



Comparison of predator–prey interaction models for fish assemblages from the neotropical region

P.A. Piana^a, L.C. Gomes^{b,*}, A.A. Agostinho^b

^a Graduate Course in Inland Aquatic Environments, Department of Biology, Maringá State University, Avenida Colombo, 5790 Maringá, Paraná, Brazil 87020-900

^b Nucleus of Research in Limnology, Ichthyology and Aquaculture (Nupelia), Department of Biology, Maringá State University, Avenida Colombo, 5790 Maringá, Paraná, Brazil 87020-900

Received 9 July 2004; received in revised form 1 June 2005; accepted 6 July 2005

Available online 8 September 2005

Abstract

Predation is one of the main fish assemblages structuring force in many aquatic ecosystems. Finding a functional relationship between predator and prey that improves our understanding of this process is a challenge to ecologists. In order to evaluate this interaction, several models have been created, each one of them representing a specific biological mechanism. Although, these models have not been intensively confronted against empirical data for some group of organisms, such as fish, they are the scientific base to predator–prey systems. In this paper, some models, with distinctive assumptions, were fitted to the same fish assemblage data set from an isolated lagoon of the upper Paraná River floodplain using non-linear procedure. Then, they were compared in order to explore the mechanisms (represented by model assumptions) that could be acting on that assemblage. We used the Lotka–Volterra model and its modifications to consider carrying capacity, saturation effect, ratio-dependence predator–prey trophic function, and environmental heterogeneity. To fit the models, all prey species were grouped as prey and the same was done to predators. Result of this approach allowed us to make four suggestions about predator–prey relationship for the environment studied: (i) predators were efficient in controlling prey populations; (ii) the best fitted model was found with the sigmoidal functional response; (iii) density-dependence presented better fit than ratio-dependence predator–prey trophic function; (iv) refuges did not present intense interference in the predator–prey relationship. Therefore, comparisons of models that represent different assumptions showed to be a good tool in evaluating main mechanisms acting on the relationship between predators and prey in a fish assemblage.

© 2005 Elsevier B.V. All rights reserved.

Keywords: Predator–prey; Modelling; Functional response; Refuge; Fish

1. Introduction

Predation is one of the main forces that affect abundance and distribution of fish assemblages in many

* Corresponding author. Tel.: +55 44 261 4662; fax: +55 44 263 1424.

E-mail address: lcgomes@nupelia.uem.br (L.C. Gomes).

aquatic ecosystems (Angermeier, 1992; Nilsson, 2001; Hixon et al., 2002). Finding a functional dependence between predator and prey, and determining the dominant mechanism is a great challenge for ecologists (Jost and Ardity, 2000), and to achieve this, several models have been developed over the past century. For example, Lotka (1925) and Volterra (1926), independently, developed a simple model with differential equations. Over time this model has been modified and adapted to specific conditions. Although the alternative models have not been sufficiently tested with empirical data (Harrison, 1995), they are the scientific basis for predator–prey systems. Each model represents a set of biological assumptions that can be analyzed by fitting and comparing its equations to data (Smith, 1996).

Among the models that represent predator–prey relationships, models which include the carrying capacity of the prey and the saturation effect in the predator functional response are more realistic (Harrison, 1995). Carrying capacity was incorporated into the models by the logistic expression developed by Verhulst (Gotelli, 2001). In relation to the saturation effect, Holling (1959) developed two alternative forms of functional responses to be used in the Lotka–Volterra predation model. His equations considered a maximum limit for the predator consumption rate. Arditi and Ginzburg (1989) suggested that predators share prey amongst themselves before they begin the search for food, and therefore the functional response depends on the ratio between prey and predators, instead of the prey density reported by Holling (1959). The above model modifications only consider population characteristics and ignore environmental heterogeneity. To address this shortcoming, Rosenzweig and MacArthur (1963) developed a series of graphic models. These authors suggested that presence of refuge can lead to a stable equilibrium. The simple premise that a certain constant number of prey is not at predation risk is used to incorporate the effect of refuges. This premise produces the effect reported by Rosenzweig and MacArthur (1963) and it also allows comparison with other models.

Theoretically, most of the above mentioned predation models suggest that predator–prey systems present oscillatory tendencies (Case, 2000). However, this prediction has not been corroborated in experiments, possibly due to the fact that predators

consume their prey completely and then die from starvation (Harrison, 1995). In addition, experiments in the laboratory, besides being expensive and time consuming, involve artificial conditions and usually consider spatial and temporal scales inappropriate for extrapolation to reality (Abrams and Ginzburg, 2000). On the other hand, time series data gathered from the environment gives a more realistic representation of predator–prey interactions and, on these data, one can apply non-linear procedures to fit models and optimize parameter estimates (Jost and Ardity, 2000).

In this paper, we fitted the Lotka–Volterra predation model and some of its modifications to a time-series dataset of the fish assemblage of Osmar Lagoon, located in the upper Paraná River floodplain. This procedure is not common in the literature and allowed us to evaluate possible factors that could be driving predation intensity. Specifically we address the following questions: (i) Are predators efficient in controlling prey populations? (ii) Which is the best functional response that represents prey consumption? (iii) Is the functional response better modeled by prey–predator ratio? (iv) Are refuges important in determining predator–prey relationships?

2. Materials and methods

2.1. Study site, sampling and dataset

Osmar Lagoon is located on Porto Rico Island in the upper Paraná River floodplain (Fig. 1), and is disconnected from the main river. The lagoon is ephemeral, with a mean depth of 1.1 m. Surface area of Osmar Lagoon is nearly 600 m², with a certain amount of floating macrophytes. Agostinho et al. (2001) and Okada et al. (2003) reported that predation is one of the main structuring forces of fish assemblages in lagoons of the upper Paraná River floodplain, especially in dry periods, and even for shorter periods of time than is considered here. Fish species that inhabit floodplain lagoons take advantage of dry periods, when their abundances increase.

Data were collected quarterly from February 2000 to May 2001, using seine nets (20 m long; 0.8 cm mesh size) in the marginal area of the lagoon. For analysis, data are presented as density (number of individuals/100 m²). In order to fit the models, the fish species

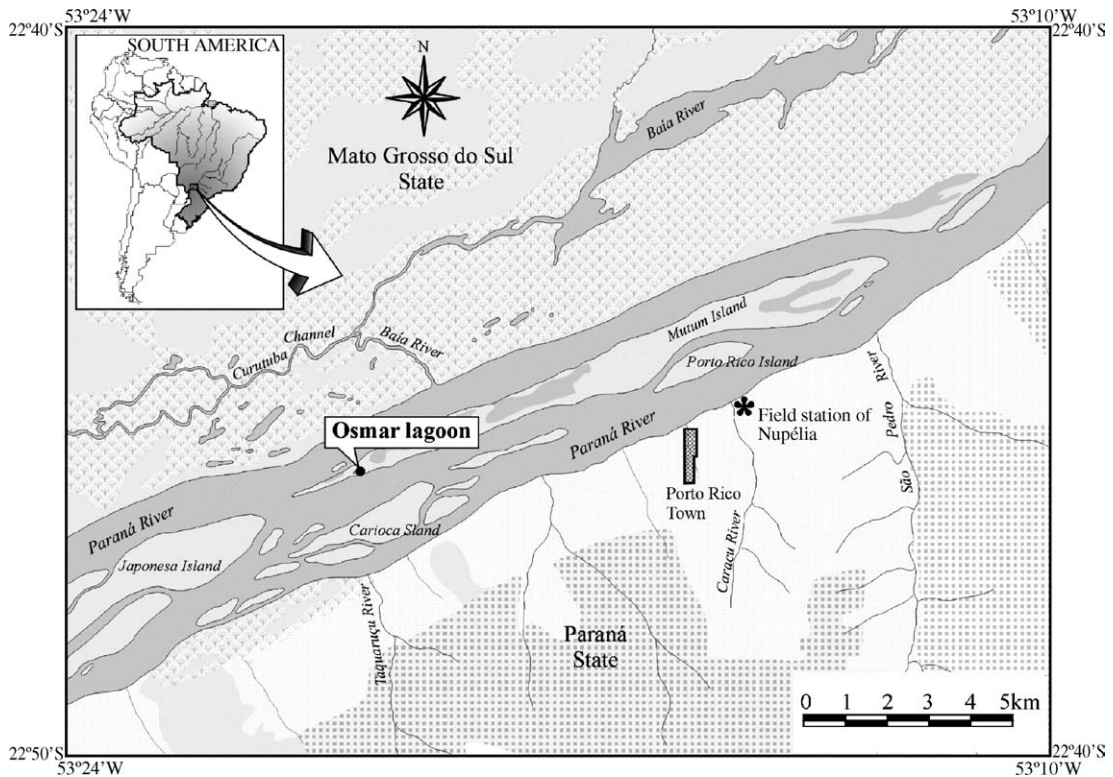


Fig. 1. Map of the upper Paraná River showing the location of the Osmar Lagoon.

collected were classified as either prey or predator species. During the study period, Osmar Lagoon remained isolated from the Paraná River due to the absence of floods. This allows us to meet the assumption of no migration (closed populations), and therefore it was possible to use the general approach of predation models.

The prey group constituted 16 small species (total length < 20 cm) that are present in the diet of piscivorous fishes (Agostinho et al., 1997; Hahn et al., 1997, 2000, 2004). This group was characterized by species with short life cycles, belonging to the families Characidae (Tetragonopterinae, Aphyocharacinae, Cheirodontinae and Characinae) and Curimatidae. All species within these families are able to complete their life cycles in isolated lagoons. They have high fecundities, and spawning is total or in batches. These species are abundant in most lagoons of the floodplain (Agostinho et al., 2001; Okada et al., 2003), especially during dry periods.

The predator group was formed by *Acestrorhynchus lacustris* and *Hoplias* aff. *malabaricus*, two species that live in lentic habitats of the floodplain. These species do not migrate for spawning (Agostinho et al., 2003), and are also very abundant in most lagoons, especially during dry periods. Both species reproduce in lentic environments of the floodplain in several batches (parceled), during the spawning season that extends from September to March (Vazzoler and Menezes, 1992; Vazzoler et al., 1997). These predators feed according to availability of prey (Hahn et al., 1997). *A. lacustris* is an opportunist active predator and the length of prey limits its predation. Mean size of prey consumed increases with the size of the predator, but larger individuals also consume small prey (Hahn et al., 2000). *H. aff. malabaricus* feeds mainly at night when it ambushes shallow areas close to the margin, usually associated with aquatic plants (Sabino and Zuanon, 1998). This species may ingest individuals of approximately its

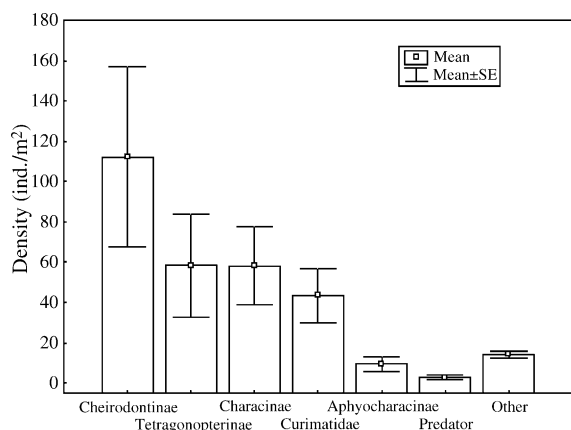


Fig. 2. Abundance (individuals/100 m²) of the fish assemblage in Osmar Lagoon, upper Paraná River floodplain, during the period from February 2000 to May 2001.

own size (Winemiller, 1989). The predator and prey species, when taken together, comprised 95.25% of the total abundance registered in Osmar Lagoon (Fig. 2).

Although the Lotka–Volterra model and its modifications have been elaborated based on interactions between populations of a prey and a predator, empirical data of two populations that only interact one with the other in natural environments are difficult to find. This is especially true in the neotropical region, because of its tremendous biodiversity and high number of small-sized species (Matthews, 1998). The high availability of small-sized prey species is allied to great dietary plasticity in the predators (Lowe-McConnell, 1987; Moyle and Cech, 1988; Wootton, 1990; Hahn et al., 1997). Therefore, to fit the models we pooled prey and predator species into groups. This approach was also used by Winemiller (1996) to study neotropical floodplain food webs and is also largely used in ecosystem modelling (e.g. Kemp and Boynton, 2004; Angelini and Agostinho, 2005; Gamito and Erzini, 2005). This procedure, however, does not impede the application of the general model approach, because it is expected that the groups formed (prey and predators) should answer as single species as shown by Murdoch et al. (2002). However, interpretation of parameters in the model changes from species characteristics to “functional characteristics” representing the mean value of a group.

2.2. Description of models

Based on the principle of mass conservation (Ginzburg, 1998) and the simplification of population dynamics processes from birth to death, the structural base for predation models that present temporary continuity is:

$$\begin{aligned} \frac{dV}{dt} &= f(V)V - g(V)P =: G_V(V, P) \\ \frac{dP}{dt} &= i(V)P - j(P)P =: G_P(V, P), \end{aligned} \quad (1)$$

where V and P are the population densities of prey and predator, respectively, G_V and G_P the integrated functions, $f(V)$ the prey growth function when predators are absent, $j(P)$ the predator growth function when prey are absent, $g(V)$ the functional response which represents the consumption of prey by a predator, and $i(V)$ is the numeric response which represents the functional response effect on predator population growth (Jost and Ardity, 2000). Modelling these four components provides the study of the predator–prey relationship. The

Table 1
Expressions used in the structural base 1 to construct models that represent distinct biological assumptions

| Expression | Biological assumptions |
|---|---|
| 1. $f(V) = r$ | Exponential growth |
| 2. $g(V) = \alpha V$ | Type I functional response |
| 3. $i(V) = \beta g(V)$ | Numerical response (linear dependence with functional response) |
| 4. $j(P) = q$ | Constant per capita death rate of the predator population |
| 5. $f(V) = r \left(1 - \frac{V}{k}\right)$ | Logistic growth (carrying capacity) |
| 6. $g(V) = \frac{sV}{(h+V)}$ | Type II functional response |
| 7. $g(V) = \frac{sV^2}{(h^2+V^2)}$ | Type III functional response |
| 8. $g(V) \Rightarrow g(V, P) = \frac{aV/P}{(h'+V/P)}$ | Ratio-dependence type II functional response |
| 9. $g(V) = \alpha(V - v)$ | Type I functional response with prey refuge |
| 10. $g(V) = \frac{s(V-v)}{[h+(V-v)]}$ | Type II functional response with prey refuge |

Parameters are: r , intrinsic rate of increase of the prey population; α , capture efficiency; β , food conversion efficiency; q , per capita death rate of the predator population; k , carrying capacity of the environment; s , maximum rate of prey consumption per predator; h , half-saturation constant; a and h' , constants equivalent to s and h ; v , constant number of prey protected by refuges.

expressions used in the structural base 1 to construct models that represent the aforementioned components are presented in Table 1.

2.3. Method of adjustment and selection criterion

In order to solve the system of differential equations, we used the Dassi subroutine (Petzold, 1982), which uses a FORTRAN code source and is based on formulas of back differentiation. This subroutine has been used to solve problems in engineering, especially for systems that present differential/algebraic equations. As required by the subroutine, equations were written in the following form:

$$F = \begin{cases} F = \sum_{i=1}^n [(V_{obs_i} - V_{est_i})^2 + (P_{obs_i} - P_{est_i})^2] & \text{objective function 1,} \\ F = \sum_{i=1}^n \left[\left(\frac{V_{obs_i} - V_{est_i}}{V_{obs_i}} \right)^2 + \left(\frac{P_{obs_i} - P_{est_i}}{P_{obs_i}} \right)^2 \right] & \text{objective function 2,} \\ F = \sum_{i=1}^n F_i = \sum_{i=1}^n \{ [w_v(V_{obs_i} - V_{est_i})]^2 + [w_p(P_{obs_i} - P_{est_i})]^2 \} \\ \frac{w_v}{w_p} = \frac{\sigma_p}{\sigma_v} \Rightarrow w_p = 1 \therefore w_v = \frac{\sigma_p}{\sigma_v} & \text{objective function 3,} \end{cases}$$

$$G \left(t, V, P, \frac{dV}{dt}, \frac{dP}{dt} \right) = 0$$

For parameter optimizations, we used the Simplex subroutine (Nelder and Mead, 1965; Edgar and Himmelblau, 1988), which also is FORTRAN based. The Simplex subroutine determines the minimum point of an objective function. Its tolerance was fixed at 1×10^{-5} , i.e. the process converged when the difference between two successive values of the objective function was less than the tolerance. The magnitude of the parameter signs was guaranteed by using the absolute value. The advantage of this subroutine is that it only needs the values of the objective function. For other methods, such as Newton–Raphson, it is necessary to calculate the derivative.

As an initial condition, the first pair of observations of predator–prey data were used, and all models were forced to start at this point. Another condition necessary to use the algorithm is the definition of the objective function to be minimized. In systems where magnitude (variation) of variables are very different, such as

the ones of predation dynamics, it is necessary to make an adjustment in the model errors to allow comparison between the groups and to give the same level of relevance.

In order to avoid priority for any group when fitting the models, we looked at the results of three objective functions. This was done only for the original Lotka–Volterra predation model, and the best function was used for further analyses. The objective functions used were: (1) the sum of the squared deviations (the least square), (2) the sum of the relative squared deviations (relative squared minimum), and (3) the sampling standard deviation of prey as a weight of the deviation of the predators and vice-versa, as follow:

where F is the objective function or the function to be minimized, n the number of data in the time series, V_{obs} the observed density of prey, V_{est} the estimated density of prey, P_{obs} the observed density of predators, P_{est} the estimated density of predators, and σ_p and σ_v are the sampling standard deviations of predator and prey groups, respectively. Other forms of functions to be minimized can be found in Harrison (1995), Hilborn and Mangel (1997) and Jost and Ardity (2000).

Qualities of the fitting were verified for the models by their percent of explanation of the weighted total variation, as follow:

$$ET = \sum_{i=1}^n \{ [w_v(V_{obs_i} - \bar{V})]^2 + [w_p(P_{obs_i} - \bar{P})]^2 \}$$

$$R^2 = \frac{ET - F}{ET}$$

where ET is defined here as the considered total variation, and \bar{V} and \bar{P} are the mean densities of prey and predators, respectively. R^2 supplies some indication of the fraction of the weighted total variation explained by a model and we used it as a criterion for

model comparisons. Harrison (1995) used a similar approach but he did not consider the weighted total variation. In addition, when a given parameter of a model was important to discriminate two mechanisms of predation, a sensitivity analysis was performed for that parameter. First, we found the values of the parameter that minimize the objective function, then the other parameters were kept fixed and the values of the parameter of interest were changed and the result of the objective function was checked (sensu Jost and Ardity, 2000). We assume that this analysis is more informative than the confidence interval because the sensitivity shows model responses when the parameter takes different values.

3. Results

To begin our analyses, we observed which objective function provided better result for the original Lotka–Volterra model. Both objective functions 1 and 2 presented potential problems. The former prioritized adjustment to prey data, possibly due to differences in the magnitude of variation in relation with predator data, whereas the second only converged when tolerance was increased. Objective function 3, however, was found to be more efficient because it represented both variables (predators and prey) in the same magnitude (Fig. 3). Therefore, all models considered here were adjusted in order to minimize this objective function. The expressions used in the structural base 1 to obtain the models that express the relationship between predator and prey, with the summary of the respective results regarding the fitting qualities, are presented in Table 2.

Table 2
Results of fitting the different models considered (M_i)

| M_i | Expression | NP | F | R^2 (%) |
|-------|----------------|----|---------|-----------|
| M_1 | 1–4 | 4 | 4.8602 | 95.12 |
| M_2 | 2–5 | 5 | 4.8603 | 95.12 |
| M_3 | 1, 3, 4 and 6 | 5 | 1.1602 | 98.83 |
| M_4 | 1, 3, 4 and 7 | 5 | 0.9638 | 99.03 |
| M_5 | 1, 3, 4 and 8 | 5 | 31.9631 | 67.88 |
| M_6 | 1, 3, 4 and 9 | 5 | 4.8602 | 95.12 |
| M_7 | 1, 3, 4 and 10 | 6 | 1.1592 | 98.84 |

Expression refers to the numbers in the text used in the structural base 1. NP, the number of estimated parameters; F , the objective function 3; R^2 , the percentage of the weighted total variation explained by the model.

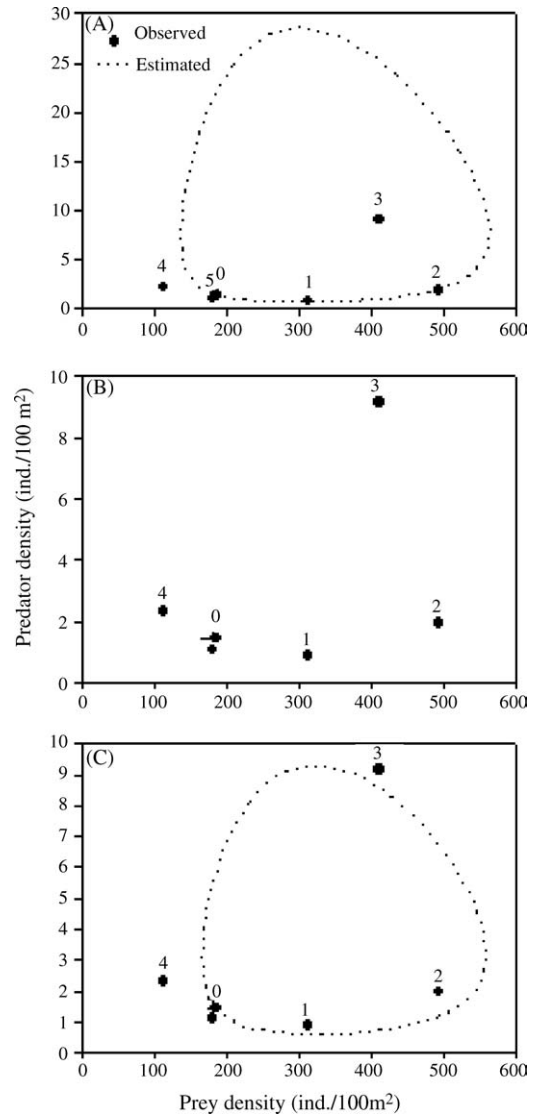


Fig. 3. Results of the Lotka–Volterra predator–prey model fitting to data from Osmar Lagoon, Paraná River floodplain. Objective functions 1 (A), 2 (B) and 3 (C) were minimized. The numbers represent the order of the time series in the population plan.

Comparing the models M_1 and M_2 (Table 2; R^2), it was observed that incorporation of carrying capacity did not increase the percent explanation of the weighted total variation. Adjusted value for the parameter k in model M_2 was well above the maximum value of population density presented by the prey group (Table 3). In this case, the parameter k can be ignored because the

Table 3
Values of the optimized parameters

| Parameters | M ₁ | M ₂ | M ₃ | M ₄ | M ₅ | M ₆ | M ₇ |
|------------|----------------|------------------------|----------------|----------------|----------------|------------------------|------------------------|
| <i>r</i> | 0.6860 | 0.6861 | 0.7419 | 0.8047 | 2.3750 | 0.6859 | 0.7408 |
| <i>α</i> | 0.2148 | 0.2148 | – | – | – | 0.2148 | – |
| <i>β</i> | 0.0469 | 0.0470 | 0.0572 | 0.0610 | 0.0101 | 0.0470 | 0.0577 |
| <i>q</i> | 3.2682 | 3.2686 | 4.4420 | 4.5387 | 1.7440 | 3.2697 | 4.4724 |
| <i>k</i> | – | 7.8 × 10 ⁰⁷ | – | – | – | – | – |
| <i>s</i> | – | – | 2.6199 | 109.1350 | – | – | 236.4070 |
| <i>h</i> | – | – | 625.2740 | 183.6720 | – | – | 617.4910 |
| <i>a</i> | – | – | – | – | 226.2440 | – | – |
| <i>h'</i> | – | – | – | – | 0.0699 | – | – |
| <i>v</i> | – | – | – | – | – | 5.6 × 10 ⁻⁷ | 1.1 × 10 ⁻⁶ |

M_{*i*} refers to the different models considered and the parameters were previously defined in the Section 2.

term that represents the unused fraction of the carrying capacity in the model tends to zero. Therefore, the equation of exponential growth is preferable over the logistic. To elucidate the effect of this result, a sensitivity analysis was performed for the parameter *k*. As the value of the carrying capacity increased, the value of the objective function decreased (Fig. 4A). Differentiate tendencies in growth when at high population densities were observed for prey in the theoretical absence of predators (Fig. 4B).

Confronting models M₁, M₃ and M₄ we observed that the best fit was obtained using the functional response type III, followed by the type II. The linear response originally used by Lotka and Volterra presented the smallest value of *R*² (Table 2).

Results of models M₃ and M₅ indicated that the functional response dependent on the prey density was preferential to ratio-dependent (Table 2). Comparing

models M₁ and M₃ with models M₆ and M₇ (Table 2), it can be observed that the use of the parameter *v* representing refuge did not contribute to a better adjustment. It was noticed that the values obtained for this parameter in models M₆ and M₇ were close to zero (Table 3). Sensitivity analysis suggested that as the number of prey not exposed to predation increases, the value of the objective function also increases, i.e. model error increases (Fig. 5).

A visual inspection of the weighted deviations between observed and estimated densities indicated that both groups (predators and prey) obtained the same level of relevance during fits and does not show temporal tendencies that could have invalidated conclusions (Fig. 6). However, the model with ratio-dependence in the functional response suggested that prey would be locally extinct, contradicting the observations (Fig. 6G).

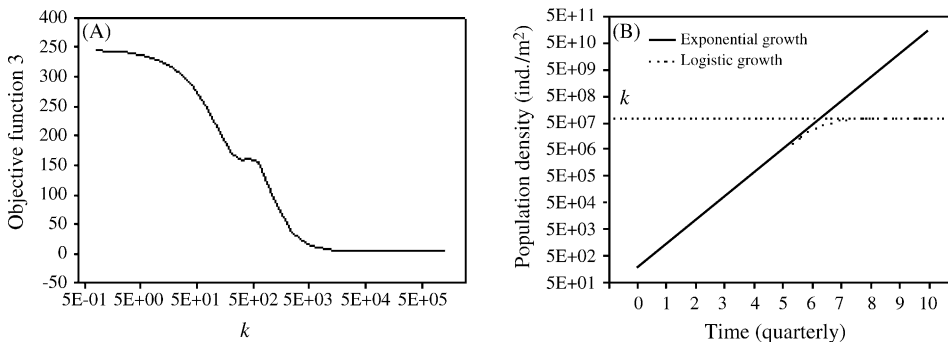


Fig. 4. Sensitivity analysis for the parameter *k* (A) and hypothetical representation of the population growth of prey when predators are absent (B).

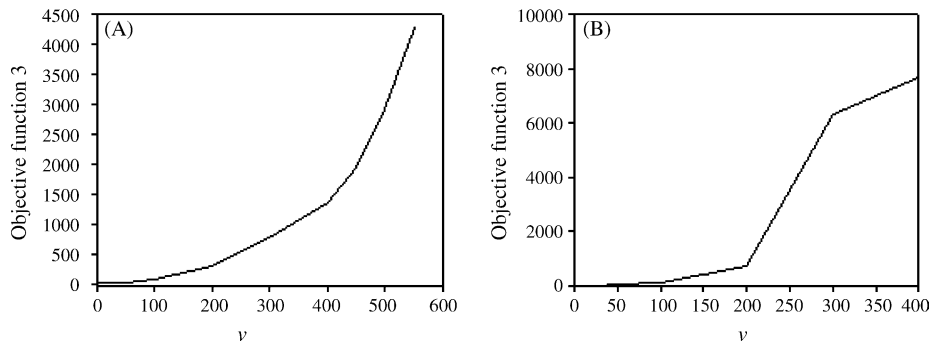


Fig. 5. Sensitivity analysis for the parameter v in the models M_6 (A) and M_7 (B).

4. Discussion

In the non-linear adjustment procedure, it is necessary to define the function to be minimized, in our study, the objective function. This can be seen as the key part of model adjustment to data (Jost and Ardity, 2000). In a similar work, Harrison (1995) used the objective functions 1 and 2 to adjust 11 different models to data obtained by Leo Luckinbill's experiments in 1973, but he also did not get good results. He observed that the adjustment prioritized density picks and he obtained better results when using a categorical factor for these. One of the ways to remove the effect of the variation scale is the Z transformation, that converts the original data into new groups of data with averages equal to zero and variances equal to 1 (Dowdy and Wearden, 1991). However, interpretation of the parameters becomes practically impossible. The advantage of using the prey sampling standard deviation as weight (or size of the uncertainty, sensu Hilborn and Mangel, 1997) to predator's deviation and vice-versa is that they give good fitting and they allow interpretation of the parameters. However, it is assumed that the degree of uncertainty for each observation is proportional to its magnitude of variation.

Usually, magnitudes of predator and prey fluctuations differ for factors above 10. For a population to present threshold fluctuation in density between two points above zero, it necessarily should be regulated by one or more factors that allow it to present tendencies to increase number of individuals when in low densities and to decrease when in high densities (Hixon et al., 2002). In population growth of a single species, it is consensus that the logistic function is preferential

and more realist than the exponential. However, in the context of interactions, more specifically predation, the interpretation is slightly different. If predators are efficient, the term that represents the part not used of the carrying capacity can be neglected, because it will not influence the adjustment of the model and predator density will be sufficient to regulate prey density. Thus, even if the predictive power and the adjustment quality have increasing tendencies with the addition of parameters (Hilborn and Mangel, 1997), results of models M_1 and M_2 , based on sensitivity analysis of the parameter k , suggest that predators maintained the prey population density at low values if compared to the values in their absence (when carrying capacity would be a limiting factor). Therefore, predators appear to be the main agent in controlling prey populations in the lagoon. This was also observed by Agostinho et al. (2001) and Okada et al. (2003) studying other lagoons in the area, where the main predator was *H. aff. malabaricus*, as in this study.

To model functional and numerical responses is not an easy task. Functional response seems to be well described by the prey-dependence approach, while the numerical response probably would be more realistic if it considers the energy quality and the load of nutrients along time, but for our purpose the linear relationship with the functional response is enough to compare models and, in this paper we are not primarily interested in numerical response. However, both functional response types II and III were adjusted in a reasonable way, with higher values of R^2 than obtained for the linear relationship in the Lotka–Volterra model. These two functional responses provided a larger flexibility along the gradient of variation of prey

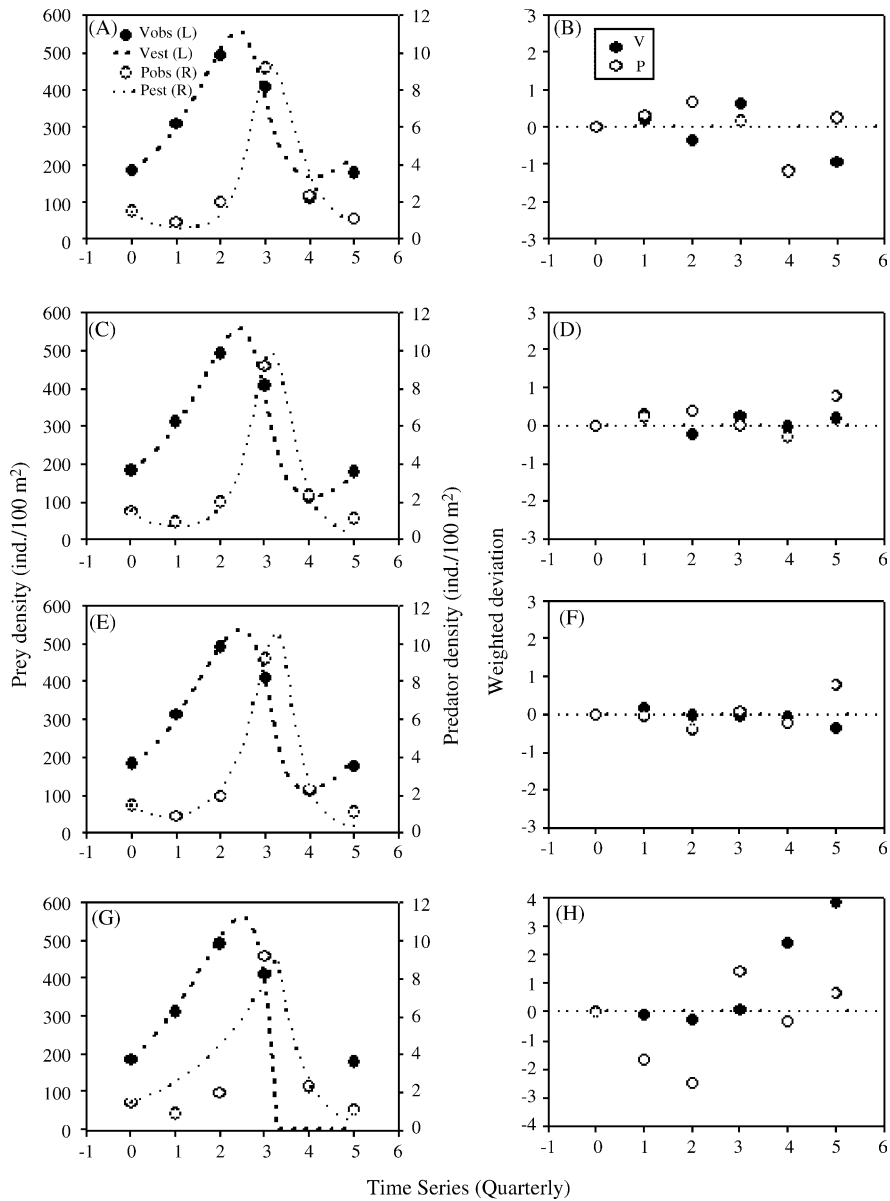


Fig. 6. Observed values of the prey (full circles) and predator (empty circles) population densities, compared with the simulated prey (stippled line) and predator (line with long dashes) densities through the models M₁ (A), M₃ (C), M₄ (E) and M₅ (G), generating the weighed deviations of the prey and predators densities (B, D, F and H, for each model, respectively).

density, resulting in better adjustment. This flexibility suggests that predators have reduced consumption rate when prey density is low, and they increase this rate gradually as prey density increases, until they reach an asymptote (maximum rate of prey consumption per predator). Two factors can produce this asymptote:

first, predators may become satiated and second, the time available for foraging is restricted (Wootton, 1990). This feeding behaviour is in agreement with optimum foraging theory, which predicts that predators maximize their cost-benefit relationship (Gerking, 1994). Harrison (1995) observed that the quality

of predator–prey models fitting for populations of *Didinium* and *Paramecium* got significantly better when he used the sigmoidal form of functional response.

Although the use of functional responses is intuitive and necessary to describe the dynamics involved in systems of predators and prey, notable problems may emerge with this approach (Berryman, 1992). For instance, functional response types II and III were formulated in short time scales (minutes or hours), while the differential equations, in which they are inserted, operate in longer temporal scales (months or years). To overcome this problem, Arditi and Ginzburg (1989) suggested that functional responses should be expressed as a function of the ratio between prey and predator. The main justification, defended by several authors (Arditi and Ginzburg, 1989; Arditi et al., 1991; Arditi and Saïah, 1992; Gutierrez, 1992), is based on the fact that predators share prey amongst themselves before they begin the search for food. Other studies showed that when imposing this assumption on classic models of predation, it generates a positive inclination in the predator isocline, avoiding the paradox of enrichment described by Rosenzweig (1971) (Arditi and Ginzburg, 1989; Berryman, 1992; Ginzburg and Akçakaya, 1992). However, the results obtained here (Fig. 6G and H), when compared with both functional responses of Holling (1959), did not support this mechanism. In fact, both piscivores from this study do not hunt in group or present other social behavior (Paiva, 1972). Abrams (1994) and Gleeson (1994) criticize the work of Arditi and Ginzburg (1989) because it was based on empirical evidence, escaping from the traditional process of formulation of functional responses. Harrison (1995) concluded that ratio-dependent functional response definitively did not act in the experiments of Luckinbill.

Indirectly, it is possible to make some inferences on the role of spatial heterogeneity on the predator–prey system. Usually, presence of refuges produces a more stable system. Among the classic experiments of Gause in 1934 (Smith, 1996), cycles of population fluctuations appeared for predators and prey only after the incorporation of spatial heterogeneity. Subsequent studies, using the premise that spatial heterogeneity supplies micro-habitats where the risk of predation is minimum or absent, indicated that the incorporation of refuges in modelling functional response may

act as a stabilization factor for the system or may drive predator's population to extinction depending of how prey use it (Ruxton, 1995; Ramos-Jiliberto and González-Olivares, 2000; González-Olivares and Ramos-Jiliberto, 2003). This subject was also revised by Srinivasu and Gayatri (2005). Results obtained by the models M_6 and M_7 , indicated that, if refuges existed, they were not necessary to represent the relationship between predator and prey in Osmar Lagoon. This could be due to the fact that the predator *H. aff. malabaricus* feeds near macrophytes in shallow areas (Sabino and Zuanon, 1998). The interference of refuges on predation can be more strongly linked to periods of low prey population density, when the risk of local extinction is larger. This result has implications both to fisheries management and conservation, given the system is stable and without refuges. Creating refuges from predation could disrupt the system leading to increases or decreases in predator and/or prey populations.

5. Conclusion

Fitting a set of functions to data provides opportunity to study ecological interactions, with definition of the objective function as the key stage that will determine subsequent conclusions. Predator–prey relationships for which the magnitudes of the scales of density variation differ, in most cases for factors above 10, need to be weighted to provide the same level of relevance for both populations. We suggest the use of the sampling standard deviation as a weighting factor. As a result of this approach, we can draw four conclusions regarding the dominant mechanisms that acted in the relationship between predator and prey fishes in Osmar Lagoon. First, predators maintained the prey population density at values below those that would theoretically occur in the absence of predation, and, apparently, they constitute the main controlling factor of prey populations. Second, the best adjustment was obtained using the sigmoidal functional response that provided larger flexibility in the rate of consumption along the gradient of prey variation. Third, the functional response of predators only depended on the prey-density and not on the ratio-density. Fourth, refuges did not interfere in an outstanding way in the relationship between predators and prey. We emphasize that these

conclusions are limited to the system and the time studied.

Acknowledgements

We thank the Brazilian Long Term Ecological Research Program (Programa Ecológico de Longa Duração, PELD) Site 6 for financing this research. We also thank the Nucleus of Research in Limnology, Ichthyology and Aquaculture (Nupelia) of Maringá State University, Brazil for providing the infrastructure necessary to conduct this study.

References

- Abrams, P.A., 1994. The fallacies of “ratio-dependence” predation. *Ecology* 75 (6), 1842–1850.
- Abrams, P.A., Ginzburg, L.R., 2000. The nature of predation: prey-dependent, ratio dependent or neither? *Tree* 15 (8), 337–341.
- Agostinho, A.A., Hahn, N.S., Gomes, L.C., Bini, L.M., 1997. Estrutura trófica. In: Vazzoler, A.E.A.M., Agostinho, A.A., Hahn, N.S. (Eds.), *A Planície de Inundação do Alto Rio Paraná: Aspectos Físicos, Biológicos e Socioeconômicos*, Eduem, Maringá, pp. 229–248.
- Agostinho, A.A., Gomes, L.C., Zalewski, M., 2001. The importance of floodplains for the dynamics of fish communities of the upper river Paraná. *Ecohydrol. Hydrobiol.* 1 (1–2), 209–217.
- Agostinho, A.A., Gomes, L.C., Suzuki, H.I., Júlio, H.F., 2003. Migratory fish from the upper Paraná River basin, Brazil. In: Carolsfeld, J., Harvey, B., Ross, C., Baer, A. (Eds.), *Migratory Fishes of South America: Biology, Social Importance and Conservation Status*. World Fisheries Trust, the World Bank and the International Development Research Centre, Victoria. pp. 19–99.
- Angelini, R., Agostinho, A.A., 2005. Food web model of the upper Paraná River floodplain: description and aggregation effects. *Ecol. Model.* 181, 109–121.
- Angermeier, P.L., 1992. Predation by rock bass on other stream fishes: experimental effects of depth and cover. *Environ. Biol. Fish.* 34, 171–180.
- Arditi, R., Ginzburg, L.R., 1989. Coupling in predator–prey theory dynamics: ratio-dependence. *J. Theor. Biol.* 139 (6), 311–326.
- Arditi, R., Saïah, H., 1992. Empirical evidence of the role of heterogeneity in ratio-dependent consumption. *Ecology* 73, 1544–1551.
- Arditi, R., Ginzburg, L.R., Akçakaya, H.R., 1991. Variation in plankton densities among lakes: a case for ratio-dependent predation models. *Am. Nat.* 138 (5), 1287–1296.
- Berryman, A.A., 1992. The origins and evolutions of predator–prey theory. *Ecology* 73, 1530–1535.
- Case, T.J., 2000. *An Illustrated Guide of Theoretical Ecology*. Oxford University Press, New York, p. 449.
- Dowdy, S., Wearden, S., 1991. *Statistics for Research*, 2nd ed. Wiley, New York, p. 629.
- Edgar, T.F., Himmelblau, D.M., 1988. *Optimization of Chemical Processes*. McGraw-Hill, New York, p. 672.
- Gamito, S., Erzini, K., 2005. Trophic food web and ecosystem attributes of a water reservoir of the Ria Formosa (south Portugal). *Ecol. Model.* 181, 509–520.
- Gerking, S.D., 1994. *Feeding Ecology of Fish*. Academic Press, San Diego, p. 416.
- Ginzburg, L.R., 1998. Assuming reproduction to be a function of consumption raises doubts about some popular predator–prey models. *J. Anim. Ecol.* 67, 325–327.
- Ginzburg, L.R., Akçakaya, H.R., 1992. Consequences of ratio-dependent predation for steady-state properties of ecosystems. *Ecology* 73 (5), 1536–1543.
- Gleeson, S.K., 1994. Density dependence is better than ratio dependence. *Ecology* 75 (6), 1834–1835.
- González-Olivares, E., Ramos-Jiliberto, R., 2003. Dynamic consequences of prey refuges in a simple model system: more prey, fewer predators and enhanced stability. *Ecol. Model.* 166, 135–146.
- Gotelli, N.J., 2001. *A Primer of Ecology*, 3rd ed. Sinauer Associates, Massachusetts, p. 265.
- Gutiérrez, A.P., 1992. Physiological basis of ratio-dependent predator–prey theory: the metabolic pool model as a paradigm. *Ecology* 73 (5), 1552–1563.
- Hahn, N.S., Andrian, I.F., Fugi, R., Almeida, V.L.L., 1997. Ecologia trófica. In: Vazzoler, A.E.A.M., Agostinho, A.A., Hahn, N.S. (Eds.), *A Planície de Inundação do Alto Rio Paraná: Aspectos Físicos, Biológicos e Socioeconômicos*, Eduem, Maringá, pp. 209–228.
- Hahn, N.S., Delariva, R.L., Loureiro, V.E., 2000. Feeding of *Acestorhynchus lacustris* (Characidae): a post impoundment studies on Itaipu Reservoir, upper Paraná River. *Braz. Arch. Biol. Technol.* 43 (2), 207–213.
- Hahn, N.S., Fugi, R., Andrian, I.F., 2004. Trophic ecology of the fish assemblages. In: Thomaz, S.M., Agostinho, A.A., Hahn, N.S. (Eds.), *The Upper Paraná River and its Floodplain: Physical Aspects, Ecology and Conservation*. Backhuys Publishers, Leiden, pp. 247–270.
- Harrison, G.W., 1995. Comparing predator–prey models to Luckinbill’s experiments with *Didinium* and *Paramecium*. *Ecology* 76 (2), 357–374.
- Hilborn, R., Mangel, M., 1997. *The Ecological Detective: Confronting Models with Data*. Princeton University Press, Princeton, p. 315.
- Hixon, M.A., Palaca, S.W., Sandin, S.A., 2002. Population regulation: historical context and contemporary challenges of open versus closed systems. *Ecology* 83 (6), 1490–1508.
- Holling, C.S., 1959. The components of predation as revealed by a small mammal predation of the european pine sawfly. *Can. Entomol.* 91, 293–320.
- Jost, C., Arditi, R., 2000. Identifying predator–prey processes from time-series. *Theor. Popul. Biol.* 57, 325–337.
- Kemp, W.M., Boynton, W.R., 2004. Productivity, trophic structure, and energy flow in the steady-state ecosystems of silver springs. *Fla. Ecol. Model.* 178, 43–49.

- Lotka, A.J., 1925. Elements of Mathematical Biology. Dover, New York, c1956. 465 p. (formerly published under the title Elements of Physical Biology, 1925).
- Lowe-McConnell, R.H., 1987. Ecological Studies in Tropical Fish Communities. Cambridge University Press, Cambridge, p. 382.
- Matthews, W.J., 1998. Patterns in Freshwater Fish Ecology. Chapman & Hall, New York, p. 756.
- Moyle, P.B., Cech Jr., J.J., 1988. Fishes: An Introduction to Ichthyology, 2nd ed. Prentice-Hall, Englewood Cliffs, p. 559.
- Murdoch, W.W., Kendal, B.E., Nisbet, R.M., Briggs, C.J., McCauley, E., Bolser, R., 2002. Single-species models for many-species food webs. *Nature* 417, 541–543.
- Nelder, J.A., Mead, R., 1965. A simplex method for function minimization. *Comput. J.* 7, 308–315.
- Nilsson, P.A., 2001. Predator behaviour and prey density: evaluating density-dependent intraspecific interactions on predator functional responses. *Ecology* 70, 14–19.
- Okada, K.O., Agostinho, A.A., Petrere Jr., M., Penczak, T., 2003. Factors affecting fish diversity and abundance in drying pools and lagoons in the upper Paraná river basin, Brazil. *Ecohydrol. Hydrobiol.* 3, 97–110.
- Paiva, M.P., 1972. Fisiocologia da traíra, *Hoplias malabaricus* (Bloch), no nordeste brasileiro: crescimento, resistência à salinidade, alimentação e reprodução. Doctoral Thesis. Universidade de São Paulo, São Paulo. 140 p.
- Petzold, L.R., 1982. A description of DASSL: a differential/algebraic equation system solver. Rep. Sand 82-8637. Sandia National Laboratory, Livermore.
- Ramos-Jiliberto, R., González-Olivares, E., 2000. Relating behavior to population dynamics: a predator–prey metaphysiological model emphasizing zooplankton diel vertical migration as an inducible response. *Ecol. Model.* 127, 221–233.
- Rosenzweig, M.L., 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171 (6), 385–397.
- Rosenzweig, M.L., MacArthur, R.H., 1963. Graphical representation and stability conditions of predator–prey interactions. *Am. Nat.* 97, 209–223.
- Ruxton, G.D., 1995. Short term refuge use and stability of predator–prey models. *Theor. Popul. Biol.* 47, 1–17.
- Sabino, J., Zuanon, J., 1998. A stream fish assemblage in central Amazonian: distribution, activity patterns and feeding behavior. *Ichyol. Explor. Fresh.* 8 (3), 201–210.
- Smith, R.L., 1996. Ecology and Field Biology, 5th ed. Harper Collins, New York, p. 824.
- Srinivasu, P.D.N., Gayatri, I.L., 2005. Influence of prey reserve capacity on predator–prey dynamics. *Ecol. Model.* 181, 191–202.
- Vazzoler, A.E.A.M., Menezes, N.A., 1992. Síntese dos conhecimentos sobre o comportamento reprodutivo dos Characiformes da América do sul (Teleostei, Ostariophysii). *Rev. Brasil. Biol.* 52 (4), 627–640.
- Vazzoler, A.E.A.M., Suziki, H.I., Marques, E.E., Lizama, M.A.P., 1997. Primeira maturação gonadal, períodos e áreas de reprodução. In: Vazzoler, A.E.A.M., Agostinho, A.A., Hahn, N.S. (Eds.), A Planície de Inundação do Alto Rio Paraná: Aspectos Físicos, Biológicos e Socioeconômicos, Eduem, Maringá, 249–266 pp.
- Volterra, V., 1926. Fluctuations in the abundance of a species considered mathematically. *Nature* 118, 556–560.
- Winemiller, K.O., 1989. Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia* 81, 225–241.
- Winemiller, K.O., 1996. Factors driving temporal and spatial variation in aquatic floodplain food webs. In: Polis, G.A., Winemiller, K.O. (Eds.), Food Webs: Integration of Patterns and Dynamics. Chapman & Hall, New York, pp. 298–312.
- Wootton, R.J., 1990. Ecology of Teleost Fishes. Chapman & Hall, New York, p. 404.