Remarkable euryhalinity of a marine fish *Lutjanus novemfasciatus* in mangrove nurseries

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Abiotic environmental stress is a fundamental driver of population and community dynamics across diverse ecosystems (Menge and Sutherland 1987). In this context, specialist species persisting at great altitudes or depths, in near-boiling or subfreezing temperatures, through droughts or monsoons, and over prolonged bouts of resource deprivation highlight the adaptability of life on Earth. Notably, environmental stress, or harshness, incorporates "extremeness" along gradients such as oxygen or temperature, but it is also defined by the magnitude and tempo of variability in these environmental conditions (Peck et al. 2006). Even, extreme-tolerant species may require stable conditions to maintain fitness, while species capable of physiological plasticity are better adapted to niches characterized by environmental variability (Chevin and Hoffmann 2017).

Across the transition from freshwater to marine conditions in coastal aquatic habitats, osmoregulatory constraints are keys to gauge environmental stress. Faunal diversity is often depressed in brackish estuaries relative to upstream (freshwater) or downstream (marine) systems due to the physiological burdens of osmoregulation under widely varying salinity (Odum 1988). Fishes with adaptations for euryhalinity (i.e., broad salinity tolerance, such as fishes in cichlid, mugilid, and antherinid families) are known to survive at very high salinities (>70 practical salinity units [PSU]), although these extreme conditions are often defined by relatively stable over weekly to yearly scales (Brauner et al. 2012). Similarly, diadromous fishes that traverse marine–freshwater boundaries as a part of their life history exhibit wide salinity tolerances during their ontogeny. Bull sharks (*Carcharhinus leucas*) are also recognized for their ability to cross marine–freshwater boundaries, but these transitions generally occur over weekly scales, and bull shark movement is linked with minimizing energetic costs associated with osmoregulation (Heupel and Simpfendorfer 2008). Comparatively, there are few examples of fishes that thrive in consistently changing salinities and cycling hyper- and hypo-osmotic stress. Some estuarine residents, such as marsh-associated killifishes, exhibit low metabolic burdens when exposed to rapid salinity change (Marshall 2013). However, even within this guild (e.g., Atlantic killifish [*Fundulus heteroclitus*]), abilities to compensate for osmotic shock may be greater among natives to typically freshwater habitats, while individuals in brackish or marine environments struggle to maintain osmotic homeostasis and take longer to recover following salinity shifts (Whitehead et al. 2011). We are unaware of euryhalinity expressed by marine fishes exposed to freshwater-marine salinity transitions (0–35 PSU) that cycle over short time scales (hours).

In early 2013, during scouting trips to mangrove-dominated creeks on Isla Isabela (S 0°57′25″, W 90°57′54″), Galápagos, we observed what appeared to be intense mixing of freshwater and saltwater and rapid salinity transitions correlated with tidal cycles. Mixing was apparent to the naked eye as a prominent underwater "mirage" effect during mid-tidal stages in this semi-diurnal system (Fig. 1), while transitions seemed obvious based on stark differences in taste of water during high (salty) and low (fresh) tides. Salinity patterns appeared to be driven by ocean-water inflows during high tides, and significant groundwater discharge during low tides sourced from rainwater that passed through Isabela's porous volcanic basalt rock (Trueman and d'Ozouville 2010). Despite these perceived large environmental shifts every six hours, we also observed that juvenile Pacific
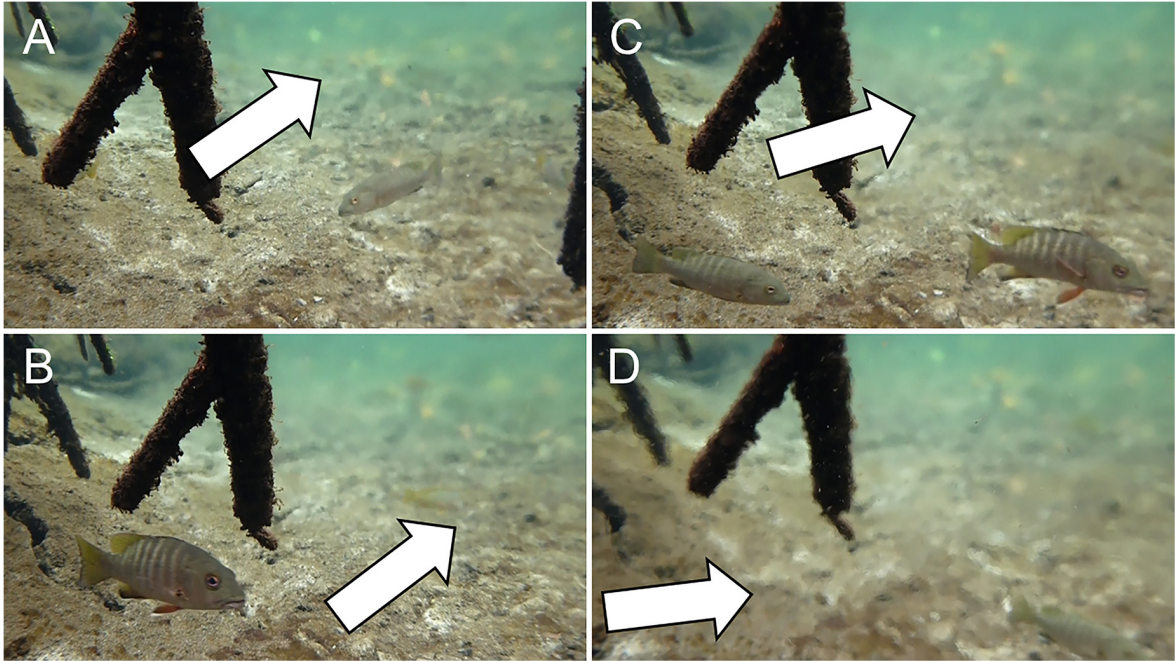
Fig. 1. Pacific dog snapper (*Lutjanus novemfasciatus*) occupying red mangrove (*Rhizophora mangle*) nursery habitat during a period of intense mixing of seawater and groundwater. Mixing is evident by visual distortion of underwater images (panels A–D; white arrows), resulting in a mirage effect. Still images were captured from a video taken during a tidal shift in which snapper interacted with the salinity-driven mirage effect. This video is included in the online supplementary material (Video S1).

dog snapper (*Lutjanus novemfasciatus*) appeared as resident within these mangrove creeks regardless of tidal stage and local salinity (Fig. 1; Video S1), while several other fishes appeared present only during high tides (e.g., blacktip sharks [*Carcharhinus limbatus*]). We also noted that emerging groundwater turned creeks into quasi-river systems during low tides, and that snappers appeared to use mangrove prop roots as flow refugia during these periods.

To confirm residency of dog snapper in the context of extreme salinity variability, we tagged 20 fish (mean total length 265 ± 68 mm) with acoustic transmitters (VEMCO; V7-4x, 90–150-s chirp rate, 246-d lifespan) during July 2013 across two mangrove-lined creeks along southeastern Isabela. These "eastern" (S 0°57′44″, W 90°57′31″; 11 fish tagged) and "western" (S 0°57′34″, W 90°59′42″; 9 fish tagged) creeks were ~4 km apart, dominated by red mangrove (*Rhizophora mangle*), connected to fully marine coastal bays, defined by main-stem channels ~10-m wide by ~2-m deep (during high tide; ~1.5-m range), and extended ~200 m from mouth to head. Twelve passive acoustic receivers (VEMCO; VR2W) were moored throughout two mangrove creeks to detect presence of fish (limiting acoustic "blindspots" across tidal cycles; $N = 5$ and 7 receivers in eastern and western creeks, respectively) and gate the mouth of each creek to detect if and when tagged fish exited (egressed) or entered

(ingressed) either system to or from the adjacent coastal bays. Egress was defined as a "last" detection at a creek mouth, followed by >3 h with no detections at any hydrophones in a creek, with ingress back into a creek defined by the subsequent detection at a creek mouth before "up-creek" movement. Tidal level (pressure; Van Essen DI500), salinity (conductivity; Van Essen DI271), and temperature (both loggers) were recorded every 10 min during this observational effort. Loggers were moored 0.5 m above the channel bottom at the midpoint between the mouth and head of each creek. Receivers and loggers were maintained regularly with final downloads in June 2014, providing a year of continuous fish tracking and corresponding environmental observations.

As suspected, extreme salinity changes in these creeks cycled twice a day ranging between <10 to 35+ PSU in the eastern creek, and <2 to 35+ PSU in the western creek (Fig. 2A, B). Across semidiurnal tides, we observed routine ~4 and ~5.5 PSU per hour shifts in salinity in eastern and western creeks, respectively. In contrast, the maximum diel temperature range during 2013–2014 in these two creeks was only ~5°C. Despite the large shifts in salinities, tagged snapper remained in these two creeks during ~93% (averaged across fish) of possible observations in six hours bracketing each high tide (i.e., high salinities), and ~91% (averaged across fish) of possible observations in the six hours bracketing all
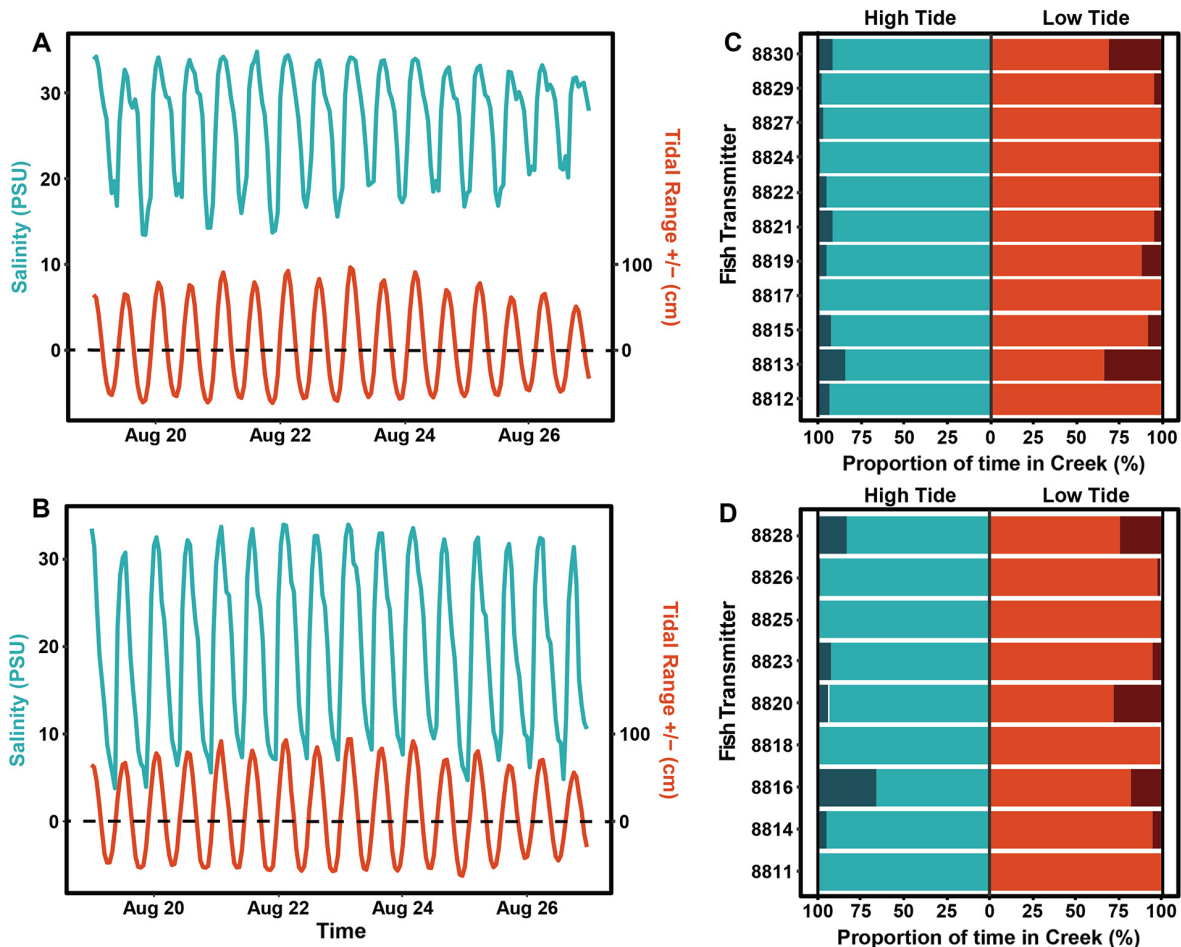
FIG. 2. Tidally driven water level and salinity in mangrove creeks on Isabela, Galápagos, during a one-week period in November 2013, representative of abiotic cycles throughout 2013–2014 in eastern (A) and western (B) creeks. Percentage of time during 2013–2014 that acoustically tagged Pacific dog snapper (*Lutjanus novemfasciatus*) occupied mangrove habitat during high-tide (salinities typically approaching 35 PSU in each creek) and low-tide (salinities dropping to 10 PSU or 5 PSU for eastern and western creeks, respectively) periods in eastern (C) and western (D) creeks. High- and low-tide intervals were defined during each 12-h tidal cycle as opposing 6-h blocks, including the three hours before and after maximum or minimum water levels, respectively. In (C–D), bright teal (high-tide interval) or orange (low-tide interval) indicate when fishes were present in mangrove creeks, while dark teal and dark orange indicate when fish egressed from the mangrove creeks and into the adjacent coastal bay (i.e., last detection at the creek mouth, followed by extended periods of no detections, followed by detection at creek mouth before movement "up creek").

low tides (i.e., low salinities), throughout 2013–2014 (Fig. 2C, D). It is implausible that dog snapper refuged in pockets of high-salinity water during low tides or low-salinity water during high tides, as we routinely observed snappers swimming through areas of visible mixing of saltwater and freshwater. We also made several transects along the main stem of both creeks with a CastAway CTD (Conductivity, Temperature, and Depth), recording 2–10 PSU or >30 PSU across the entire systems during low and high tides, respectively. Lastly, 75% and 95% of all snapper detections in the eastern and western creeks, respectively, were at "mid-creek" hydrophones, rather than at hydrophones adjacent to the mouth or head of these systems.

Despite the marine lineage of snappers (Family: Lutjanidae), dog snapper appear capable of remarkable euryhalinity in putative nurseries with semidiurnal salinity fluctuations spanning <5 to 35 PSU. Notably, snapper would have only had to egress ~200 m during each low tide into the adjacent coastal bays to track more isohaline (marine) conditions, but instead exhibited high site fidelity in creeks. The physiological mechanisms, if any, these snapper employ to express euryhalinity represent a subject for further investigation. Given the short time scales over which salinity cycles in these creeks, rapid control of seawater-type ionocytes might maintain NaCl balance without notable metabolic costs for these juveniles (Daborn et al. 2001, Marshall 2013). Up- and

down-regulations of ionocytes, however, are more typically studied in freshwater and brackish taxa, and it is unclear whether these models of ionocyte dynamics can be easily applied to marine species. Alternatively, salinities of 2 PSU are isosmotic to blood. Therefore, snappers were likely not required to respond to alternating hypo- (<2 PSU) and hyper-osmotic (>5 PSU) conditions (Marshall 2013). Still, we suspect some potential for osmotic stress, given that fishes other than snapper egress from these creeks during low tides. In this context, dog snapper expand our understanding of the range of environmental tolerances fauna may demonstrate with respect to abiotic variability.

It remains unknown whether dog snapper is capable of similar euryhalinity across its range (e.g., eastern equatorial Pacific, and Mexico to Peru), or if our observations represent local acclimation or selective survival and tolerance for extreme salinity variability (sensu Carr et al. 2018). Even across the Galápagos, rainfall patterns and freshwater discharge into mangrove creeks varies among islands (Trueman and d'Ozouville 2010), potentially leading to highly localized selective pressure for euryhalinity among snapper.

The wide salinity tolerances exhibited by dog snapper not only demonstrate how behavioral or physiological plasticity may buffer taxa against potential abiotic stress over evolutionary timescales, but also highlight critical questions regarding the response(s) of nearshore marine fauna in an era of rapid global change. In particular, how freshwater, euryhaline, and marine taxa respond to location-specific increases in precipitation or saltwater intrusion may be one determinant of the resilience or vulnerability of these ecosystems (Kennish 2002). Dog snapper residency within mangrove creeks despite potential energetic demands of salinity variability may also reinforce the overall fitness benefits for juvenile fishes provided by coastal biogenic habitats (Lefcheck et al. 2019). The structural refuge defining these habitats can increase foraging opportunities and decrease predation risk for juvenile fishes, a pattern corroborated by the high survival rate of tagged dog snapper (>80% survival of fish in the array during 2013–2014, with the remaining 20% representing either mortality or permanent emigration).

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3582/suppinfo

Open Research

Data (Plumlee et al. 2021) are freely available on Figshare: https://doi.org/10.6084/m9.figshare.14467068.v1.