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MATRIX MODELS FOR ANALYZING THE POPULATION DYNAMICS OF THE BRAZILIAN MANGROVE CRAB Ucides cordatus L. (DECAPODA: UCIDIDAE)

Modelos matriciais para a análise da dinâmica populacional de *Ucides cordatus L.* (Decapoda: Ucididae)

Marcos de Miranda Leão Leite[1], **Dalva Maria Silva-Matos**[2], **Raquel Negrão Baldoni**[3], **José Roberto Feitosa-Silva**[4], **Cynthia Yuri Ogawa**[5], **Luís Ernesto Arruda Bezerra**[6]

[1]PhD in Ecology and Natural Resources, Graduate Program in Ecology and Natural Resources - PPGERN, Universidade Federal do Ceará - UFC, Avenida Mister Hull s/n Pici, 60.455-760, Fortaleza, CE, Brazil.
Faculdade Luciano Feijão – Sobral-CE
[2]Universidade Federal de São Carlos - UFSCar, Rodovia Washington Luís s/n, 13.565-905, São Carlos, SP, Brazil.
[3]PhD in Ecology and Natural Resources, Graduate Program in Ecology and Natural Resources - PPGERN, Universidade Federal de São Carlos - UFSCar, Rodovia Washington Luís s/n, 13.565-905, São Carlos, SP, Brazil.
[4]Department of Biology, Universidade Federal do Ceará - UFC, Avenida Mister Hull s/n, Pici, 60.455-760, Fortaleza, CE, Brazil.
[5]Instituto de Ciências Do Mar - LABOMAR, Universidade Federal do Ceará - UFC, Avenida da Abolição 3207, Meireles, 60.165-081, Fortaleza, CE, Brazil.
E-mail author: 1975.mirandaleao@gmail.com

ABSTRACT

Ucides cordatus is an important yet declining fishery resource in mangrove ecosystems along the Brazilian coast. This study uses a matrix model to investigate the population dynamics of this species. Specimens were collected monthly using traps from July 2011 and June 2012 in a mangrove area of the Jaguaribe River (Ceará, Northeast Brazil). Population dynamics were analyzed using the size/stage-structured matrix model proposed by Lefkovitch. Carapace width was measured with a stainless steel caliper (accuracy: 0.05 mm). The final sample included 223 female specimens, with an average carapace width of 48.4 mm. Matrix modeling results indicate that the sampled population is expanding (λ=1.30), and the demographic parameter “survival and growth rate” is crucial for maintaining the population.

Keywords: Population dynamics; fisheries management; demography.

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RESUMO

Ucides cordatus *é um recurso pesqueiro dos manguezais da costa brasileira e declínios de suas populações têm sido reportados em diferentes regiões do país. No presente trabalho, foi utilizado um modelo matricial para dar suporte à compreensão da dinâmica de uma população dessa espécie. O estudo foi realizado no manguezal do rio Jaguaribe, estado do Ceará, nordeste do Brasil. Os espécimes foram amostrados mensalmente entre julho de 2011 a junho de 2012. Os caranguejos foram coletados por meio do uso de armadilhas tipo forjo. Para a análise matricial foi utilizado o modelo proposto por Lefkovich, baseado na estrutura de tamanho/estágios. Para isso, os animais tiveram a largura do cefalotórax mensurada por meio de um paquímetro de aço de precisão de 0.05 mm. Foram amostradas 223 fêmeas. A média da largura do cefalotórax foi de 48.4 mm. O resultado da modelagem matricial indicou que a população analisada se encontra em expansão (λ=1.30) e que as taxas vitais relativas à sobrevivência e crescimento são cruciais para a manutenção da população.*

Palavras-chave*: Dinâmica populacional; manejo pesqueiro; demografia.*

INTRODUCTION

Matrix models are useful tools to analyze the population dynamics of plants and animals since they estimate status and identify the demographic parameters/vital rates that most influence the population growth rate (Caswell, 2011). Furthermore, these models provide data for estimating numbers of individuals exploited by extractive activities such as fishing without impairing the viability of populations (Heppel *et al*., 1996; Miller, 2001; Gross *et al*., 2002; Freckleton *et al*., 2003; Rogers-Bennet & Leaf, 2006), which helps define criteria for exploited species management. Criteria for the exploitation of species can be defined using sensitivity and elasticity analyses that identify the critical and priority life cycle phases/vital rates for population abundance and conservation efforts (Begon *et al*., 2007). The most commonly used models are the Leslie matrix model for age-structured populations and the Lefkovitch matrix model for size or stage-structured populations (Aberg, 1992). Models based on size/stages are ideally used when age is not a good performance predictor of vital rates, such as survival and reproduction (Miller, 2001; Grady & Valiela, 2006). In general, this model takes into account the complexity of species life cycles based on survival rate and permanence in the same stage/size or transition from one stage/size to another.

The mangrove crab *Ucides cordatus* occurs along the Atlantic coast of the American continent, from Florida (USA) to the state of Santa Catarina (Brazil) (Melo, 1996). This semi-terrestrial crab inhabits the intertidal zone of estuarine regions and digs galleries in the soil that can reach depths of 2m (Alcântara-Filho, 1978). It is considered an economically important fishing resource of the Brazilian estuarine regions (Banci *et al*., 2017; João & Pinheiro, 2018; Machado *et al*., 2018; Pinheiro et al., 2018; Souza & Pinheiro, 2021; Mota *et al*., 2023; Pinheiro *et al*., 2023) and involves a wide supply chain (Ivo & Gesteira, 1999; Glaser & Diele, 2004; Dias-Neto, 2011; Pinheiro *et al*., 2016; Cortês, 2019). Outside Brazil, *U. cordatus* is an economically significant fishing resource in Suriname and the Dominican Republic (Nascimento, 1993). This crustacean is manually captured using artisanal methods, although other fishing gear may also be used (Dias-Neto, 2011; Pinheiro *et al*., 2018; Cortês, 2019). Moreover, it is selectively captured by size and sex and the females are generally returned to the mangrove (Paiva, 1997) together with specimens with cephalothorax less than 6.0 cm wide, which is the minimum catch size established by IBAMA (Ordinance No. 034/03-N, 24.06.2003) (Diele *et al*., 2005; Leite *et al*., 2006). In addition to this legal restriction, the market demands larger individuals, preferably males (Botelho et al., 2000; Passos & Di Beneditto, 2005; Fernandes & Carvalho, 2007). A decline in populations of *U.*

cordatus has been reported in different coastal regions of Brazil (Diele *et al*., 2005; Legat *et al*., 2005; Mendonça & Pereira, 2009; Santos *et al*., 2018; Pinheiro *et al*., 2023) and the crustacean has been included in the list of species threatened by overexploitation (MMA - Ministério do Meio Ambiente, 2004). However, more recently, its status was changed to "near threatened" due to a 28% decline in the species´ population size in Brazilian mangroves (Pinheiro *et al*., 2016; Mota *et al*., 2023; Pinheiro *et al*., 2023).

The rational exploitation of renewable resources is directly related to sustainable development. In this regard, economic and biological factors for the rational use of renewable resources have been considered (Freckleton *et al*., 2003; Grady & Valiela, 2006). Generally speaking, when the criteria for capturing individuals is larger size, as in the case of *U. cordatus*, fishing should only occur after reproduction to ensure stability of the population (Zhang *et al*., 2000). The aim of this paper is to understand the population dynamics of the mangrove crab *Ucides cordatus* using matrix modeling and evaluate the population status (decline, equilibrium, or growth) of this species at the study site. Additionally, this paper assesses the current form of exploitation and projects the persistence of stocks based on the following question: "Which life cycle stages are critical for maintaining population abundance?”

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MATERIALS AND METHODS

Study site

The study area is located in a mangrove of the Jaguaribe River (4°26'15'' S - 37°48'45'' W), municipality of Aracati, east coast of the state of Ceará, northeast Brazil. The Jaguaribe River Basin is around 633 km long, divided into five sub-basins, and drains a total area of 72,043 km^2 (Marins *et al*., 2003). In the estuarine region, the mangrove covers an area of 11.64 km^2 (Semace, 2006). Regional climate is mild semi-arid tropical with two well-defined seasons, although dry and rainy periods can exceed average rates (Marins *et al*., 2003). Average temperature ranges between 26 and 28^{o}C (Ipece, 2010). The period of greatest rainfall is from January to May, with a maximum average of 237.8 mm in March. From June to December, the minimum average does not exceed 47.7 mm, while in September, minimum average rainfall is 2.4 mm (Ipece, 2010).

Sampling

Individuals of *U. cordatus* were collected monthly from July 2011 to June 2012 in commercial fishing areas of the community, during low tide periods, using 50 “forjo” crab traps, in each area. This trap is placed in a way that the entrance to the galleries is closed after the crab tries to eat the bait, which consists of red mangrove *Rhizophora mangle* leaves (Carvalho & Igarashi, 2009). During the collections, the traps were placed in the afternoon and collected the next morning, totaling an approximate period of 12 hours. The captured individuals were subjected to thermal shock in a container with ice. They were then transported to the laboratory where sex was recorded by observing morphology of the abdomen (Pinheiro & Fiscarelli, 2001). Cephalothorax width (CW) of the collected crabs was measured using a caliper with 0.05 mm accuracy.

Population dynamics

For matrix analysis, a life table was previously used as a demographic tool. The life table for *U. cordatus* was built according to the method proposed by Murie (1944, *apud* Deevey, 1947), according to the number of individuals killed and age structure of the population. Since chronological marks indicating age were not visible, the individuals were sorted by stage rather than age. To simplify the model, the different stages of development were based on biological criteria of common characteristics for each of the individuals. In this study, the biological criterion was increased percentage of the species seedling (Diele & Koch, 2010) and size at the beginning of sexual maturation (Leite *et al.*, 2013). A life table was created for the analyzed time interval (2011/2012). The number of stages and their respective intervals were determined as follows: juvenile (20-30 mm), pre-reproductive (30-40 mm), reproductive (40-50 mm), adult I (50-60 mm), adult II (60-70 mm), and senile (70-80 mm).

To calculate the number of survivors (S), total captured individuals should be alive at birth and upon entering the first size class (Murie, 1944 *apud* Deevey, 1947). Thus, it was assumed that the individuals killed by capture would be alive when entering the first size class and, therefore, belong to the same "cohort" that would have been "monitored". Therefore, a sequence of the number of survivors (S) was obtained by backcalculation (Leite *et al.*, 2012). The stages (x) and other parameters of the table were also estimated according to these authors. In addition to survival rates, fertility data is required to construct the matrix (Crouse *et al.*, 1987). Therefore, the model describes the dynamics from the stratum of the population composed of females (Brault & Caswell, 1993).

To construct the life table, the following parameters adapted by Baldoni (2010) were also considered:

Survival rate (sigma-σ_{ij}): the survival rate calculated as number of individuals who survived (S) to the subsequent stage divided by the number of initial individuals (N).

Transition rate (gamma-γ_{ij}): the transition rate of individuals from one stage (x) to the next (x+1) calculated by considering the number of crabs in each subsequent stage divided by the number of crabs from the previous stage.

The data generated from the life table were analyzed using matrix models. The matrix model used to calculate the population growth rate, sensitivity, and elasticity of each demographic parameter of the transition matrix was based on the model proposed by Lefkovitch (1965). In this model, the matrix elements represent the demographic parameters for each size class or stage rather than age (Caswell, 2001). The transition matrix (A) was constructed as follows:

$$\mathbf{A} = \begin{bmatrix} P_1 & 0 & F_3 & F_4 & F_5 & F_6 \\ G_1 & P_2 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 \end{bmatrix}$$

In this matrix, **P** represents the probability of surviving and remaining at the same stage; **G** is the probability of survival and growth to the next stage, and **F** represents fertility (Crowder et al., 1994; Caswell, 2001). The probabilities were calculated according to Caswell (2001), as follows:

$$P = \sigma * (1-\gamma)$$
$$G = \sigma * \gamma$$

Fertility rate (F): the fertility rate was calculated using the proposed formula (Grady & Valiela, 2006): $Fi = P_i m_i + G_{mi+1}$; where F: fecundity; P= probability of surviving and remaining in the same size class/stage; G= probability of survival and growth to the next size class/stage; m= yield per recruit. This yield was obtained by dividing the number of crabs in the smallest stage at the beginning of the survey by the number of adult females (Gotelli, 2009) from the first stage in which the females are sexually mature, around 45 mm cephalothorax width (Leite et al., 2013).

The population growth rate (lambda - λ) is provided by the eigenvalue of the matrix (Pertierra *et al.*, 1997). Growth rate (λ) is a measure of the balance between survival and reproduction; therefore, when $\lambda>1$, the population is growing; when $\lambda<1$, the population is declining, and when λ=1, the population is in equilibrium (Fujiwara & Caswell, 2001). Analyses on the sensitivity of the population growth rate (λ) were performed as a function of changes in the probability that regulates both the transition from stage "I" to any other stage and permanence in "i" (Miller, 2001). Through sensitivity, it is possible to evaluate how the population growth rate responds to changes in demographic rates and identify the parameters to which λ is most dependent (Caswell, 2001). In this study, the sensitivity of (λ) was calculated using the model proposed by Caswell (2001), in which the change in the transition matrix element was calculated as:

$$S_{ij} = \delta\lambda/\lambda a_{ij} = v_i w_i/(v,w)$$

where S_{ij} is the sensitivity of (λ) to changes of the matrix element a_{ij} and v and "w" are the left and right dominant eigenvectors, respectively. Since the probabilities of permanence and transition range from 0 to 1, fecundity is not so limited and it is, therefore, useful to refer to the elasticity of (λ) (Miller, 2001). This is defined as the proportional contribution of a demographic parameter to the population growth rate (de Kroon et al., 2000). According to Caswell (2001), elasticities are calculated as:

$$e_{ij} = a_{ij}/\lambda = \delta\lambda/\delta a_{ij}$$

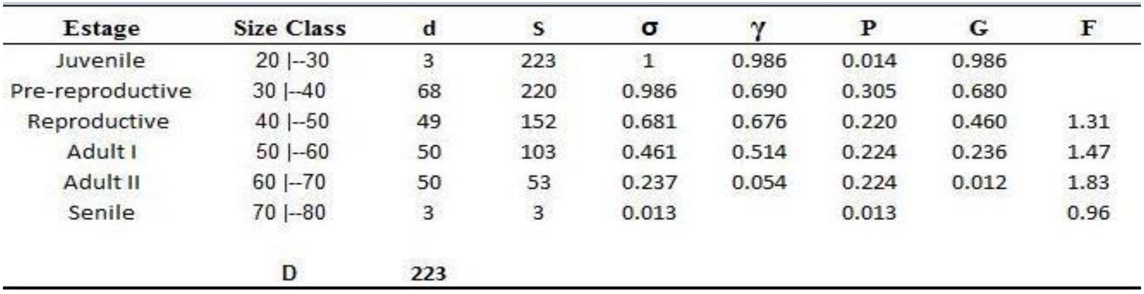
where a_{ij} is a matrix element and λ is the population growth rate.

Since the elasticities are additives, the sum of these elasticities for each stage defines the proportional contribution of the matrix element a_{ij} to global population growth, (λ) (Miller, 2001; Grady & Valiela, 2006). To perform the matrix calculations, the "Popbio" package (Stubben & Milligan, 2007) was used in R software.

RESULTS

A total of 223 crab females were sampled during the study period. Cephalothorax width (CW) ranged from 26.5 to 71.0 mm (mean ± SD: 48.4 ± 11.8 mm). The lowest proportions of survivors (σ) in the survey (2011/2012) occurred in the most advanced ontogenetic stages, namely "adult II" and "senile", with 23.7% and 1.3%, respectively. Moreover, the highest transition rates (γ) were observed in the transitions from "juvenile" to "pre-reproductive" (98.6%), "pre-reproductive" to "reproductive" (69.0%), and "reproductive" to "adult I" (67.6%). The lowest transition rate was observed in the passage from "adult II" to "senile" (5.4%). Fertility rates increased from the "reproductive" stage to the "adult II" stage as the "senile" stage decreased in the analyzed annual interval (Table 1).

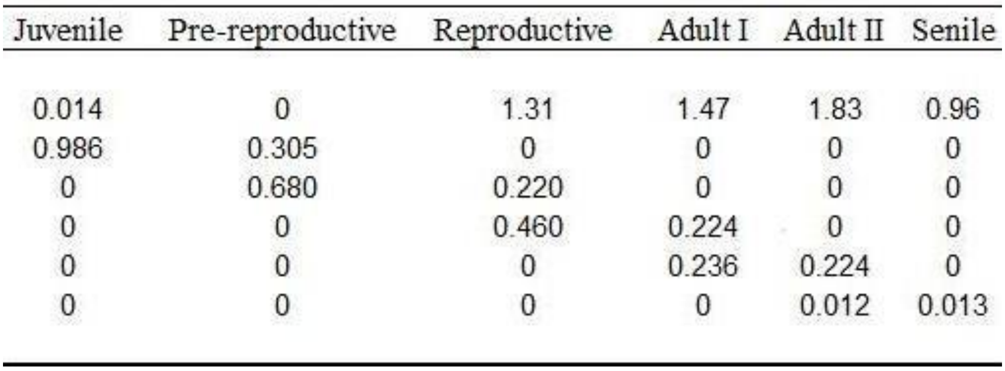
Table 1 - Life table of the mangrove crab *Ucides cordatus* in the mangrove of Jaguaribe River, northeast Brazil, for the annual interval (2011/2012). D: total deaths; d: number of deaths per stage; σ: survival rate; γ: transition rate; P: probability of survival and permanence at the same stage; G: probability of survival and growth to the next stage; F: fertility rate



Estage	Size Class	d	S	σ	γ	P	G	F
Juvenile	20 |--30	3	223	1	0.986	0.014	0.986	
Pre-reproductive	30 |--40	68	220	0.986	0.690	0.305	0.680	
Reproductive	40 |--50	49	152	0.681	0.676	0.220	0.460	1.31
Adult I	50 |--60	50	103	0.461	0.514	0.224	0.236	1.47
Adult II	60 |--70	50	53	0.237	0.054	0.224	0.012	1.83
Senile	70 |--80	3	3	0.013		0.013		0.96
	D	223						

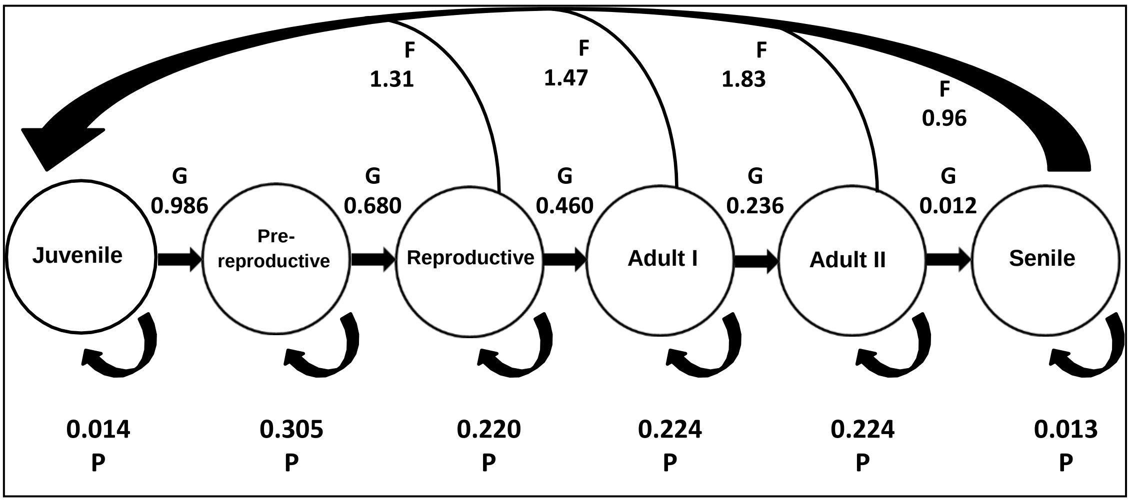
The transition matrix generated from the vital rates obtained in the life table for 2011/2012 indicated that the population of *U. cordatus* from the mangrove of Jaguaribe River is growing (λ=1.30). Furthermore, in the transition matrix, individuals have a high probability of survival (G) from the "juvenile" stage until reaching sexual maturity. Individuals in the "adult I" and "adult II" categories obtained the highest fertility rates and potentially the highest reproductive values for the population (Table 2).

Table 2 - Transition matrix obtained for the population of *U. cordatus* in the mangrove of Jaguaribe River, northeast Brazil, in the interval (2011/2012)



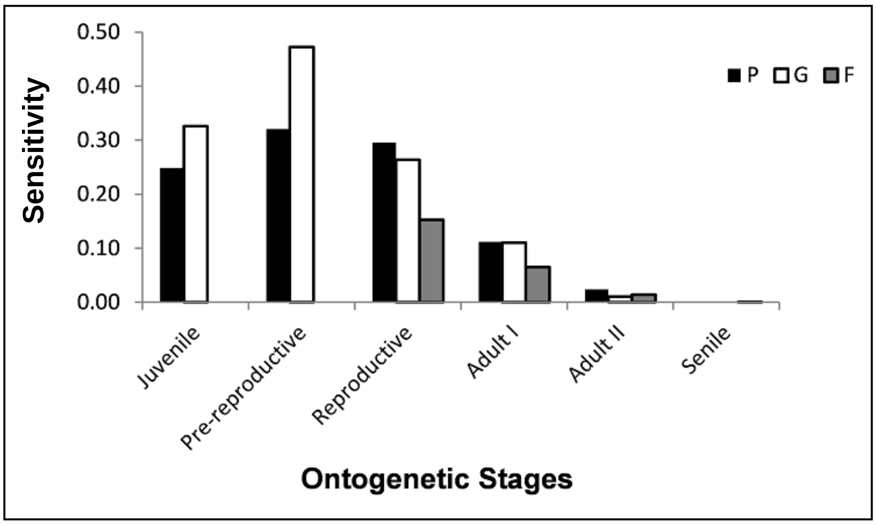
Juvenile	Pre-reproductive	Reproductive	Adult I	Adult II	Senile
0.014	0	1.31	1.47	1.83	0.96
0.986	0.305	0	0	0	0
0	0.680	0.220	0	0	0
0	0	0.460	0.224	0	0
0	0	0	0.236	0.224	0
0	0	0	0	0.012	0.013

Figure 1 - Simplified arrow diagram of the mangrove crab *Ucides cordatus* in the mangrove of Jaguaribe River, generated from the vital rates obtained in the transition matrix in the analyzed time interval. (P): probability of survival and permanence at the same stage; (G): probability of survival and growth to the next stage; (F): fertility rate



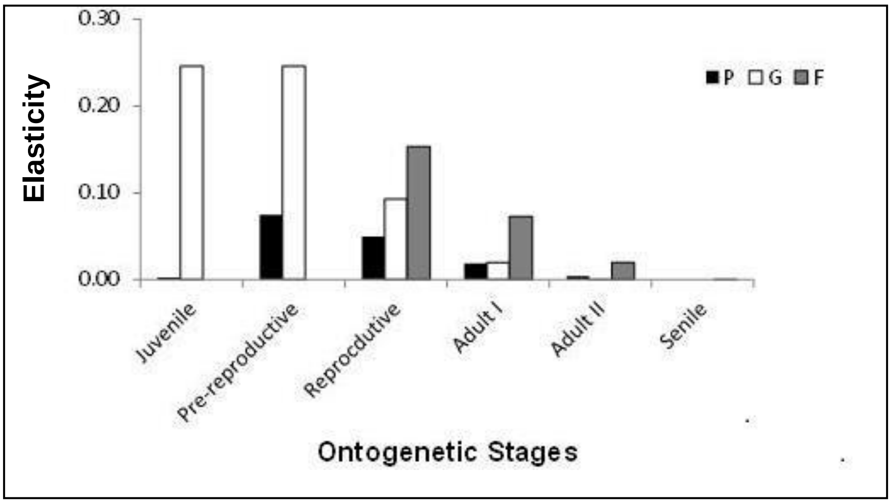
The greatest sensitivity of λ to a change of a matrix element was observed in the transition from the "pre-reproductive" (30-40 mm) to "reproductive" (40-50 mm) stages in the analyzed annual interval (Figure 2).

Figure 2 - Sensitivity of λ to the change in probability of survival and permanence in the same stage (P); probability of survival and growth to the next stage (G); and fertility rate (F)



The matrix elements for vital survival and growth rates from "juveniles" (20-30 mm) to "pre-reproductive" (30-40 mm) and from this stage to "reproductive" (40-50 mm) showed the highest elasticities in the analyzed time interval (Figure 3). Thus, surviving and moving to the next stage is the vital rate with the highest proportional contributions and the rate that best explains the λ value, followed by the fertility rate of reproductive individuals and the probability of an individual surviving and remaining in the same stage.

Figure 3 - Elasticity of λ to changes in survival and permanence in the same stage (P); probability of survival and growth to the next stage (G); and fertility rate (F)



DISCUSSION

In terms of local dynamic processes, matrix modeling indicated that the growth rate of the *U. cordatus* population was 30% per year (λ=1.30). Populations in equilibrium exhibit a population growth rate of around 1 (Fujiwara & Caswell, 2001). Therefore, the studied population is expanding. This result differs from the findings of Miller (2001), who used matrix models and identified a decline of a blue crab *Callinectes sapidus* population at a rate of 25% per year. The population of crab species studied by this author is subjected to unsustainable fisheries that catch small individuals and mature, ovigerous females. These demographic categories play an important role in regulating the population dynamics of the species. Thus, this may have influenced the decrease in population growth rate.

The population biology of *U. cordatus* at the same site of the present study and found that males reach sexual maturity when they are 15% larger than the females, size structure indicates relative stability of the population, and the sex ratio is deviated for males. Thus, there was no strong evidence of overexploitation (Leite *et al*., 2013). According to the authors and the assessment of these indicators, the analyzed population is apparently not suffering the negative effects caused by selective fishing, such as changes in population structure, related to reduced body size, decreased size for sexual maturity, and deviation of sex ratio (Roy *et al*., 2003; Sato & Goshima, 2006; Fenberg & Roy, 2007). However, Pinheiro *et al*. (2023) observed a drastic reduction in the abundance of *U. cordatus* in the mangroves of Iguape (southeast Brazil) related to anthropogenic impacts which inducing habitat loss. To preserve the species' populations, these authors recommend designating this area as a fishing exclusion zone.

The fishing of *U. cordatus* is selective by sex and size (Botelho *et al*., 2000; Passos & Di Beneditto, 2005; Fernandes & Carvalho, 2007) and females are generally returned to the mangrove (Paiva, 1997; Diele & Koch, 2010). Therefore, it is considered a potentially sustainable fishery (Diele, 2000). By reducing the fishing pressure on females, the effect of this extrinsic cause of death on the stratum of the population chiefly responsible for regulating population dynamics, through fecundity and recruitment, can be substantially reduced. In this regard, the population growth indicated by modeling may reflect these factors, as opposed to the findings of Miller (2001) for *C. sapidus*.

For *U. cordatus*, the finite rate of population increase (λ) was more sensitive to the transition from “pre-reproductive” to “reproductive” stages, while elasticity analyses revealed that the survival and growth of juveniles up to the “reproductive” stage contributed more proportionally to (λ). According to these results, the main processes that interfere with population dynamics are linked to survival and growth, followed by fecundity. The importance of vital rates for population growth may vary between different taxa. For the species of the Atlantic horseshoe crab *Limulus polyphemus*, the population growth rate was more sensitive to late juvenile survival rates than to other stages (Grady & Valiela, 2006). Therefore, these authors recommend that the capture of individuals before sexual maturity should be avoided.

In contrast, in vertebrate species, (λ) may be more sensitive to changes in the survival of adults (Crouse *et al*., 1987; Brault & Caswell, 1993; Heppell *et al*., 1996), to which protection and management should be directed. In the present study, the transition of individuals from the juvenile to adult stages is critical for population maintenance; therefore, efforts should focus on protection to allow individuals to grow, reach sexual maturity, and reproduce. This process that supports the viability and persistence of the population is not under pressure due to the exploitation characteristics of *U. cordatus*. In this regard, the results of matrix modeling revealed that individuals have a high probability of surviving, reaching sexual maturity, and contributing to population replacement. According to Miller (2001), matrix models have some weaknesses despite their usefulness in the study of population dynamics. Specifically in his study, the life story of the blue crab *Callinectes sapidus* involves an inherent spatial component related to larval dispersion and this spatial variability is not incorporated into the model.

To guarantee the conservation of this fishery resource, the current form of exploitation based on selecting catch by size and sex can be maintained. Additionally, environmental agencies must increase enforcement efforts to protected the species during its reproductive season and prevent the extraction of ovigerous females and animals with carapace width of less than 6.0cm. However, factors of this population (sexual dimorphism, sex ratio, size at sexual maturity) should not be altered. Given the economic importance of *U. cordatus* along the Brazilian coast, its populations and exploitation should be monitored to detect population attributes and ensure the necessary management measures. Finally, it is essential to preserve the mangrove areas that serve for larvae settlement, nursery, and refuge of juveniles for their survival, growth, and reproduction

(Miller, 2001; Diele *et al*., 2005, Schimidt & Diele, 2009; Pinheiro *et al*., 2023).

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