No mullet, no gain: cooperation between dolphins and cast net fishermen in southern Brazil

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ABSTRACT. We report on the interaction between common bottlenose dolphins, *Tursiops truncatus* (Montagu, 1821) and cast net fishermen in southern coast of Brazil. The fishery was monitored in the mouth of the Tramandaí River Estuary to investigate the seasonality of catches and their relationships with a set of variables: presence/absence and number of bottlenose dolphins, fishing area, temperature, salinity, wind and water flow direction in the channel. The mullet, *Mugil liza* Valenciennes, 1836 is the target species and was the dominant fish in the catches (77% of total catch; 50% in frequency; 0.2 ind. x f-1). The use of GLM models helped to reveal that the number of the bottlenose dolphins, time of year (months) and spatial variation of fishing activity were the main factors explaining the presence and abundance of mullet in the fishermen’s catches. The presences of bottlenose dolphins in the fishing area raise the probability of fishermen catch larger number of mullets with smaller fishing effort. However, the size of the mullet is influenced basically by seasonality. The mullets are the “currency” of bottlenose dolphins and fishermen interaction. There are reasons for concern about the sustainability of the southern Brazilian *M. liza* stock, once the decrease of this fishing resource can lead this rare and traditional fishery to the extinction.


INTRODUCTION

In many fisheries, fishers look for signs of animals, such as birds or mammals, in order to find fish schools (Chilvers and Corkeron 2001, Chua and Grosvalet 2001). However, the interaction between cetaceans and artisanal fishers is a rare phenomenon described in few places, including parts of Australia, Mauritania, Myanmar, India and Brazil (Fairholme 1856, Busnel 1973, Pryor et al. 1990, Smith et al. 2009, Kumar et al. 2012). Certain species of Delphinidae, such as *Orcadella brevirostris* (Owen in Gray, 1866), *Tursiops truncatus* (Montagu, 1821) and *Sousa chinensis* (Osbeck, 1765) are known to aid fishers in their catches (Simões-Lopes 1991, Kumar et al. 2012, D’Lima et al. 2014).

The interactive fisheries with dolphins can be performed from land or by boat, using passive fishing gear (gill nets and traps) or active fishing gear (cast nets, hand nets and spears) (Fairholme 1856, Busnel 1973, Peterson et al. 2008, D’Lima et al. 2014). Generally, the interaction occurs in two different ways: initiated by the fishermen (Busnel 1973, Fairholme 1856) or initiated by the cetaceans (Simões-Lopes et al. 1998). In the land-based fishery the interaction typically takes the form when cetaceans driving shoals of fish towards shallower waters as a food capture strategy. Usually occurs near shorelines adjacent to the mouth of estuaries, where fishermen are waiting for the arrival of the shoals to catch fish. Fish of the family Mugilidae, which generally use estuaries as nursery and feeding grounds before eventually migrating to marine environments for spawning (Vieira and Scalabrin 1991, Whitfield et al. 2012, Lemos et al. 2014), are the most common target species of these interactive fisheries (Fairholme 1856, Busnel 1973, Pryor et al. 1990, Kumar et al. 2012, D’Lima et al. 2014).

In Brazil, the interaction between the common bottlenose dolphins, *T. truncatus*, and cast net fishermen, called ‘tarrafeiros’, is restricted to the southern coast (Simões-Lopes 1991) and has been observed and described in the estuarine systems of Laguna (28°S; 48°W) and Tramandaí River Estuary (TRE) (29°S; 50°W) (Pryor et al. 1990, Simões-Lopes 1991, Simões-Lopes et al. 1998, Zappes et al. 2011). In these regions the *T. truncatus* interact with tarrafeiros to catch the mullet *Mugil liza* Valencienes, 1836. This interaction begins when the bottlenose dolphins herd shoals of mullet to shallower areas of the estuarine banks (Pryor et al. 1990, Simões-Lopes 1991, Simões-Lopes et al. 1998).
Fishermen stand side-by-side along the banks, waiting for the dolphin signals to cast their nets toward the school. The theory of interaction is that the tarrafeiros increase their catch and capture larger individuals by casting their nets over mullet schools herded by bottlenose dolphins, whereas the bottlenose dolphins are able to catch mullets more easily because the throwing nets disrupts the schools (Simões-Lopes et al. 1998). This interspecific relationship can be considered cooperation (Pryor et al. 1990, Simões-Lopes 1991, Simões-Lopes et al. 1998, Simões-Lopes et al. 2016), being called “cooperative fishery”.

Acquiring fishery data (e.g., fishing effort, catch rates, species size distribution) during an extensive period, especially in inaccessible fishing grounds, with unpredictable spatial and temporal dynamics is not an easy task (Berkes et al. 2001, Cetra and Petrere 2014, Oviedo and Bursztyn 2017). It is expected that the assessment of artisanal cooperative fishery between the common bottlenose dolphins and tarrafeiros at TRE to be even more complex. There can be, at least four groups of variables that interact with each other and oscillate in time and space: fishermen, bottlenose dolphins, mullet and environmental conditions.

The few fishery studies available at TRE did not cover a one-year period and have focused on the interaction between bottlenose dolphins and fishermen per se, particularly the behavior of the bottlenose dolphins and their relationship with the fisherman (Simões-Lopes 1991, Simões-Lopes et al. 1998, Zappes et al. 2011, Simões-Lopes et al. 2016). The temporal and quantitative assessment of catches and interspecific relationships of cooperative fishery with environmental factors are fundamental to support sustainable management proposals that ensure the maintenance of this rare artisanal fishery. In this context, our goal therefore was to study the cooperative fishery at TRE over a one-year period to assess the relative importance of *M. liza* in the cast net fishery and to understand the degree of dependence between tarrafeiros and bottlenose dolphins under the influence of environmental conditions.

**MATERIAL AND METHODS**

The Tramandaí River Estuary (TRE) (30-km²) is located in southern Brazil (29°58’33.93”S; 50°7’16.78”W) and is connected to the Atlantic Ocean by a permanent channel (1.5 km long and 100 m wide) (Würdig 1988). The main tributary is the Tramandaí River, which has a drainage basin of approximately 2500 km². The average salinity in the estuary varies from 0 to 11 and exhibits daily variation (Chomenko and Schäfer 1984, Kapusta et al. 2006). Water temperature varies seasonally, with highest and lowest average values occurring in austral summer (29 °C) and winter (16 °C), respectively (Kapusta et al. 2006). The semi-diurnal astronomical tide (mean amplitude of 0.25 m) plays a secondary role to meteorological tides (Villwock and Tomazelli 1995, Tabajara and Dillenburg 1997), which may reach as high as 2 m but usually average 1.20 m (Toldo et al. 2006, Guimarães et al. 2015). The estuarine system is shallow (1.0–1.4 m depth), except the main channel (2.5–5 m depth) (Tabajara and Dillenburg 1997).

Sampling was conducted in an area of approximately 700 m in length located on the south bank of the mouth of the TRE, which was sectioned into five adjacent fishing sectors (i.e., sampling sectors) of similar sizes: S1 (29°58’38.22”S, 50°7’15.97”W), S2 (29°58’36.30”S; 50°7’15.97”W), S3 (29°58’39.86”S; 50°7’20.67”W), S4 (29°58’42.84”S; 50°7’24.21”W) and S5 (29°58’46.30”S; 50°7’29.04”W) (Fig. 1).

Fishermen activities were observed weekly between June 2014 and May 2015. Each observation period had an average

![Figure 1. Study area and sampled fishing sectors (sampling sectors) in the Tramandaí River Estuary (TRE) in southern Brazil. The circles represent the sectors sampled.](image)
dolphins in the sampled sector, temperature, salinity, wind and water flow direction in the channel. Predictive variables were tested for collinearity using the Spearman coefficient prior to model formulation (Beger and Possingham 2008). Thus, when collinearity was detected between two variables, the variable interpreted to have greater ecological importance was maintained in the analysis. Only season and month were highly correlated, and month was selected to increase the accuracy of the models (Table 1). In addition, the interactions between predictive variables were tested. The seasonal variation of the predictive variables is available in Figs 2–7.

The high frequency of zeros in the data matrix (> 40%) required the construction of two models (McCullagh and Nelder 1989, Courrat et al. 2009). The first model was a coupled sub-model testing for the presence or absence of mullet in the samples and used the binomial family with the “logit” link function (McCullagh and Nelder 1989). The second sub-model was used to test the positive abundance of mullet catches, for which a gamma distribution model with the “log” link function was employed (Myers and Pepin 1990).

To choose the best model, we followed the “backward stepwise” procedure by selecting the template that had the lowest Akaike Information Criterion (AIC) value (Burnham and Anderson 2002). In addition, a drop1 function in software “R” was used to compare the full model with a model in which the interaction was dropped using a chi-square test (Zuur et al. 2007). All models were tested for overdispersion, and the final model was fitted only with significant predictor (p < 0.05) (Rodrigues et al. 2014). The percentage of the total deviance explained, and the relative contribution of each predictor were independently verified for each model (binomial and gamma) (França et al. 2011, Rodrigues et al. 2014).

CPUE of each season, for 10-mm length class (CPUE-LC%) of mullet individuals was calculated following the formula: \( y = n_{i} \times N_{i}^{-1} \times f_{i}^{-1} \), where \( y \) is the CPUE-LC%, \( n \) is the total number of individuals caught on each sample \( i \), \( N_{i} \) is the total number

Table 1. Spearman (rho) correlations among variables.

<table>
<thead>
<tr>
<th>Month</th>
<th>Fishing sector</th>
<th>Season</th>
<th>Temperature</th>
<th>Salinity</th>
<th>Wind</th>
<th>Regime channel</th>
<th>Number of dolphins</th>
</tr>
</thead>
<tbody>
<tr>
<td>Month</td>
<td>1</td>
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<td>Fishing sector</td>
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<tr>
<td>Season</td>
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<td>-0.12*</td>
<td>1</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
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<td>-0.17*</td>
<td>-0.39*</td>
<td>1</td>
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</tr>
<tr>
<td>Salinity</td>
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<td>-0.08</td>
<td>0.40*</td>
<td>-0.25*</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wind</td>
<td>0.03</td>
<td>-0.06</td>
<td>0.09</td>
<td>-0.04</td>
<td>0.03</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Regime channel</td>
<td>-0.23*</td>
<td>-0.01</td>
<td>-0.22*</td>
<td>-0.01</td>
<td>-0.30*</td>
<td>-0.19*</td>
<td>1</td>
</tr>
<tr>
<td>Number of dolphins</td>
<td>-0.09</td>
<td>0.41*</td>
<td>-0.08</td>
<td>-0.02</td>
<td>0.06</td>
<td>-0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>* p &lt; 0.05.</td>
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</table>

Generalized linear models (GLM) were used to investigate the relationship between mullet catch and a set of predictor variables, including month, season, fishing sector, number of bottlenose dolphins in the sampled sector, temperature, salinity, wind and water flow direction in the channel. Predictive variables were tested for collinearity using the Spearman coefficient prior to model formulation (Beger and Possingham 2008). Thus, when collinearity was detected between two variables, the variable interpreted to have greater ecological importance was maintained in the analysis. Only season and month were highly correlated, and month was selected to increase the accuracy of the models (Table 1). In addition, the interactions between predictive variables were tested. The seasonal variation of the predictive variables is available in Figs 2–7.

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Figures 2–7. Seasonal variation of the predictive variables: (2) Mean and standard deviation of water temperature, min. 15 °C and max. 27 °C; (3) Mean and standard deviation of salinity, min. 1 PSU and max. 36 PSU; (4) Mean and standard deviation of number of dolphins, min. 0 and max. 5; (5) Frequency of occurrence% of water flow direction (ebb, flood, slack water) in the entrance channel; (6) Frequency of occurrence% of wind direction (Northerly, Southerly, Easterly); (7) Frequency of occurrence% of the fishing sector (S1, S2, S3, S4 or S5).

of measured individuals and (f) is the fishing effort (Garcia et al. 2001, Vieira 2006, Ceni et al. 2016).

The factorial ANOVA was used to test the influence of season and the presence and absence of bottlenose dolphins on the dependent variables of fishing effort and total length of *M. liza*. Post-hoc significant differences were evaluated using Tukey’s test (Zar 1984).

Statistical analyzes were performed with R software (R Development Core Team 2015). We used 95% confidence intervals and a significance level of *p* < 0.05 in all analyses.

**RESULTS**

From June 2014 to May 2015, based on a total of 443 samples, 815 fish of 16 species were identified. The number of species varied seasonally. The species richness (S) was highest in autumn (S = 12) and lowest in winter (S = 3). The seasonal variations of Total CPUE (spring = 0.40 ind × f⁻¹; summer = 0.11 ind × f⁻¹) were not significant (ANOVA, *F* = 0.59; *P* > 0.05) (Table 2).

*Mugil liza* composed 77% of the total fish caught and was the only species classified as dominant. Mullet abundance was highest in autumn (0.25 ind × f⁻¹) and lowest in summer (0.09 ind × f⁻¹), but no statistically significant differences among seasons were detected (Table 2; ANOVA, *F* = 0.83; *P* > 0.05). The remaining species were occasional (not abundant and infrequent), except for Argentine menhaden *Brevoortia pectinata* (Jenyns, 1842), which was abundant but not frequent in autumn and spring (Table 2).

The best GLM model accounting for the presence or absence of mullet in the catches explained 12% of the total deviance (Table 3). The model consisted of two predictors: month, which contributed 8.5% of the deviance, and the number of bottlenose dolphins, which contributed 3.5%. The probability of catching mullet was highest in April, May and Jun (autumn) and October, November and December (spring) (Fig. 9) and consistent with the increase in the numbers of bottlenose dolphins in the fishing sectors (Fig. 8).

The best model for explaining *M. liza* abundance (CPUE) consisted of three predictors that were responsible for 46% of the total explained deviance: fishing sector, month and number of bottlenose dolphins (Table 3). The single predictor with the highest level of explicability was number of bottlenose dolphins (24.9%). The interaction between fishing sector and month was significant, with the two variables accounting for 8.8% and 5.5% of the total explained deviance, respectively (Table 3). The expected abundance of mullet increased with the number of bottlenose dolphins (Fig. 10) and can be associated with the displacement of fishermen toward the inner portion of the sampling area (Fig. 12). The GLM modeling did not reveal monthly significant variations in the expected abundances of the mullet (Fig. 11).

Seasonal differences in fishing effort were not statistically significant (Table 4). However, fishermen significantly reduced their fishing effort when bottlenose dolphins were present, except in spring (Table 4, Fig. 13). The lowest fishing effort was observed in autumn and winter in the presence of bottlenose dolphins (Fig. 13).
Table 2. List of species caught by cast net fishermen in cooperation with dolphins at the entrance channel of the ESTR, along with frequency of occurrence (%FO) and number of individuals per unit of effort (CPUE). Species were classified as: abundant and frequent (++), abundant and infrequent (+–), frequent and not abundant (–+), infrequent and not abundant (absence of the signals) and absent (–).

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency of Occurrence</th>
<th>CPUE</th>
<th>Frequency of Occurrence</th>
<th>CPUE</th>
<th>Frequency of Occurrence</th>
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<th>Frequency of Occurrence</th>
<th>CPUE</th>
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<tr>
<td></td>
<td>Summer</td>
<td>Winter</td>
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<td>FO% (Ind × f^-1)</td>
<td>FO% (Ind × f^-1)</td>
<td>FO% (Ind × f^-1)</td>
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<tr>
<td>Mugil liza</td>
<td>38.33++</td>
<td>52.81++</td>
<td>48.00++</td>
<td>62.71++</td>
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<tr>
<td>Brevoortia pectinata</td>
<td>3.33</td>
<td>1.12</td>
<td>0.56</td>
<td>3.39</td>
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<tr>
<td>Genidens sp.</td>
<td>–</td>
<td>1.12</td>
<td>0.56</td>
<td>3.39</td>
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<td>Eucinostomus melanopterus</td>
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<td>0.56</td>
<td>0.56</td>
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<tr>
<td>Centropomus sp.</td>
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<tr>
<td>Mugil curema</td>
<td>3.33</td>
<td>0.56</td>
<td>0.56</td>
<td>3.39</td>
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<td>0.56</td>
<td>3.39</td>
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<td>Caranx latus</td>
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<td>0.56</td>
<td>0.56</td>
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<td>Selene vomer</td>
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<tr>
<td>Acestrothynchus pantaneiro</td>
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<td>0.56</td>
<td>0.56</td>
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<tr>
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<td>0.56</td>
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<td>Trachinotus carolinus</td>
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Table 3. Analyses of deviances for the generalized linear model that best explains the occurrence (binomial model) and abundance (gamma model) of mullets. Degrees of freedom (d.f.); residual deviance (Res. Dev); deviance explained in percentage (%Dev. Expl); significance (Sig.).

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<td>Occurrence</td>
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<tr>
<td>Binomial Model (0 or 1)</td>
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<td>516.87</td>
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<tr>
<td>Main effects</td>
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</tr>
<tr>
<td>~ Month + Number of dolphins</td>
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<td>361</td>
<td>472.86</td>
<td>8.53</td>
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<tr>
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<td>454.99</td>
<td>3.47</td>
<td>***</td>
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<tr>
<td>Total explained</td>
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<tr>
<td>Abundance</td>
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<tr>
<td>Gama model [Log (CPUE+1)]</td>
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<td>189</td>
<td>158.5</td>
<td>***</td>
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<tr>
<td>Main effects</td>
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<tr>
<td>~ (Fishing area*Month) + Number of dolphins</td>
<td></td>
<td>185</td>
<td>144.53</td>
<td>8.86</td>
<td>***</td>
</tr>
<tr>
<td>Number of dolphins</td>
<td></td>
<td>174</td>
<td>135.82</td>
<td>5.52</td>
<td>–</td>
</tr>
<tr>
<td>Fishing area*Month</td>
<td></td>
<td>173</td>
<td>96.45</td>
<td>24.97</td>
<td>***</td>
</tr>
<tr>
<td>Total explained</td>
<td></td>
<td>163</td>
<td>85.96</td>
<td>6.65</td>
<td>*</td>
</tr>
</tbody>
</table>

(*) p < 0.05; (**) p < 0.01; (***) p < 0.001; (–) p > 0.05.

Mullets ranged in size from 121 to 655 mm (TL) (Figs 14–17) and exhibited statistically significant seasonal differences in size distribution (Table 5). Larger individuals were captured in autumn (mean = 444 ± 72 mm TL) and winter (mean = 423 ± 73 mm TL) and smaller in summer (mean = 348 ± 94 mm TL) and spring (mean = 381 ± 67 mm TL) (Figs 14–17).

The presence/absence of bottlenose dolphins did not have any significant effects on mullet size (Table 5). However, the interaction of the presence/absence of bottlenose dolphins with season resulted in a significant effect in summer only. In this season, mullet body size was significantly larger in the presence (mean = 396 ± 81 mm LT) than in the absence (mean = 251 ± 76 mm LT) of bottlenose dolphins (Table 5; Fig. 18).
Figures 8–9. Expected occurrence of *Mugil liza* for predictors of the binomial model. Number of dolphins (8) and month (9); the black lines indicate the moving averages; dark gray areas represent the 95% confidence intervals of the predictions.

Figures 10–12. Expected abundance of *Mugil liza* for predictors of the gamma model. Number of dolphins (10), month (11) and fishing area (12); the black line indicates the moving average; dark gray areas represent the 95% confidence intervals of the predictions.

Figure 13. Seasonal variation in fishing effort. Means and standard deviations of the effort in the presence or absence of dolphins.

Table 4. Seasonal comparisons of fishing effort and relationships with the presence or absence of dolphins. Factorial ANOVA results indicate sum of squares (SSQ), degrees of freedom (d.f.), average square (MS), F value and Tukey’s test.

<table>
<thead>
<tr>
<th>Effect</th>
<th>SSQ</th>
<th>d.f.</th>
<th>MS</th>
<th>F</th>
<th>p</th>
<th>Comparisons</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dolphins</td>
<td>188.5</td>
<td>1</td>
<td>188.5</td>
<td>177.552</td>
<td>***</td>
<td>Summer (Presence) x Summer (Absence)</td>
<td>***</td>
</tr>
<tr>
<td>Season</td>
<td>5.4</td>
<td>3</td>
<td>1.8</td>
<td>1.698</td>
<td>–</td>
<td>Autumn (Presence) x Autumn (Absence)</td>
<td>***</td>
</tr>
<tr>
<td>Season * Dolphins</td>
<td>7.6</td>
<td>3</td>
<td>2.54</td>
<td>2.389</td>
<td>–</td>
<td>Winter (Presence) x Winter (Absence)</td>
<td>***</td>
</tr>
<tr>
<td>Residuals</td>
<td>386.5</td>
<td>364</td>
<td>1.06</td>
<td>–</td>
<td></td>
<td>Spring (Presence) x Spring (Absence)</td>
<td>–</td>
</tr>
</tbody>
</table>

(*** p < 0.01, (-) p > 0.05.)
Figures 14–17. Catch per unit effort (CPUE-LC%) by body size classes (10 mm) of the mullet. (14) summer, (15) autumn, (16) winter and (17) spring.

Figure 18. Seasonal variation in total length (mean and standard deviation) of *Mugil liza* caught in the presence or absence of dolphins.

Table 5. Seasonal comparison of body size (total length, mm) of mullets with the presence or absence of dolphins. Factorial ANOVA results indicate sum of squares (SSQ), degrees of freedom (d.f.), average square (MS), F value and Tukey's test.

<table>
<thead>
<tr>
<th>Effect</th>
<th>SSQ</th>
<th>d.f.</th>
<th>MS</th>
<th>F</th>
<th>p</th>
<th>Comparisons</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>541669</td>
<td>3</td>
<td>180556</td>
<td>35.642</td>
<td>***</td>
<td>Summer (Presence)</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x Summer (Absence)</td>
<td></td>
</tr>
<tr>
<td>Dolphins</td>
<td>14041</td>
<td>1</td>
<td>14041</td>
<td>2.772</td>
<td>–</td>
<td>Autumn (Presence)</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x Autumn (Absence)</td>
<td>–</td>
</tr>
<tr>
<td>Season* Dolphins</td>
<td>141467</td>
<td>3</td>
<td>47156</td>
<td>9.309</td>
<td>***</td>
<td>Winter (Presence)</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x Winter (Absence)</td>
<td>–</td>
</tr>
<tr>
<td>Residuals</td>
<td>2502548</td>
<td>494</td>
<td>5066</td>
<td></td>
<td>–</td>
<td>Spring (Presence)</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x Spring (Absence)</td>
<td>–</td>
</tr>
</tbody>
</table>

(***): p < 0.01, (-) p > 0.05.
DISCUSSION

Cast net is a traditional fishing method that has been used since the Neolithic Age (Edo 2007). Although Taylor and Gerking (1978) suggested that cast net have low efficiency, artisanal fishermen adapted the technique to improve capture effectiveness (Berkes et al. 2001). In southern Brazil, the primary target species of cast net fishermen are mullet, silversides (Atherinidae) and shrimp (Harayashiki et al. 2011). More than 70% of the fish caught by cast net fishermen (tarrafeiros) in the mouth of the Tramandaí River Estuary (TRE) are *M. liza*, suggesting that this fishing method is highly selective for this species in this region. *Mugil liza* is an important traditional fishery resource for artisanal fishermen in the southern states of Brazil and is considered of high economic, cultural and social relevance (Diegues 2004, Klippel et al. 2005, Peres et al. 2007, Kalikoski and Vasconcellos 2013). Approximately 40 tarrafeiros are officially licensed to fish in the TRE (Zappes et al. 2011). Mullet is the main target species, and source of income and food security for this group of fishermen, locally.

According to Zappes et al. (2011), tarrafeiros in Tramandaí city believe that the presence of bottlenose dolphins increases mullet capture efficiency by reducing fishing effort and increasing total catch. Simões-Lopes et al. (1998) reported a positive relationship between fishing efficiency and the presence of bottlenose dolphins, although their study was based on a limited three-month sampling period. Our results carried out over a one-year period and considering a wide set of variables (wind, water temperature, salinity, channel regime and spatial distribution of tarrafeiros) are consistent with these preliminary observations. Moreover, our extended and standardized observations allowed us to statistically demonstrate that the presence of bottlenose dolphins reduces fishing effort and increases the capture probabilities of mullet.

According to Simões-Lopes et al. (1998) the tarrafeiros wait for signals from the bottlenose dolphins, which usually consist of “head slaps” (when a dolphin raises its head out of the water and slaps the surface with its throat), indicating the appropriate time to throw the cast nets and the location of the mullet shoals, an interaction that seems to increase fish capture efficiency. We also observed that in the absence of bottlenose dolphins fishermen tend to randomly throw their nets, targeting no specific location in the water, thereby significantly reducing fish capture efficiency and, consequently, increasing fishing effort.

Bottlenose dolphins use the estuaries for feeding, sheltering and resting area (Irvine et al. 1981, Hanson and Defran 1993, Simões-Lopes and Fabian 1999). The presence of bottlenose dolphins at TRE does not necessarily indicate that they are interacting with the fishermen. However, our results demonstrated that the presence of bottlenose dolphins change the fishing strategy of the tarrafeiros. We can assume that the presence and the number of bottlenose dolphins in a given sector may be related to the availability of mullets. The fishermen look at the bottlenose dolphins and run to the sector where they are and, consequently, increase mullet catch probabilities. Therefore, we cannot consider that only the interactions between fishermen and bottlenose dolphins generate effects on fishing. The simple fact of the presence of the bottlenose dolphins in the TRE positively influences the fishing behavior of the tarrafeiros.

Only in spring the fishing effort was not influenced by the presence/absence of bottlenose dolphins, which may be due to the reduction in the occurrence of bottlenose dolphins in the sampling area (Fig. 4). The highest number of samples in the absence of bottlenose dolphins was recorded in spring, although there was a high frequency of occurrence of mullet in the catches (%FO > 62). *Tursiops truncatus* is an opportunistic predator, and their occurrence in coastal areas and estuaries varies seasonally, typically associated with the availability of food resources (Defran et al. 1999, Hanson and Defran 1993, Irvine et al. 1981, Shane et al. 1986). Simões-Lopes and Fabian (1999) demonstrated that the residence pattern of *T. truncatus* in the Laguna estuary (about 250 km north of the TRE) varies seasonally, with fewer bottlenose dolphins observed in spring/summer than in autumn/winter. The mullet *M. liza* inhabits the estuaries of southern Brazil throughout the year (Lemos et al. 2014) and cast net fishermen of the TRE catch mullet all year round regardless of the presence of bottlenose dolphins. Therefore, although the presence of bottlenose dolphins increases mullet capture efficiency by tarrafeiros, these fishermen are also able to catch mullet when bottlenose dolphins are less frequent or absent.

Our results reveal that the body size distribution of mullets caught varies significantly with season in the study area. In the coastal regions of southern Brazil, the adult mullets move in large schools from the estuaries to the marine environment during the reproductive migration in austral autumn and winter (Vieira and Scalabrini 1991, Vieira et al. 2008, Lemos et al. 2014). Most *M. liza* individuals caught in autumn and winter in the TRE are adults, and larger than the average total length of first maturity (*L_m*= 408-mm; Lemos et al. 2014). Also, many of the females caught showed well-developed ovaries. The average size of mullets caught in autumn/winter was larger than in spring and summer.

Simões-Lopes et al. (1998) suggested that the body sizes of mullets caught by tarrafeiros are influenced by interactions between bottlenose dolphins and fishermen. According to these authors, bottlenose dolphins preferentially select larger mullet; consequently, mullets captured would also have larger body sizes. Our results did not corroborate this claim. We did not observe a significant difference in the body size of mullets caught when the bottlenose dolphins were present or absent at TRE. The interpretation of the differences in the body size of mullets caught in the study area may be explained when the interaction between the presence/absence of bottlenose dolphins and seasonality is considered. Only in summer the fishermen significantly catch larger mullets when bottlenose dolphins...
are present. This can be explained by the fact that after the reproductive period (autumn/winter) adult individuals of *M. liza* move from the marine environment to the estuaries and coastal region of southern Brazil in small and sporadic schools, mixing with juvenile individuals (Herbst and Hanazaki 2014, Lemos et al. 2014). In this work, the size analysis of individuals caught in summer showed a predominance of juveniles and the occurrence of few adults, only. We believe that this mixture of cohorts associated with the opportunistic behavior of *T. truncatus* and the tarrafeiros is the explanation for this result. Therefore, fishermen and bottlenose dolphins capture mullets that are available in the environment, where their sizes vary seasonally according to the life cycle of *M. liza*.

Several authors demonstrate the importance of water temperature variation and salinity in the reproductive/migratory cycle of *M. liza* (Vieira and Scalabrin 1991, Vieira 1991, Vieira et al. 2008, Lemos et al. 2014, 2016). According to them, the decrease in water temperature and the increase in salinity in the estuaries, associated with the southern wind that promote the intrusion of marine water in estuaries during the austral autumn act as “triggers” for sexually mature individuals of *M. liza* runs to the ocean. In this reproductive migration period, called the ‘corrida da tainha’, artisanal fishermen intensify fishing efforts throughout the southern Brazilian coast, raising the quantities of mullets caught within the estuaries (Vieira et al. 2008, Herbst and Hanazaki 2014, Lemos et al. 2016, Sant’Ana et al. 2017). Nevertheless, water temperature and salinity did not have representative effects on the explicability of the models of occurrence and abundance of mullet in the cast net fishery at TRE.

The interactions between mullets, bottlenose dolphins, fishermen and environmental variables are complex, and difficult to distinguish the possible cause-and-effect relationships. The use of GLM models helped to reveal that the time of year (months) followed by the number of bottlenose dolphins were the main factors explaining the presence of mullet in the fishermen’s catches. The number of bottlenose dolphins and the spatial distribution of fishermen along the banks of the entrance channel of TRE together explained more than 30% of mullet CPUE. Fishermen follow the movement of bottlenose dolphins over the channel, and thus the fishing sector used appears to vary seasonally: during autumn and winter the fishing occurs in the interior of the channel in the estuary, whereas during spring and summer the fishing occurs primarily near the adjacent coastal zone. Therefore, the higher the number of bottlenose dolphins in a specific fishing sector, the higher the probability that tarrafeiros will catch mullet in higher quantities.

No significant seasonal variations of mullet abundance were observed. This is unusual because it is known that in periods of reproductive aggregation of *M. liza* the catches of artisanal fisheries increased notably (Vieira et al. 2008, Herbst and Hanazaki 2014, Lemos et al. 2014). This may be associated with the way cast nets operate and the fishing dynamics. Unlike gillnet fishing, for example, where large sets of nets remain anchored for 24 hours away from the coast in estuarine channels (Kalikoski and Vasconcellos 2013), the tarrafeiros remain in the sand with limited throwing distance and often performed blindly. Thus, the mullets available for the tarrafeiros are in the shallow areas, while the dense shoals move in deeper and inaccessible areas of the channel. The importance of bottlenose dolphins (demonstrated in the models) is precisely to make mullets accessible for fishermen, bringing the fish from deeper regions to shallow areas, increasing the chances of catching them (Simões-Lopes et al. 1998). This behavior is pronounced during the autumn, when the concentration of mullets in the estuary increases. On the other hand, when the abundance of mullet is reduced in the estuary (spring and summer) tarrafeiros direct their efforts to the estuarine mouth near the ocean (sector S1 and S2; Figs 1–7), usually without the presence of the bottlenose dolphins. In this situation mullet schools are a mixture of large adults, returning from marine reproductive areas, and mid-size juveniles that use the surf zone as transient nursery area (Vieira and Scalabrin 1991, Lemos et al. 2014). Therefore, catches and fishing effort tend to remain constant throughout the year.

Historically, estuaries around the world are being degraded by anthropic activities, resulting in the depletion of aquatic life (Lotze et al. 2006). The TRE is located between two vocational towns, influenced by tourism, real estate business and oil industry, challenging the resilience of the system. Local artisanal fishermen report that environment protection of the estuary is neglected and should be one of the main causes of mullet abundance reduction and low frequency of bottlenose dolphins in the region. Zappes et al. (2011) reported on the apprehensiveness of tarrafeiros and suggested that the main factors that hamper the cooperative fishing in TRE are: lack of vessel traffic control, the presence of illegal (unregulated) fishermen and the growing of industrial fishing activity in southern Brazil.

According to Daura-Jorge et al. (2012) social connections between *T. truncatus* individuals facilitate the maintenance of cooperative behavior with fishermen through social learning and may be interpreted as a “cultural process”. In southern Brazil, fishing for mullet is a cultural tradition, also. Both bottlenose dolphins and fishermen visit coastal and estuarine environments because those are the preferential habitats of their common prey. The mutual benefit of this cooperation is catching mullet, but the implications of mullet population dynamics and fishery exploitation for this complex human-dolphin relationship have been neglected in prior studies.

*Mugil liza* migration period overlaps with the industrial purse seine fleet fishing season (May-July) when the licensed fleet is motivated to capture mullet by the high value of the roe (Lemos et al. 2016, Sant’Ana et al. 2017). Although Patos Lagoon is considered the main nursery area of mullet in southern Brazil (Vieira and Scalabrin 1991, Herbst and Hanazaki 2014, Lemos et al. 2014), juveniles are fished all year at southern Brazilian estuaries (Lemos et al. 2014). Since 2004 *M. liza* was ranked as overexploited (MMA 2004) and the actual management plan for
the species (MPA/MMA 2014) is still not effective. According to Lemos et al. 2016, it is imperative to manage the mullet resource at adequate levels to prevent the stock collapse. There is strong scientific evidence that the southern population of *M. liza* (Mai et al. 2014) is overfished, particularly due to fishing pressure during the reproductive migration period (Gonzáles-Castro et al. 2015, Lemos et al. 2014, Sant’Ana et al. 2017). Increasing concern about the viability of the southern population of *M. liza* has led Brazilian authorities to enact stricter regulations on fishing, but these measures have been largely ineffective, systematically transgressed and, apparently, inadequate for ensuring the maintenance of mullet population abundance, as showed by the results of the latest published stock assessment of this species (Sant’Ana et al. 2017). There is, therefore, a clear need for better management to safeguard the sustainability of the southern population of *M. liza*.

Although the coastal population of *T. truncatus* is not endangered (Hammond et al. 2012) their conservation is relevant to tarrafeiros at TRE. The cast net fishermen in this estuary should also be protected. The artisanal fishermen suffer from economic exclusion, social marginalization, class exploitation, political disempowerment, environmental change, ecological marginalization, loss of identity, and disconnection from resources and from other fishermen (Nayak et al. 2014). Therefore, the management measures for the population of *M. liza* in southern Brazil is fundamental to ensure the maintenance of the basis of the rare and beneficial interaction between humans and bottlenose dolphins.

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Cooperation between dolphins and cast net fishermen


M. L. Santos et al.


Editorial responsibility: Cassiano Monteiro Neto

Author Contributions: MLS VML and JPV designed the experiment, analyzed the data, wrote the paper; MLS conducted the experiment.
Competing Interests: The authors have declared that no competing interests exist.

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