Research Square

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Wind speed and dissolved oxygen predict mullet jumping in a subtropical estuary

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Abstract

Mullet (Mugilidae) are well known for frequently leaping out of the water, yet the ecological and physiological drivers of this behavior remain debated. Hoese's internal diving bell hypothesis proposed that mullet jump to obtain atmospheric air using the pharyngobranchial region when aquatic oxygen uptake is limited. Building on this hypothesis, we tested whether wind speed predicted mullet jumping independently of dissolved oxygen under natural field conditions in Big Sarasota Bay, a shallow subtropical estuary on the Gulf coast of Florida. From February to May 2025, we conducted 126 one-hour visual observation periods and recorded mullet jumps, dissolved oxygen, wind speed, and additional environmental variables. Jumping was most frequent under calm, lower-oxygen conditions. An additive negative binomial model received greater support than models containing either predictor alone, and both wind speed and dissolved oxygen remained significant when analyzed together. An exploratory segmented analysis identified a candidate wind-speed breakpoint near 6.3 mph. These findings extend the internal diving bell hypothesis by indicating that natural variation in wind-driven mixing may help determine when oxygen-related jumping occurs.

Introduction

Big Sarasota Bay is a shallow subtropical estuary located within the Sarasota Bay Watershed on the south-central Gulf coast of peninsular Florida. It supports diverse estuarine organisms and is bordered by a densely developed human population, making it vulnerable to rapid changes in water quality. This area of Florida averages 53 inches of rain annually (Sarasota County Water Atlas 2025), which is a main contributor to Big Sarasota Bay receiving many land-based pollutants, including fertilizers, pesticides, cleaning products, oil, and other contaminants, via runoff during rain events. Additionally, Big Sarasota Bay has three major intertidal connections with the Gulf: New Pass, Big Sarasota Pass, and Longboat Pass. Therefore, planktonic organisms, including harmful algal species, and anthropogenic pollutants can easily wash into the bay and remain there in high concentrations. With potential environmental degradations entering this bay from multiple sources, Big Sarasota Bay may therefore be susceptible to water-quality stressors, including elevated temperature and salinity, uneven dissolved oxygen distribution, and eutrophication associated with blooms of the red tide-forming dinoflagellate *Karenia brevis* and other algae (Sarasota County Water Atlas 2025). Similar harmful algal bloom events in estuarine systems can strongly alter dissolved oxygen dynamics by producing daytime oxygen supersaturation followed by nighttime hypoxia, conditions that may reduce fish abundance and alter fish behavior (Bornman et al. 2023).

Organisms that live in tropical and subtropical estuaries frequently have mechanisms for adapting to low oxygen conditions. Mullets are common throughout the Sarasota Bay Watershed and other coastal waters globally. Of particular importance to Big Sarasota Bay are striped mullet (*Mugil cephalus* Linnaeus 1758) and white mullet (*Mugil curema* Valenciennes 1836). *Mugil cephalus* is a cosmopolitan and euryhaline species of ecological and commercial importance, particularly in Southwest Florida, which leads the United States in mullet production (Jacot 1920; Marin 2018). Due to the co-occurrence of *M.*

cephalus and *M. curema* in Big Sarasota Bay, and the inability to accurately identify species during jumping observations, we refer to both species collectively as “mullet” throughout the paper.

Despite its small overall size of 54 square miles, Big Sarasota Bay is relatively shallow, with an average year-round depth of less than two meters (Fig. 1a; Goodwin 1989). Additionally, wind speed has been directly linked to the even mixing of oxygen in surface waters in shallow bays and estuaries (Sarasota County Water Atlas 2025; Liu et al. 2022; Turner et al. 1987). In shallow estuaries, wind can increase surface mixing and re-aeration, potentially reducing the severity and spatial patchiness of low-oxygen conditions. However, whether wind speed predicts mullet jumping independently of dissolved oxygen measured at the observation site has received little direct evaluation under natural field conditions.

Mullet are highly adaptable, tolerating broad changes in salinity and temperature that are common in dynamic estuarine habitats (Marium et al. 2023). Most species of mullet, but especially *M. cephalus*, are well known for their impressive and frequent leaps from the water, sometimes from predators or boats, but other times seemingly at random (Florida Museum of Natural History 2025; Thomson 1966). Researchers have hypothesized several reasons for this behavior, including using jumps as an escape tactic from predators (Holder 1903), a method of cleaning parasites off of the body (Thomson 1966), a means of getting more oxygen (Hoese 1985; Cech and Wohlschlag 1973), and even potential as a play behavior (Holder 1903). Although several explanations have been proposed, the “internal diving bell” hypothesis has emerged as one of the strongest physiological explanations for why mullet jump under low-oxygen conditions (Hoese 1985).

Most fish species rely on their gills to extract dissolved oxygen from the water and cannot directly use atmospheric oxygen unless they have specialized air-breathing adaptations, such as lungs or labyrinth organs (Carter 1931; Johansen 1970; Graham 1997). Mullet possess firmer gill filaments that do not shrink or collapse when taken out of water (Hoese 1985). Additionally, mullet species are capable of isolating part of these gill filaments with the use of their pharyngeal branchial organs; this allows them to take in oxygen directly from air rather than dissolved in water (Capanna et al. 1974). Under the internal diving bell hypothesis, mullet leap from the water to trap atmospheric air within this specialized pharyngobranchial region, allowing temporary gas exchange when dissolved oxygen in the water column is insufficient (Hoese 1985). As a part of his study, Hoese (1985) caught and then euthanized *M. cephalus* specimens from areas with low oxygen levels and found gas bubbles within the pharyngeal branchial organ and the gills for over 15 minutes after being out of the water in almost every specimen. This supports the theory that mullet can not only take in oxygen through the air, but can also store it internally for a short period. The angle at which the mullet leap from the water or gulp air at the surface seems to be advantageous to this function as well (Capanna et al. 1974). While this adaptation gives mullet the ability to acquire atmospheric oxygen, they still use gills as the primary mechanism for oxygen acquisition and are ultimately more adapted for oxygen intake via water (Jordan and Evermann 1901).

Hoese’s “Internal Diving Bell Hypothesis” (1985) showed that mullet jump frequencies are inversely correlated with dissolved oxygen concentrations. Dissolved oxygen concentrations in an environment

vary between time of day, time of year, tide stages, temperature, salinity, depth, and the organisms present in the water (Sarasota County Water Atlas 2025; Breitburg et al. 2018; Bornman et al. 2023). Dissolved oxygen levels are also directly influenced by and influence other water parameters such as temperature, pH, and salinity. Levels of dissolved oxygen are easily disturbed, especially within coastal and estuarine systems. Warming temperatures, sewage and nutrient runoff from the land and harmful algal blooms can all directly contribute to and exacerbate existing low levels of dissolved oxygen in the water column (Breitburg et al. 2018). Additionally, intercoastal waterway dredging and other types of coastal development directly impact estuaries and can indirectly affect dissolved oxygen. Activities such as the destruction of seagrass meadows and mangrove fringes can influence oxygen production, habitat structure, and water-column mixing. Sarasota Bay is therefore an ideal natural system for evaluating whether mullet jumping behavior reflects short-term changes in dissolved oxygen and wind-driven re-aeration.

Hoese (1985) established that mullet jumping is inversely related to dissolved oxygen and that the pharyngobranchial region can retain atmospheric gas. A remaining ecological question is how natural physical conditions determine when this behavior occurs in the field. We therefore evaluated whether wind speed predicted mullet jumping independently of measured dissolved oxygen and whether the wind-jump relationship showed evidence of a nonlinear threshold. This extends the internal diving bell hypothesis by incorporating wind-driven mixing as a potential environmental mechanism rather than simply testing the oxygen-jump relationship in another location. Our observations also occurred during a non-breeding seasonal window in Big Sarasota Bay (Kilby 1948), whereas Hoese's observations were collected in Louisiana and Texas estuaries across multiple seasons.

We predicted that mullet jump counts would decrease with increasing dissolved oxygen, decrease with increasing wind speed, and be better explained by an additive model containing both predictors than by models containing either predictor alone. We further explored whether the relationship between wind speed and jumping changed across the observed wind-speed range.

Methods

Study Design

Ten preliminary one hour-long field observations were made in April 2024 at randomized times from the central-eastern coast of Big Sarasota Bay on the Sarasota/Manatee County line in Florida (27.384678, -82.565201). Preliminary observations suggested a negative association between wind speed and mullet jump counts, motivating the formal 2025 study.

In 2025, observations were independently collected by six different individuals (students in a Scientific Research Tutorial course) at randomized times throughout the four-month period (February 5-May 7). Observations consisted of visually surveying the central-eastern coast (mainland side) of Big Sarasota Bay, with the vantage point of observation being a large dock on the waterfront at New College of Florida

(Fig. 1b). The approximate surface area of observation was 53,016 m^2 (based on current aerial imagery of the site). Maps were prepared in ArcGIS Online using the web map created by Sands (2026). Basemap and imagery providers are identified in the figure caption. Physical features of the observation area included a deeper (~ 2 m deep; historically dredged) area directly in front of the dock and a seagrass bed further to the west. The line of clear sight was limited to the edge of the seagrass bed. Observation windows were exactly one hour in length, and a Xylem ProQuatro YSI was air-calibrated for dissolved oxygen prior to each observation event. Salinity was calibrated once weekly. Each observation event consisted of recording the date, time, salinity (ppt), dissolved oxygen saturation (%), water temperature (°C), and water depth (m). Dissolved oxygen concentration (mg/L) was calculated from the instrument-recorded percent saturation using temperature- and salinity-dependent oxygen-solubility equations. Because standard ProQuatro percent-saturation measurements incorporate barometric pressure through the instrument's built-in barometer and calibration procedure, no additional pressure correction was applied. Additional data collected included tide (source: National Oceanic and Atmospheric Administration (NOAA) Tides and Currents 2025), wind speed and air temperature (source: weather station located at Sarasota/Bradenton International Airport, 800 m from the study site), *Karenia brevis* presence (source: NOAA and Gulf of America Coastal Ocean Observing System's Harmful Algal Bloom Forecast 2025), and enterococci bacteria presence (source: Suncoast Waterkeeper, with samples taken weekly from the observation location).

During each observation, any mullet leaping from the water was recorded as one "mullet jump." If a fish jumped multiple times in quick succession, the sequence was counted as a single jump. Because dissolved oxygen was not measured during the pilot period, the 10 pilot observations were excluded from all statistical analyses reported here. Statistical analyses were therefore based on 126 formal observation periods.

Statistical Analysis

Data were recorded in a shared Google Sheet (equivalent to Microsoft Excel), where individuals in the course were responsible for inputting their own data from each observation. Data were loaded into and analyzed in R version 4.4.1 (R Core Team 2024) using RStudio version 2026.05.0 + 218 (Posit Team 2026). Analyses used the packages tidyverse, MASS, mgcv, segmented, ggplot2, patchwork, broom, and gt. To evaluate environmental predictors of mullet jumping, we assessed relationships among dissolved oxygen, wind speed, and the number of mullet jumps observed during each one-hour observation period.

The relationship between wind speed and dissolved oxygen was first evaluated using diagnostic tests to determine whether parametric assumptions were met. Normality was assessed using Shapiro-Wilk tests. Because the variables did not meet assumptions of normality, Spearman's rank correlation was used to evaluate the strength and direction of the association between wind speed and dissolved oxygen.

Candidate models included linear, nonlinear generalized additive models (GAMs), quadratic, spline, and segmented regression models. Candidate models were compared using Akaike's Information Criterion (AIC), with lower AIC values interpreted as stronger relative support. Model selection also considered

biological interpretability, particularly whether more complex models provided insight beyond simpler alternatives.

Mullet jumping frequency was analyzed as count data. Because jump counts showed greater variability than expected under a Poisson distribution, negative binomial regression was used for count-based analyses. This approach allowed us to model changes in expected jump counts as a function of wind speed and dissolved oxygen while accounting for overdispersion among observations.

Results

Mullet jump counts were strongly overdispersed under a Poisson model (overdispersion ratio = 35.45), supporting the use of negative binomial regression for analyses with jump count as the response variable. Among negative binomial models predicting mullet jumps, the additive model including both wind speed and dissolved oxygen had the lowest AIC, indicating better support than models with either predictor alone: wind speed + dissolved oxygen AIC = 1014.33, wind speed only AIC = 1029.66, and dissolved oxygen only AIC = 1045.48.

Wind speed was weakly positively associated with dissolved oxygen concentration in our study (Fig. 2a; Table 1). Spearman correlation indicated a positive relationship between wind speed and dissolved oxygen ($\rho = 0.29$, $p = 0.0014$). Linear regression similarly indicated that dissolved oxygen increased with wind speed, with an estimated increase of 0.094 mg/L dissolved oxygen per 1 mph increase in wind speed (95% CI: 0.043 to 0.145; $p < 0.001$; $R^2 = 0.10$).

Dissolved oxygen was negatively associated with mullet jumping (Fig. 2b; Table 1). Spearman correlation indicated that jump counts were higher when dissolved oxygen was lower ($\rho = -0.43$, $p < 0.001$). In the negative binomial model, dissolved oxygen was a significant predictor of jump counts ($\beta = -0.406$, 95% CI: -0.548 to -0.263; $p < 0.001$). The corresponding incidence rate ratio (IRR) was 0.67 (95% CI: 0.58 to 0.77), indicating that each 1 mg/L increase in dissolved oxygen was associated with an approximately 33% decrease in expected mullet jump counts.

Wind speed showed the strongest pairwise association with mullet jumping (Fig. 2c; Table 1). Spearman correlation indicated a negative relationship between wind speed and jump counts ($\rho = -0.56$, $p < 0.001$). In the negative binomial model, wind speed was a significant predictor of jump counts ($\beta = -0.179$, 95% CI: -0.222 to -0.137; $p < 0.001$). The incidence rate ratio was 0.84 (95% CI: 0.80 to 0.87), indicating that each 1 mph increase in wind speed was associated with an approximately 16% decrease in expected mullet jump counts.

Because the relationship between wind speed and mullet jumping appeared to change across the observed wind-speed range, an exploratory segmented regression was used to estimate a candidate threshold. This analysis identified a breakpoint at 6.27 mph (95% CI: 5.60 to 6.94 mph), with jump counts declining steeply below this value and remaining comparatively low above it (Fig. 2c; Table 1). A Davies test indicated statistical support for a change in slope in the wind speed-jump count relationship ($p <$

0.001), suggesting that the association between wind speed and jumping was not constant across the observed wind-speed range. Because this threshold analysis was exploratory and based on segmented regression rather than the primary negative binomial count model, the estimated breakpoint should be interpreted as a candidate threshold rather than a definitive biological cutoff. An additional exploratory segmented regression analysis is presented in the Appendix (Fig. 3).

When wind speed and dissolved oxygen were included as covariates in the same negative binomial model, both predictors remained significant. Wind speed was negatively associated with jump counts after accounting for dissolved oxygen ($\beta = -0.151$, 95% CI: -0.193 to -0.109; $p < 0.001$; IRR = 0.86), and dissolved oxygen was also negatively associated with jump counts after accounting for wind speed ($\beta = -0.303$, 95% CI: -0.438 to -0.168; $p < 0.001$; IRR = 0.74). These results indicate that both lower wind speed and lower dissolved oxygen were independently associated with increased mullet jumping, with the strongest visual and pairwise relationship occurring between wind speed and jump counts.

Table 1 Summary of relationships among wind speed, dissolved oxygen, and mullet jumping. Spearman correlations describe pairwise associations among variables. Linear regression was used for the relationship between wind speed and dissolved oxygen. Negative binomial generalized linear models were used for jump-count responses because mullet jumps were count data and were strongly overdispersed. Incidence rate ratios indicate the proportional change in expected jump counts for each one-unit increase in the predictor. The segmented threshold analysis was used as an exploratory analysis to estimate the wind-speed breakpoint. Bold p-values indicate $p < 0.05$.

Relationship	Analysis	Effect size	Estimate [95% CI]	p-value
Wind speed and dissolved oxygen	Spearman correlation + linear regression	Spearman ρ = 0.29; R^2 = 0.10	β = 0.094 [0.043, 0.145] DO change per 1 mph wind increase	Spearman **p = 0.0014** Model **p < 0.001**
Dissolved oxygen and mullet jumps	Negative binomial GLM	Spearman ρ = −0.43; IRR = 0.67	DO β = −0.406 [− 0.548, − 0.263] IRR = 0.67 [0.58, 0.77]	Spearman **p < 0.001** NB **p < 0.001**
Wind speed and mullet jumps	Negative binomial GLM; segmented threshold	Spearman ρ = −0.56; IRR = 0.84	Wind β = −0.179 [− 0.222, − 0.137] IRR = 0.84 [0.80, 0.87] Breakpoint = 6.27 [5.60, 6.94] mph	Spearman **p < 0.001** NB **p < 0.001**
Wind speed, dissolved oxygen, and mullet jumps	Additive negative binomial GLM	Wind IRR = 0.86; DO IRR = 0.74	Wind β = −0.151 [− 0.193, − 0.109] DO β = −0.303 [− 0.438, − 0.168]	Wind **p < 0.001** DO **p < 0.001**

Discussion

The principal contribution of this study is evidence that wind speed explains variation in mullet jumping beyond its association with dissolved oxygen. Jump counts were highest under calm, lower-oxygen conditions, and both wind speed and dissolved oxygen remained significant when included in the same negative binomial model. Thus, the wind-jump relationship was not explained solely by the tendency for dissolved oxygen to increase with wind speed. These findings extend Hoese's (1985) internal diving bell hypothesis by identifying wind-driven mixing as a potential ecological influence on when oxygen-related jumping occurs under natural field conditions. Although the observational design cannot establish causation, the results are consistent with jumping functioning, at least in part, as a short-term respiratory behavior in shallow estuarine habitats where oxygen conditions can vary rapidly (Cech and Wohlschlag 1973; Hoese 1985).

Wind speed showed the strongest pairwise relationship with mullet jumping. Jump counts declined as wind speed increased, and exploratory segmented regression identified a candidate breakpoint at approximately 6.27 mph. Wind speed and dissolved oxygen were only weakly correlated, and both retained significant effects in the additive model. This suggests that wind speed may capture aspects of short-term mixing, oxygen patchiness, or surface conditions that were not fully represented by a single dissolved oxygen measurement taken at the observation location. Below this threshold, jump frequency

decreased sharply with increasing wind speed, whereas above this threshold, jump counts remained comparatively low and the relationship weakened. This pattern suggests that very calm conditions may be especially important for triggering increased jumping activity. In shallow estuaries, wind can increase surface mixing and re-aeration, potentially reducing the spatial patchiness or severity of low-oxygen conditions (Turner et al. 1987; Liu et al. 2022; Sarasota County Water Atlas 2025). Therefore, low wind speed may increase the likelihood that mullet encounter localized oxygen limitation, particularly near the surface or in areas where biological oxygen demand is high.

The wind-speed breakpoint should be interpreted cautiously. Only a small number of observations occurred at or below approximately 6 mph, and additional data collected during calm periods could shift the estimated threshold or reveal a more continuous relationship. In addition, dissolved oxygen rarely fell below 4 mg/L during this study, and hypoxia, typically defined as dissolved oxygen concentrations below approximately 2 mg/L, was not observed (Salazar et al. 2026). As a result, these data do not represent a direct test of mullet behavior under extreme hypoxic stress. Instead, the results suggest that mullet jumping increases across the lower range of oxygen conditions observed in this estuary. This may indicate that jumping responds not only to severe hypoxia, but also to more moderate reductions in oxygen availability, especially when combined with calm conditions that limit wind-driven mixing.

The physiological mechanism underlying this pattern is plausible. Mullet possess a specialized pharyngobranchial structure capable of holding gas, and Hoese (1985) argued that the height and orientation of mullet jumps are sufficient to ventilate this cavity with atmospheric air. Earlier work also showed that striped mullet respond physiologically to hypoxic conditions, supporting the idea that oxygen availability can influence behavior in this species (Cech and Wohlschlag 1973). This behavior may be particularly useful when oxygen demand increases during rapid swimming, predator avoidance, migration, or other energetically demanding activities (Peterson 1976; Hoese 1985). Under these conditions, aquatic oxygen uptake through the gills may not fully meet metabolic demand, especially in warm, shallow, eutrophic waters. The negative association between dissolved oxygen and jump frequency observed here is therefore consistent with the interpretation of jumping as a respiratory behavior rather than only an escape or disturbance response.

It is important to note that mullet jumping is unlikely to have a single function. Predator escape remains an important alternative explanation. Mullet have long been described as leaping in response to pursuit or disturbance, and predator-associated jumps may involve multiple fish jumping from the same area or repeated jumps by an individual fish attempting to evade a predator (Holder 1903; Olla and Samet 1974; Whitfield 2016). Predators of mullet, including piscivorous fishes, sharks, dolphins, and birds, are common in estuarine habitats (Thomson 1966; Blaber 1987; Barros and Cockcroft 1991; Barros et al. 2004; Whitfield and Blaber 1979; Jackson 1984; Dias et al. 2012). In this study, predators were observed during 27 observation periods. Importantly, predator data were qualitative and likely incomplete because many aquatic predators could not be reliably detected from shore. Future studies could improve on this limitation by using drone footage, underwater cameras, or paired surface and subsurface observations to separate predator-driven jumps from jumps that appear unrelated to pursuit.

Parasite removal is another possible function of jumping. Breaching and jumping behaviors in other aquatic animals, including dolphins, rays, and sharks, have been associated with removal of external parasites or remoras (Ritter 2002; Weihs et al. 2007; Klimley et al. 2025; Nolan et al. 2026). Gulf sturgeons may jump as a form of acoustic communication that helps maintain group cohesion in holding areas (Sulak et al. 2002). Similar functions have not been ruled out for mullet. However, parasite load was not measured in this study, and observations from shore could not distinguish jumps associated with irritation or parasite removal from jumps associated with oxygen acquisition. Laboratory or mesocosm studies that manipulate parasite load, dissolved oxygen, and predator cues independently would be useful for testing these competing explanations. Such studies could also evaluate whether individual state, school size, or social isolation affects jumping frequency, since isolated mullet may show higher ventilation frequencies under hypoxic conditions (Lefrançois et al. 2009).

A further contribution of this study is the simultaneous measurement of conspicuous behavior and environmental conditions in wild fish. Laboratory experiments are essential for isolating respiratory mechanisms, but they cannot fully reproduce the interacting variation in wind, dissolved oxygen, temperature, salinity, tide, predator activity, and human disturbance experienced by mullet in an estuary. The field design therefore allowed us to determine whether oxygen-linked jumping patterns remain detectable amid natural environmental variability. Its corresponding limitation is that the individual contributions of these covarying factors cannot be interpreted as experimentally causal.

The association between low dissolved oxygen and increased jumping also has implications for understanding how estuarine fishes respond to changing coastal environments. Shallow subtropical estuaries are vulnerable to warming, eutrophication, harmful algal blooms, and short-term oxygen fluctuations (Breitburg et al. 2018; Sarasota County Water Atlas 2025). Harmful algal blooms can alter dissolved oxygen dynamics through daytime photosynthetic oxygen production, nighttime respiration, and bloom decay, and high phytoplankton biomass has been associated with reduced mullet abundance or avoidance behavior in other estuarine systems (Bornman et al. 2023). Some bloom-forming species can also impair gill function directly through ichthyotoxic effects, further limiting a fish's ability to extract oxygen from the water (Bornman et al. 2022). Although mullet may possess behavioral and physiological mechanisms for coping with low oxygen, these adaptations do not make them immune to poor water-quality conditions; mass-mortality events affecting mullet have been linked to environmental contamination and degraded estuarine conditions (Wang et al. 2011). Even when average dissolved oxygen values appear moderate, fish may encounter short-term or spatially localized reductions in oxygen that are not captured by a single-point measurement. Mullet jumping may therefore provide a conspicuous behavioral signal of environmental conditions associated with oxygen limitation, although its value as an indicator requires further validation.

At the same time, mullet jumps should not yet be treated as a validated indicator of hypoxia. This study supports the idea that jumping frequency is associated with lower dissolved oxygen and lower wind speed, but additional validation is needed before the behavior can be used confidently in monitoring programs. Future work should include observations during early morning periods, nighttime transitions,

summer high-temperature conditions, and documented hypoxic events. Expanding the study across multiple sites, seasons, and habitat types would also help determine whether the wind-speed threshold observed here is specific to Big Sarasota Bay or reflects a broader behavioral pattern in mullet. Long-term dissolved oxygen records suggest that oxygen conditions in Sarasota Bay may appear relatively stable at broad temporal scales (Fig. 4), but short-term variation caused by tides, wind, temperature, algal production, respiration, and bloom decay may still be biologically meaningful to fish (Sarasota County Water Atlas 2025).

This behavioral response may become increasingly important as coastal waters continue to warm. Global oxygen concentrations in marine and coastal waters are declining, in part because warmer water holds less dissolved oxygen and because warming can strengthen stratification and weaken circulation (Breitburg et al. 2018). At the same time, ectothermic fishes generally experience increased metabolic demand at higher temperatures, which can raise oxygen requirements and reduce tolerance to low-oxygen conditions (Farrell 2002; Marium et al. 2023). Warming estuaries may provide less dissolved oxygen while fish require more oxygen to maintain basic metabolic function. For mullet living in shallow, warm, eutrophic estuaries, the conditions under which aerial oxygen uptake could be advantageous may become more frequent.

Overall, our findings extend the internal diving bell hypothesis from a relationship between dissolved oxygen and jumping to a broader ecological framework involving wind-driven mixing. Wind speed and dissolved oxygen explained independent variation in jump counts, and exploratory analysis identified a candidate transition in the wind-jump relationship near 6.3 mph. These results suggest that calm conditions may help determine when moderate reductions in oxygen availability elicit increased jumping, even in the absence of severe hypoxia. Mullet jumping should not yet be treated as a validated indicator of oxygen stress, but it provides a conspicuous behavior through which the responses of estuarine fishes to short-term environmental variation can be investigated.

Declarations

Funding: No funding was received for this project.

Competing interests: The authors do not have any competing interests to declare.

Author contributions: Lydia Ubry conceived the project and led data collection and the first manuscript draft, Samantha Levell assisted with study design and implementation, primarily conducted the data analysis, and primarily contributed to manuscript editing.

Data availability: Data available upon reasonable request.

Ethics approval: Not applicable. This study involved non-invasive observations of free-ranging fish; no animals were captured, handled, or manipulated.

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Figures



Figure 1

a Study location on Big Sarasota Bay (Sands 2026a). **b** Close-up of the observation area; the yellow outline indicates the approximately 53,016 m² observation area (Sands 2026b). Maps created using ArcGIS Online. World Imagery sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

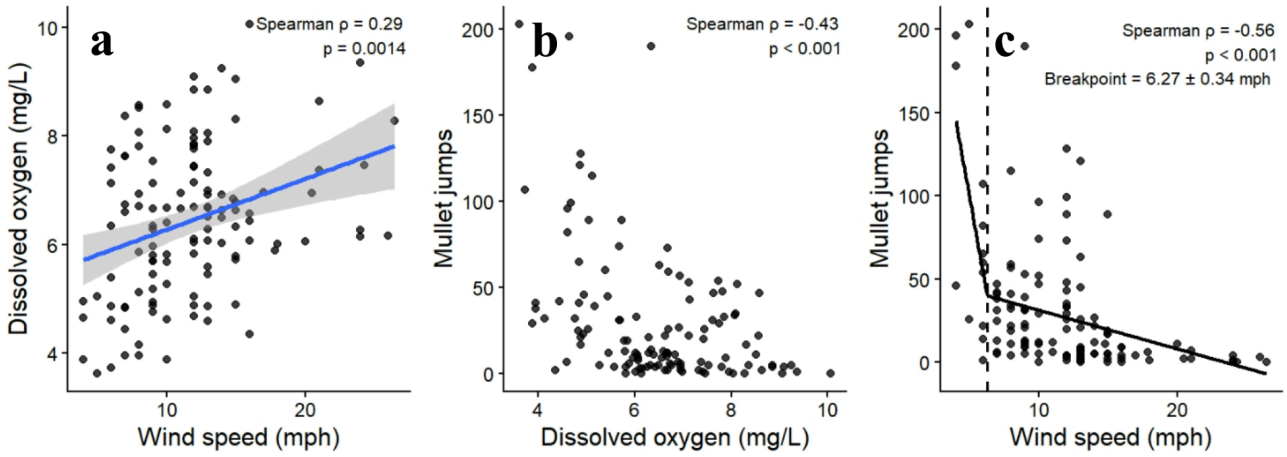


Figure 2

Relationships among wind speed, dissolved oxygen, and mullet jumping behavior. Points represent individual one-hour observation periods. Spearman correlations are shown for pairwise associations. Wind speed was positively associated with dissolved oxygen (**a**), and both lower dissolved oxygen (**b**) and lower wind speed (**c**) were associated with higher jump counts. Panel c shows an exploratory segmented regression identifying a candidate wind-speed breakpoint at 6.27 ± 0.34 mph. Formal count-based analyses used negative binomial regression because jump counts were strongly overdispersed.

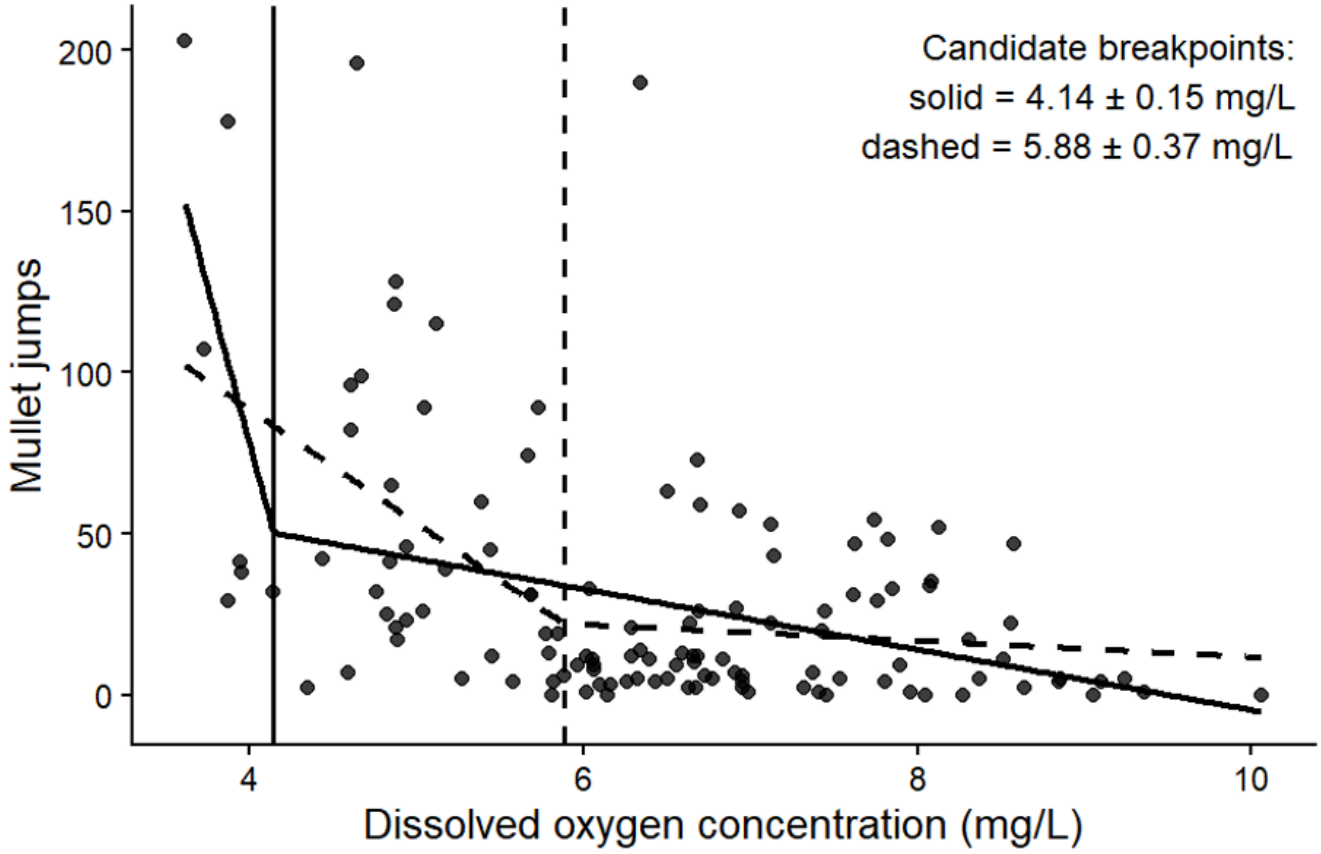


Figure 3

Exploratory segmented regression models showing candidate dissolved oxygen breakpoints in the relationship between dissolved oxygen concentration and mullet jump counts. The solid line indicates a candidate breakpoint at 4.14 ± 0.15 mg/L, and the dashed line indicates a second candidate breakpoint at 5.88 ± 0.37 mg/L. These thresholds are presented as exploratory visualizations rather than primary inferential models.

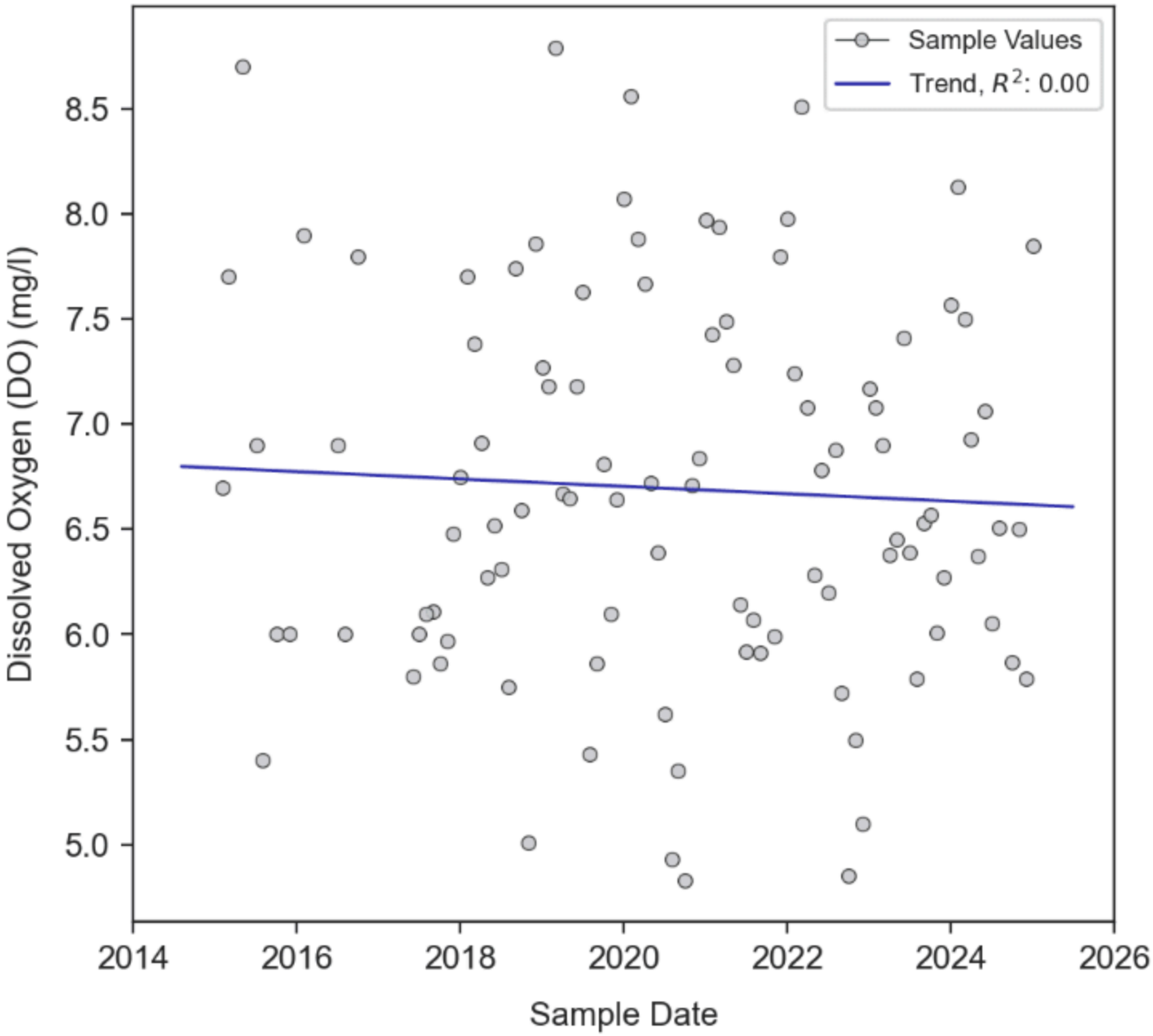


Figure 4

Ten-year dissolved oxygen record for the study site, with a fitted linear regression line. Data are from Sarasota County Water Atlas monitoring station SARASOTA BAY E US-4, 2015–2025.