



# Foraging synchrony drives resilience in human–dolphin mutualism

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Interactions between humans and nature have profound consequences, which rarely are mutually beneficial. Further, behavioral and environmental changes can turn human–wildlife cooperative interactions into conflicts, threatening their continued existence. By tracking fine-scale behavioral interactions between artisanal fishers and wild dolphins targeting migratory mullets, we reveal that foraging synchrony is key to benefiting both predators. Dolphins herd mullet schools toward the coast, increasing prey availability within the reach of the net-casting fishers, who gain higher foraging success—but only when matching the casting behavior with the dolphins' foraging cues. In turn, when dolphins approach the fishers' nets closely and cue fishers in, they dive for longer and modify their active foraging echolocation to match the time it takes for nets to sink and close over mullets—but only when fishers respond to their foraging cues appropriately. Using long-term demographic surveys, we show that cooperative foraging generates socioeconomic benefits for net-casting fishers and ca. 13% survival benefits for cooperative dolphins by minimizing spatial overlap with bycatch-prone fisheries. However, recent declines in mullet availability are threatening these short- and long-term benefits by reducing the foraging success of net-casting fishers and increasing the exposure of dolphins to bycatch in the alternative fisheries. Using a numerical model parametrized with our empirical data, we predict that environmental and behavioral changes are pushing this traditional human–dolphin cooperation toward extinction. We propose two possible conservation actions targeting fishers' behavior that could prevent the erosion of this century-old fishery, thereby safeguarding one of the last remaining cases of human–wildlife cooperation.

behavior | cooperation | culture | social foraging | wildlife conservation

Humans' ability to learn to interact with nature in transformative ways has been key to our global ecological success (1, 2) but also to a global ecological crisis (3). Our recent history has been marked by escalating human–wildlife conflicts (4), at the cost of natural, often cultural, practices that can mutually benefit both humans and wildlife (5). This process is illustrated by declines in historical human–wildlife cooperation whereby humans and free-living animals actively coordinate their behavior to achieve a common beneficial outcome (6, 7). Particularly, artisanal fisheries assisted by cetaceans (Fig. 1A) are disappearing amid a recent surge of conflicts between cetaceans and industrial fisheries (8, 9). Theoretical work shows how the nature of ecological interactions can flip between positive and negative, as changes in resource availability or behavior shifts the cost–benefit ratio for the interacting parties (10–12). However, predicting such dynamics in human–wildlife interactions is challenging (7, 13) and requires unpacking how the interplay between environmental factors and behavioral mechanisms confer benefits to the interacting individuals.

We reveal the mechanisms underlying cooperative foraging between humans and wild dolphins, and ask whether this cultural practice can persist, as a mutually beneficial interaction, in the face of current and predicted environmental and behavioral changes. For over a century, individual bottlenose dolphins (*Tursiops truncatus gephyreus*) have cooperated with artisanal net-casting fishers in southern Brazil (Fig. 1B) to catch the same prey, primarily migratory mullet (*Mugil liza*) (14, 15). This fishery has been key in providing ecosystem services to the community—including both resources and intangible assets such as social belongingness and ecological knowledge (16, 17)—while its symbolic value contributes substantially to the local cultural identity (6, 18, 19). Yet it remains unclear how cooperating dolphins and fishers synchronize foraging efforts, how both predators benefit in the short term and long term from coordinated foraging, and whether these benefits are sensitive to fluctuations in prey availability, potentially making such rare ecological interaction vulnerable to overfishing arising from other fisheries (20, 21). We address these questions by i) simultaneously tracking mullet, dolphins,

## Significance

Understanding the conditions under which human–wildlife interactions flip between mutually beneficial and antagonistic is a challenging yet critical endeavor to align human interests and wildlife protection. We study these conditions in a century-old cultural practice involving artisanal fishers who forage cooperatively with wild dolphins. By combining fine-scale behavioral tracking, long-term demographic surveys, and numerical simulations, we show that foraging synchrony is the key driver generating short- and long-term benefits for humans and dolphins. We then quantify the consequences of environmental changes, showing how recent declines in prey availability and foraging specialization can push the mutualism toward extinction. We propose conservation actions to prevent one of the last remaining human–wildlife cooperation from turning into one more human–wildlife conflict.

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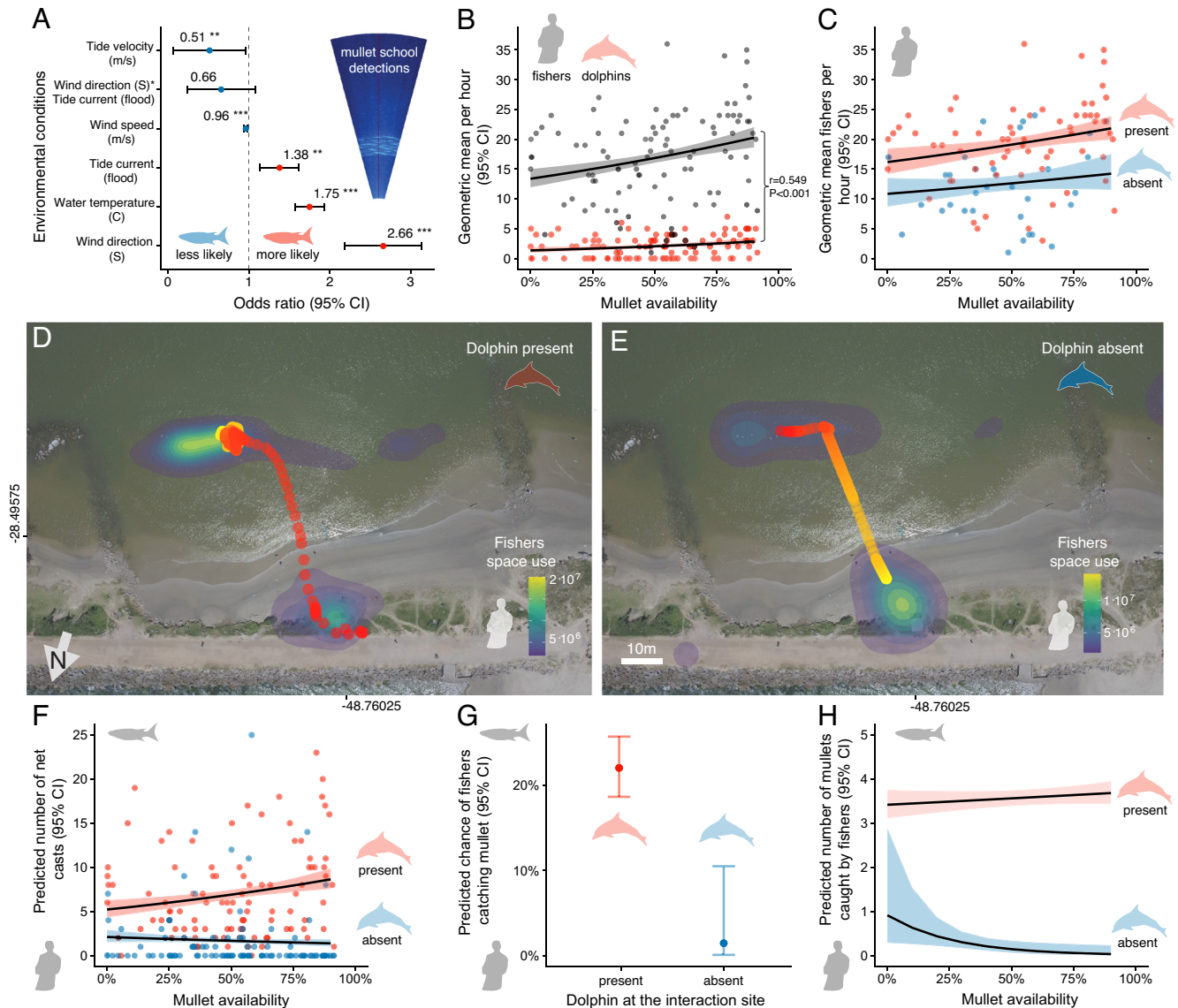
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267 h of behavioral sampling of individual dolphins and fishers, we found that both predators tend to be more numerous at the interaction site when prey availability is high (Fig. 2 A–C). This raises a fundamental question: Are dolphins and fishers independently attracted to the site when conditions are best for catching fish, or do they attract and respond to one another? Dolphin presence increases the number of fishers, regardless of mullet availability (*SI Appendix, Supplementary text 1*), and stimulates a behavioral change among fishers. Equipping fishers with GPS wristbands shows that fishers rapidly move into the water when dolphins arrive (Fig. 2 D and E), while behavioral observations ( $n = 4,090$  events; *SI Appendix, Tables S2 and S3*) show that fishers cast nets at a higher rate when dolphins are present (Fig. 2F).

Thus, while dolphins may be attracted by mullets (Fig. 2B), fisher's behavioral responses demonstrate their active attraction to dolphins. Quantifying the success of net-casting events explains this strong response: when dolphins are present, fishers are 17 times more likely to catch mullet (Fig. 2G), and catch nearly four times more mullet (Fig. 2H), largely independently of their foraging effort and mullet availability (*SI Appendix, Supplementary text 2*). Dolphins clearly generate foraging benefits to fishers and stimulate beneficial actions in response to increased mullet availability that is not present when dolphins are absent. But it is hitherto unclear how.

We demonstrate how dolphins benefit fishers by integrating drone-based tracking to quantify the synchrony and outcomes

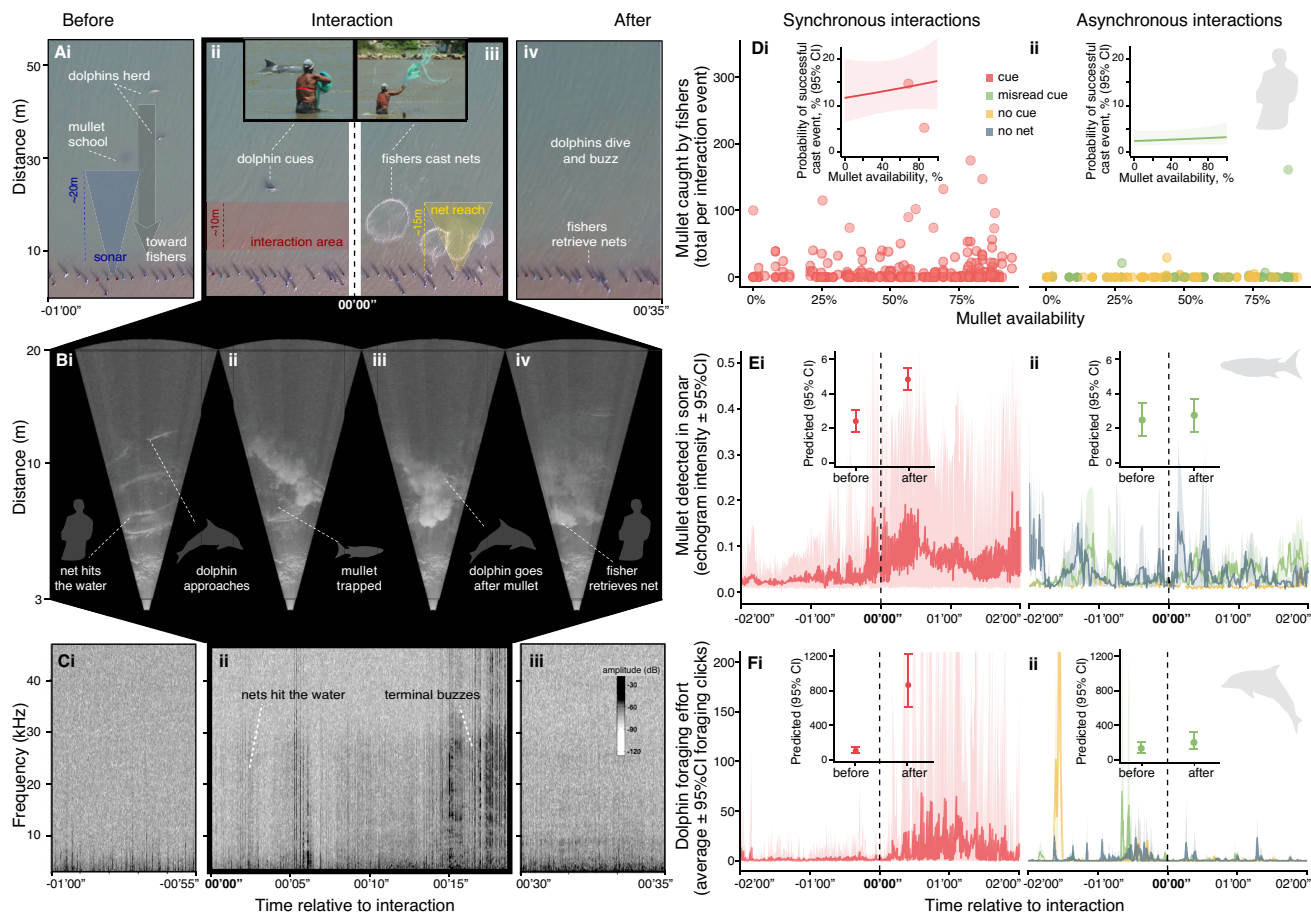


**Fig. 2.** Mullet, dolphin, and fisher co-occurrence and attraction. (A–C) Environmental conditions related to mullet availability at a fine scale (sonar detections; *Inset*) influence the presence of fishers and dolphins. (A) The odds of mullet school detection vary as a function of environmental variables (GLMM1,  $N = 102$ ; *SI Appendix, Table S5*). (B) Fishers, and dolphins to a lesser extent, are more numerous as suitable conditions for mullet increases (GLM2 and GLM3, respectively,  $N = 99$  interaction events; *SI Appendix, Table S5*). (C) Dolphin presence increases the number of fishers more than mullet availability does (GLM4,  $N = 99$ ; *SI Appendix, Table S5*), and GPS tracking demonstrates that fishers enter and remain for longer in the water (high kernel density along the edge of the canal) when (D) dolphins are present than (E) when they are absent (high density at the beach). Individual tracks exemplify (D) a fisher slowly leaving the water when dolphins departed and (E) a fisher rapidly entering the water when a dolphin arrived (yellow = start; red = end of track). (F) Fishers are more likely to cast nets when dolphins are present, and with increasing mullet availability, but not when dolphins are absent (GLM5,  $N = 198$ ; *SI Appendix, Table S5*). Fishers accrue higher foraging success in the presence than in the absence of dolphins, more so than the effects of fishing effort and mullet availability, both in terms of (G) chances of catching any mullet (Odds ratio = 17.07, CI = 3.65–304.24,  $P = 0.005$ ; GLM6,  $N = 751$  net-casting events; *SI Appendix, Table S5*) and (H) total mullet caught (Incidence Rate Ratio = 3.75, 95%CI = 1.35 to 13.80,  $P = 0.025$ ; GLM7,  $N = 751$ ; *SI Appendix, Table S5*).

of their foraging interactions (*SI Appendix, Supplementary text 3*). We identified four different types of cooperative interactions varying in synchrony of predators' actions and reactions (*SI Appendix, Table S8*). During synchronous interactions ("cue": 45.8% of 2,805 independent events), both predators coordinate their actions (Fig. 3 *A–C*): dolphins approach fishers closely (net–dolphin distance  $\pm$  SD = 12.05  $\pm$  3.95 m), make a behavioral cue (commonly, a sudden deep dive (15): *Movie S2*) that fishers interpret as the right moment to react and immediately cast their nets (reaction time  $\pm$  SD = 7.80  $\pm$  5.38 s). By contrast, the other three types of interactions are asynchronous and defined by mismatched actions and reactions: either only one predator acts or fishers react incorrectly. The former includes fishers casting nets without any dolphin cue ("no cue": 33.9% of events) and dolphins making a cue without fishers casting in response ("no net": 8.6%). The latter ("misread cue": 11.7%) represents dolphins approaching and making a cue but fishers casting nets too late (reaction time  $\pm$  SD = 21.39  $\pm$  43.95 s) or too far from dolphins (net–dolphin distance  $\pm$  SD = 21.54  $\pm$  10.31 m). Our behavioral sampling shows that most of fishers'

foraging success—74% of the 433 interactions where they caught mullet, and 86% of all 4,955 mullets caught (Fig. 3 *D*)—comes from synchronous interactions with dolphins (*SI Appendix, Supplementary text 4*). Our underwater imaging reveals the likely mechanism: an increase in mullet detections near the edge of the canal, where the fishers stand, during synchronous (Fig. 3 *E, i*) but not during any type of asynchronous interactions (Fig. 3 *E, ii*). Therefore, dolphins benefit fishers by herding mullet schools towards them, creating temporary high-quality patches just before giving a cue (*Movie S1*), and signaling when prey are within reach of fishers' nets. But, do dolphins also benefit from herding mullet and, subsequently, interacting with fishers?

During interviews with the most experienced fishers, 98% reported that dolphins gain foraging benefits from synchronous interactions. While measuring the dolphins' catch is notoriously more challenging than the fishers', we posit that if dolphins experience a higher prey capture rate when interacting with fishers, then they should consistently modify their behavior and invest more in active foraging after the fishers' nets are cast in synchrony



**Fig. 3.** Foraging coordination and mutual benefits of dolphins and fishers. A typical synchronous foraging interaction seen from above and underwater: (*A, i*) Dolphins herd mullet towards fishers standing at a steep bank, (*A, ii*) and give a cue (*Inset*) when they temporarily turn the interaction area into a high-quality patch for (*A, iii*) fishers, who cast nets (*Inset*), and (*A, iv*) for themselves (*B, i–iv*) who approach nets underwater (sonar imaging), and (*C, i–iii*) and echolocate intensely ("terminal buzzes" in the spectrogram) after nets hit the water and sink over mullets. (*D, i*) Fishers catch more mullet (irrespective of availability and foraging effort) from synchronous interactions than (*D, ii*) any type of asynchronous interactions (*Insets*: predicted foraging success; GLM18 (N = 604 interactions): *SI Appendix, Table S15*), because (*E, i*) mullet detections in the sonar increase after dolphins give a cue (vertical dashed line) in synchronous, (*E, ii*) but not in any type of asynchronous, interactions (*Insets*: predicted mullet detections 2-min before and after interaction; GLM15 (N = 92): *SI Appendix, Table S13*). Dolphins increase the emission rate of active foraging clicks ("terminal buzzes") after fishers cast nets in response to (*F, i*) synchronous, but (*F, ii*) not any type of asynchronous, interactions (*Insets*: predicted terminal buzz clicks 2-min before and after interactions; GLM20 (N = 86): *SI Appendix, Table S19*). When fishers catch fish, dolphins can also benefit by (*B, ii–iv*) extracting mullet directly from the nets (stills from underwater sonar videos providing a top-down view of net, mullet, and dolphin: *Movie S4*). Synchronous are the typical cooperative interactions ("cue", red): dolphin approaches fishers, makes a behavioral cue, and fishers cast nets subsequently (*Movie S2*). Asynchronous interactions represent behavioral mismatches: dolphin approaches and cues but fishers cast nets at the wrong time and place ("misread cue", green); fishers cast without dolphin cue ("no cue", yellow); dolphin cues but fishers do not cast ("no net", blue) (*SI Appendix, Table S8*).

with their cue. We present three lines of empirical evidence to support this hypothesis (*SI Appendix, Supplementary text 5*). First, synchronous interactions stimulate active foraging by dolphins. When actively foraging, dolphins increase echolocation click rates resulting in “terminal buzzes” with very short inter-click intervals ( $<0.016$  s; Fig. 3 C) as they home in on prey (22). By integrating automated detection and classification of echolocation clicks, we show that foraging dolphins produce disproportionately more “terminal buzzes” in response to fishers casting nets in synchrony with their cue (Fig. 3 F, *i*) compared to any type of asynchronous interactions (Fig. 3 F, *ii*). Second, synchronous interactions have a distinct temporal sequence of dolphin reactions (Fig. 3 A–C). Dolphins dive for longer ( $123.8 \pm 75.7$  s after the cue) and emit “buzz” clicks sooner after synchronous interactions in which fishers catch fish ( $12.00 \pm 9.67$  s) compared to unsuccessful synchronous interactions (diving =  $100.4 \pm 77.7$  s, buzzes =  $21.06 \pm 25.23$  s) or any type of asynchronous interactions (diving =  $78.2 \pm 50.2$  s; buzzes =  $28.91 \pm 25.32$  s). These differences suggest that when dolphins coordinate their behavior with the behavior of fishers, they remain underwater for longer after the cue, buzzing more (and before) the nets sink and close over the mullet school (nets sink  $19.62 \pm 5.19$  s after hitting the water), attempting to complete their foraging bout by capturing mullet. Third, dolphins might benefit from aggregating mullet against fishers or from nets disrupting their schools and reducing the confusion effect (15), but our overhead and underwater imaging reveals that dolphins can also directly select trapped mullet from fishers’ nets (Fig. 3B and *Movies S3 and S4*). This finding corroborates how fishers perceive the dolphins’ gain: 61% reported that they feel when dolphins “pull one or two mullets” from their nets. Taken together, our natural experiment comparing the multiplatform tracking data across interaction types demonstrates how foraging synchrony can link the successes of fishers and dolphins.

## Cooperative Foraging Generates Long-Term Benefits but Is in Decline

Next, we show that although generating survival benefits for dolphins and socioeconomic benefits for net-casting fishers, cooperative foraging is in decline. As it has long been recognized by the fishers (15), individual dolphins vary in their tendency to interact with the net-casting fishery. Unlike “non-cooperative” dolphins that forage independently over the entire lagoon, “cooperative” and “occasional cooperative” dolphins forage with net-casting fishers, but cooperative dolphins interact more often with fishers, concentrate their home-ranges around interaction sites (23), and are perceived by fishers as producing more catches than the occasional cooperative dolphins (*SI Appendix, Supplementary text 6*). We used our 12-y boat-based population surveys to quantify the home range and frequency of interaction with the net-casting fishery for each individual dolphin and assign them to each of the foraging tactics (Fig. 4). By building mark-recapture models, we found that cooperative and occasional cooperative dolphins gain a *ca.* 13% survival benefit over non-cooperative dolphins (Fig. 4 B, *i*), while having similar recruitment rates (Fig. 4 B, *ii*). Despite this long-term survival benefit, individual dolphins’ frequencies of interactions with net-casting fishers have been declining over the same period (Fig. 4 C, *i–iii*). Our survey data revealed that this decline coincides with changes in dolphins’ social structure (Fig. 4 C, *iv–vi*) and home-ranges (Fig. 4 D, *ii and iv–vi* and *SI Appendix, Supplementary text 7*), as observed in other dolphin populations that have lost another specialized foraging tactic (24). Recent declines in dolphin–fisher interactions have not been linked to changes in dolphin population size (mean  $\pm$  SD =  $54.7 \pm 3.8$  individuals; no trends in Fig. 4B) or

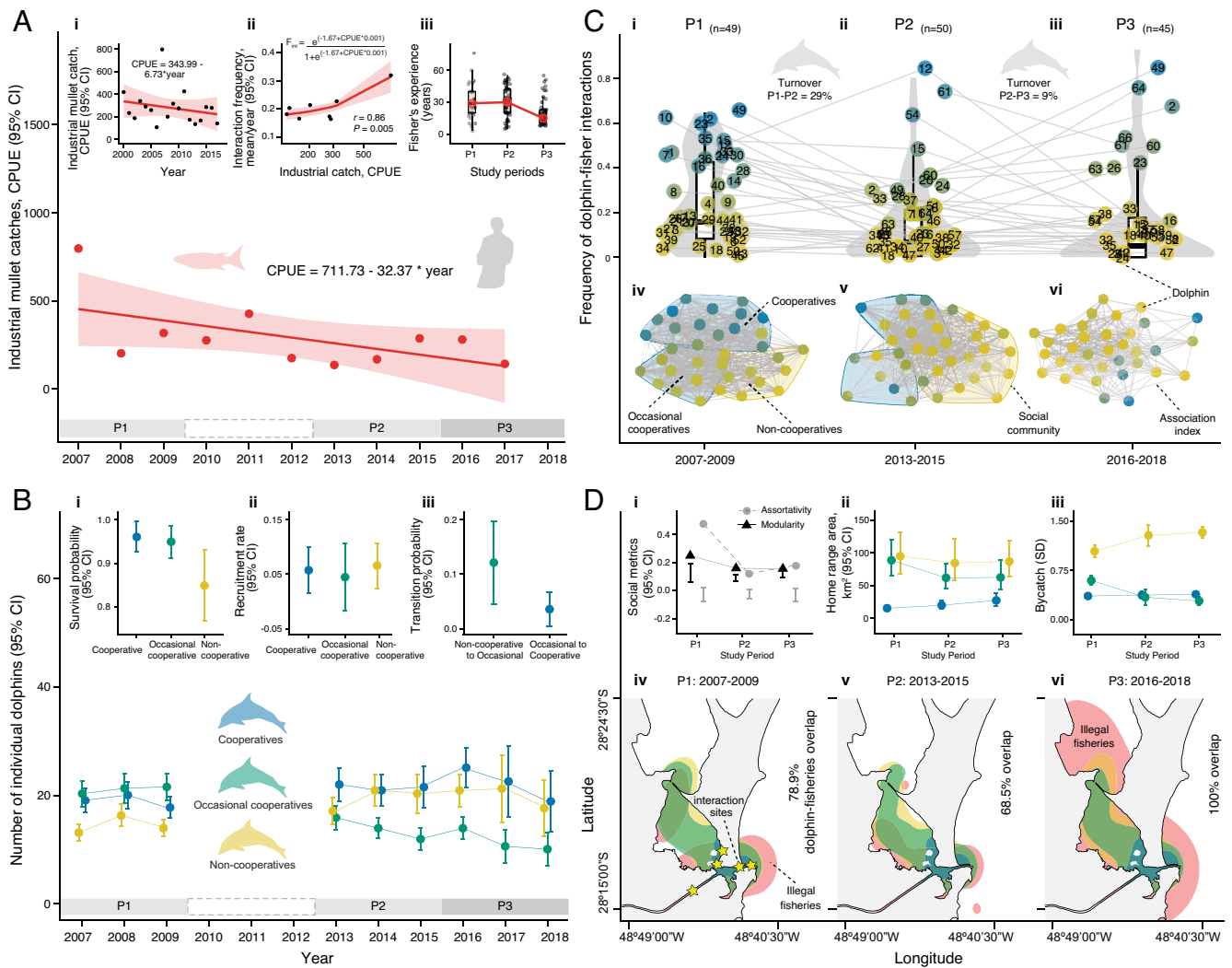
population turnover (Fig. 4C), but mirror individual changes in foraging (Fig. 4 C, *i–iii* and B, *iii*) and declines in resource availability (Pearson’s  $r = 0.86$ ,  $P = 0.005$ ; Fig. 4 A, *ii*). As with many of the world’s unmanaged fisheries (21), the mullet stock across southern Brazil (Fig. 4A) is locally overexploited by the regional small-scale and industrial fisheries (20), potentially contributing to declining local mullet availability (*SI Appendix, Supplementary text 8*) and a corresponding declining willingness by dolphins and artisanal net-casting fishers to interact.

As seen among dolphins, our long-term land-based monitoring also captures individual variation in fisher behavior over time. Individual net-casting fishers vary in experience (16), which our drone-based tracking translates to variation in foraging synchrony with dolphins and catching success (25) (*SI Appendix, Supplementary text 9*). Interviews over the past 16 y reveal economic, cultural and social benefits of this traditional fishery (16–18, 26), but also a decrease in the fishers’ experience of net-casting with dolphins (Fig. 4 A, *iii*). Such net-casting fishers comprise a small subset of the diverse artisanal fishing community that uses a wider array of fishing methods (16). Some fishing gear used by fishers who do not net-cast with dolphins, such as trammel netting, are deployed across the lagoon and throughout the dolphins’ distribution, despite being illegal (Fig. 4 D, *iv–vi*), and are now a major cause of dolphin mortality—6 of 12 carcasses stranded in 2016 to 2018 were entangled. This bycatch mortality is additive to the natural mortality rates (27) and our data reveal that non-cooperative dolphins are, on average, 3.3 times more likely to be bycaught than cooperative dolphins (Fig. 4 D, *iii*), potentially because moving over large areas increases exposure and susceptibility of non-cooperative dolphins to such bycatch-prone illegal fisheries (*SI Appendix, Supplementary text 10*). Taken together, our long-term data suggest that spending more time at the interaction sites is therefore a key, indirect pathway through which cooperative dolphins gain long-term survival benefits.

## Local Behavioral Changes Can Buffer the Mutualism Against Regional Environmental Changes

We have demonstrated that the foraging success of net-casting fishers and dolphins is interdependent, but that three key components of this mutualistic system—local mullet availability, dolphins’ interactions, and fisher experience—are declining. Such changes, plus individual foraging variation among fishers and dolphins, could jeopardize the synchrony that is key for their mutual success. Mutualisms are sensitive to fluctuations in resource availability and in the participants’ behavior that change their accrued benefits (10–13), which could explain past extinctions of human–cetacean cooperation (Fig. 1). Given such growing pressures, how long can this rare cultural fishery persist?

We combine our fine-scale understanding of dolphin–fisher interactions (Figs. 2 and 3) with our long-term demographic data (Fig. 4) to parametrize a numerical model (Fig. 5) that evaluates how three scenarios of changes in local mullet availability and fisher behavior would impact the long-term persistence of this mutualistic system (*SI Appendix, Supplementary text 11*). In the best-case scenario (Fig. 5 B, *i*), high mullet availability and high net-casting fisher engagement persist, maintaining the foraging benefits for both predators, and the survival benefits dolphins receive through reduced bycatch, thereby keeping dolphin abundance constant (Fig. 5 C, *i*). However, mullet declines reduce the interaction benefits, thus its frequency. The current decline is predicted to increase bycatch rates of non-cooperative dolphins, but the interaction with net-casting fishers could still buffer the bycatch rates of cooperative and

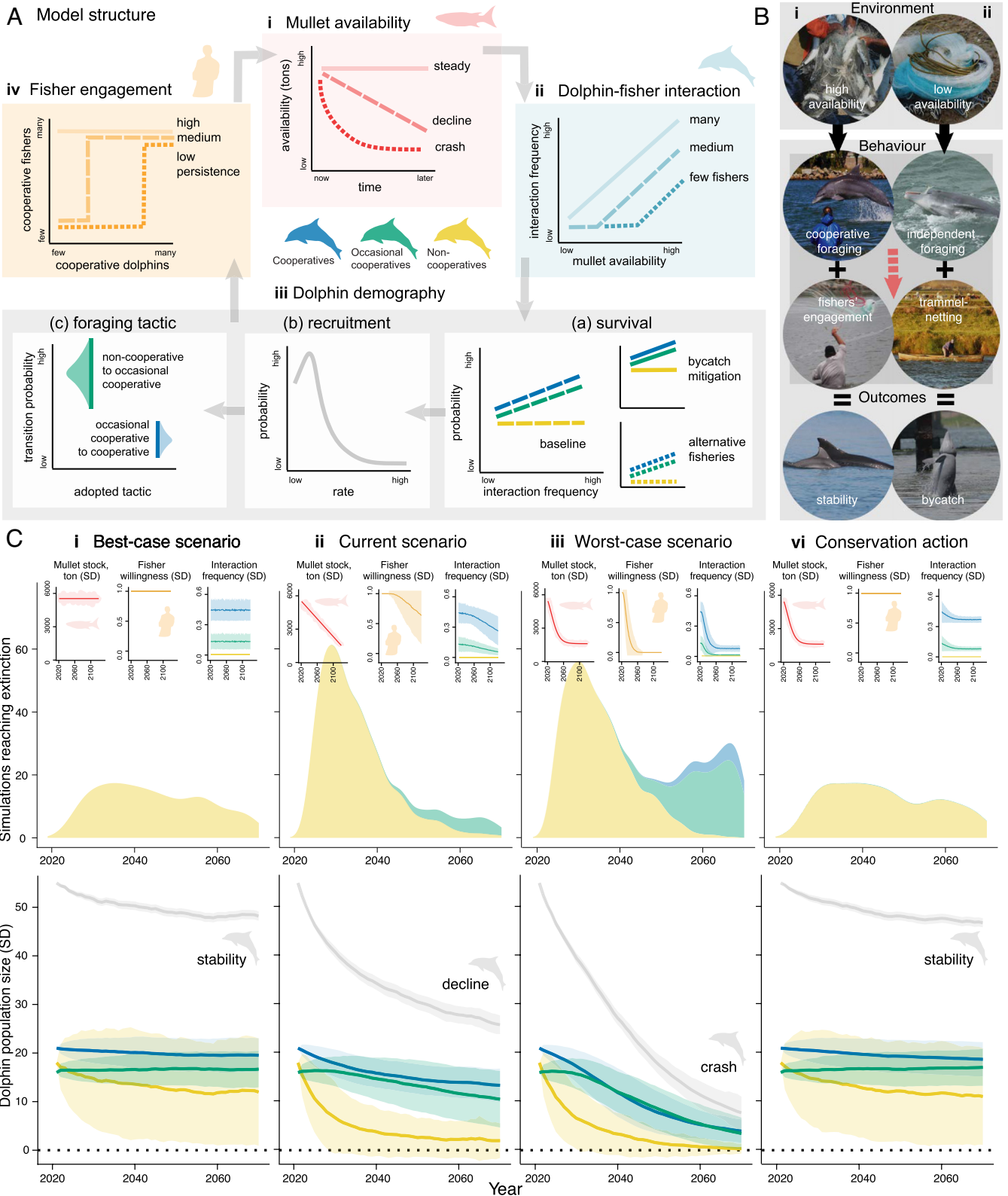


**Fig. 4.** Temporal trends in the human–dolphin mutualistic system. (A) Possible decline in mullet availability shown by the reduced catch per unit of effort (CPUE) of the regional industrial fleet (since 2007: LM32 (N = 11); (A, i): since 2000, LM31 (N = 19); *SI Appendix, Table S23*). (A, ii) Mullet availability correlates with average dolphin–fisher interaction frequency (LM29 (N = 8); *SI Appendix, Table S23*). (A, iii) Net-casting fisher experience (years cooperating with dolphins) also decreases across study periods (P1 = 2007 to 2009, N = 38; P2 = 2013 to 2015, N = 53; P3 = 2016 to 2018, N = 49 individual fishers). (B) Dolphin population size (color-code: foraging tactics) is stable over 12 y, despite (C) high turnover in population composition. (B, i) Cooperative (n = 23) and occasional cooperative dolphins (n = 21) have on average 13% higher survival relative to non-cooperatives (n = 21 individual dolphins), but (B, ii) the recruitment rate is similar. (B, iii) Dolphins transit more often from non-cooperative to occasional cooperative than from occasional cooperative to cooperative foraging tactics. (C, i–iii) Variation among dolphins in interaction frequency with artisanal fishers, with the overall rate dropping recently (more skewed density distribution and boxplots of individual frequencies from study periods P1 to P3), (C, iv–vi) dismantling the assortment of the dolphin social network (D, i) once structured into communities matching foraging tactics (polygons: communities; numbered nodes: individual dolphins; color-code: interaction frequency). There are corresponding changes in (D, ii) dolphin home range (slight increase in 90% kernel densities of cooperative dolphins; GLM28; *SI Appendix, Table S21*), leading to (D, iv–vi) increasing overlap (percentages shown) with illegal fisheries (red shades) across study periods, therefore (D, iii) causing greater human–dolphin conflicts, i.e., bycatch of (primarily non-cooperative) dolphins.

occasional cooperative dolphins (Fig. 5 C, ii). In the worst-case scenario (Fig. 5 B, ii), a collapse in mullet availability decreases the cooperative interaction frequency further, thus reducing the engagement of cooperative net-casting fishers and dolphins, likely promoting inter- and intraspecific competition and also exposing cooperative dolphins to bycatch. Here, the cooperative foraging system is predicted to go extinct over the next 40 to 60 y (Fig. 5 C, iii). Faced with a crash in prey availability, we implement three further scenarios to demonstrate how some possible local conservation actions targeting the fishers' behavior could promote resilience of the mutualistic system (*SI Appendix, Supplementary text 12*). We simulated a bottom-up action that incentivizes fishers to continue interacting at normal rates even when the interaction benefits are reduced, and a top-down action enforcing the removal of fishing gear that causes bycatch (*SI Appendix, Figs. S33 and S34*). Our model predicts that only by combining these actions would this human–wildlife mutualism persist (Fig. 5 C, iv).

## Safeguarding an Interspecific Cultural Unit

Our study highlighting the importance of behavioral synchrony within human–wildlife interactions—here, cooperative foraging between fishers and dolphins—generates insights into ecological interaction dynamics, and the conditions under which they can flip from positive to negative (7, 10, 12, 13)—here, from mutually beneficial to antagonistic. Crashes in mullet availability can reduce mutual benefits, causing fishers to abandon their cultural fishery and exposing dolphins to bycatch from indiscriminate fishing practices, ultimately turning this rare human–wildlife mutualism into yet one more conflict. Human–wildlife conflicts have severe consequences for cetaceans (28), as demonstrated by the recent decimation of vaquita (*Phocoena sinus*) (8) and baiji dolphins (*Lipotes vexillifer*) (29). Local conservation actions targeting the maintenance of foraging synchrony between artisanal fishers and cooperative dolphins—through incentivizing the



**Fig. 5.** Persistence of the human-dolphin mutualistic system. Structure of the numerical model: (A, i) mullet availability affects (A, ii) interaction frequency under different fisher engagement, with consequences to (A, iii) dolphin survival which, combined with (A, iv) a flat recruitment probability and (A, v) transitions between foraging tactics, affects (A, vi) net-casting fisher engagement in cooperating with dolphins, feeding back onto the dolphin-fisher interaction frequency. Hypothesized mechanisms of the extreme scenarios, (B, i) best-case and (B, ii) worst-case, indicating fishers' behavior as the target of local conservation actions (dashed arrow). (C) Model predictions across scenarios: simulations reaching extinction per year (out of 1,000 replicates), and dolphin population trajectory over time (color-code: foraging tactic; grey: whole population). *Insets* show mullet availability, fisher engagement, and dolphin-fisher interaction frequency. In the (C, i) "best-case" scenario, mullet stock is constant, keeping fishers engaged in interacting at high frequencies with dolphins; (C, ii) "current" scenario predicts that mullet stock declines linearly and fishers are reduced engagement in the interaction; (C, iii) "worst-case," the stock crashes, reducing both fisher and dolphin willingness to cooperate. (C, iv) Combining top-down and bottom-up conservation actions to incentivize fisher engagement when the mullet stock crashes can maintain the interaction frequency and the dolphin population stable (*SI Appendix, Supplementary texts 11 and 12*).

cultural and policing the detrimental fisheries—could prevent the extinction of this small, genetically distinct dolphin population (30). Safeguarding cultural behaviors that benefit both humans and wildlife not only encourages their coexistence (31) but is also emblematic of how the conservation of “culturally significant units” advances the conservation of biodiversity (6, 32). This endeavor requires additional research (*SI Appendix, Supplementary text 13*) and tailored conservation strategies (6) before human impacts further erode animal genetic and behavioral diversities (3, 33).

## Materials and Methods

### Data Sampling and Processing.

**Dolphin–mullet–fisher interactions.** We recorded interactions between dolphins, mullets, and artisanal fishers from over and underwater at the main interaction site in Laguna, southern Brazil (Fig. 1A and B; 28°20'S 48°50'W), during 44 d in 2018 and 2019 during the peak (May–June) of the mullet reproductive migration season, when the dolphin–fisher interactions are intensified (15). During a nearly complete sampling totaling 267.3 h of direct observation, we collected six data types simultaneously with a multiplatform tracking system (Fig. 1C): i) an Adaptive Resolution Imaging Sonar camera (SoundMetrics ARIS3000, frequency range: 1.8 to 3 MHz) to quantify mullet availability in the murky waters; ii) all-event behavioral sampling to quantify the number and behavior of dolphins and fishers, and the fishing success of fishers; iii) photography (Canon 7D, 70–300 mm lenses) to identify dolphins through natural marks; iv) GPS wristbands (Huawei Band Pro 2) to track fishers' movement; v) unmanned aerial vehicles (drones DJI Phantom3, Mavic 3) to describe the synchrony between dolphins' actions (space use, diving) and the fishers' reactions (net-casting timing, location, distance); vi) omnidirectional hydrophones (Aquarian H2a 0.01–100 kHz, –180 dB) to quantify the dolphins' foraging effort. Every day we interviewed experienced fishers, and every hour we recorded in situ the water (temperature, transparency, salinity, pH), wind (speed, direction), and tide (state, direction, velocity) conditions known to influence mullet presence (34).

We created a proxy for mullet availability over time by relating the detection of mullets in the sonar imaging to the environmental data. We processed 105 h of underwater footage by filtering off background noise to extract targets in motion (mullet), compressed video frames into echograms where pixel intensity indicated mullet presence, and classified each minute as with or without mullet detection. We processed 104 h of overhead footage (35) to characterize interaction events in terms of distance, angle and timing of the dolphin's approach toward fishers, timing and quality of the fishers' response, and dolphins' space use and diving patterns before and after interactions. We processed photographs of dorsal fins to identify individual dolphins based on natural marks following photoidentification protocols (36). We processed 189 h of acoustic recordings to quantify the dolphins' active foraging. With a custom energy detection algorithm, we detected echolocation clicks and fit univariate finite Gaussian mixture models to the resultant temporal series of inter-click intervals to tease apart three echolocation processes (37, 38). Clicks were classified into “terminal buzzes” (used by dolphins when actively foraging, typically associated with attempted prey capture), “regular clicks” (used for navigation and scanning the surroundings), and “inter-train clicks” (a mixed situation, with pauses between trains of clicks) (37, 38). We used terminal buzz clicks to infer active dolphin foraging effort. Full details on sampling methods, effort and data processing at *SI Appendix, Supplementary methods* (Data sampling: Dolphin–mullet–fisher interaction; Data processing).

**Dolphin, mullet, and fisher populations.** To monitor the dolphins' population and social dynamics, we carried out systematic boat-based photoidentification surveys across the entire 200 km<sup>2</sup> lagoon system in three sampling periods over 12 y (P1 = 2007 to 2009; P2 = 2013 to 2015; P3 = 2016 to 2018). Each survey covered a 30-km predefined route evenly (Fig. 1B) for 5 h of good weather conditions; the number of surveys was similar across periods (P1 = 47, P2 = 49, P3 = 46 d). Upon sighting a group of dolphins, we defined the behavioral state (resting, traveling, socializing, foraging, foraging with fishers) and photographed all dorsal fins for individual identification. We also used opportunistic and systematic beach surveys that recovered stranded animals throughout the entire study area between 2013 and 2018 to identify individual dolphins and infer *causa mortis* through necropsy.

To monitor mullet availability over time, we relied on fisheries data at the local and regional scales. We combined the underwater sonar imaging with the counts of individual mullets caught by net-casting fishers to assess availability at the local fine-scale where the dolphin–fisher interaction happens. We used the yearly catches of the regional artisanal and industrial fleet disembarked in southern Brazil (39) to assess the biomass of mullet available for dolphins and fishers at the regional large scales.

To monitor the population of artisanal net-casting fishers, we used 191 semi-structured interviews conducted by our research group with 177 individual fishers during four campaigns between 2004 and 2019, spaced out by ca. 5 y (16–18, 26). Key artisanal fishers were identified through the snowball and purposive sampling, and the interviews were conducted individually and only when the fisher agreed and signed an informed consent form (16–18, 26). All questionnaires included information on socioeconomics, fishers' perceptions about the benefits of the interaction for the dolphins, their experience in, and reliance on, fishing with dolphins, their perceptions about threats to dolphins, and their willingness to keep practicing this traditional fishery. To investigate the spatiotemporal distribution of other fisheries practiced by the larger fishing community across the entire lagoon system that can threaten dolphins directly or indirectly, we mined 2,524 daily reports of the local environment military police reports, and compiled records of illegal fishing gear (such as trammel nets) confiscated during the three sampling periods (P1 to P3). The data on dolphins were sampled under research permits by the Brazilian Ministry of Environment (SISBio #47876-1, #64956-1), and the studies on fishers were approved by the Committee for Ethics in Research with Humans of the Universidade Federal de Santa Catarina, Brazil (CEPSH#52308116.9.0000.0121, #06457419.6.0000.0121). Full details at *SI Appendix, Supplementary methods* (Subject details and ethical considerations; Data sampling: Dolphin population; Mullet population; Fisher population).

### Data Analyses.

**Dolphin–mullet–fisher interactions.** We first tested how environmental conditions directly influence the mullet availability, thereby indirectly influencing the presence of dolphins and fishers, at the interaction site. We build a generalized linear mixed model with the number of minutes per hour with mullet detection in the sonar as a function of water, wind and tide conditions, controlling for between-day variation. We then used the predictions of this model as a proxy for fine-scale mullet availability and investigated whether it influenced the number of dolphins and fishers at the interaction site. Finally, we used GPS tracking to investigate whether the fishers' movement and foraging relate to the presence of foraging dolphins.

Next, we used the multiplatform tracking data to quantify the foraging behavior of both fishers and dolphins and to assess whether their foraging success depends on the synchrony of their actions and reactions. First, using the land- and drone-based behavioral observations, we characterized dolphin–fisher cooperation interaction events as synchronous or asynchronous (*SI Appendix, Table S8*). Before each interaction event, we evaluated the dolphins' approach toward, and the resulting mullet availability at, the edge of the canal to test whether dolphins herd mullet schools towards fishers. At the interaction moment, we evaluated how fishers cast their nets and how dolphins react, to test whether fishers respond in a coordinated way, and whether dolphins respond to the nets being cast. After each event, we evaluated the dolphins' diving and acoustic behavior, and the fishers' catch, to test for evidence of foraging success. To measure the dolphins' approach to fishers, fishers' reactions, and dolphin diving, we used 6-min drone video clips centered around the interaction moment to quantify distances and angles between dolphins and fishers, fishers' casting timing and performance, and dolphin inter-breath intervals. To measure the dolphins' herding behavior toward the coast, we used sonar footage to quantify the intensity of mullet detections around the interaction. To measure the dolphins' reactions to the nets, we used the acoustic data to quantify their active foraging echolocation (“terminal buzzes”), and drone and sonar imaging to investigate whether dolphins interact directly with the nets. Finally, we inspect the fishers' nets to count, measure and weigh their catch. We evaluated relationships between these variables between synchronous and asynchronous interactions by building a set of generalized linear (mixed) models. Full details at *SI Appendix, Supplementary methods* (Data analyses: Interaction data).

**Dolphin, mullet, and fisher populations.** We first investigated how individual dolphins vary in foraging tactics by calculating individual frequencies of



interaction with net-casting fishers and ranging areas (90% and 50% kernel densities). We then used the individual variation in interaction frequency and ranging to categorize dolphins as “cooperatives” (forage frequently with fishers and concentrated around interaction sites), “occasional cooperatives” (forage less frequently with fishers around interaction sites and across the lagoon), and “non-cooperative dolphins” (forage independently across the lagoon). Second, we investigated if the population-level frequency of dolphin–fisher interactions declined over the study periods (P1 to P3), and whether such decline was related to dolphin population turnover, changes in dolphin foraging, and in mullet availability. We investigated how mullet availability fluctuated over time with linear models of total catch and catch per unit of effort of the regional fleet. Third, we tested whether declines in dolphin–fisher interactions affected the ranging and social behavior of dolphins that use different foraging tactics, by modeling home ranges and the social network structure into communities assorted around foraging tactics across the study periods. Fourth, we built a set of Robust Design (40) mark-recapture models, combining open and closed population models and Pradel temporal symmetry approach (41), to estimate key dolphin population parameters (abundance, apparent survival, emigration probability, capturability, recruitment probability) and investigate how these parameters they change across years and foraging tactics. Finally, we investigated whether dolphins change foraging tactics over time, and how these tactics provide long-term benefits for dolphins by building a set of multistate mark-recapture models (42) that estimated the transition probability between tactics and tactic-specific survival probability.

Next, we used the interviews with net-casting fishers to explore their willingness to interact with dolphins, and how experience and economic reliance in this fishing practice changed across study periods. As per the insights of the interviews with the most experienced net-casting fishers who cooperate with dolphins, we investigated temporal changes in the spatial distribution of the alternative fisheries that can cause dolphin bycatch (e.g., gill- and trammel-netting) when deployed by the local fishing community at large. We modelled the spatial distribution by estimating kernel density maps of the illegal gear confiscated by the police, and quantifying their overlap with the dolphins’ home ranges across study periods. Finally, we combined the stranding data from beach monitoring with the abundance and survival estimates from multistate mark-recapture models to estimate the mortality of dolphins through bycatch across study periods. Full details at [SI Appendix, Supplementary methods](#) (Data analyses: Population data).

### Numerical Model Simulations.

**Modeling overview.** We built a numerical model describing the interdependencies among mullet availability, dolphins’ actions, and fishers’ reactions to evaluate the resilience of their mutualism facing regional environmental and local behavioral changes. We parametrized the model with the long-term empirical data on the population and behavior of dolphins and fishers, and fisheries data on the availability of mullets. Biological processes occurred in the following order for 100 time steps (Fig. 5A): (i) mullet availability is defined and (ii) it influences the interaction frequency between net-casting fishers and dolphins; (iii) the numbers of dolphins per foraging tactic (non-cooperative, occasional cooperative and cooperative) that survive are defined based on their frequencies of interaction, which are influenced by mullet availability and fishers’ willingness to interact; given the total number of dolphins, new dolphins are recruited into the adult pool, and adult dolphins adopt or not the tactic of foraging with fishers (i.e., transition to and from the non-cooperative and occasional cooperative tactics, and to and from occasional cooperative and cooperative tactics); (iv) finally, the number of dolphins of different foraging tactics influence the fishers’ willingness to interact.

**Simulated scenarios.** We first used the numerical model to generate three scenarios of regional changes in the mullet availability and local changes in the dolphins’ and fishers’ behavior to investigate the dolphin population stability and the persistence of the dolphin–fisher mutualism over time. In the “best-case” scenario, the regional mullet stock remains constant, net-casting fishers are

very engaged in interacting with dolphins (Fig. 5C, *i*); in the “current” scenario, the mullet stock declines slowly and linearly, and fishers become less engaged in net-casting with dolphins (Fig. 5C, *ii*); and in the “worse-case” scenario, the stock crashes (declines fast, nonlinearly) and fishers are quick to abandon the interaction with dolphins (Fig. 5C, *iii*). Next, we generate three other scenarios to investigate whether some conservation actions targeting fishers’ behavior can counterbalance regional changes in mullet availability and safeguard this mutualism. Building upon the worse-case scenario of mullet stock crash, we simulated a “top-down” scenario of increased policing to remove alternative fisheries that causes dolphin bycatch; a “bottom-up” scenario of increased governmental and infrastructure incentives that add value to traditional fisheries to keep net-casting fishers engaged in interacting with dolphins; and an “integrative action” scenario in which the top-down and bottom-up approaches are combined (Fig. 5C, *vi*). We run 1,000 replicates of each scenario to investigate the dolphin population trajectory over 100 y and compare the proportion of replicates in which dolphins went extinct across scenarios. Full details at [SI Appendix, Supplementary methods](#) (Data analyses: Simulation data).

**Data, Materials, and Software Availability.** Empirical data and computer code to replicate main analyses, results and figures available at (43).

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