

A matrix population model of the “janitor fish” *Pterygoplichthys* (Pisces: Loricariidae) in the Marikina River, Luzon island, Philippines and the possibility of controlling this invasive species

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A life stage-based Leftokovich matrix was used to model the population of the invasive “janitor fish” *Pterygoplichthys* in Marikina River, Luzon, Philippines. The matrix elements were derived from field and laboratory studies of life history and ecology, and the published literature. The population growth rate λ , rate of increase r and other life history parameters were derived from the model. The estimated λ is 1.079, and an r of 0.076 which suggests invasiveness. Matrix sensitivity and elasticity estimates suggest that the population is density

independent and that juveniles are most prone to mortalities while adult and juvenile survivability is essential in ensuring population growth. Manipulation of survival probabilities in the model suggests that decreasing survival probabilities from 0.99 to 0.10 of juveniles and adults offers the best approach to controlling this population. The practicality of implementing management strategies are evaluated given the biological and ecological characteristics of the species.

KEYWORDS

Pterygoplichthys, population matrix model, janitor fish, Marikina River, invasive species, pollution

INTRODUCTION

The armoured sailfin catfish, *Pterygoplichthys* Gill, 1858 (Figure 1) is considered to be an invasive species in the Philippines, Mexico, Taiwan, Puerto Rico and the United States (Bunkley-Williams et al. 1994, Chavez et al. 2006, Liang and Wu 2005, Vallejo 2006) where they have established populations and displaced indigenous fish and invertebrate communities. The

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Figure 1. Adult *Pterygoplichthys* from the Marikina River

rapidity of their establishment in these areas is remarkable among freshwater fish species for they are able to establish populations in clean to polluted freshwater environments and thereby occupy various habitats. In the Philippines, two species have been known to have been introduced in the late 1980s to early 1990s in Laguna de Bay. These are *P. pardalis* (Castelnau, 1855) and *P. disjunctivus* (Weber, 1991, Chavez et al. 2006) and they eventually dispersed to the Marikina River watershed. However there is evidence that these species have hybridized based on recent studies on DNA barcoding. The fish have been reported from Negros, Candaba wetlands, Magat Dam and the Agusan Marsh in Mindanao (Hubilla and Kis 2006). These sites are far from the sites of original introduction in Luzon.

An understanding of the population dynamics of this species is essential in studying its potential to spread to other parts of the country where they pose a serious threat to fisheries, aquaculture and civil engineering works. This information is also essential in proposing a possible control. However there are methodological problems in using age-based methods in estimating mortality which is essential in population dynamics studies. Dissection of the fish revealed very small otoliths which do not show settlement and growth increments. This makes ageing the fish impractical using these methods and a stage based population model was used instead. The objective of the study is to determine the per capita population growth rate estimate λ from a population matrix model and its natural

logarithm r . These parameters are then used to assess if possible control measures, which decrease survival probability among life stage classes, are practical or not.

MATERIALS AND METHODS

Sources of biological information

Information on the biology of the fish as an invasive was gathered from the literature, online databases and on-going studies on the reproductive phenology and invasive potential of the fish (Bunkley-Williams et al. 1994, Chavez et al. 2006, Liang and Wu 2005, Samat et al. 2008, Vallejo 2006). For fecundity estimation, 200 fish were collected from the field, size and weight were measured and gonads were dissected. Information on fecundity, length of the fry stage, size at maturity, length-weight relationship, and condition factor were used in subsequent population modelling analyses (Jumawan et al. 2010, Vallejo et al. 2010). The assumption in the subsequent analyses is that the Marikina River population is density independent.

Leftkovich matrix modelling and estimation of population biological parameter values

A stage-based matrix model (Leftkovich 1965) was constructed using four life stages: egg (E), fry (F), juvenile stage (J), and adult (A) stages (Equation 1). Based on natural history observations in the field, the fish are mouthbrooders with

brooding behaviour exhibited by males. The large eggs (0.2-0.5 mm) are brooded for at least a month in burrows along the riverbank. Based on our estimates, fecundity averages at 2216 eggs per female, which is less than what was observed in Malaysia (3480 eggs/female) (Samat et al. 2008). However, as in Malaysia, the standard length (SL) at gonadal maturity was at 20 cm. Best gonadal condition was observed with fish at 30-40 cm SL. Larger sized fish have lower fecundity. The sex ratio is 1:1.

Unlike in Malaysia, the Marikina River population shows one peak-spawning period (June-July) a year. This coincides with the start of the rainy season. Recent gonadal condition studies support this observation. Decrease in gonado-somatic index in Marikina River fish is significant in July-August (Jumawan et al. 2010). In Malaysia, where rainfall is more evenly distributed year round, the species spawns throughout the year. Recruitment of fry and small juveniles from cryptic habitats to the shallow riverbanks happens in August to September.

The fish do not have a larval stage as they hatch as fully-formed fry (0.2 cm SL) after the male had brooded them. Based on the field and laboratory observations we have made, approximately 50% of the eggs do not hatch since the male has a limited capability of brooding them effectively. Thus in the matrix model, the initial hatching estimate is 1108, which is half of estimated mean fecundity.

Methodological difficulties in ageing fish constrained us to use stage-based population models. Population attributes were assessed by life stages rather than age. The matrix model and its population vector describe the survival, growth and reproduction attributes of the population (Equation 1),

$$\begin{bmatrix} E_{t+1} \\ F_{t+1} \\ J_{t+1} \\ A_{t+1} \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 & R_E \\ G_F & P_F & 0 & 0 \\ 0 & G_J & P_J & 0 \\ 0 & 0 & G_A & P_A \end{bmatrix} \begin{bmatrix} E_t \\ F_t \\ J_t \\ A_t \end{bmatrix}$$

Equation 1. Leftkovitch matrix of the Marikina River Pterygoplichthys population

where R_E is the viable reproductive contribution from the egg stage, G_F is the mortality of the fry, P_F is the survival probability of the fry, G_J is the mortality estimate during the juvenile stage, P_J is the survival probability of the juveniles, G_A is the mortality of adults and P_A is the survival probability of adults.

Based on field and initial laboratory observations, the egg

brooding stage is 1 month long and the fry stage (0.2 to 1.5 cm SL) is from 1- 2 months long (Jumawan et al. 2010). In captive conditions, the fish could live up to 15 years but is likely to have a shorter lifespan in the wild. Thus, it is assumed that the adults (> 20 cm SL) are between 1-4 years of age. The juvenile (1.5-19 cm SL) stage can be from 0.8-1 year. These life stage-age categorizations are very arbitrary and are based on natural history and aquaculture observations and what have been published in the literature; there is no suitable morphometric way of ageing the fish aside from conducting controlled laboratory age-growth studies, which are on going. However, it is likely that once the fish come out of their cryptic stage, they undergo faster growth as juveniles and young adults. This is supported by recent studies of Marikina River populations, which suggest a significant growth inflection (resulting from a faster exponential growth rate) beginning from when the fish are about 25- 30 cm SL (Jumawan et al. 2010, Vallejo et al. 2010). The probable reason is that males tend to grow faster ($r = 2.2$) as compared to females ($r = 2.1$) and may reflect on full sexual maturity and development (Jumawan et al. 2010). While sex ratios are approximately 1:1 if all adult sizes are considered (Vallejo et al. 2010), there are more males in larger size classes than females (Jumawan et al. 2010). Adult females show a modified group-synchronous mode of ovarian development that allows for multiple spawnings within a single season. However, multiple spawnings have not been confirmed for the Marikina populations (Vallejo et al. 2010). Jumawan et al. (2010) did not estimate a slowing down of growth rates in the populations that they examined. This information is not explicitly used in the Leftkovitch matrix modelling. The matrix yields a set of eigenvalues where the dominant real eigenvalue λ represents the population growth rate. The natural logarithm of λ gives the parameter r which is the rate of increase. It is assumed that λ and r were estimated yearly as based on the yearly spawning of the fish. Life stage survival and mortality probabilities were estimated per week.

Mortality estimates per life stage were computed from the allometric weight-natural mortality function (Lorenzen 1996, Lorenzen 2000) (Equation 2) which allows for the estimation of instantaneous mortality per length class.

$$M_W = M_u W^b$$

Equation 2. Allometric weight-natural mortality function

where M_w is the estimated natural mortality at weight W , M_u is the natural mortality at unit weight (gm) also known as instantaneous mortality and b is the allometric scaling factor. This b is unknown and has to be estimated for different environments and climates. For this purpose, Lorenzen's (1996) estimate for tropical river ecosystems $b = -0.289$ was used.

$$P_{lifestage} = e^{-M_{lifestage}}$$

Equation 3. Estimation of survival probability

To determine the fry, juvenile and adult mortalities, the mean of instantaneous mortalities per each life-stage class was computed. These estimates are used to compute the survival probability per life stage class according to Equation 3, where $M_{lifestage}$ is the instantaneous mortality estimate for each life stage.

The above-mentioned estimates were included in the Leftkovich matrix. Population growth rate λ was extracted from the matrix by getting the dominant eigenvalue. Matrix elasticity and sensitivity were also computed according to standard methods (Caswell and Takada 2004) (Equations 4 and 5), since these are parameters used to identify which matrix elements are most responsive to variation. Elasticities and sensitivities also characterize effects of environmental perturbations on populations and the proportional contribution to λ , and measure the magnitude of natural selection gradients on populations (Caswell and Takeda 2004). Population parameters for number of replacements, estimated growth rate per annum, estimated generation time and the average age at spawning were also collected to populate the matrix from Jumawan et al. (2010) data. After the elasticity and sensitivity of matrix elements had been estimated, the survival probability per life stage was also manipulated at 0.8, 0.5, 0.2 and 0.1, and the resulting new matrix parameters calculated. All matrix calculations were done using Octave (Eaton 2010) and PopTools (Hood 2009).

$$e_{ij} = \frac{a_{ij} \partial \lambda}{\lambda \partial a_{ij}}$$

Equation 4. Elasticity

$$\frac{\partial \lambda}{\partial x} = \sum_{ij} \frac{\partial \lambda \partial a_{ij}}{\partial a_{ij} \partial x}$$

Equation 5. Sensitivity

RESULTS

The *Pterygoplichtys* population growth rate was estimated at $\lambda = 1.079$. Matrix elements PJ and PA showed the largest elasticities (0.4098 and 0.3952, respectively). This suggests that juvenile and adult survivability is more important in this moderately long lived catfish species which exhibits K selection traits. Matrix element GJ showed the highest sensitivity at 47.96 followed by GA at 3.39 (Table 2). This suggests that juvenile populations are most vulnerable to environmental perturbation.

Table 1. Leftkovich matrix analysis estimates of population parameters. The dominant positive eigenvalue is the population growth rate λ .

Eigenvalues			Eigenvectors (R&L)	
Real	Imaginary		Age/stage structure	Reproductive value
1.079	0		54.6%	0.0%
0.845	0		44.9%	0.0%
0.685	0		0.4%	11.6%
-0.00626	0		0.1%	88.3%
r	0.076	(rate of increase)		
Ro	114.07	(expected number of replacements)		
T	61.811	(generation time - time for increase of Ro)		
mul	215.240	(mean age of parents of offspring of a cohort)		

Table 2. Matrix elements, computation method, values, elasticity and sensitivity estimate

Matrix element	Value	Computation	Elasticity	Sensitivity
R _A	1108	E[Fecundity]*0.5	0	0.000005
P _F	0.62	e ^{-M_F}	0.036	0.086
P _J	0.99	e ^{-M_J}	0.036	0.446
P _A	0.99	e ^{-M_A}	0.036	0.432
G _F	0.38	1-e ^{-M_F}	0.050	0.105
G _J	0.01	1-e ^{-M_J}	0.050	47.96
G _A	0.01	1-e ^{-M_A}	0.395	3.390

Since λ is > 1 , it can be assumed that the population is growing. The mean number of replacements for the first cohort of juveniles is 114 fish. The estimated generation time is 61 weeks and the average age of parents during spawning is 215.24 weeks. This suggests that larger adults (30-40 cm SL), in the 2-3 year age class, are most fecund and conditioned (Samat 2008, Jumawan et al. 2010) to spawn, with individual adult females able to contribute 88% of the population (Table 1). The r estimate of 0.076 suggests invasiveness. A species that is not invasive will have an r approaching 0. The inconsistency between the estimated generation time and the age of when most adults are fecund may be attributed to Jumawan et al.'s (2010) hypothesis that females are maturing at smaller sizes.

Manipulation of survival probabilities and the corresponding λ are given in Table 3. The models suggest that 90% reduction of survival probabilities in juveniles and adults give a lower λ than 1. Targeting just one age class for heavy exploitation only marginally reduces λ below 1. The consequent r will be negative, which means a rate of decrease.

DISCUSSION

It appears that a high survival rate per cohort is the main reason *Pterygoplichthys* has become invasive in the Marikina River. Its egg viability under the model is estimated at 37.5%. This proportion hatches to become fry, which have a survival probability of 62.4%. Juveniles have a survival rate of 99.18%, while reproductive adults have a 98.8% survival rate. This means that almost all juveniles end up as reproductive adults in the absence of predators. The fish appears to be long lived for a tropical catfish. Aquarium records suggest that members of the Loricariidae can survive in captivity for 15 years Ekstrom 2002. However it is reasonable to assume that most individuals in the wild can live for half that time, or 7 years. It is also likely that they are reproductive until the end of their lifespan.

An interesting result of this modelling study is that the estimated generation time is less than the time estimated for parents (male and female) to be most fecund. The only possible explanation here is that females are starting to mature sexually at smaller sizes and is a sign of extreme directed selection which is commonly observed in animals under domestication (Owagu et al. 2007). This has been hypothesized by Jumawan et al. (2010). However they do not note if the same trends can be observed with the males. The dominance of males in larger size classes suggests that there is higher

female mortality due to a greater reproductive investment. With females spending more energy resources in reproduction in adverse environmental conditions, their mortality is expected to be higher (Jumawan et al. 2010). However while this analysis used in this study does not estimate female only mortality, it is likely that the hypothesized sex related mortality difference is not large enough to offset population growth trajectories. Clearly more studies are needed along this line and there is a need to further refine estimates of initial size at female sexual maturity.

The largest matrix elasticities were estimated for PJ and PA which supports the conclusion that juveniles and adults have high survival rates and that survival of these life stage classes is important in population increase. In population viability theory, a reduction of estimated matrix elasticity would imply the vulnerability of these cohorts to mortality (Caswell and Takada 2004). GJ shows the highest sensitivity followed by GA. This would suggest that juvenile fish especially smalls ones will be

Table 3. Survival probability in each life stage class and estimated λ .

Survival probability		
	λ	Life stage class
0.99	1.07	Juveniles and adults
0.8	1.03	Juveniles and adults
0.5	1.01	Juveniles and adults
0.2	1.00	Juveniles and adults
0.1	0.99	juveniles only
0.1	0.99	adults only
0.1	0.99	Fry
0.1	0.36	all life stages
0.1	0.64	Juveniles and adults

most vulnerable to mortality, presumably to predation. This is typical of fish which employ brood care (Lowe-McConnell 1987). Survival in brooded fry is typically greater than that in fish that are not brooded. As small juveniles these fishes are prone to predation until they reach an “escape size” after which they are immune to predation. Presumably this “window” for predation is narrow for the fish as they rapidly grow and quickly develop the hard dermal armour that gives them their name. In Florida USA where piscivorous birds are present, the major *Pterygoplichthys* predators are diurnal birds like herons, egrets and cormorants. These birds can only prey on small juveniles 10-20 cm SL (Nico 2010). Larger fish are preyed on by alligators and caimans (Borteiro et al. 2009).

Species that establish themselves as invasive generally have no natural predators in the new environment (Carlton 1996, Caswell and Takada 2004, Huey et al. 2005, Jia et al. 2009, Karatayev et al. 2009, Wangkulangkul and Lheknim 2008). *Pterygoplichthys* species are detritivorous (Lowe-McConnell 1987, Samat 2008) and this makes them adapted to polluted environments. This is particularly true for the Marikina River where untreated sewage is a major source of pollutants. Being a waterway impacted by urbanization, the natural fish community here has been largely modified as water quality decreased due to pollution (DENR 2008, Vallejo 2006). *Pterygoplichthys* being tolerant of poor water quality and low dissolved oxygen content thus proliferated. There is evidence that urban land use change extending to the headwaters of the Marikina River is facilitating spread of the fish further upstream.

Control of *Pterygoplichthys* will be effective if a large proportion of juvenile and adult populations are caught. If the PJ of juveniles is reduced to 10% the resulting λ will be < 1 but only marginally at 0.99 ($r = -0.01$), thus guaranteeing minimal population decline. If PA of adults is reduced to 10%, λ will be at 1.0 ($r = 0$). A similar result was estimated if fry survival PF was reduced to 10% which can only be done if the burrows of the male brooders are destroyed or made unusable. This is impractical. Reduction by 90% of the survival of adults and juveniles gives a better chance for population control $\lambda = 0.64$ ($r = -0.45$). The best model scenario is when the survival rate of all life stages is reduced by 90%, which results in $\lambda = 0.36$ ($r = -1.021$).

Introduction of natural biocontrol agents such as piscivorous birds to the Marikina River may be an attractive option but will require massive ecological restoration of riparian habitats which are now built up. At present this is not feasible since privately owned land will have to be expropriated by the state. Crocodilians were once part of the Marikina-Pasig River and Laguna de Bay watershed biota. However, the reintroduction of crocodilians is also not feasible due to the presence of human habitation. Biocontrol is not feasible in the Marikina River. The more practical approach is to find an economic use for the fish which supports a high-value fishery.

The massive removal of 90% of the population of juveniles and adults is a huge task and will entail massive costs, but may not guarantee extirpation for invasive species. The famous extinction of once numerous species, like the passenger pigeon (*Ectopistes migratorius*), suggests that massive environmental change combined with hunting may cause population crashes leading to extirpation. The passenger pigeon, however, has particular life history characteristics, such as large breeding flocks in mature woodland, and is a specialist granivore (Bucher 1992). Felling of eastern North American forests and high hunting pressure resulted in the extinction of this once numerous bird species. The passenger pigeon was not an invasive species, but endemic to the eastern United States. However, for most invasive species such as the urban tolerant and trophic generalist Laughing Gull (*Larus atricilla*), massive culling in Canada resulted in a 70% decline in population, but this did not stop range expansion and biological invasion by this species (Blackwell et al. 2004). Researchers applying a similar stage-based model for controlling the invasion of the Indo-Pacific lionfish (*Pterois volitans*) in the Tropical Atlantic suggest that removal of 27% of adult stock may halt the invasion, but given the spatial scale at which the invasion has happened, this will entail huge costs (Morris et al. 2010).

The results of this analysis suggests that controlling the proliferation of this species will be extremely difficult unless steps are taken to remove a large proportion of juveniles and initiate massive river rehabilitation that will improve the water quality of the Marikina River. Both strategies will entail huge costs and is not financially attractive given that no economic value has been found for the fish.

The invasion of *Pterygoplichthys* shows a clear example of the need to prevent biological invasion, early detection and rapid management response in case of accidental or intentional introductions. Given that initial invasion occurred more than 20 years ago, it may be too late for eradication.

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CONTRIBUTION OF INDIVIDUAL AUTHORS

Benjamin Vallejo, Jr. was the study leader, collected field and ecological data, and performed population numerical modelling. Kristine A. Soriano collected the fish and reproductive life history and gonadal data from the field and laboratory.

CONFLICTS OF INTEREST

There are no conflicts of interest in this study

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