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Effects of age-specific natural mortality in sequential fisheries: management implications

Efectos de la mortalidad natural a la edad en pesquerías secuenciales: implicaciones de manejo

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Abstract
Sequential fisheries represent the technological interdependence of two or more fleets exploiting different population components of a species. Exploitation rates per fleet (E_m) are affected by the value of natural mortality (M), which is traditionally constant. However, this sequential characteristic requires mortality-at-age vectors (M_a) representing the differential probability of death between the juvenile (high) and adult (low) components. This study evaluates the bias in the estimation of exploitation rates-at-age by fleet ($E_{a,t,m}$) when using constant M over M_a in the sequential white shrimp (*Litopenaeus vannamei*) fishery and further explores the effect under a catchability-at-age ($q_{a,t}$). The results indicated that applying a constant M in a sequential fishery can overestimate total $E_{a,t,m}$ values by 66%, mainly affecting the small-scale fleet, caused by a large positive bias in younger ages (up to 321%). A moderate positive bias in $E_{a,t,IF}$ was also present in the industrial fleet's migration ages (from 50% to 100%). Consequently, the E overestimation will generate a higher fishing intensity, compromising sustainability and sequential management objectives. Additionally, incorporating $q_{a,t}$ introduced the effects of the sequential accessibility and availability of the stock in the modeling. Finally, M_a and $q_{a,t}$ were fundamental for an adequate assessment and management of sequential fisheries. Its application to highly exploited fisheries could redirect exploitation strategies towards components with a higher probability of death, such as juveniles, diminishing the fishing effort over the scarce reproductive adults and improving the fishery's performance.
Keywords: Sequential fishery, exploitation rates, mortality-at-age, gnomonic interval, shrimp, Mexico.

Resumen
Las pesquerías secuenciales se basan en la interdependencia tecnológica de dos o más flotas que explotan distintos componentes poblacionales de una especie. Las tasas de explotación por flota (E_m) son afectadas por el valor de la mortalidad natural (M), que tradicionalmente es constante. Sin embargo, la naturaleza secuencial requiere vectores de mortalidad a la edad (M_a) que representen tanto las altas tasas de mortalidad en juveniles como las bajas y estables en adultos. El presente estudio evaluó el sesgo en las tasas de explotación por edad por flota ($E_{a,t,m}$) al usar M constante sobre M_a en la pesquería secuencial del camarón blanco (*Litopenaeus vannamei*); además, exploró el efecto con una capturabilidad a la edad ($q_{a,t}$). Los resultados mostraron que al emplear M constante en una pesquería secuencial se sobrestima la $E_{a,t,m}$ en 66%, lo que afecta principalmente a la flota artesanal por el mayor sesgo sobre las edades más jóvenes (hasta 321%). También se observó una sobrestimación de $E_{a,t,m}$ en las edades de migración (de 50%-100%) para la flota industrial. La sobrestimación de $E_{a,t,m}$ generará mayor intensidad de pesca, comprometiendo la sustentabilidad y la posibilidad de alcanzar los objetivos de manejo. Adicionalmente, la incorporación de $q_{a,t}$ permitió introducir los efectos de accesibilidad y disponibilidad secuencial del recurso a la pesca en la modelación. La incorporación de M_a y $q_{a,t}$ es fundamental para la evaluación y el manejo de pesquerías secuenciales, donde, incluso en pesquerías altamente explotadas se pudieran redirigir estrategias de captura hacia componentes con mayor probabilidad de muerte, como son los juveniles, protegiendo a los adultos reproductores y mejorando el desempeño de la pesquería.
Palabras clave: Pesquería secuencial, tasas de cosecha, mortalidad a la edad, intervalo gnomónico, camarón, México.

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Introduction

In a marine population, natural mortality (*M*) is defined as the rate of loss due to natural causes. *M* can be influenced by several factors such as predation, cannibalism, disease, food availability, and oceanographic variables (Pauly 1980, Hampton 2000). This parameter is considered one of the most influential in population dynamics and stock assessment models, and one of the most difficult to estimate accurately (Kenchington 2014, Punt *et al*. 2021). It is common to assume a constant *M* value in assessment models. However, many studies have shown that *M* is strongly related to life stages, age, and length and can be variable over time (Caddy 1996, Lorenzen 1996, Chu *et al*. 2008, Johnson *et al*. 2014). Using a constant *M* for all ages and/or over time can lead to biases in the estimated quantities in assessment models, as the magnitude of *M* is related to stock status and productivity, harvest rates, and estimation of objective reference points.

The estimation of *M* includes methods based on empirical equations, catch curves (Ricker 1975), and tagging-recapture (Pine *et al*. 2003, Pollock *et al*. 2004). The most common methods are those based on empirical equations because they demand little information, such as species life-history parameters [*e.g.*, curvature parameter (*K*), infinite length (L_∞), maximum age, age/length at sexual maturity, etc.] and, in some cases, environmental variables (*e.g.*, sea surface temperature) (Alverson & Carney 1975, Rikhter & Efanov 1976, Pauly 1980, Roff 1984, Chen & Watanabe 1989, Zhang & Megrey 2006, Lorenzen *et al*. 2022).

Some empirical equations focused on estimating variable *M*, either at age (M_a), length (M_l), or weight (M_w) (Table 1). However, by relying on the parameter estimates themselves, these models may be biased and subject to considerable uncertainty (Vetter 1988, Zheng 2003, Kenchington 2014).

Table 1

Empirical equations to estimate natural mortality-at-age (M_a), length (M_l) or weight (M_w)

Empirical equation	*Estimation parameters*	*Reference*
$M_a = \begin{cases} \dfrac{K}{1- e^{-K(ts-t_0)}}, & t \leq t_s \\ \dfrac{K}{1-e^{-K(ts-t_0)} [1 - K (t - t_s) + 0.5K^2 (t - t_s)^2]}, & t \geq t_s \end{cases}$	Growth rates	Chen & Watanabe (1989)
$M_a = M_\infty \dfrac{L_\infty}{L_t} = \dfrac{M_\infty L_\infty}{L_\infty (1-e^{-K(t-t_0)})} = \dfrac{M_\infty}{1-e^{-K(t-t_0)}}$	von Bertalanffy growth function (VBGF)	Beyer (1989)
$M_l = 1.73 l^{-1.61} L_\infty{}^{1.44} K$	Population lengths	Gislason *et al.* (2010)
$M_l = K \left(\dfrac{L_\infty}{l} \right)^{1.5}$	Population lengths	Charnov*et al.* (2012)
$M_w = w^{-0.333}$	Weight	Ursin (1967)
$M_w = 3.00 w^{-0.288}$	Weight	Lorenzen (1996)
$M_w = w^{-0.25} e^{26.25-6960/(T+273)}$	Weight and temperature	Jennings & Dulvy (2008)

Where: M_a is the mortality-at-age *a*; *K* is the curvature parameter of the von Bertalanffy equation; t_0 is the theoretical length the fish would be at age 0; t_s is the age at which senescence begins; L_∞ is the infinite length; L_t is the length at time t; M_∞ is the natural mortality of the infinitely oldest fish; M_l is the mortality-at-length l in centimeters; w is the weight in grams; *T* is the temperature in Kelvin (°C + 273).

Another approach for estimating *M* relies on dividing the life cycle of the organism into “gnomonic” time intervals (Caddy 1996) with the characteristic that the time intervals increase progressively with age. This division into intervals indicates stages of biological and ecological relevance in the ontogeny of the organisms associated with a mortality vector M_i. The resulting M_i predict high mortality in the early life stages (*i.e.*, eggs and larvae stages) with a steep drop over a brief period and rapidly converging on an *M*-value asymptote for ages approaching maturity (Caddy 1996) (Fig. 1).

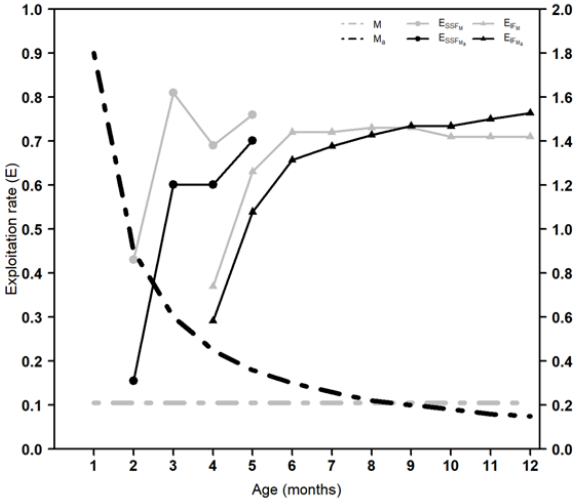

Fig. 1. Exploitation rates per age for the small-scale (E_{SSF}) and industrial fleets (E_{IF}) in a sequential shrimp fishery. Lines in grey represent the exploitation rates based on constant natural mortality (*M*) for the small-scale (E_{SSF_M}, circle marks), and industrial fleets (E_{IF_M}, triangles marks). Lines in black represent the exploitation rates based on natural mortality at age (M_a) for the small-scale ($E_{SSF_{M_a}}$, circle marks) and industrial fleets ($E_{IF_{M_a}}$, triangles marks). Discontinuous grey and black lines represent the constant natural mortality (*M*) and natural mortality at age (M_a), respectively.

Modifications to Caddy’s (1996) approach was done by Martínez-Aguilar *et al.* (2005) which included an extension of multi-annual species, variability in fecundity, and improvement of the criteria to adjust the number of gnomonic intervals to the duration of life stages. Afterward Torrejón-Magallanes *et al.* (2021)[1] performed a mathematical simplification of the method and created a package called *gnomonicM* (Torrejón-Magallanes 2021).[1]

The application of this approach, both in its original formulation and subsequent modifications, has been applied to various marine taxa with different life histories, estimating logical *M* values with biological sense (Ramírez-Rodríguez & Arreguín-Sánchez 2003, Giménez-Hurtado *et al.* 2009, Aranceta-Garza *et al.* 2016). Despite these attempts, the concept of gnomonic time interval in fisheries management has been scarcely applied (Caddy 2018, Aranceta-Garza *et al.* 2021).

Age-dependent natural mortality applied to sequential fisheries: A case study of Mexican Pacific white shrimp

Sequential fisheries are based on the technological interdependencies generated from the interaction of two or more heterogeneous fleets, usually composed of a coastal fleet (typically representing the small-scale fishery “SSF”), and an industrial fleet “IF”, that exploit different components of the species population structure, such as the juveniles and adults. This interdependency generates sequential externalities, where the intensification of the effort of one fleet will negatively affect the performance of the other and vice-versa (Anderson & Seijo 2010). Thus, applying natural mortality-at-age (M_a), denoting the probabilities of death within the population age structure, will be fundamental to correctly estimate the total mortality and harvest rate for the stock assessment, management, and decision making.

The sequential fisheries represent substantial employment and food security source to many coastal communities worldwide (FAO 2021, Gillet 2008). Worldwide, they are represented by diadromous fishes (Criddle 1996, Laukkanen 2003), marine fishes (Ye & Beddington 1996, López-Rocha *et al.* 2009, Caddy 2018), crustaceans (Arreguín-Sánchez & Castro-Meléndez 2000, Pascoe *et al.* 2016, Aranceta-Garza *et al.* 2021), and mollusks (Velázquez-Abunader *et al.* 2013), featuring the sequential penaeid shrimp fisheries as

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[1] Torrejón-Magallanes J. 2021. *gnomonicM*: estimate natural mortality for different life stages. R package version 1.0.1 (1.0.1).

the most representative due to their commercial and social importance (FAO 2021, Gillet 2008).

In Mexico, the shrimp sequential fishery represents the most important fishery in economic and social terms (CONAPESCA 2018). Its total yield is based on the exploitation of three species: the brown shrimp, *Farfantepenaeus californiensis* (Holmes 1900), blue shrimp *Litopenaeus stylirostris* (Stimpson 1874), and white shrimp *Litopenaeus vannamei* (Boone 1831). These penaeid shrimps have a short life span (about <2 years) and develop between coastal and marine habitats (García 1988, Gillet 2008). The adults aggregate in the depths to copulate, then release fertilized eggs into the water column to develop their pelagic larval phases until settlement as post-larvae (or inshore recruitment) in coastal lagoons or shallow bays (averaging 15 days). During their coastal phase, juveniles grow for three or four months until they become pre-adults and begin their reproductive migration (marine recruitment) to the bottoms of the continental shelf. Based on their biological cycle, a sequential fishery operates with an artisanal or small-scale fleet targeting the juvenile component using cast nets and non-motorized boats or *cayucos*, sometimes supported by channel closing devices called *tapos* to prevent the reproductive emigration. On the other hand, the industrial fleet targets the adult component using industrial trawlers with trawling nets in marine waters.

Most shrimp fisheries use similar management instruments to regulate the activity depending primarily on the growth and reproductive closures, spatial segregation of fleets, and fishing gear regulations (Gulland & Rothschild 1984). The status of the Mexican Pacific white shrimp populations varies across their geographic distribution (*i.e.*, along the Pacific coast), presenting maximum sustainable yields or signs of overexploitation (Cervantes-Hernández *et al.* 2008, Rivera-Velázquez *et al.* 2009, Madrid-Vera *et al.* 2012, Ramos-Cruz 2013). The main factors contributing to the white shrimp stock overexploitation are excess in fishing effort (particularly for the SSF), growth and/or reproductive overexploitation, illegal fishing, and weak institutional capacities to regulate all units of effort (particularly for SSF during the fishing and closed seasons) (Gillet 2008). Furthermore, another factor contributing to the suboptimal state of sequential fisheries is the bias in estimating the parameters applied in the stock assessment model, where the effects and potential consequences within the Mexican sequential fisheries have not been fully addressed.

This study, based on the Mexican sequential shrimp fishery, analyzes the effect of using constant M to estimate the fleets' exploitation rates compared with a natural mortality-at-age (M_a). This effect is explored under two scenarios: *i)* including a constant catchability assumption simulating poor-data fishery conditions and, *ii)* using a catchability-at-age vector ($q_{a,t}$). Finally, management implications derived from each case are discussed.

Material and methods

The white shrimp (*L. vannamei*) fishery data for the 2014-2015 season in southern Sinaloa comes from Aranceta-Garza *et al.* (2021). Furthermore, constant natural mortality (M) and natural mortality-at-age vector (M_a) applied to shrimp were obtained from Aranceta-Garza *et al.* (2016) (Fig. 1).

The original formulation by Caddy (1996) and subsequent modifications of the procedure are described below. The gnomonic model for M_i is based on the negative exponential function:

$$N_i = \begin{cases} FM \cdot e^{-(M_i \cdot \Delta_i)};\ for\ i = 1 \\ N_{i\text{-}1} \cdot e^{-(M_i \cdot \Delta_i)};\ for\ i > 1 \end{cases} \qquad \text{Eq. 1}$$

Where: the independent variable is Δ_i which represents the duration of the i^{th} gnomonic interval [i = 1,2,3,...,n], M_i is the average value of the natural mortality rate, and N_i represents the survivors of the previous Δ_i. The initial population for the first gnomonic interval is assumed to be the average lifetime fecundity (FM) or the total number of hatched eggs.

The estimation of M_i for each Δ_i requires biological information such as (a) the duration of the first life stage corresponding to the first gnomonic interval (Δ_1), (b) the FM, (c) the longevity of the species (Caddy 1996), and, according to Martínez-Aguilar *et al.* (2005), (d) the number of gnomonic intervals, which is calibrated with independent information about life stages' durations reflecting the species' life history.

Torrejón-Magallanes *et al.* (2021) estimate the duration of the other gnomonic intervals

$(i \geq 2)$:

$$\Delta_i = \Delta_i \alpha (\alpha + 1^{(i-2)} \quad \text{Eq. 2}$$

Where: Δ_i is the duration of the gnomonic interval when $i \geq 2$, α is a proportionality constant.

M_i is proportional to the duration of each life stage, thus:

$$M_i = \frac{G}{\theta_i - \theta_{i-1}} \quad \text{Eq. 3}$$

Where: G is the proportion of the overall M, which is constant for all gnomonic intervals, represented as the product of $M_i \cdot \Delta_i$ and $\theta_i = {}^{(\Delta_i / \zeta_n)} / 365$, representing the annual proportional duration of each interval, where ζ_n is the longevity of the species in days. According to Torrejón-Magallanes *et al.* (2021), G is estimated as:

$$G = -ln \left[\left(\frac{2}{FM} \right)^{1/n} \right] \quad \text{Eq. 4}$$

Where: n is the total number of gnomonic intervals.

Once the average natural mortality by gnomonic interval (M_i) was estimated, the average lengths by interval were converted to ages using the inverse von Bertalanffy growth equation (Sparre & Venema 1988), with the VBGF parameters for *L. vannamei* (Aranceta-Garza *et al.* 2021). An exponential model was fitted to the M_a values by gnomonic interval to calculate the value at each age (Fig. 1). In contrast, the value of M when it is considered constant was 0.21 according to Lluch (1974).

Estimation of exploitation rate by fleet

The estimation of the monthly exploitation rate at each age by fleet ($E_{a,t,m}$) was according to Sparre & Venema (1988):

$$E_{a,t,m} = \frac{F_{a,t,m}}{(F_{a,t,m} + M_x)} \quad \text{Eq. 5}$$

Where: the exploitation rate (E) of the fleet (m) over age (a) and time (t) will be equal to the ratio of fishing mortality ($F_{a,t,m}$) over total mortality (Z), described as the sum of fishing mortalities by fleet.

Fishing mortality (F) by fleet (m) over age (a) and month (t) was calculated:

$$F_{a,t,m} = q_{x,m} \, s_{a,m} \, f_{a,t,m} \quad \text{Eq. 6}$$

Where: $q_{x,m}$ is the catchability coefficient per fleet, where (x) indicates either a constant or age-varying catchability, $s_{a,m}$ is the selectivity, and $f_{a,t,m}$ is the unit of effort of each fleet.

Estimation of catchability, selectivity, and effort by fleet

Catchability

In this study, catchability represents the proportion of biomass caught by a unit of effort related to factors such as size/age of the fish, population structure, differences in fleets, population density, and amount of fishing (Arreguín-Sánchez 1996). Catchability-at-age ($q_{a,t,m}$) was estimated based on Arreguín-Sánchez (1996), Arreguín-Sánchez & Pitcher (1999), Martínez-Aguilar *et al.* (1999)[2] using the data for the sequential white shrimp fishery from Aranceta-Garza *et al.* (2021). The constant catchability was calculated as the average catchability-at-age for each fleet ($\bar{q}_m$) and the $q_{a,t,m}$ vectors are show in *Table 2*.

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[2] Martínez-Aguilar S, E Morales-Bojórquez, F Arreguín-Sánchez, F de Anda-Montañez. 1999. Catchability: Programa computarizado para estimar el coeficiente de capturabilidad en función de la longitud. Centro Regional de Investigación Pesquera La Paz-INP/Centro Interdisciplinario de Ciencias Marinas-INP/Centro de Investigaciones Biológicas del Noroeste SC. México. 16p.

Table 2

Values of constant catchability ($\bar{q}_m$) and catchability-at-age ($q_{a,t,m}$) for the small-scale and industrial fleets in the sequential white shrimp fishery

Small-scale fishery age structure

	1	2	3	4	5
Sep.	1.7×10^{-7}	1.84×10^{-7}	2.19×10^{-7}	3.35×10^{-7}	2.17×10^{-6}
Oct.		2.79×10^{-7}	2.14×10^{-7}	3.27×10^{-7}	9.84×10^{-7}
Nov.		4.79×10^{-8}	2.01×10^{-6}	7.71×10^{-7}	
Dec.		1.64×10^{-8}	5.16×10^{-8}	1.44×10^{-8}	
q_{SSF}	*5.2×10^{-7}*				

Industrial fishery age structure

	4	5	6	7	8	9	10	11	12
Oct.	0.00012	0.00062	0.00073	0.00066	0.00073	0.00287	0.00206	0.00185	0.00213
Nov.	0.00067	0.00052	0.00054	0.00067	0.00030	0.00282			
Dec.	0.00057	0.00006	0.00019	0.00021	0.00029	0.00003	0.00081	0.00047	0.00098
Jan.	0.00004	0.00029	0.00043	0.00014	0.00022	0.00112	0.00073	0.00046	0.00066
Feb.		0.00006	0.00014	0.00063	0.00067	0.00021			
Mar.	0.00018	0.00043	0.00021	0.00018	0.00018	0.00029	0.00076	0.00076	0.00102
q_{IF}	*0.00065*								

Selectivity

The selectivity for each fleet was estimated according to Sparre & Venema (1988) following Lluch-Belda (1974, 1977) (Table 3), considering the official mesh sizes for the industrial trawl (*i.e*, mesh size of 2 ½ inches) and the artisanal cast nets (*i.e.*, 1 ½ inch):

$$S_L = \frac{1}{(1+e^{(S_1 - S_2 L)})} \qquad \text{Eq. 7}$$

$$S_1 = L_{50\%} Ln(3) / (L_{75\%} - L_{50\%}) \qquad \text{Eq. 8}$$

$$S_2 = ln(3) / (L_{75\%} - L_{50\%}) \qquad \text{Eq. 9}$$

$$L_{25\%} = (S_1 - Ln(3)) / S_2 \qquad \text{Eq. 10}$$

$$L_{50\%} = S_1 / S_2 \qquad \text{Eq. 11}$$

$$L_{75\%} = (S_1 + Ln(3)) / S_2 \qquad \text{Eq. 12}$$

Table 3
Selectivity parameters for small-scale and industrial fleets from Lluch-Belda (1974)

Parameter	*Small-scale fleet*	*Industrial fleet*
L_{50}	114.47	139.68
L_{75}	124.14	149.35
s_1	13.01	15.87
s_2	0.11	0.11

Fishing effort

Fishing effort ($f_{a,t,m}$) was obtained from Aranceta-Garza *et al*. (2021) for the sequential white shrimp fishery. Effort units for the small-scale effort (f_{SSF_t}) were set in total fishermen cast net throws per month, where each month (t) is represented as total effective fishing days, calculated as:

$$f_{SSF_t} = \mathrm{D}_d \tau_d \varepsilon_d \qquad \text{Eq. 13}$$

Where: D_d is the effective fishing days per month, τ_d is the number of casts per fishing day, and ε_d is the number of fishermen per day.

Table 4
Estimated monthly effort per fleet for the sequential white shrimp fishery. From Aranceta-Garza *et al*. (2021)

Small-scale effort

	Effective fishing days per month (D_d)	*Cast-net throws per day* (τ_d)	*Fishermen per day* (ε_d)
Sep.	23	50	2 000
Oct.	25	150	1 000
Nov.	25	67	1 000
Dec.	25	74	1 000

Industrial fleet effort

	Total effective fishing days per month (D_d)	*Industrial vessels per month* (Y_t)
Oct.	17	72
Nov.	21	29
Dec.	28	43
Jan.	23	74
Feb.	31	70
Mar.	22	10

The industrial effort units were calculated as total industrial vessels per month, where each month (t) is represented as total effective fishing days, calculated as:

$$f_{t_{IF}} = D_d \gamma_t \qquad \text{Eq. 14}$$

Where: D_d is the effective fishing days, γ_t is the number of industrial vessels in the month t. *Table 4* shows the effort values used for their estimation.

$$\omega_{a,t,m} \frac{\left(\dot{E}_{a,t,m} - E_{a,t,m}\right)}{E_{a,t,m}} \qquad \text{Eq. 15}$$

Where: $\dot{E}_{a,t,m}$ is the exploitation rate value under the assumption of constant M, and $E_{a,t,m}$ is the estimated exploitation rate value of the vector of M_a.

Results

Exploitation rates in the sequential shrimp fishery with constant catchability

Exploitation rates by fleet and age ($E_{a,m}$) resulted from both constant M and M_a under a constant catchability are shown in *figure 1*. The general pattern showed a maximum overestimation of $E_{a,m}$ values at the youngest ages, which represents a considerable positive bias for the small-scale fleet ($E_{a,SSF}$). Likewise, the overestimation decreased towards the ages of migration and sexual maturity (Fig. 1) for the industrial fleet exploitation rates ($E_{a,IF}$). Finally, at adult ages (a≥9) the application of constant M underestimates $E_{a,IF}$ (Fig. 1).

The relative percentage error ($\omega_{a,t,m}$) in $E_{a,m}$ based on constant M or M_a was maximum at the youngest age recruited to the fishery by each fleet (Table 5; *i.e.*, age 2: 186%SSF, age 4: 29%IF). The values of $E_{a,m}$ ranging from ages one to eigth were overestimated when constant M is assumed, representing a positive bias over 66% of the early exploited ages and a negative bias over 44% for the rest of the adult ages (Fig. 1).

Exploitation rates in the sequential shrimp fishery with catchability-at-age vector

Exploitation rates by fleet, age, and month ($E_{a,t,m}$), under a catchability-at-age vector (Fig. 2) showed similar trends to the previous section (*i.e.*, assuming a constant $\bar{q}_m$). The highest positive bias of exploitation rates was at early ages with a subsequent decrease towards migration and maturity ages, with a negative bias towards the last ages (see Fig. 2 months: October, December, January, and March).

Table 5

Relative percentage error (ω) in the exploitation rate values for small-scale ($\omega_{a,SSF}$)) and industrial ($\omega_{a,IF}$) fleets under constant catchabilitȳ (q_m) in a sequential white shrimp (*Litopenaues vannamei*) fishery

	Ages recruited to the fishery										
	2	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*
$\omega_{a,SSF}$	1.86	0.35	0.15	0.08							
$\omega_{a,IF}$			0.29	0.19	0.12	0.06	0.02	-0.01	-0.04	-0.07	-0.08

*SSF: small-scale fishery; *IF*: Industrial fishery.

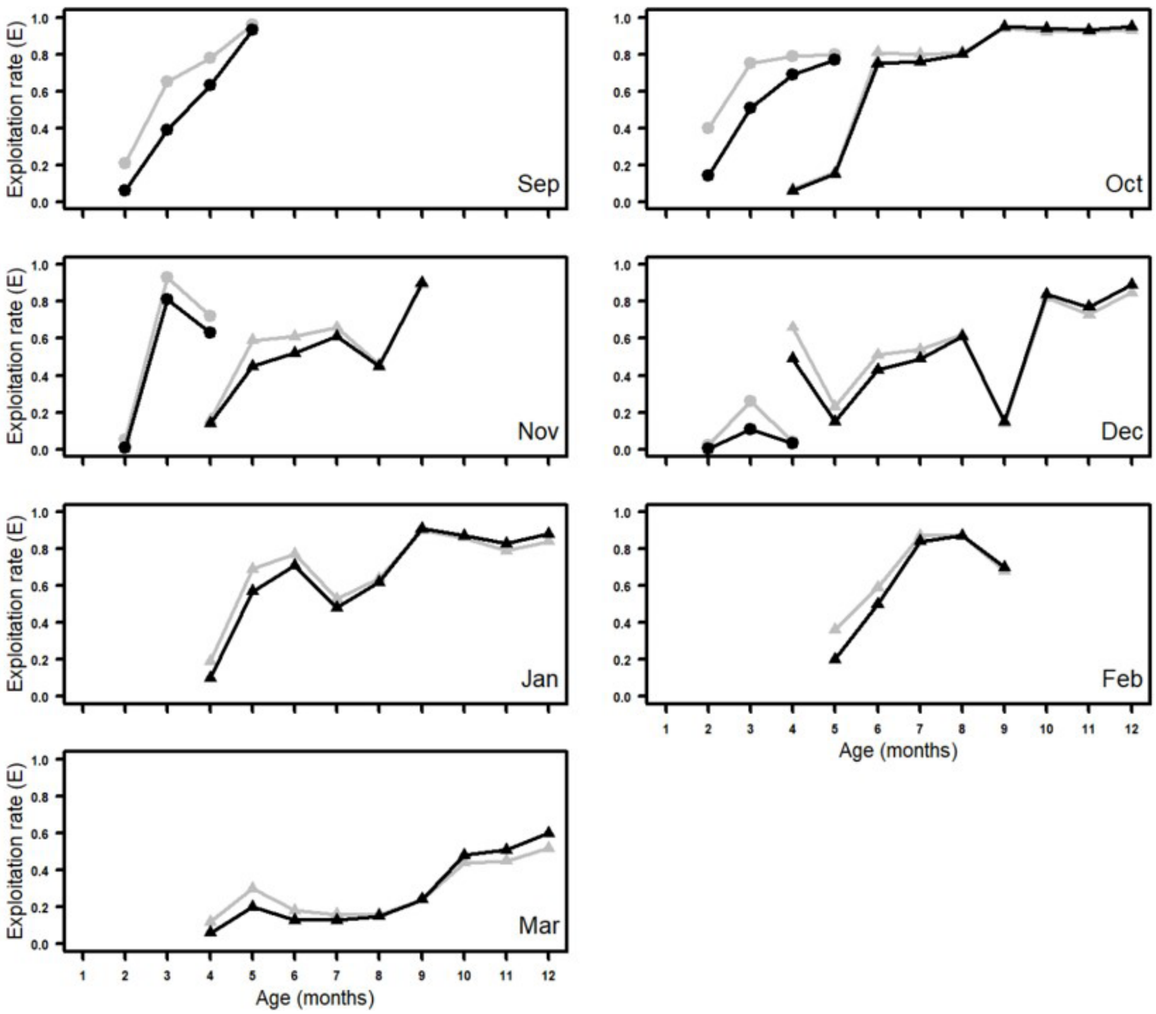

Fig. 2. Exploitation rates ($E_{a,t}$) by age and time (in months) in a sequential white shrimp (*Litopenaues vannamei*) fishery. Lines in grey represent the exploitation rates based on constant natural mortality (*M*) and a catchability-at-age vector ($q_{a,t}$) for the small-scale (circle marks) and industrial fleets (triangles marks). Lines in black represent the exploitation rates based on natural mortality at age (M_a) and a catchability-at-age vector ($q_{a,t}$) for the small-scale (circle marks) and industrial fleets (triangles marks). The global trend shows the largest bias of exploitation rates during the season's initial months and over the small-scale fleet's juvenile component. Then, it reduces towards the adult component for the industrial fleet.

The exploitation rates for the small-scale fleet ($E_{a,t,SSF}$) presented the highest overestimation under M (up to 321%$_{\text{SSF}}$, Table 6). During the SSF fishing season, the values of $E_{a,t,SSF}$ decreased progressively caused by the catchability-at-age vector ($q_{a,t}$) (Table 6), showing maximum values ($E_{a,t,SSF}$≈0.9) in September (*i.e.*, start of the fishing season), and minimum values ($E_{a,t,SSF}$≈0.26) in December (*i.e.*, the end of the season for SSF) (Fig. 2). In addition, low and similar values were presented at the same age group using either M or M_a influenced by low catchability-at age values (Fig. 2: Nov: Age 2 and Dec: Ages 2 and 4). For the industrial fleet, $E_{a,t,IF}$ values also varied during the fishing season (Oct-Mar) influenced by $q_{a,t}$, where the highest overestimated $E_{a,t,IF}$ values (up to 100%$_{\text{IF}}$, Table 6) were associated with marine migration and recruitment ages.

Table 6

Relative percentage error ($\omega_{a,t,m}$) in the exploitation rate values per month for the small-scale (SSF) and industrial (IF) fleets under a catchability-at-age vector ($q_{a,t}$) in a sequential white shrimp (*Litopenaues vannamei*) fishery

	Ages recruited to the fishery										
$\omega_{SSF_{a,t}}$	2	3	4	5	6	7	8	9	10	11	12
Sep.	2.58	0.65	0.25	0.03							
Oct.	1.96	0.47	0.16	0.03	0.12	0.06	0.02	-0.01	-0.04	-0.07	-0.08
Nov.	3.12	0.14	0.14								
Dec.	3.21	1.37	0.34								
$\varpi_{SSF_{a,t}}$	**2.72**	**0.65**	**0.22**	**0.031**							
S.D.	**0.577**	**0.520**	**0.094**	**0.002**							
$\omega_{IF_{a,t}}$											
Oct.			0.16	0.03	0.08	0.04	0.01	0.00	-0.01	-0.02	-0.02
Nov.			0.14	0.29	0.17	0.08	0.04	-0.01			
Dec.			0.34	0.54	0.21	0.10	0.03	-0.04	-0.03	-0.06	-0.04
Jan.			0.92	0.22	0.10	0.10	0.02	0.00	-0.02	-0.05	-0.04
Feb.				0.45	0.17	0.03	0.01	-0.02			
Mar.			1.00	0.50	0.35	0.19	0.06	-0.04	-0.08	-0.12	-0.14
$\varpi_{\omega_{IF_{a,t}}}$			**0.512**	**0.340**	**0.179**	**0.090**	**0.028**	**-0.018**	**-0.035**	**-0.062**	**-0.062**
S.D.			**0.420**	**0.195**	**0.097**	**0.056**	**0.018**	**0.018**	**0.031**	**0.044**	**0.052**

Discussion

Management implications

The natural mortality-at-age vector (M_a) estimated from a gnomonic approach for the white shrimp sequential fishery predicted a differential probability of death among ages, maximum over the first life stages followed by a decrement and stabilization towards sexual maturity and adult stages. A constant M will erroneously assign the same probability of death to the entire population structure, affecting the total mortality rate (Z) and, consequently, the exploitation rates estimations for each fleet (E_m), producing a systematic bias for the entire sequential fishery. For the case of the sequential white shrimp fishery under a constant catchability, the total exploitation rates presented a positive bias of 66%, with the highest error shown at the youngest ages (affecting the SSF fleet considerably) related to its high probability of death. The remaining 44% resulted in a negative bias for the adult component (affecting the industrial fleet) related to the converging of an M-value asymptote with a mild negative slope.

The application of either a constant catchability ($\bar{q}_m$) or catchability-at-age ($q_{a,t}$) showed a similar trend of bias (ω_m) along the population structure. However, the main disadvantage of using q_m was the loss of information related to biological processes (*i.e.*, recruitment, migration, and reproduction) during the ontogeny of the species, which must be considered necessary for the successful management of sequential fisheries. Alternatively, $q_{a,t}$ showed a monthly variability by age and fleet in $E_{a,t,m}$ values, which were directly related to the biological processes of shrimp, based on the accessibility and availability of the biomass in ages during the fishing season (Arreguín-Sánchez 1996). The progressive decrease in $E_{a,t,SSF}$ values (Fig. 2) were caused by the migration of pre-adult organisms to the marine-bottom habitat and the SSF fishing mortality. Similarly, the $E_{a,t,IF}$ values (Fig. 2) varied because of the recruitment processes to marine waters (ages 4-6), reproductive aggregations (ages +7), and industrial fishing mortality (Aranceta-Garza *et al.* 2020). Other studies have employed the catchability-at-age approach successfully to represent other specific biological processes affecting the fishery, such as Pacific sardine (Martínez-Aguilar *et al.* 2009), red grouper (López-Rocha *et al.* 2009), and *Octopus maya* (Velázquez-Abunader *et al.* 2013).

The use of constant M in the sequential fisheries will overestimate the exploitation rate values, especially for the artisanal-juvenile component. The estimated bias under constant M ranged from 328% to 71% for ages 2-4 for SSF, and 71 to -29% for ages 4-12 for IF (Table 6 and Fig. 2). Other studies in non-sequential fisheries reported similar percentages of bias due to errors in M ranging from 10% to 36% (Pascual & Iribarne 1993), 50% to 200% (Kenchington 2014), and 70% to 220% (Punt *et al.* 2021). Moreover, Punt *et al.* (2021) have also reported errors in the estimation of biomass and fishery reference points derived from bias in the estimation of M, which affect the stock assessment and, consequently, diminishes the ability to achieve management objectives. Furthermore, a $E_{a,t,m}$ overestimation will result in higher exploitation rates than using M_a hindering the sustainability of the resource. In the case of shrimp, their intrinsic characteristics of high fecundity and short life cycle provide higher resiliency to fishing pressures than other long-lived, late maturity, and/or less fecund species. However, overestimation in $E_{a,t,m}$ will exacerbate the current deteriorated stock status of some Mexican Pacific shrimp populations, mainly in southern regions (Cervantes-Hernández *et al.* 2008, Rivera-Velázquez *et al.* 2009, Madrid-Vera *et al.* 2012, Ramos-Cruz 2013). In addition, this overestimation in the exploitation rate for the small-scale fleet will be critical for the sustainable sequential management of the resource since they start the season one month earlier than the industrial fleet (Table 6 and Fig. 2), where an unbiased harvest rate will be fundamental for the escape of shrimp to marine waters that will sustain the industrial fishery.

Historically, fisheries were managed under the paradigm proposed by Beverton & Holt (1959) based on constant M for adults, which emphasizes that all "fish" should be allowed to grow and reproduce at least once, thus achieving their maximum yield. This theory thrived when fisheries were in a development phase targeting high adult biomass and correctly applying a constant adult M in their fishery assessments. However, the current fishery status has changed to fully exploited or overexploited (FAO 2021), where the adult component have become scarce, which would be the case for several artisanal fisheries in Latin America (Arreguín-Sánchez & Arcos-Huitrón 2011). Based on this status, Caddy & Seijo (2002) proposed a paradigm shift based on M-at-age vector by increasing the exploitation rate (to a certain level) on the juvenile component, given its predicted high probability of M, thus, reducing fishing pressure on the less abundant adult component with a lower probability of death.

In sequential fisheries, management becomes more complex due to technological interdependence between fleets, where the estimation of a M_a vector becomes critical in the assessment for achieving management goals. Also, this implies higher management challenges and institutional capacities to succeed. Specifically, several management measures have been proposed in sequential penaeid fisheries to optimize performance (Gillet 2008).

The elimination of the industrial component in overfished fisheries in Asia has been proposed to protect the livelihood of small-scale fishers (Butcher 2004) or, conversely, to reduce the least efficient fleets (*e.g.*, SSF) to achieve the maximum economic yield applied in countries such as Australia (Pascoe *et al.* 2012). However, in developing countries, such as Mexico, the shrimp fishery represents a source of food, employment, and livelihood for many coastal communities, where effort removal strategies, mainly for small-scale fishers, are not politically accepted (Nance *et al.* 2008).

Other authors propose to apply a management measure based on a balanced harvest strategy, "BH" (Caddy 2018. Law *et al.* 2012, Zhou *et al.* 2019). The BH equals or "balances" the fishing mortality (F) per fishing gear (g) at each age (a) with the corresponding vectors of M_a (i.e., $\sum F_{a,g}=M_a$). In this way, the juvenile component would be exploited at higher rates than adults, resulting in higher sustainable yields (Law *et al.* 2012) and promoting adult conservation according to the paradigm of Caddy & Seijo (2002). Also, the BH strategy confers the advantage that F's are predefined by M_a, corresponding to the biology of the resource. Caddy (2018) applied this strategy in a theoretical example in a multi-gear fishery for hake, showing that protecting age 1 recruits and older spawning stock ages achieved the highest yield and maximum conservation of spawning biomass. The current state of the Mexican shrimp fishery (*i.e.*, maximum exploitation or overexploitation) could benefit largely from applying a BH strategy. For the white shrimp sequential fishery case, the estimated F's per age and fleet were higher than M_a values caused by an excess in fishing effort for both fleets. To achieve a BH strategy, the authorities must establish an effective effort control, especially at the SSF level, which represents a major challenge given the current institutional capacities in Mexico. Other alternative management strategies have proposed the spatial regulation of the industrial effort, showing high predicted benefits in all the bioeconomic performance variables (*i.e.*, biomass, catch, present value) for IF, and avoiding economic damage to any artisanal fisher (Aranceta-Garza *et al.* 2021). Selectivity-at-age per fleet could also be explored similarly to Caddy (2018) to establish a range of optimum exploited ages that could increase the fishery-biological performance under the predefined state of small-scale overcapitalization.

Conclusion

The application of constant natural mortality in sequential fisheries generated a systematic error in the fishery's exploitation rates, consequently affecting the fishery evaluation, management, and estimation of reference points. The proper management of sequential fisheries, whose essence is the exploitation of juveniles and adults, requires the incorporation of a natural mortality-at-age vector (M_a) to correctly estimate the exploitation rates applied by each fleet on the corresponding population structure. Additionally, incorporating a catchability-at-age vector ($q_{a,t}$) acknowledges the variability caused by biological processes that affect the fishing dynamics of the fleets, defined as the differential accessibility and availability to the population structure elements in space and time.

The assumption of constant natural mortality in the sequential fishery will overestimate exploitation rates, with an inverse relationship to age (or the component with the highest probability of natural death). The resulting positive bias on the fleet's exploitation rates will primarily impact the small-scale fleet caused by its dependence on the juvenile component. This bias will cause sequential externalities created by higher fishing intensity between fleets, increasing the risk of not achieving the fishery management objectives (*i.e.*, B_{MSY}). Additionally, fisheries under high exploitation levels and weak institutional capabilities may benefit from developing strategies based on M_a increasing the exploitation rates of the juvenile component to certain levels, and conserving the reduced reproductive component, whose predicted probability of death will be lower and stable. Thus, applying an M_a and a $q_{a,t}$ will be essential in managing sequential fisheries, especially under high exploitation rates, to achieve the fishery management objectives.

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