



Assessing the potential for red tide (*Karenia brevis*) algal bloom impacts on Atlantic tarpon (*Megalops atlanticus*) along the southwestern coast of Florida

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Abstract This study investigated the potential effects of red tide events (blooms of the toxin-producing dinoflagellate, *Karenia brevis*) on Atlantic tarpon (*Megalops atlanticus*), a long-lived migratory game fish, along the southwestern coast of Florida. In this region, red tides have long been associated with mass mortality events of marine organisms and other deleterious effects on coastal ecosystems. To estimate the impacts of red tide on tarpon and the recreational fishery they support, we used a mixed-methods approach that combined multiple data sources including fish

kill data, local ecological knowledge (LEK) interviews, angler catch logs, and acoustic telemetry. Our results suggested tarpon are somewhat tolerant to red tide blooms; but, when blooms did overlap with tarpon peak abundance and became dense and large, tarpon were reported to leave the affected area, suffered mortality, or both. Furthermore, in recent years, LEK data suggested an increase in the persistence and overlap of red tide blooms with peak tarpon abundance that coincided with their spawning season. In contrast, using acoustic telemetry data, we did not detect any pattern in tarpon presence during red tide events, further suggesting that tarpon may be adaptive to the effects of red tide. Finally, to evaluate

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monitoring methods, data quality, and collection, we used a strengths, weaknesses, opportunities, and threats analysis and found all could be improved through increased engagement with LEK and collaboration among researchers. Ultimately, combining multiple data sources helped elucidate how red tide exposure influences tarpon and the recreational fishery that targets them.

Keywords Brevetoxins · Gulf of Mexico · Harmful algal blooms · Local ecological knowledge · Recreational fishery

Introduction

The Atlantic tarpon (*Megalops atlanticus*) is a migratory, long-lived, and late maturing fish that is found in coastal waters throughout the Atlantic Ocean, Caribbean Sea, and Gulf of Mexico (McMillen-Jackson et al. 2005; Luo et al. 2020). Southwest Florida (USA) is of particular importance to Atlantic tarpon, hereafter referred to as tarpon, across all life history stages. For juveniles, the surrounding estuarine habitats, composed of mangrove-lined tidal creeks, salt marshes, and coastal ponds, serve as critical developmental habitat (Wilson et al. 2019). Thousands of large mature tarpon migrate annually to Charlotte Harbor and Tampa Bay in the late spring and early summer (April–July) prior to moving offshore to spawn (Crabtree et al. 1997; Luo et al. 2020).

This region also supports an extensive catch-and-release recreational fishery for juveniles and adults that contributes millions of dollars to local

economies. For example, in Charlotte Harbor, where the first hook and line captured tarpon was recorded in 1885 (White and Brennen 2010), the fishery was estimated to contribute \$110 million annually to the local economy in 2009 and 2010, which is the only economic data of this kind available (Fedler 2011). Although widely sought after as a catch-and-release only gamefish by residents and tourists (Camp et al. 2018), tarpon are currently listed as Vulnerable by the International Union for Conservation of Nature (IUCN) with a likely decreasing population trend (Adams et al. 2019a). Their Vulnerable status is largely attributed to degraded juvenile habitat, depredation, commercial/subsistence harvest in some areas (e.g., Mexico, Cuba, Brazil), angling-related mortality, and water quality (Adams et al. 2014, 2019a; Wilson et al. 2019; Luo et al. 2020).

Red tides, naturally occurring blooms of the toxic dinoflagellate *Karenia brevis*, have long impacted many species of marine life along Florida's Gulf of Mexico coast, with annual reports from the eastern Gulf of Mexico dating back to 1844 (Ingersoll 1881; Steidinger 2009). While *K. brevis* can be found at background levels (≤ 1000 cells/L) year-round in the Gulf of Mexico, harmful blooms and fish mortality tend to occur when concentrations reach 100,000 cells/L (Quick and Henderson 1974; Landsberg and Steidinger 1998). At lethal concentrations, *K. brevis* kills a range of fish species across life history stages along with higher vertebrates and invertebrates (Steidinger et al. 1973; Riley et al. 1989; Warlen et al. 1998; Landsberg 2002; Flewelling et al. 2005, 2010; Fire et al. 2008; Landsberg et al. 2009; Gravinese et al. 2020).

Toxicity of red tide blooms can vary with amount and concentration of neurotoxic ichthyotoxin (brevetoxins) in the water (Landsberg et al. 2009). Lysis of *K. brevis* cells releases brevetoxins that when absorbed across gill membranes (Abbot et al. 1975; Baden et al. 1989) can cause loss of muscle coordination, convulsions, paralysis, and respiratory failure resulting in death (Baden et al. 1989; Landsberg 2002). Fish are also killed when toxic cells are consumed, either directly through direct exposure or ingestion of water or vectored prey, during a red tide bloom (Tester et al. 2000; Landsberg 2002; Naar et al. 2007), after one has dissipated (Flewelling et al. 2005; Landsberg et al. 2009), or both. Indeed, mortality events related to red tide can sometimes be lagged

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by days to months (Gannon et al. 2009; Landsberg et al. 2009; McIntosh and Morse 2015). Furthermore, mortalities can also occur in hypoxic conditions stemming from decaying *K. brevis* cells and other dead organisms (Dupont et al. 2010; Gravinese et al. 2020; Milbrandt et al. 2021). Ultimately, species-specific susceptibility to both lethal and sublethal *K. brevis* effects is largely dependent on the intersection of their innate tolerance, life history stage, dispersal ability, and behavioral ecology/environmental conditions, as well as bloom toxicity dynamics and distribution (Walters et al. 2013).

Except for 2011, the southwest coast of Florida has experienced red tide blooms annually since 2000 (NOAA Harmful Algae Blooms Observing System n.d.) and recreational anglers are now highlighting red tide as a major conservation concern for tarpon. Given the typical movement patterns of tarpon (Griffin et al. 2018; Friess et al. 2021), their exposure to red tides may be occurring often. For this study, we used a parallel mixed-methods approach (Kinnebrew et al. 2021) to better understand how the species reacts to red tide blooms and how red tides may affect the fishery. Specifically, these potential impacts were examined across multiple spatiotemporal scales through the use of reported fish kill events, interviews with expert fishing guides (i.e., local ecological knowledge, LEK), recreational catch logs, and acoustic telemetry. Lastly, we applied a strengths, weaknesses, opportunities, and threats (SWOT) analysis (Houben et al. 1999) to assess monitoring of red tide in relation to this species and other applicable marine species.

Methods

Red tide sampling and estimates

The study area encompassed the adjacent coastal areas of Pinellas, Hillsborough, Manatee, Sarasota, Charlotte, and Lee counties, Florida. Red tide monitoring data (temporally and spatially), as indicated by *K. brevis* cell counts per liter (see Walters et al. 2013 for methodology details), were obtained from the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute (FWRI) (<https://myfwc.com/research/redtide/monitoring/database/>). As red tide became detected and associated with

individual events, due to its heterogeneous nature, sampling frequency and density increased to monitor its intensity and geographic range across time (<https://myfwc.com/media/13075/executive-summary-for-database.pdf>).

To obtain monthly averaged cells/L, we first aggregated samples by month, and averaged the cell count per 5 km² area on a cartographic grid. We used the autoKrig function of the automap package (Hiemstra 2013) to interpolate (ordinary kriging) cell counts across the area of interest (see below for each analysis) for each month. *Karenia brevis* cell counts are commonly categorized by a standard scale: present/background (≤ 1000 cells/L), very low (> 1000 – $10,000$ cells/L), low ($> 10,000$ – $100,000$ cells/L), medium ($> 100,000$ – $1,000,000$ cells/L), or high ($> 1,000,000$ cells/L) (<https://myfwc.com/research/redtide/statewide/>). To ensure *K. brevis* interpolation accuracy, interpolations were visually compared to the monthly reported *K. brevis* sample concentrations (cells/L) archived on the FWRI website, <https://www.flickr.com/photos/myfwc/sets/72157635398013168/>.

For red tide analyses involving statistical modeling (i.e., recreational catch logs and acoustic telemetry), we first interpolated log-transformed *K. brevis* values for the defined geographic area of focus (again, see below for each analysis), and then categorized each month as having a red tide event that was either “not elevated” or “elevated” using a threshold of when fish kills become probable, i.e., log-transformed counts $> 100,000$ cells/L. R (v. 3.6.2; R Core Team 2019) and RStudio (v. 1.4.953) were used to conduct all statistical analyses.

Mortality reporting

Data on fish kills involving tarpon were obtained from the State of Florida's FWRI Marine Fish Kill Hotline database. The relative frequency and assigned causes of fish kills involving tarpon reported from 02 February 1977 through 12 August 2021 were summarized at three geographic levels, (1) state, (2) southwestern region (<https://myfwc.com/fishing/freshwater/regulations/regions/>), and (3) county (Pinellas, Hillsborough, Manatee, Sarasota, Charlotte, and Lee counties). Tarpon fish kills were compared to monthly *K. brevis* counts and their approximate locations were plotted spatially

for periods of high mortality and for months with available *K. brevis* data. While fish kill data collected via reporting provided the best available data on tarpon fish kills, it should be noted that multiple factors may affect accuracy, such as willingness and ability of observer to report, location of fish kill (high density vs low density human population, shoreline/mangrove vs seawall), elapsed time from fish kill to the time reported, and by active (swimming prior to death) and passive (currents, tides, wind) transport of affected fish.

Expert interviews

A semi-structured interview approach (McIntosh and Morse 2015) was conducted by one of the authors (AJA) to obtain the perspectives of professional recreational fishing guides and expert recreational anglers on the effect of red tide on tarpon. The interviews were based on a questionnaire of 20 predetermined primary questions that were intentionally open-ended to generate discussion (Supplemental Table 1). Interviews were structured in three sections: (1) foundational questions to determine duration of guiding and/or angling experience, fishing area, and fishing methods; (2) questions to establish the general temporal and spatial patterns of fishing effort for tarpon; and (3) questions to gauge interviewee perspectives on the relationships between red tide, tarpon, and their fishing effort.

We identified and targeted experienced interviewees through social networking, as well as through one of the authors (AJA) who had preexisting familiarity with the regional private and for-hire angling communities, which was gained through extensive professional research and outreach activities and personal participation in the fishery. We also used the “snowball technique” by contacting known regional experts to request assistance identifying and approaching other experienced anglers within the fishery, and during interviews, some fishing guides recommended that we contact other specific experts in their social networks (Perez-Cobb et al. 2014). Interviewees were contacted by phone, text, or email and all that responded agreed to be interviewed. The interviewer took notes during interviews and all interviews were recorded (audio) with the permission of the interviewee for later reference.

Catch data

To determine if tarpon catch counts were influenced by red tide status (i.e., not elevated vs. elevated), we examined tarpon catch records of members of the Cape Coral Tarpon Hunters Club (<https://www.capecoraltarponhunters.com>) from March through September 2011–2020, which is the typical fishing season for tarpon in the region. While it was not possible to incorporate angling effort, Cape Coral Tarpon Hunters Club was selected as a source for catch data due to their historical recording of tarpon catches, as well as being in an area (southern Charlotte Harbor) that has been known to be impacted by red tide blooms. The designated fishing area for the club was from Captiva Pass (26.613 N, −82.223 W) to Gordon’s Pass (26.090 N, −81.802 W) with no boundary to the west. For the area where the majority of tarpon were captured, between Captiva Pass to Lovers Key State Park (26.387 N, −81.879 W), monthly *K. brevis* concentrations across the area were interpolated, and then averaged, and subsequently, months were categorized as having not elevated (log-transformed counts $\leq 100,000$ cells/L) or elevated (log-transformed counts $> 100,000$ cells/L) red tide events.

A generalized linear mixed-effects model (GLMM) with a negative binomial distribution using the glmmTMB package (Magnusson et al. 2017) was used to determine if tarpon catches were impacted by red tide blooms. The full model consisted of monthly catch counts as the dependent variable, red tide concentrations and month as categorical independent variables, and year as a random effect. A second modified model was developed with red tide concentrations lagged by 1 month since the biological effects of blooms may occur or persist days to months after the initial bloom (Gannon et al. 2009; Landsberg et al. 2009; McIntosh and Morse 2015). The packages DHARMA (Hartig 2017), performance (Lüdtke et al. 2021), and SjPlot (Lüdtke 2018) were then used for selecting between the two models, and for validation and interpretation, e.g., normality, homogeneity of variance, zero inflation, autocorrelation, and marginal effects.

Acoustic telemetry data

To examine if tarpon presence increased or decreased as a function of monthly red tide events and their concentrations (not elevated vs. elevated), we first

summarized daily presences across each month from the region. Specifically, data were collected from 13 fixed-station acoustic receiver arrays from the study area shared via the Integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTAG) regional tracking network (Friess et al. 2021). All detection data were derived from an ongoing tarpon acoustic telemetry tracking project (see Griffin et al. 2018, 2022). Due to data limitations, only detection data from mature individuals (≥ 128.5 cm fork length, Crabtree et al. 1997) were used since movement patterns differ between life stages (Kurth et al. 2019).

Although extensive receiver coverage existed across the study area (Supplemental Fig. 1), irregular deployments and retrievals of arrays, as well as a temporal mismatch between typical red tide months and peak tarpon abundance across receiver aggregates, prevented quantitative comparisons across years. Thus, the final dataset included only receivers deployed prior to July 2018 or retrieved after July 2019 and tarpon presence was examined from January 2018 to April 2021 in two areas that had reliable detection coverage for analyses: the Tampa Bay nearshore area and the Charlotte Harbor inshore estuarine area (Fig. 1). Subsequently, *K. brevis* concentrations were interpolated across these two areas to identify when red tide blooms occurred (Fig. 1). Although inshore Charlotte Harbor receivers were consistent in detection coverage, due to *K. brevis* data sampling limitations, *K. brevis* data were only interpolated in the nearshore region. In addition, this nearshore area serves as a proxy for red tide events since elevated concentrations of *K. brevis* typically occur offshore prior to moving into inshore areas. Therefore, if tarpon significantly modified their space use during or following red tide blooms, we expected to observe absences in nearshore regions (e.g., Tampa Bay nearshore) and/or an increased presence in inshore areas (e.g., Charlotte Harbor inshore) where *K. brevis* concentrations are expected to be lower since salinities of < 24 ppt act as a physiological barrier (Vargo 2009).

Detection days (DDs) per month were defined as a transmitter being detected within the given area on a given calendar day and were summed by area and calendar month to give monthly area-specific detection days. When a transmitter was detected more than once during a day, its DD count remained at one, and when multiple transmitters were detected on the same

day in the focal area, their DDs were summed. DDs per month at the regional level were then used as the dependent variables in GLMs using a negative binomial distribution.

The independent variables of the full candidate models included monthly red tide concentrations (categorical), defined using the threshold as not elevated (log-transformed $\leq 100,000$ cells/L) or elevated (log-transformed $> 100,000$ cells/L), and general expected tarpon abundance for each region (categorical), defined as higher (March–November for Tampa Bay, March–October for Charlotte Harbor) and lower (December–February for Tampa Bay and November–February for Charlotte Harbor). Expected abundance was included as a fixed effect to account for the many zero DDs in the winter months when tarpon are largely absent, as supported by exploratory analysis, LEK, and results from Friess et al. (2021). Each area's respective monthly mean receiver count (log-transformed) was included as an offset to account for variable receiver deployments and detection coverage. In addition, an offset of available tags (log-transformed) was included in each full model since tarpon tagging was variable across the study period. The number of available transmitters was based on tagging date. Within the available transmitters offset, we also incorporated approximate monthly estimates of survival rates from natural mortality estimates (Hewitt and Hoenig 2005) by using the Eq. 4.22/maximum age, defined as 70 years (Ault et al. 2008). Each model for each area underwent validation and interpretation procedures as described in the above section. Subsequently, all modeling processes were implemented again but using the independent variable, categorical monthly red tide concentrations lagged by 1 month.

SWOT analysis

To better understand and inform future monitoring efforts of red tide and its potential impacts on tarpon and similar species, we conducted three separate SWOT analyses on: (1) monitoring of fish kills, (2) engaging with guides and anglers via interviews and catch data as sources of LEK, and (3) using acoustic telemetry to track movements in potential response to red tide events. In this case, by means of qualitative user inputs (i.e., the collective group of co-authors in this study), SWOT analysis broadly categorizes

strengths and weaknesses as intrinsic factors, and opportunities and threats as extrinsic factors (Houben et al. 1999). Strengths are associated with inherently positive qualities of the focal entity, while weaknesses are the intrinsic risks of losing those strengths. Conversely, opportunities are the ability and potential for continued sustainability and improvement of the focal entity, while threats are the risk that may hinder the entities success due to external factors. Although SWOT is commonly used for strategic planning purposes in business and industry (Learned et al. 1969; Fleisher and Bensoussan 2003), it has been applied in the field of ecology to assess sustainable tourism (Navarro-Martínez et al. 2020), animal reintroductions (Trujillo 2005; White et al. 2015), and conduct environmental impact assessments (Paliwal 2006; Geneletti et al. 2007). As such, given the mixed-methods approach of our study, we thought it prudent to examine each method through this lens, especially as they related to future monitoring of the relationship between red tide incidence and tarpon space use and related mortality events.

Results

Red tide estimates

Monthly *K. brevis* interpolations were similar to those from FWRI sampling results, as reported by <https://www.flickr.com/photos/myfwc/sets/72157635398013168/> (e.g., Fig. 3).

Fish kill events

Of the 356 reported fish kill events between February 1977 and August 2021 involving tarpon (independent of size), 29% ($n=103$) were attributed to red tide, and ranked second only to “unknown reasons” (37%, $n=132$) (Supplemental Table 2). Southwest Florida waters accounted for the greatest proportion of reported red tide associated tarpon mortality events (81%, $n=83$, Table 1). By county, the greatest number of events were reported from Pinellas ($n=23$) and Lee ($n=23$), followed by Charlotte ($n=16$) and Sarasota ($n=12$) (Fig. 2a). The two largest periods of reported red tide tarpon mortality events occurred between Sarasota and Lee counties from June to September 2018 and between Pinellas and Charlotte from

Table 1 Red tide associated tarpon mortality events across Florida regions from 02 February 1977 to 12 August 2021. The number of events was summed at the regional level and their proportions were derived

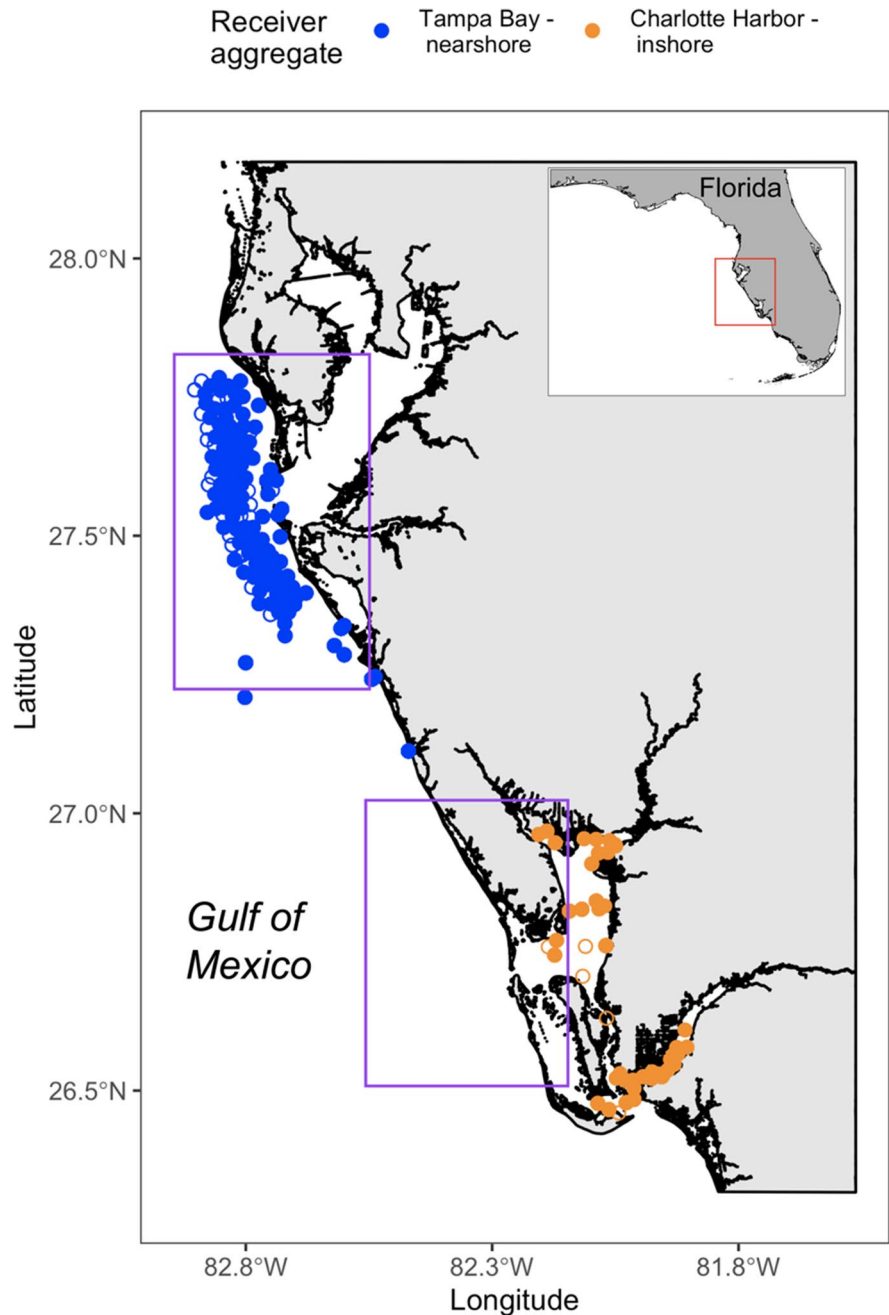
Region	Red tide tarpon fish kill event count	Proportion
SW	83	0.81
S	11	0.11
NW	4	0.04
NE	3	0.03
NC	2	0.02

April to August 2021 (Fig. 2b). It should be noted that at the time of analysis (August 2021), red tide was still present and, thus, more tarpon kills may have been subsequently reported in 2021. According to the interpolated *K. brevis* counts and reports from summer 2018, approximate locations of tarpon mortality events were largely located along the barrier islands and were within medium to higher concentrations of *K. brevis* for its given or prior month (Fig. 3).

Expert interviews

Results from expert interviews are presented in summary form so that responses are not attributed to any individual (Supplemental Table 1). Twelve professional fishing guides and one expert recreational angler were interviewed during July 2021. Interviews lasted between 30 and 45 min. Twelve interviews were conducted by phone, and one interview was conducted in person. Six interviewees primarily fished near Tampa Bay area and seven primarily fished near Charlotte Harbor. The experience of fishing guides focusing on tarpon ranged from 9 to 50 years (26.2 ± 13.5 SD). Although all experts focused on tarpon for at least part of the year, the months when they were targeted varied. Peak tarpon season was generally April–June, with four guides only fishing for the species in these peak months, while two others targeted tarpon to some extent throughout the year. Many experts reported that they target tarpon outside of peak months when tarpon abundance, weather, and client preference allow. The mean number of days tarpon were targeted each year ranged from 50 to 200 (83.1 ± 38.9 SD). The primary fishing methods were using bait via conventional rod and reel tackle ($n=8$) and fly

Fig. 1 Study area (red box) and receiver locations used for analysis (blue and orange circles) involving daily detections across Tampa Bay and Charlotte Harbor regions, Florida. Filled circles indicate where tarpon (*Megalops atlanticus*) were detected and open circles indicate locations without detections between January 2018 and April 2021. Purple boxes indicate where monthly red tide (*Karenia brevis*) estimates were interpolated. See Supplemental Fig. 1 for location of additional receivers not used for analysis



fishing ($n=5$). Although to a great extent, the location of fishing for tarpon changed due to weather, boating and fishing traffic, tarpon movements, and red tide occurrence, some guides focused on the Gulf of Mexico, some on passes (inlets) between the estuaries and Gulf of Mexico, and some on areas within the estuary. Others distributed their effort among the three zones relatively equally.

All respondents used personal observations and communication with other guides to determine if red tide was present and assess the spatial extent of blooms. Red tide intensity was determined by guide experience and on-water observations. For example, low-intensity blooms were present when guides claimed they could smell or “taste” red tide in the air, moderate when baitfish in the livewell would die,

and high when widespread fish kills occurred. Eleven guides also reported that they obtained information from the weekly red tide report email from FWRI which they felt was a useful guide, but that given the dynamic nature of red tide blooms they also relied on personal observations.

All respondents reported changes in tarpon abundance and behavior when red tide was present, with tarpon actively moving to avoid dense red tide concentrations. The distance of movement appeared to depend in part on red tide intensity and spatial extent of occurrence. Ten respondents reported that tarpon movements were usually local, in that they did not leave the guide's normal fishing range (~25–35 km). However, when red tide was believed to be intense enough to initiate tarpon movements, it was noted that they would move from red tide impacted areas to areas of little to no red tide, often <20 km away. During red tide blooms, respondents changed fishing patterns by actively moving to find areas to which tarpon had relocated. Alternatively, some would target other species such as snook (*Centropomus undecimalis*) and redfish (*Sciaenops ocellatus*), residing in areas not affected by red tide (e.g., low salinity areas within the estuary).

Respondents reported that once tarpon found “clean” water, they often remained in the “safe” area for extended periods or until the spatial pattern of red tide occurrence changed. In these locations, fishing pressure could be very high since tarpon seemed to be more concentrated. Once red tide events intensified and became widespread, the consensus was that tarpon may completely evacuate the area and move long distances offshore or alongshore (e.g., from Charlotte Harbor to Tampa Bay) to escape red tide. However, it was noted that tarpon were more likely to remain longer in intense or widespread red tide conditions if respondents believed they had not yet spawned (early season; April–June) compared to when respondents believed they had already spawned (late season; July–August). Finally, it was occasionally reported that tarpon moved into low salinity areas of estuaries during red tide events, but this was reported to be relatively uncommon compared to the previously described movements.

A high proportion of respondents ($n=10$) reported that tarpon appeared to be tolerant of low to perhaps moderate levels of red tide as reflected by tarpon remaining in such affected areas. However, tarpon

appeared to become less catchable as red tide intensity increased. Responses to questions about tarpon catchability and endurance (e.g., shorter fight times) when hooked during red tide blooms varied from no change to a decline in both. This appeared to be related to the intensity and spatial configuration of blooms. As described above, since tarpon were believed to select for locations where *K. brevis* cell counts were relatively lower, catchability and endurance remained unchanged. However, respondents reported that when red tide intensity was moderate or higher and tarpon were still present, catchability was believed to decline.

Sightings of dead tarpon by respondents during red tide blooms were rare, and when dead tarpon did occur, they were few in number. The exception to this was the red tide event in 2018, when numerous sightings of dead tarpon were documented by interviewees during the tarpon fishing season. Respondents attributed the apparent tolerance of tarpon to red tide, in part, to observations that they sometimes actively fed on other smaller fish affected by red tide, e.g., pinfish (*Lagodon rhomboides*) and pigfish (*Orthopristis chrysoptera*). Ten respondents (77%) reported that tarpon seemed to take advantage of red tide as a feeding opportunity. Although observed by nine respondents, it was reported as an occasional event and not during every bloom.

All respondents reported that red tide is more frequent now than in the past years, while seven reported that red tide has become more intense, and six reported that red tides are more widespread when blooms occur. Six respondents reported that in the past, when red tide blooms were generally shorter-lived and patchier, making it relatively easy to fish around and causing minor impacts on tarpon fishing. Ten respondents reported that red tide did not often occur during peak tarpon season (April–June) in the past but would sometimes occur during the late-tarpon season months (e.g., October). Thus, the occurrence of red tide during tarpon season was reported as a relatively new phenomenon. Furthermore, most respondents ($n=9$) were able to remember past seasons when red tide was particularly bad, but other than the 2018 event, most were not able to identify the year. All respondents that were able to remember the influence of red tide during the 2018 season primarily fished in the Charlotte Harbor region and stated that overall tarpon behavior was different than

in previous years. In general, during the 2018 red tide event, tarpon remained in the local fishing area in the early season, but as the red tide became more intense in mid- to late-season, most tarpon left the area.

Catch data

As recorded by the Cape Coral Tarpon Hunters Club across 10 seasons (2011–2020), there was an average of $257.40 (\pm 99.4)$ catches per season with April having the greatest number caught (62.0 ± 31.3), followed by July (43.2 ± 35.4), September (39.3 ± 22.6), August (36.6 ± 20.4), June (32.1 ± 21.0), March (25.7 ± 17.3), and May (25.4 ± 9.6) (Fig. 4).

Although only 2 months (August and September 2018) were identified as having an elevated red tide event, both models found a significant effect of *K. brevis* concentrations and month on catch counts; however, the model that had lagged concentrations performed best with an AIC of 622.8 compared to 625.4 (Supplemental Table 3). For the unlagged and lagged models, respectively, when red tide blooms were not elevated, catch counts were 8.1 (GLMM; CI 2.6–25.82; $p < 0.001$) and 10.34 (CI 3.2–33.2; $p < 0.001$) times as likely compared to when red tide blooms were elevated (Supplemental Table 3). Marginal effect plots highlighted that catch rates were expected to be highest in April for both models and confirmed that as red tide blooms were elevated, tarpon catches were expected to decrease (Fig. 5).

Acoustic telemetry

Detection data from January 2018 to April 2021 were collected from a total of 35 mature tarpon (149.5 ± 14.0 SD, fork length, cm) tagged between April 2017 and August 2020. Available tags able to be detected across each month, which accounted for survival estimates, ranged from 8.6 to 43.8 tags (31.7 ± 11.5). For analyses focused on Tampa Bay and Charlotte Harbor portions of the study area, respectively, DD ranged from 0 to 32 (5.1 ± 7.7) and from 0 to 18 (2.7 ± 4.0), and average receiver count ranged from 24.1 to 39.0 (34.0 ± 3.3) and from 47.0 to 59.0 (57.3 ± 3.3).

While tarpon abundance was higher across the spring and summer months, there were few red tide events during this period and we found no significant

effect of red tide bloom concentrations, i.e., not elevated or elevated, on tarpon DD for any model (unlagged and lagged by one month) (Supplemental Table 4).

SWOT analysis

SWOT analyses demonstrated the potential benefits of examining fish kills (e.g., red tide lethality and species vulnerability), sourcing LEK (e.g., catch logs and users with valuable knowledge of the system), and using acoustic telemetry to potentially monitor animal movements (e.g., ability to examine fine-scale movements) (Table 2). The most important opportunities in each category included increased engagement and outreach to gather information on fish kills and from LEK, as well as embracing collaborative efforts among researchers when using acoustic telemetry to evaluate red tide effects. Specifically, disjointed detection coverage by arrays meant for other purposes limited our ability to detect any potential red tide effects on tarpon movements. Furthermore, because of opportunistic and irregular sampling of *K. brevis*, findings that were derived from their interpolated concentrations should be interpreted cautiously since sampling methodologies were biased. Considering the spatiotemporal complexity of *K. brevis* blooms, more robust sampling methods (e.g., increased sampling efforts and or use of satellite imagery) in the future may help to resolve methodological mismatches for future studies wishing to evaluate finer-scale red tide impacts (e.g., corresponding fish mortality events or space use with *K. brevis* concentrations). In all categories, the quality of data and challenges to incorporate data were found to jeopardize the strengths and opportunities of each attribute.

Discussion

It is well documented that red tide blooms have greatly affected invertebrate and vertebrate behavior and survival (Steidinger et al. 1973; Baden et al. 1989; Landsberg 2002; Landsberg et al. 2009), yet, in the case of tarpon, little is known about their impacts. The results from this simple parallel mixed-methods approach (Kinnebrew et al. 2021) suggest tarpon are resilient to red tide blooms to some extent, depending on the timing, intensity, distribution, and duration

Table 2 Results from three separate strengths, weaknesses, opportunities, and threats analyses on monitoring efforts of red tide involving (1) fish kills, (2) sourcing local ecologicalknowledge (e.g., catch logs and users with valuable knowledge of the system), and (3) acoustic telemetry to track movements in response to red tide (*Karenia brevis*) events**Monitoring fish kills****Strengths (internal)**

Documented the lethality of red tide events
 Provided a relative understanding of the vulnerability/resilience of tarpon to red tide

Opportunities (external)

Foster stakeholder participation and knowledge exchange using more effective outreach initiatives
 Increased effort to ensure quality assurance/quality control at each event and in records

Weaknesses (internal)

Quality assurance/quality control required for each entry
 Multiple species are grouped together when reported and likely some are unaccounted for
 No reliable numeric output per species affected by red tide

Threats (external)

Lack of willingness and ability of observers to report fish kills
 Location of fish kill (high density vs low density human population; shoreline/mangrove vs seawall)
 Elapsed time from fish kill to the time reported
 Active (swimming prior to death) and passive (currents, tides, wind) transport of affected fish

Sourcing local ecological knowledge (e.g., catch logs and users with valuable knowledge of the system)**Strengths (internal)**

Expert knowledge and regular interaction with the ecosystem
 Regular monitoring of gamefish presence and behaviors in relation to environmental parameters
 Regular communication among other local ecological knowledge experts

Opportunities (external)

Create a working group to facilitate knowledge exchange and incorporation into management
 Identify particularly vulnerable habitat areas or areas that provide refuge during red tide events
 Quantitatively assess the economic impacts of red tide on recreational angling sector
 Increase volunteer sampling of *K. brevis*

Weaknesses (internal)

Untapped source of knowledge and data by management agencies
 Perspectives and skill level can vary greatly between local ecological informants
 Observations regarding *K. brevis* concentrations are qualitative
 Individual and local observations may not represent large-scale spatio-temporal patterns and trends

Threats (external)

Mistrust in sharing information regarding fishing locations
 Lack of trust in management and other government agencies to enact positive environmental change
 No formal structure to source, incorporate, or ground truth local ecological knowledge or catch data

Acoustic telemetry to track movements in response to red tide events**Strengths (internal)**

Best available method to monitor long-term and movements
 Method caters to multi-species analyses

Weaknesses (internal)

Variable receiver placement both in time and space
 Variable transmitters' availability in system (e.g., battery lives and disjunct tagging efforts across research groups)
 Data inherently difficult to analyze

Opportunities (external)

Embrace researcher collaboration (e.g., tagging and monitoring effort, data sharing)
 Promising technology to attract funding
 Advance in statistical methods and user-friendly programs

Threats (external)

Non-uniform detection coverage when red tide is and is not occurring
 Inability to correlate brevetoxin toxicity with detection data, only *K. brevis* cell counts available
 Difficulty in quantitatively documenting the overlap between *K. brevis* dynamics and receivers and arrays
 High tagging sample sizes difficult but important to acquire
 Funding availability

of each bloom. Although infrequent, when red tide events did overlap with tarpon peak abundance, fish kills involving tarpon did occur, but as informed by LEK, were rare in-part due to the ability of tarpon to actively disperse. Furthermore, we found no differences in tarpon presence or absence during or

following red tide events based on acoustic telemetry data. However, the effects of red tide on tarpon abundance may have been masked by the temporal mismatch between peak tarpon abundance and typical red tide months (i.e., detection days were already low). Regardless, when intense red tide events did

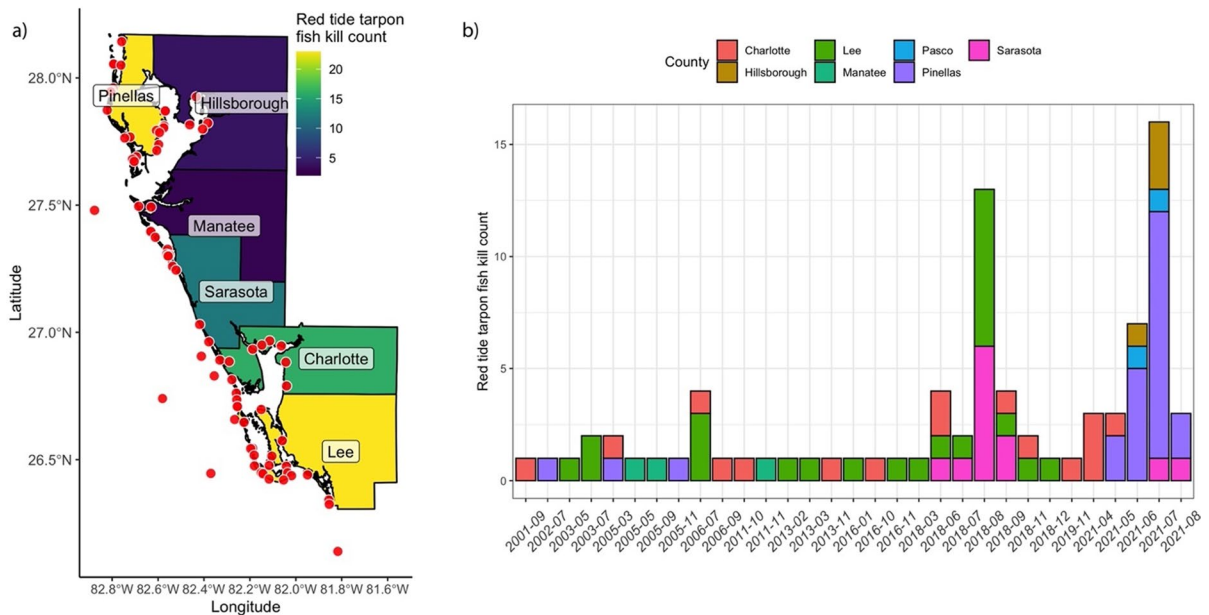


Fig. 2 Red tide (*Karenia brevis*) associated tarpon (*Megalops atlanticus*) mortality events in southwest Florida from 02 February 1977 to 12 August 2021. The overall number of events at

the county level with red dots indicating approximate locations of observations (a) and events at the county level across time (non-continuous year-month dates) (b)

overlap with peak tarpon abundance, the fishery was negatively impacted, as supported by the analysis of the Cape Coral Tarpon Hunters Club catch logs. Considering the LEK results suggest that red tide blooms may be overlapping with peak tarpon abundance more often, the effects of red tide on tarpon should continue to be monitored since this threat will almost certainly persist into the future.

With the capability to move > 30 km per day (Griffin et al. 2018), it is not surprising that tarpon were reported to modify their space use in relation to red tide events. Although the ability of fish to detect *K. brevis* has not been experimentally tested, these data support that tarpon may have an exposure threshold before initiating movements from areas of high red tide concentration. Of course, if tarpon remained in the affected areas and absorbed sufficient levels of brevetoxins across their gill membranes (Abbot et al. 1975; Baden et al. 1989), mortalities might ensue as reflected in the 2018 red tide blooms when 27 fish kills involving tarpon were documented.

Tarpon may also be negatively impacted by the consumption and ingestion of prey containing sub-lethal and lethal doses of brevetoxin. As informed by guides and anglers and since tarpon are capable of

consuming a wide diversity of prey (Ault et al. 2008), it is not surprising that tarpon would opportunistically feed on fish that were impaired by exposure to red tide (e.g., loss of equilibrium and corkscrew swimming; Stuart and Baden 1988; Kennedy et al. 1992), thus reaching elevated levels of brevetoxins via ingestion. It has been experimentally demonstrated that fish and shellfish can accumulate brevetoxins and subsequently transfer them to higher trophic levels through consumption (Tester et al. 2000; Naar et al. 2007). For example, in 2004, a mass common bottlenose dolphin (*Tursiops truncatus*) mortality event occurred in an area devoid of elevated *K. brevis* concentrations, but Flewelling et al. (2005) discovered and attributed the deaths to their stomach contents that contained planktivorous menhaden (*Brevoortia* spp.) with high levels of brevetoxins. When examining the prevalence of brevetoxins in a number of common forage fish found in Sarasota Bay, including pinfish, pigfish, striped mullet (*Mugil cephalus*), and spot (*Leiostomus xanthurus*), Fire et al. (2008) found individuals contained high levels of toxins during and following red tide events, and suggested extended consumption of these prey may lead to sub-lethal health impacts for common bottlenose dolphins. Interestingly, common filter

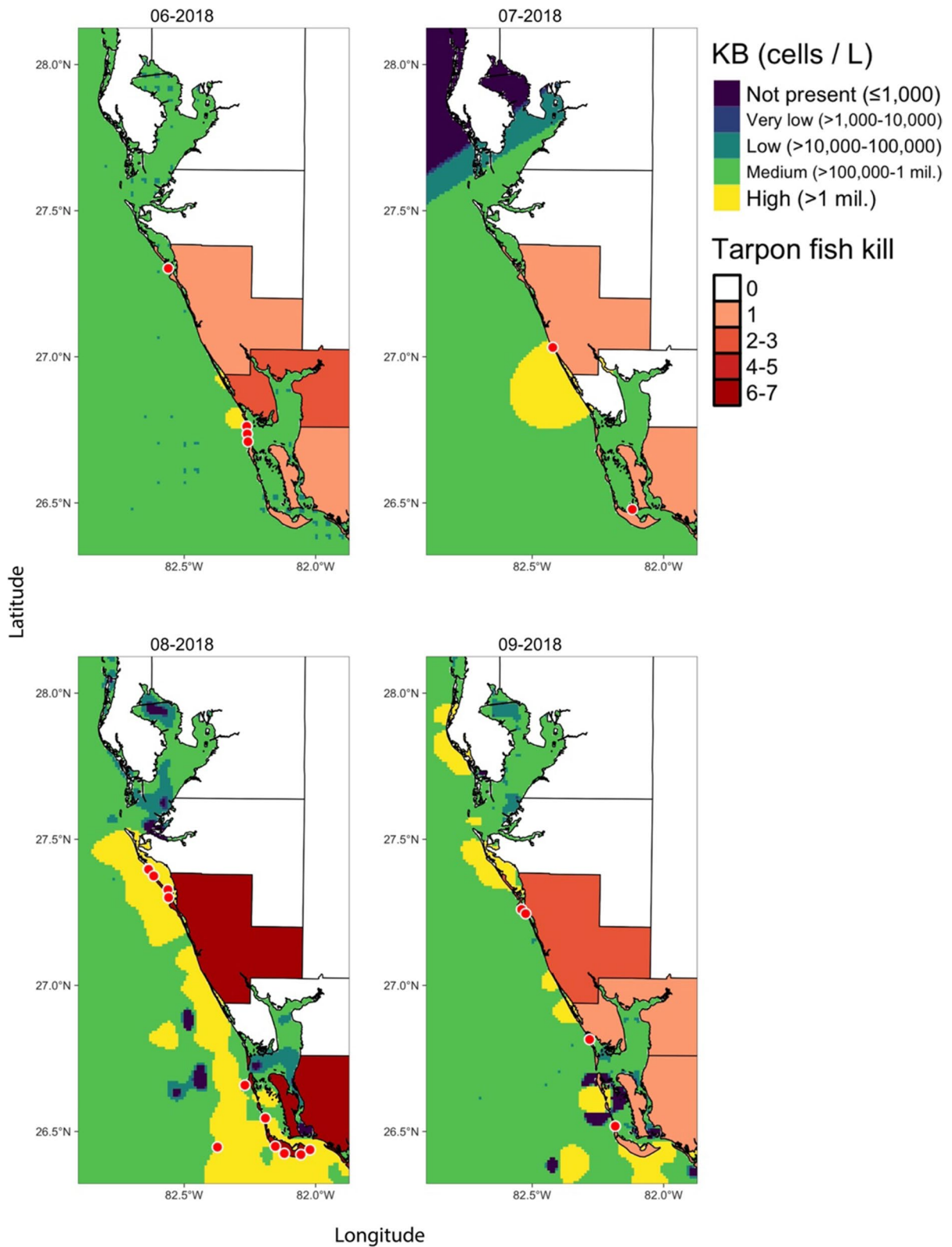


Fig. 3 Red tide (*Karenia brevis*; KB) associated tarpon (*Megalops atlanticus*) mortality events in the southwest region of Florida from June to September 2018. The number of events was summed at the county level and *K. brevis* counts (cells/L) were interpolated and categorized based on sampled concentrations. Red dots indicate approximate locations of observations

feeding clupeid prey of tarpon in this study area (e.g., Atlantic threadfin herring, *Opisthonema oglinum*, and scaled sardines, *Harengula jaguana*; personal communication, Captain Edward Glorioso) were found to increase in abundance surrounding red tide events (Gannon et al. 2009; Berens McCabe et al. 2021). If clupeids are better able to tolerate brevetoxins compared to other species or if they locally modified space use to avoid heavy *K. brevis* concentrations, this highlights the likelihood that tarpon are exposed to brevetoxins via ingestion. Although little is known of the long-term effects on fish with chronic exposure to brevetoxins, experimentally using the freshwater fish medaka (*Oryzias latipes*), Colman and Ramsdell (2003) highlighted exposure could lead to the maternal transfer of toxins to oocytes and, subsequently, reduce survival of offspring. Since blooms sometimes coincide with tarpon presence in the spring and early summer months when gonadal development mainly occurs (Crabtree et al. 1997), reproductive success may be reduced if mature females become sufficiently exposed to red tide through direct exposure or by ingestion.

Beyond direct exposure to red tide and its sublethal and lethal effects on tarpon, severe red tide blooms may indirectly affect tarpon by altering community structure that may support their prey base. For example, following an intense and 13-month protracted bloom in 2005 (Liu et al. 2016), Gannon et al. (2009) found fish population density (except clupeids) and species richness throughout Sarasota Bay declined significantly. Specifically, catch-per-unit-effort was found to decrease across eight fish guilds (again, excluding clupeids), ranging from −57% in mangrove habitats to −88% in the Gulf (Gannon et al. 2009). In another example following the 2005 bloom, Walters et al. (2013) highlighted the potential for species-specific long-term effects of severe red tides after documenting a significant reduction in Tampa Bay sand seatrout (*Cynoscion arenarius*) spawning aggregations due to a likely mass mortality event. Subsequently, a 4-year depression in juvenile abundance

was observed (Walters et al. 2013). For other species, including those that are believed to be common prey for tarpon such as pinfish, pigfish, scaled sardine, Atlantic threadfin herring, ladyfish (*Elops saurus*), and mullet (*Mugil* spp.), the recovery time following red tide blooms was expected to occur within 1 year, but depending on the timing, severity, and duration of the bloom, it could take up to 3 years (McCabe et al. 2010). This loss of prey due to red tide mortalities and its associated community structure changes was an item of concern expressed by five of the expert fishers in this study.

Ultimately, the fishery may also be threatened if red tide blooms continue to overlap with the peak tarpon fishing season, as suggested by the LEK reported here. If red tide blooms are increasing in prevalence and also changing temporally to coincide with peak tarpon abundance, as suggested by Brand and Compton (2007), anglers may continue to shift fishing effort. For example, when major blooms were patchy, anglers were forced to modify their fishing methods to locate tarpon in areas of low *K. brevis* concentrations. As bloom density intensified and tarpon were restricted to smaller areas, angler reported fishing pressure could greatly intensify as fish became concentrated in less toxic waters. Although there was little to no perceived difference in tarpon endurance (e.g., fight times) during blooms, survival may be jeopardized if red tide has any synergistic or compounding effects with other angling related stressors (e.g., physiological or traumatic injury, Gilman et al. 2013). Considering tarpon post-release mortality estimates during non-bloom conditions are relatively high, 13–27% (Guindon 2011; Luo et al. 2020), it is important to determine if angling during blooms decreases survival.

Regardless of angling effects, when blooms became dense and spatially homogenous, tarpon catchability was reported to decline. In agreement, catch logs, collected across 10 seasons by the Cape Coral Tarpon Hunters Club, supported that when red tide blooms were elevated (e.g., summer 2018), tarpon catches were expected to decline. This potential reduction in catches due to red tide could threaten the lucrative fishery that was estimated (2009–2010) to regionally contribute an estimated \$110 million per year (Fedler 2011). Because the fishery is heavily supported by visiting tarpon anglers (Camp et al. 2018), the decline in catches combined with human

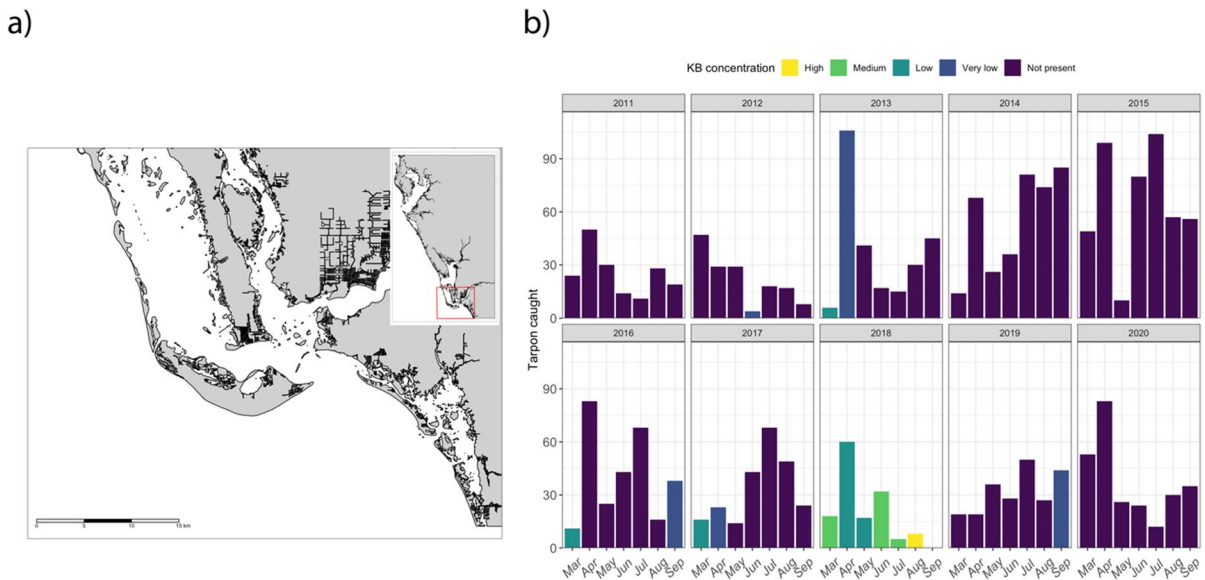
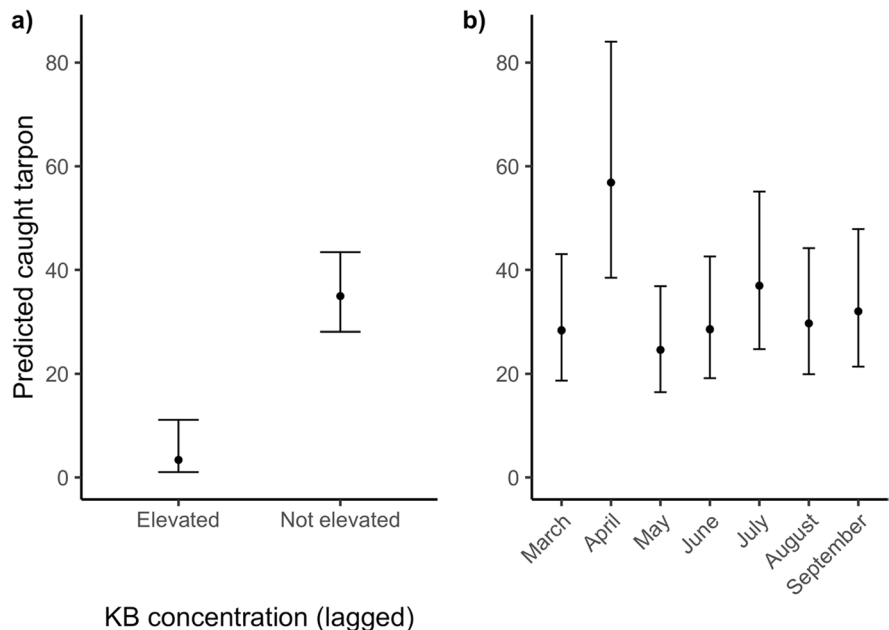


Fig. 4 General fishing area of the Cape Coral Tarpon Hunters Club (a) and monthly tarpon (*Megalops atlanticus*) catch counts across 10 seasons (2011–2020). (b) Averaged red tide (*Karenia brevis*; KB) concentrations are indicated and cat-

egorized based on sampled and interpolated concentrations (cells/L). Due to no recorded catches in September 2018, no *K. brevis* concentration values were shown

Fig. 5 Marginal effects plots in model 2 that evaluated the relationship between the number of tarpon (*Megalops atlanticus*) caught by the Cape Coral Tarpon Hunters Club tournament (2011–2020) by red tide (*Karenia brevis*; KB) concentrations lagged by 1 month (a) and month as an independent variable (b). KB concentrations in panel a were defined as not elevated ($\leq 100,000$ cells/L) and elevated ($> 100,000$ cells/L)



health concerns related to red tide may pose a threat to tourism (Bechard 2019). Previously, Brand and Compton (2007) argued that red tide since the 1950s had increased in intensity, duration, seasonality, and

geographic spread, which they attributed to anthropogenic nutrient inputs. This is in agreement with information provided by LEK, in which expert recreational tarpon anglers reported blooms were increasingly

overlapping with peak tarpon abundance in time and space, suggesting the tarpon fishery may continue to confront red tide effects.

More recently, Medina et al. (2022) linked red tide intensity and bloom dynamics to anthropogenic nutrient input sources. Specifically, they linked discharges from the Caloosahatchee River (further linking nutrient sources to the upper reaches of the watershed) to red tide intensity and bloom dynamics. Given the high level of anthropogenic nutrient inputs into coastal waters along Florida's Gulf of Mexico coast from surface (river, creek) inputs and groundwater discharges, it is highly likely that, as suggested by Brand and Compton (2007), current red tide dynamics (intensity, duration, frequency, geographic spread) are heavily influenced (enhanced) by anthropogenic nutrients. For example, Scott et al. (2006) found a 20-fold increase in nitrate concentrations in Florida's largest freshwater springs between 1992 and 2001. These high-nutrient underground freshwater outflows reach the Gulf of Mexico. Miller et al. (1990) found that groundwater inflow into tidal rivers is similar in volume to the flow of rivers above the tide line during the dry season. Moreover, Hu et al. (2006) estimated that the groundwater entering Tampa Bay inputs dissolved organic nitrogen that is approximately 35% of the amount discharged by all central Florida rivers entering the Gulf of Mexico combined. Lastly, Brewton et al. (2022) demonstrated that septic system effluent has contaminated both groundwater and surface water sources in Southwest Florida and contributes to the intensification of harmful algal blooms, such as red tide events. Thus, the overall influence of anthropogenic nutrients on red tide dynamics in the Gulf of Mexico is likely considerable.

Using SWOT analysis, we determined that the data from each monitoring method (i.e., fish kill reports, sources of LEK, and tracking) were complementary in terms of highlighting general tarpon vulnerability and resilience to red tide. Lacking consistent acoustic telemetry detection coverage in areas that regularly detect tarpon, combined with the limited instances when red tide blooms overlapped with peak tarpon detections, our ability to make direct comparisons between tarpon presence/absence and red tide presence/absence was limited. Beyond inter-institutional and agency collaboration to monitor red tide effects, having an established and cohesive acoustic telemetry array across the region rather than smaller study- or

species-specific arrays would benefit red tide and inter-annual monitoring efforts. Furthermore, we determined engagement with stakeholders and collaboration were priorities for future research efforts, but, again, data quality and trust were critical for success. It is well established that trust is essential for enabling effective knowledge exchange among diverse actors (Cvitanovic et al. 2021). As suggested by Hoagland et al. (2014), a public mobile website that provided real-time updates and a centralized platform on current and projected *K. brevis* blooms would provide recreational anglers an explicit system to avoid areas of high *K. brevis* concentration. Such a platform could then also enhance fish kill monitoring and volunteer water sampling (i.e., community science; Charles et al. 2020) through engagement with LEK experts who regularly encounter red tide blooms first. Furthermore, incorporating LEK experts is likely to build trust within agency groups (Fernandez-Gimenez et al. 2008), one of the major threats found in the SWOT analysis. In this study, because trust was already established with LEK experts due to regular engagement between several authors and the larger tarpon angling community, we were better able to understand the interaction between tarpon and red tide along the southwestern coast of Florida. Nonetheless, there remain opportunities to more fully embrace knowledge co-production and co-assessment to empower all stakeholders and ensure that research is inclusive and relevant (Cooke et al. 2021).

LEK is becoming increasingly recognized as an important component of fish research, especially for species that are endangered or support managed fisheries (e.g., Farr et al. 2018; Poulakis and Grubbs 2019). For example, Adams et al. (2019b) used the interviews with recreational fishing guides in The Bahamas to identify possible pre-spawning aggregation sites for bonefish (*Albula vulpes*), an economically important species throughout its range (Danylchuk et al. 2007; Adams et al. 2014), and combined this LEK with multiple research methods (a parallel mixed-methods approach; Kinnebrew et al. 2021) as part of a protocol to document bonefish pre-spawning aggregation sites. Perez-Cobb et al. (2014) used a mixed-methods approach that included LEK to reveal disconnects between fisheries management, the user groups, and both fisheries that were being managed and those unmanaged because of managers' lack of understanding of user demographics. Indeed, LEK

can provide both a comparison with and context for more standard research approaches that together can provide a more realistic view of a subject (Brook and McLachlan 2005). For our study, the interdisciplinary approach that combined LEK with other research and monitoring techniques improved our interpretation of results and contextualized findings to better understand monitoring needs and the potential population-level effects of red tide on tarpon.

This study supports previous research findings that sufficient information to understand a topic can be obtained from a small number of interviews. For example, Guest et al. (2006) found that information saturation occurred after 12 interviews. Similarly, Muellmann et al. (2021) found that respondent information variation was minimal after 10 interviews. However, Hennink et al. (2017) further examined levels of saturation. They found that fewer interviews (nine) were needed to reach code saturation (the point when no additional issues are identified and the codebook begins to stabilize), whereas 16–24 interviews were needed to reach meaning saturation (the point when we fully understand issues, and when no further dimensions, nuances, or insights of issues can be found). In our study, the LEK interviews were used as a complementary component of a multi-methods approach, and numerous co-authors have extensive knowledge of the local fishery. The commonality of responses among the 13 experts interviewed here, combined with the multi-methods approach and author knowledge of the fishery, supports that an appropriate sample size was used for this study.

Conclusion

While the immediate and long-term effects of red tide on tarpon appear to be complex and remain challenging to fully understand, our study has highlighted that tarpon appear to be resilient to low and moderate concentrations due to their ability to disperse into areas devoid of *K. brevis*. However, when blooms did occur during tarpon peak abundance and became homogeneous and widespread across the study area, multiple data sources suggested tarpon become susceptible to mortality or leave the affected area entirely. While

the long-term population level effects are unknown for tarpon, we should expect deleterious effects for the fishery if blooms continue to overlap with tarpon abundance, as LEK experts reported. Given the direct links between anthropogenic inputs and red tide dynamics, the increasing nutrient load in Florida's surface waters and groundwater that enter coastal waters, it is probable that red tide events will continue to increase in frequency, duration, intensity, and geographic extent, thus continued monitoring and future studies must consider incorporating multiple data sources, including from LEK experts. However, it will be critical for parallel methods to be rigorous and used systematically to take full advantage of the data and ensure they can be used to inform conservation, policy, and management, and to monitor recovery if policymakers do address the anthropogenic nutrient issues. As shown here, the effects of red tide on economically and culturally important fisheries are likely to increase. To ensure that Florida retains its claim as Fishing Capitol of the World, reduction of nutrient inputs must become a statewide priority.

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Data availability Data are available upon reasonable request.

Declarations

Aaron Adams, Andy Danylchuk, and Steven Cooke are Guest Editors of this special issue, but they had no involvement in the peer review of this article and had no access to information regarding its peer review.

Ethical approval All tagging procedures were conducted in accordance with the American Association for Laboratory Animal Science (IACUC protocol 2016–0049, University of Massachusetts).

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