it is produced by white muscle [67]. While lactate is not a direct product of the neuroendocrine stress response, it can be a useful measure when combined with other biometrics to evaluate stressor intensity, whole-organism response, and susceptibility to post-release mortality [68-70]. Therefore, cortisol and lactate emerge as useful indicators to evaluate the intensity of angling stress in *S. pulcher* and other gamefishes, with cortisol reflective of the neuroendocrine response to stress and lactate indicative of intensive physical activity derived from behavioral (swimming) responses. Glucose, on the other hand, has been considered a less reliable indicator of angling stress and intensity, since glucoregulation occurs along several different pathways and increased metabolism may balance increased glucose synthesis during exhaustive exercise [67,71].

Prolonged angling times of up to 20 minutes are not unusual in the *S. pulcher* recreational fishery where this species is known for becoming entangled in rock or kelp strands and must be worked free. Stress responses reported here were similar to those of other marine and freshwater teleosts, where plasma cortisol levels >10 ng/mL indicate a degree of physiological stress that increases with angling time [35,57,61,72-72]. However, interspecific variation, and differences in capture methods and angling conditions, complicate direct comparisons between species and studies.

S. pulcher continued to experience elevated physiological stress during 2 hours following hook-and-line capture when they were further held in on-board tanks (confinement). Plasma cortisol and glucose levels peaked at around 45 minutes and then leveled off thereafter, while lactate levels increased progressively throughout the 2 hours treatment period. The leveling off in cortisol levels is presumably due, in large part, to continued elevated cortisol exerting negative feedback on the HPI axis leading to reduced rate of cortisol synthesis [17,24,32]. While plasma glucose followed the same pattern (i.e., leveling off at an elevated level), lactate exhibited progressively increasing concentrations throughout the 2-h period. Fish movement and activity during the 2-hours confinement was somewhat restricted due to small holding tanks, suggesting that the most substantial cause of the increasing lactate was the response to the intensive exercise during the initial angling and handling, combined with a slow rate of clearance of lactic acid in the muscle and lactate in the bloodstream [57,67,71,74].

The overall rate and magnitude of the *S. pulcher* stress responses are generally comparable to those observed in other gamefishes studied, including kelp bass [75,], shortnose sturgeon (*Ancipencer brevirostrum*), [76,77], starry flounder (*Platichthys stellatus*), [38], roach (*Rutilus rutilus*), [78, 79], fat snook (*Centropomus parallelus*), Lennox et al. [80], golden dorado (*Salminus brasiliensus*), Gagne et al. [81], and bonefish *Albula spp*., [82]. When fish are the most physiologically stressed is when they are likely to be the most impaired and susceptible to predation and post-release mortality. Despite the substantial physiological responses to capture-related stressors in *S. pulcher*, they were found in this study to be capable of rapid physiological recovery if released back into their natural environment. Fish that were released and later recaptured, including some individuals at liberty for only18 h, exhibited cortisol levels that had fully returned to baseline. *S. pulcher* are known to rest overnight in home shelters [9,83,84], which may facilitate their recovery given the lower metabolic demands during this period. While the cortisol clearance rate for *S. pulcher* is unknown, it likely lies within the range reported for other teleosts, from 30.3 ml/kg/h (Salmo gairdneri, Brown et al. [85] to 270 ml/kg/h Onchorynchus nerka,[35].

Given the overnight recovery of cortisol to basal levels, it was notable that there was high variability in glucose and lactate concentrations in recaptured individuals. While not readily explainable, this may indicate persistent perturbations in metabolites post-stress response and/or differences in recent foraging and activity prior to recapture. It was also noted that *S. pulcher* which were recaptured and sampled at >10 min post-hooking (i.e., not rapidly blood sampled) exhibited significantly elevated cortisol and glucose levels, comparable to fish angled for 20 min. This finding suggests that repeat capture may result in stress responses that are greater in magnitude, a point worthy of further study and which would be relevant to fisheries management in areas of high fishing pressure where individuals may experience frequent catch and release.

In contrast to the rapid recovery of caught and released *S. pulcher*, confinement post-capture resulted in elevated cortisol and glucose levels for as long as 30 d and 14 d, respectively, reflecting the chronic stress fish experience in captivity. Lactate levels, however, remained at or below baseline levels through the 30 d confinement period, suggesting that fish were less active and less mobile in captivity than they would be in the wild. In general, these findings suggest that it may be inappropriate to use captive fish when evaluating physiological stress recovery, and that monitoring fish in their natural environment should be implemented in study design whenever possible [86].

While *S. pulcher* exhibited significant physiological responses to angling and capture stress, we did not observe any significant behavioral changes, a contrast which highlights the value of pairing physiological and behavioral endpoints when evaluating angling impacts on gamefish populations. We expected *S. pulcher*, like other home-ranging species, to exhibit reduced activity and a greater preference for core range areas immediately following release [11,49,50], with a gradual resumption of normal behavior simultaneous with physiological recovery. However, we found no difference between angled (stressed) fish and control fish in any of the behavioral metrics evaluated. Unfortunately, efforts to feed female *S. pulcher* the baited transmitters were unsuccessful, and so there were no female control fish to compare with the behavior of females caught and released. It is also possible that we were unable to detect subtle behavioral impacts from angling due to the high individual variation observed among both control and angled fish. Topping et al. [87] reported similar variation in behavior for *S. pulcher* in the CIMLR, and also found that males use significantly more area and exhibit higher rates of movement than females. This sexual dimorphic behavior may be due to body size, i.e. larger males require more resources, or because male *S. pulcher* are territorial and maintain a harem of smaller females to mate with [88-94].

Conclusion

This study finds that fishing regulations like bag limits and size restrictions, which result in catch and release practices, appear to cause only temporary physiological disturbance in *S. pulcher*. When returned to their natural environment, they exhibit high survival, rapid physiological recovery, and no measurable impact on movement behavior. Such findings suggest that management priorities for this popular southern California gamefish should focus on reducing harvest rates and educating anglers on best handling practices. Given that prolonged angling clearly elicits elevated stress in a variety of gamefishes, including *S. pulcher*, we recommend reducing fight times by using appropriate gear and landing fish quickly without playing on the line. Best practices minimizing capture related stress are important for undersized fish, which anglers are required to release, but also particularly for large females in the population. While reproductive input by large females is vital for population sustainability these individuals are currently only released voluntarily, often by conservation-minded anglers. Although *S. pulcher* appear to exhibit high survival rates and rapid post-release recovery, there may be cumulative effects from repeated catch and release or additive effects of other environmental stressors that warrant further investigation. Results from this study add to a growing body of literature that aims to understand how anglers impact the gamefish they target and how the health and sustainability of recreational fisheries may be ensured.

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