

Age-specific natural mortality - implications for stock assessment and management of Mexican fisheries

Mortalidad natural específica por edad: implicaciones para la evaluación de poblaciones y el manejo de las pesquerías mexicanas

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Abstract

The instantaneous rate of natural mortality, M , is a key parameter estimated in fisheries stock assessments. Conventionally, M has been assumed to be constant over time and age; however, this assumption typically generates an underestimation of recruitment and an overestimation of spawning stock. If a fish stock is exploited to the limit of its biological production capacity or if it is under recruitment or growth overfishing, then it is important to increase the precision when estimating survivors at critical ages. The estimate of M -at-age/length is based on the notion that M varies with the ontogeny of a species. Almost all methods for estimating M -at-age/length are linked to estimates of individual growth to approximate the ontogeny of species. The gnomonic-interval method allows estimates of M at life history stages that are biologically and ecologically consistent with observed data, and these estimates can be translated to age or length. In Mexico, methods based on length and growth have been applied to some species of Veneridae clams, while the gnomonic-interval method has been applied to species with different life histories, such as the short lifespan penaeids shrimp (*Penaeus* spp.); long-lived species, such as the top predator red grouper (*Epinephelus morio*), and the filter-feeding species, the geoduck clam (*Panopea globosa*); and medium lifespan species with different life histories such as the small pelagics (*Sardinops caeruleus*); an intermediate trophic level of active predators, such as the giant squid (*Dosidicus gigas*); and the sea cucumber (*Isostichopus badionotus*). It should be noted that in the studied cases, the gnomonic-interval method did not consider variability over time, only for life history stages, while methods based on length and growth can be applied to estimate time-variable natural mortality, as in the case of the Venus clam (*Chione californiensis*). The analysis showed that biased estimates of population size, which occurred due to the assumption of constant natural mortality with ontogeny, were larger for short-lived than long-lived species, while the time varying estimates of M showed a bias of approximately $\pm 35\%$ in a seasonal time frame for the Venus clam *C. californiensis*.

Keywords: constant- M , M -at-age/length, ontogeny-dependent- M , stock assessment, fisheries management.

Resumen

La tasa instantánea de mortalidad natural, M , es un parámetro clave estimado en las evaluaciones de las poblaciones de peces. Convencionalmente, se ha supuesto que M es constante a lo largo del tiempo y la edad; sin embargo, este supuesto usualmente genera una subestimación del reclutamiento y una sobreestimación de la población reproductora. Si una población de peces se explota hasta el límite de su capacidad de producción biológica o si está en una condición de sobrepesca de reclutamiento o crecimiento, entonces es importante aumentar la precisión al estimar los sobrevivientes de edades críticas. La estimación de M por edad/talla se basa en la noción de que M varía con la ontogenia de una especie. Casi todos los métodos para estimar M por edad/talla están vinculados a estimaciones de crecimiento individual para aproximarse a la ontogenia de las especies. El método de intervalos gnomónicos permite estimaciones de M en etapas de la historia de vida que son biológica y ecológicamente consistentes con los datos observados,

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y estas estimaciones pueden traducirse a longitud y edad. En México, se han aplicado métodos basados en longitud y crecimiento a algunas especies de almejas Veneridae; mientras que el método de intervalos gnomónicos se ha aplicado a especies con diferentes historias de vida, como camarones peneidos de corta longevidad (*Penaeus* spp.); especies longevas, tales como el mero rojo (*Epinephelus morio*), predador tope, y la almeja de sifón (*Panopea globosa*), una especie filtradora; y especies con longevidad intermedia e historias de vida variadas tales como pequeños pelágicos (*Sardinops caeruleus*); un depredador de nivel trófico intermedio, el calamar gigante (*Dosidiscus gigas*); y el pepino de mar (*Isostichopus badionotus*). Cabe señalar que, en los casos estudiados, el método del intervalo gnomónico no consideró la variabilidad en el tiempo, sólo para las etapas de la historia de vida, mientras que los métodos basados en la longitud y el crecimiento pueden aplicarse para estimar la mortalidad natural variable en el tiempo, como en el caso de la almeja roñosa (*Chione californiensis*). El análisis mostró que las estimaciones sesgadas del tamaño de la población, que ocurrieron debido a la suposición de una mortalidad natural constante con la ontogenia, fueron mayores para las especies de vida corta que para las de vida larga; mientras que las estimaciones variables en el tiempo de M mostraron un sesgo de aproximadamente $\pm 35\%$ en un marco de tiempo estacional para la almeja roñosa *C. californiensis*.

Palabras clave: M -constante, M - a -edad/talla, M -dependiente de la ontogenia, evaluación de stock, ordenación pesquera

Introduction

Assessments of the availability of fishery resources provide an indispensable level of knowledge for managing and sustainably using fishery resources. Unlike other primary production sector activities, fishing is the only one where there are no inputs for production; that is, the yields and persistence of the resources depend entirely on the natural biomass production capacity of the populations. Toward the first half of the 20th century, information needs, strongly linked to the degree of use, were mainly related to estimating the magnitude of fishable biomass and, in particular, to identifying the stress conditions that could maximize production capacity, typically using this level as a reference. However, when resources begin to be intensely exploited and, in some cases, even exploited beyond the condition of maximum production capacity, it becomes necessary to determine the size of the spawning stock that must remain in the sea to ensure, through the success of reproduction, the replacement of fishing losses. In this context, it is important to understand in detail the mortality associated with each age. Obviously, this knowledge is also critical when fishing is strongly oriented toward organisms that have not yet reached their reproductive age, that is, juvenile organisms. Overfishing of these sectors of the population is where the concepts of overfishing during recruitment and growth stages originate.

The rate of change in the size of an exploited population is represented as

$$\frac{dN}{dt} = -Z$$

where: Z is the instantaneous total mortality rate. In a closed population, where there is no migration and time contains a complete reproductive period, typically one year, Z as two components, natural mortality, M , and fishing mortality, F .

Thus, the size of a population considering its age structure is represented as:

$$N_t = \sum_{a=r}^{a_\lambda} N_{a,t-1} e^{-(M_{a,t-1}+F_{a,t-1})} + N_{r,t} \quad \text{eq. 1}$$

where: α represents age, $a=r$ represents the age of recruitment, a_λ represents the age of maximum longevity present and $N_{r,t}$ represents the number of recruits at age r and at time t . In an exploited population, $N_{r,t}$ can represent recruitment to the fishery, and would correspond to the size of the population susceptible to being captured; then, if refers to the recruits to the population resulting from the success of reproduction, then will represent the size of the stock.

Two aspects in the previous equation are of interest. First, if the population is to be represented in terms of its biomass (as a metric of interest for management), then *equation 1* would be represented as:

$$B_t = \sum_{a=r}^{a_\lambda} N_t w_t = \sum N_{a,t-1} w_t \cdot e^{-(M_{a,t-1}+F_{a,t-1})} + N_{r,t} w_r \quad \text{eq. 2}$$

The second aspect refers to survival, represented by the expression:

$$e^{-(M_{a,t-1}+F_{a,t-1})} \quad \text{eq. 3}$$

This equation represents the proportion of survivors over time $t - 1$ at time, for example, in two successive years, and depends on the mortality due to fishing, F , and due to natural causes, M .

$F_{a,t} = S_a q_{a,t} E_t$ represents age-specific fishing mortality and at time, as a product of the fishing-gear selectivity, or the retention probability by age of the fishing gear, S_a ; the probability of capture or catchability, q , at age-specific and at time t ; and fishing effort is E , at time t . Catchability represents the interaction between the organisms of a population and the fishing gear in such a way that it varies depending on those factors that affect both the resource and the fishing effort (Arreguín-Sánchez 1996). Regarding natural mortality, one can consider different sources of mortality, such as diseases, longevity, and predation; being that predation contributes the most to mortality because diseased, injured, or older organisms have a greater probability of being consumed by predators. Also, changes of environmental patterns can be a notably source of mortality, especially in early stages of life. Although natural mortality as concept is usually easily understood, its estimation is extremely complex since it requires specific information on consumption by predators and the variation patterns of predators and preys, or the different effects of environmental changes on the living stages; and from the perspective of the target fishing resource, all these factors affect throughout its ontogeny, and are critical for the sustainability of the production capacity. This paper will discuss some aspects related to the complexity of estimating the instantaneous rate of natural mortality based on studies of population dynamics and the evaluation of fishery resources, as both serve as required information for fisheries management.

Complexity of natural mortality estimations

Toward the middle of the 20th century, the theoretical bases for evaluating fishing populations were developed, and in essence, and to date, scientific efforts have focused on achieving the best possible parameterization of the elements of *equation 1*. As mentioned above, although mortality by predation is accepted as the main and significant source of natural mortality, its estimation

from field data is complex and expensive in terms of maintaining continuous monitoring. Initially, given this complexity, it was interpreted that M could be assumed to be constant with age and time. This assumption had two key rationales: *i*) that the environment is reasonably stable, leading to the assumption that the pattern of variation over time would also be stable; that is, there would be no trend; and *ii*) that for the most part, the ages involved in fish captures were adult organisms, with minimally different sizes and similar behaviors so that the probability of retaining prey as an adult could be assumed to be constant with age. Clearly, this assumption would imply greater uncertainty related to the differences in the ontogeny of the organisms involved in the captures.

Based on these concepts, different models were proposed to estimate the natural mortality variable with age and time (Table 1). Although it is recognized that both sources of variation have limitations (Deroba & Schueller 2013, Punt *et al.* 2021), the bias involved was not especially critical to fishing mortality, which also directly depends on the amount of catch retained and the management objective. It should be noted that at that time, the relative stability of the environment allowed us to assume that the greatest source of variation in the trend of populations was fishing; additionally, the fact that the state of exploitation of fishery resources was not that intense, did not require high precision in the estimates (Arreguín-Sánchez 2022).

Currently, according to the Food and Agriculture Organization (FAO 2020), approximately 30% of the world's fisheries are moderately exploited or underexploited, which means that the remaining fisheries are being exploited at their maximum biomass production capacity (>45%), are overexploited, or are in recovery (>20%). This condition requires greater precision in mortality estimates, for example, the need to guarantee a stock of brood stock that causes an adequate level of recruits that allow the sustainability of the population or, where appropriate, to ensure the growth of enough juveniles to reach reproductive age. This required precision has motivated the development of methods that consider variability in natural mortality with length and age. At this point, the obvious question becomes, what is the consequence of assuming the natural mortality M constant?

Table 1
Models to estimate variable instantaneous rate of natural mortality

<i>Model</i>	<i>Equation</i>	<i>Comment</i>
Peterson & Wroblewski (1984)	$M_w = 1.28 \cdot w^{0.25}$	w = weight-at-age/size
Chen & Watanabe (1989)	$M_a = \frac{K}{1 - e^{-K(a_0 - a_0)}}$	$a \leq a_s, a_s$ is the age at which senescence begins
Reciprocal model (Caddy 1991)	$[M_i - A] \cdot t = [M_{i+\Delta} - A] \cdot (t+\Delta)$	A = asymptotic mortality Δ = time interval
Lorenzen (1996)	$M_w = 3.00 \cdot w^{0.288}$	w = weight-at-age/size
Jennings & Dulvy (2008)	$M_w = w^{-0.25} e^{26.25 - 6960/(a+273)}$	w = weight-at-age a
Gislason <i>et al.</i> (2010)	$M_\ell = 1.73 \cdot l^{1.61} \cdot L_\infty^{1.44} \cdot K$	ℓ = length class K and L_∞ von Bertalanffy growth parameters
Charnov <i>et al.</i> (2012)	$N_{\ell t+\Delta t} = \left[\sum_k G_{\ell,k} S_k \right] N_{k,t}$	ℓ = length class K and L_∞ von Bertalanffy growth parameters
Arreguín-Sánchez <i>et al.</i> (2012)	$M_i = \frac{G}{\theta_i - \theta_{i-1}}$ $G = -\ln \left[\left(\frac{2}{MLF} \right)^{\frac{1}{n}} \right]$	N_ℓ = stock density as length frequency. k, l = successive length classes Δt = time interval G and S = growth and survival matrices, respectively
Asymptotic mortality Gnomonic interval model (Caddy 1996, Martínez-Aguilar <i>et al.</i> 2005, Torrejón-Magallanes <i>et al.</i> 2021)	$\theta_i = (\Delta_i / t_n) / 365$ $\Delta_i = \Delta_1 \cdot \alpha \cdot (\alpha + 1)^{(i-2)}$	n = longevity MLF = mean lifetime fecundity Δ_i = gnomonic interval size (can be fitted to observed data) α = proportionality constant iteratively computed.

Consequences of assuming the M constant

For ease of calculating, assume *equation 1* for a single cohort and in the absence of fishing mortality. Additionally, consider a population vector with a value of $N_2 = 500\,000$ individuals, with longevity $a_\lambda = 10$ years. Assume a value of $M = 0.34$ is constant, and assume a variable vector of natural mortality that begins with

the same number of individuals, N_2 , and with an initial value of $M_2 = 1.1$, which changes with age at a factor of 0.6, such that $M_3 = 1.1 \cdot 0.6 = 0.66$, etc. until the age of maximum longevity, $a_\lambda = 10$; where the average of the natural mortality vector will be $\bar{M}_{2-9} = 0.34$. When estimating the size of the population with the M constant results in a value of $N = 1\,653\,390$ individuals, while with the M_a variable,

$N = 999\,923$ individuals, the first case is 65% higher than the second. If with these values, we assume that the age at first maturity $a_m = 4$ years, then the reproductive stock, up to age a_λ , is $N_m = 797\,505$ individuals with the M constant, and $N_m = 333\,488$ with the M_a variable; that is, 42% of that estimated with M constant. From these estimates, the difference between the two conditions of applying natural mortality is clear. Similarly, if the number of individuals is estimated N_1 as recruit age $a = 1$ year, then the estimator with M constant will be $N_1 = 702\,474$ individuals, while the M variable will be $N_1 = 2\,647\,245$ individuals, that is, 3.7 times higher than with M constant. Obviously, these differences, when considering real cases, lead to biases and/or errors that usually lead to problems in decision-making related to managing resources.

Considerations of variable natural mortality

If biological processes are considered throughout the ontogeny of species, then it is easy to understand that as individuals grow, the living conditions under which they develop change. Many species go through life stages and in turn inhabit wholly different communities, or individuals modify their behavior once they play a role in the population, such as their participation in reproduction or migrate from a certain age occupying different habitats. Along such stages, predator-prey relationships are also modified, as well as their response to environmental changes. These types of events are widely recognized (Cushing 1975, Caddy 1984, Gulland 1987, Shepherd & Cushing 1990, Caddy 1991, Gagliano *et al.* 2007) and show the need to obtain estimates of variable natural mortality with ontogeny and to the extent possible also at a temporal scale. Globally, there are three major approaches to consider when estimating variable natural mortality with the ontogeny of a species: *i*) one based on age; *ii*) one based on the length of the organisms; and *iii*) one based on variable intervals according to the duration of life stages.

Models based on age and size represent the ontogeny of a species through the von Bertalanffy growth equation. The difference between both approaches is the concept of length and age. In general, an age is characterized by organisms of a certain interval of lengths that show a distribution, typically normal, and are components of a cohort;

that is, these individuals originate during the period of the same reproductive event. In these cases, mortality is calculated by the survival of the total cohort from one year to the next, as indicated by *equation 2*. In this context, when a population has several cohorts present in a year, it is very likely that the size distribution of the two successive cohorts overlap to some degree, and this overlap can occur for up to two, three, or more cohorts. This means that an organism of a certain size is likely to belong to more than one specific age. However, this does not affect the estimation of mortality since it is being estimated from the change in the number of individuals in each cohort.

In the case of estimates based on lengths, the data arrangement is different since each length-class i , l_i , corresponds to a relative age a_i , and the probability that a l_i corresponds to the next relative age a_j , corresponding to the next length-class, is null. The consequence of this condition is that it assumes a certain stability in the distribution of the structure by lengths over time, which generally does not occur given that organisms tend to occupy different habitats throughout their ontogenetic development, in addition to the effects on the metabolism of individuals associated with changes in climate patterns. In essence, this means that it will be assumed that the standard deviation of the normal distributions of ages are equal in time, changing only the mean length with age. If this assumption is not met, then the assignment of the number of individuals to an age would be incorrect, and therefore, the mortality estimate is incorrect. A possible alternative to this situation would be to independently estimate the means and standard deviations of the frequency distributions for each age and, from the theoretical values on individual growth, obtain an age-length key in terms of probability and use it to convert each frequency distribution of lengths to age structure. Under this condition, an age-based method could be used.

Among the models developed in recent decades that do not depend on estimates of the growth rate, the gnomonic-interval model initially proposed by Caddy (1996) for species of short longevity stands out. In this model, the division of life stages into gnomonic intervals represents a sequence in the ontogeny of the species whose duration increases progressively according to a proportion factor that, although not discussed at the time, is assumed to be associated with attributes intrinsic to the life history of each species (John Caddy *pers. comm.*).

Martínez-Aguilar *et al.* (2005) modified this method to be applied to species of any longevity and allowed us to formally incorporate biological information to define the number corresponding to the gnomonic intervals with observed life stages where individuals are subject to the same habitat/community pressures. This approach provides the method with biological and ecological consistency compared to other methods (Table 1). Constructed in this way, this model is easily converted to ages or lengths.

The gnomonic model has been applied to different fishing resources in Mexico that correspond to species with different life histories and longevities. Such is the case for short-lived species such as several Penaeid shrimp: pink shrimp (*Penaeus duorarum* Burkenroad 1939) in the southern Gulf of Mexico (Ramírez-Rodríguez & Arreguín-Sánchez 2003), blue shrimp (*Penaeus stylirostris* Stimpson 1874), white shrimp (*Penaeus vanameii* Boone 1931), and brown shrimp (*Penaeus californiensis* Holmes 1900) (Aranceta-Garza *et al.* 2016), and the giant squid (*Dosidicus gigas* (d'Orbigny 1835)) from the Gulf of California (Martínez-Aguilar *et al.* 2010). This model has also been applied to relatively long-lived species such as the red grouper (*Epinephelus morio* (Valenciennes 1828)) (Giménez-Hurtado *et al.* 2008) and the sea cucumber (*Isostichopus badionotus* (Selenka 1867)) (Romero-Gallardo *et al.* 2018) on the Bank of Campeche, the Monterrey sardine (*Sardinops caeruleus* (Girard 1854)) from the Gulf of California (Martínez-Aguilar *et al.* 2005), and species of high longevity, such as the Venus clam (*Panopea globosa* Dall 1898) in the Mexican Pacific (González-Peláez *et al.* 2015).

It should be noted, however, that the current applications of the gnomonic-interval model do not consider variability in time, only with ontogeny. In this sense, the information on which the definition of the duration of the gnomonic intervals depends is directly linked to the information of average annual fecundity and the duration of the initial stage, typically egg. If this information is available annually, then it would be feasible to obtain a natural mortality vector based on gnomonic intervals over time, and it would be even better, if data are available on the duration of stages for different years. Thus, the interannual variation in this information could be contrasted with climate patterns, for example, to establish the effect of climate on the magnitude of spawning or on the duration of the egg or larval stages. Martínez-Aguilar *et al.* (2005) used this type

of data for the Monterrey sardine (*S. caeruleus*), even though they did not develop this approach.

Thus, when estimating natural mortality based on age or length in populations with no fishing, it is possible to use a simple method based on the Leslie matrix, as suggested by Arreguín-Sánchez *et al.* (2012) for the Venus clam (*Chione californiensis*) on the northern Pacific coast of Mexico. The method is based on abundance information expressed in frequency of lengths, according to the following expression:

$$\bar{N}_{\ell,t+\Delta t} = G_{\ell,k} \cdot S_k \cdot \bar{N}_{k,t}$$

where: \bar{N}_{ℓ} represents the vector from abundance to longitude ℓ ; k and ℓ represent successive length intervals, $t+\Delta t$ represents the period of time between the two abundance vectors; $G_{\ell,k}$ is the matrix that represents the probabilities of individual growth between length classes, estimated, in this case, according to the von Bertalanffy model; $S_k = e^{-M\Delta t}$ represents survival due to natural causes (M instantaneous natural mortality rate); and from successive data of \bar{N}_{ℓ} in time, M_{ℓ} could be estimated for different time periods.

Variable M and its impact on fisheries management

As previously noted, the consideration of the M variable with ontogeny and over time, with respect to the assumption of constant, could have consequences for decision-making due to the risk of generating biases or potentially errors in the estimates of stock's size and the state of resource exploitation. To illustrate this aspect, some species of commercial importance in Mexico were considered where, as illustrated in the previous section, estimates of M -at-age have been applied to several fishery resources that represent species with different life histories, longevity, habitat requirements, etc. Except for one case, the method based on gnomonic intervals has been applied, as shown in Table 2. Given that the method estimates natural mortality from the egg to adult stage and that in general, the early life stages are not commercially exploited, only the gnomonic intervals corresponding to commercial sizes were considered, assuming in this example mainly those that represent the adult stage and, in some cases juveniles, to include in the comparative analysis for at least the last two gnomonic intervals. For each species, the natural mortality values were available for each gnomonic interval considered (M_i). To ensure the

exercise was comparable between species, an initial number of 1 000 million individuals was arbitrarily assumed in the gnomonic interval immediately prior to that considered for the analysis. For both cases, variable and constant natural mortality, the number of individuals surviving at the end of the last gnomonic interval was calculated. Thus, for each species, the number of individuals surviving at the end of their longevity was obtained for each case of variable natural mortality M_i and constant M_c , represented as N_{if} and N_{cf} , respectively.

Table 2 shows important differences in the estimates of adult survival for the last gnomonic interval, varying the proportions of change, N_{if}/N_{cf} by a factor of 0.9 to 227.0, showing a tendency toward a greater overestimation of the population size in species with short longevities compared to species with long longevities (Fig. 1). This trend seems to be associated with the life history of the species. Thus, in general, the rates of change in short-lived populations are faster, for example, the growth and survival of a cohort occurs in a short period of time, which accentuates the overestimation. The opposite

Table 2.

Natural mortality (M_i) for exploited gnomonic stages reported in literature, for several fish stocks of Mexico. Comparison with constant natural mortality assumption is also shown. N_{if} = number at the last gnomonic interval computed with M variable; N_{cf} = number at the last gnomonic interval computed with M constant (Mc); e.m. and l.m. = early maturity and late maturity. Initial number for each case was arbitrary, just to show differences between M variable and constant. GC = Gulf of California, SGM = Southern Gulf of Mexico; CB = Campeche Bank

Scientific name	Common name	Location	Longevity (years)*	Gnomonic interval*	M_i^*	N_{if}	Mc	N_{cf}	$\frac{N_{if}}{N_{cf}}$	Reference
<i>Dosidiscus gigas</i>	jumbo squid	GC	1.2	Subadult	13	14	6.55	2 062	147	Martínez-Aguilar et al. (2010)
				Adult	5.1					
<i>Penaeus duorarum</i>	pink shrimp	SGM	1.3	Preadult	6	246	3.01	2 448	10	Ramírez-Rodríguez & Arreguín-Sánchez (2003)
				Adult	2.3					
<i>Penaeus vannamei</i>	white shrimp	GC	1	Preadult	8.4	12	3.62	716	60	Aranceta-Garza et al. (2016)
				Adult	2.9					
<i>Penaeus stylirostris</i>	blue shrimp	GC	1.1	Preadult	7.9	30	3.35	1 242	41	Aranceta-Garza et al. (2016)
				Adult	2.5					
<i>Penaeus californiensis</i>	brown shrimp	GC	1.5	Preadult	8.7	33	2.45	7 484	227	Aranceta-Garza et al. (2016)
				Adult	1.63					
<i>Sardinops caeruleus</i>	monterrey sardine	GC	7	Early Adult	1.00	122	0.55	105	0.86	Martínez-Aguilar et al. (2005)
				Adult	0.70					
				Late adult	0.40					
<i>Isostichopus badionotus</i> e.m.	sea cucumber	CB, SGM	10	Juvenile	2.29	67	0.69	252	3.76	Romero-Gallardo et al. (2018)
				Adult	0.41					
<i>Isostichopus badionotus</i> l.m.	sea cucumber	CB, SGM	10.1	Juvenile	0.69	252	0.68	256	1.02	Romero-Gallardo et al. (2018)
				Adult	0.72					
<i>Epinephelus morio</i>	red grouper	CB, SGM	19	subadult II	0.50	449	0.15	429	0.96	Romero-Gallardo et al. (2018)
				Adult I	0.20					
				Adult II	0.10					
<i>Panopea globosa</i>	geoduck clam	GC	49	juvenile	2.6	7.750	0.15	6 979	0.90	González-Peláez et al. (2015)
				late juvenile	2.21					
				dult	0.05					

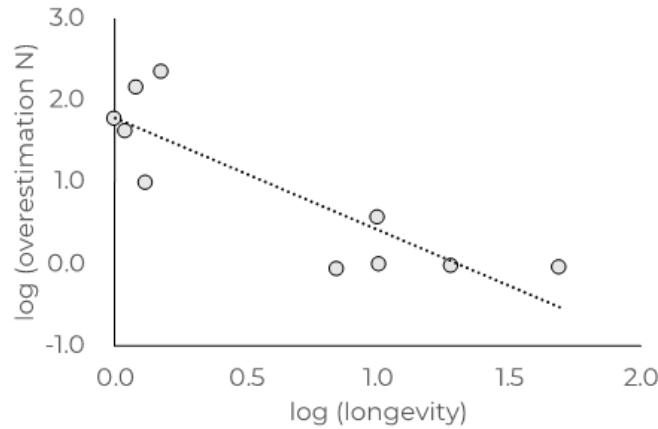


Fig. 1. Trend of the population size overestimation factor by assuming a constant natural mortality with respect to a variable. A tendency toward greater overestimation is clearly identified in species with short longevity compared to species with medium and long longevity.

is the case with long-lived species, where these rates of change are not only slower, but the changes are distributed over time and between generations.

On the other hand, the estimation of natural mortality based on growth information and lengths using the Leslie matrix for nonexploited populations reported by Arreguín-Sánchez *et al.* (2012) allows us to observe the variability in natural mortality over time and with ontogeny. In this particular case of the Venus clam *C. californiensis*, the mortality at length for different intra-annual periods shows very little variability between sizes but not over time (Fig. 2). Assuming a constant value of M-at-length for each period, a weighted average value was estimated for each period. Thus, the authors showed a pattern of variation

that suggests a seasonal behavior, with the highest values being observed toward the summer (July-August) with respect to the remainder of the year.

As in the previous case, a constant value of natural mortality was obtained as the weighted average value, and in this case, the relative abundance was used as a weighting factor, as shown in Figure 3. When the patterns of variable and constant natural mortality were used to estimate the size of the population, it was biased in 35% of the estimates according to the time of year.

For the Venus clam, the highest values of natural mortality coincided with the spawning season. If, for example, one of the conservation measures of an exploited species is to maintain a certain critical level of the reproductive stock,

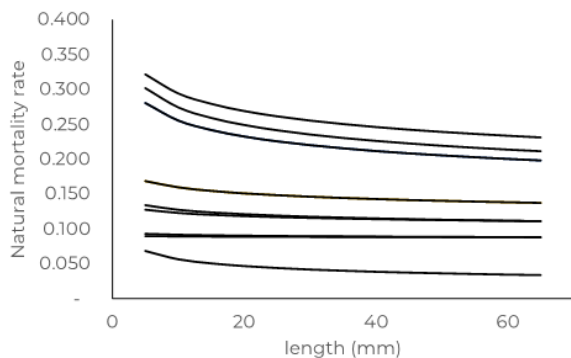


Fig. 2. Estimates of natural mortality-at-length for the Venus clam *Chione californiensis* on the northern coast of the Mexican Pacific. Each trend corresponds to monthly estimation at different times of the year. Note that for each case, the natural mortality at length tends to be constant. For more data on this species, see the reference in Table 1.

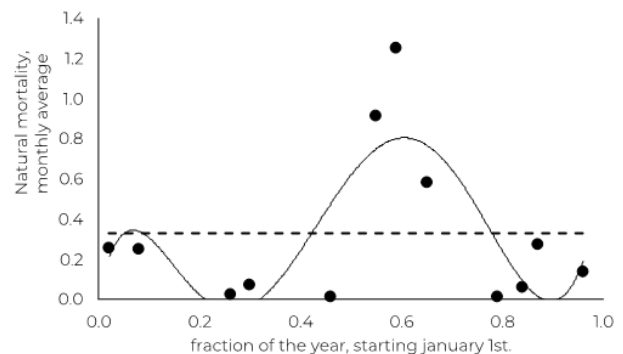


Fig. 3. Estimates of time-varying natural mortality for the Venus clam *Chione californiensis* on the northern Mexican Pacific coast. For more data on this species, see the reference in Table 1 (adapted from Arreguín-Sánchez *et al.* 2012).

then the precision with which the size of the reproductive stock is estimated would be relevant.

The concept in the illustrated cases showed the type of potential bias that can be incurred by assuming a constant natural mortality value with age when evaluating exploited stocks. The size of the bias seems to be inverse to the longevity of the species (Fig. 1), although this indication will have to be investigated in greater detail considering information on the life histories of species. The effect of the temporal variability in natural mortality is also notable. Even when few cases were reviewed, the possible consequences of assuming constant natural mortality on population size estimates can be of great relevance, especially for species that are in a state of excessive fishing or in recovery, or those for which there is special interest in their protection.

Currently many fishery resources are exploited to their maximum biomass production capacity. Under these conditions, it is necessary to include criteria in management decisions that help prevent growth and recruitment overfishing. For these cases, it is necessary to gain precision in the mortality estimates of both juveniles, to guarantee enough organisms from reaching adult stages and effectively contributing to reproduction; as well as the survival of reproductive adults that allows the supply of recruits and the persistence of the population. Part of this precision underlies the estimation of natural mortality, in such a way that the consideration of M -at-age is relevant for an accurate estimation of fishing mortality, in such a way that management measures are efficient. In the case of Mexican fisheries, the need for and importance of properly evaluating the natural mortality rate will largely depend on the state of exploitation of the stocks, to the extent that the resource is more pressured by fishing, the greater the need for an accurate estimate of natural mortality. It is also relevant, even in socioeconomic terms, when it comes to sequential fisheries, such as Penaeid shrimp, where a small-scale fleet typically exploits juvenile stages, while industrial fleets take advantage of adults. In these cases, a good estimate of natural mortality will contribute to a better definition of partial harvest rates by fleet. A different situation arises when the fleets compete for the same resource, with a particular biological sector of population predominating in their catches, as observed in the case

of the grouper fishery in the Bank of Campeche where a small-scale coastal fleet retain more juveniles than adults, and *vice versa*, with the semi-industrial fleet. In both cases, a high precision in the estimation of fishing mortality can be decisive for the management of the resource. In general, as mentioned above, specific survival will depend on the life history of the species, and the relative importance of assessing natural mortality as accurately as possible will largely depend on the state of resource exploitation.

Regarding the methods to be used to estimate variable natural mortality with age, it is difficult to recommend any one in particular, since, in most cases, it will largely depend on the information available. All the methods and their possible forms of solution when applying them have assumptions that must be considered. In general, those methods that are less restrictive and more representative of biological processes could be the most recommended. For example, as mentioned before, length-based methods assume that each length corresponds to a single relative age, contrasting against real ages were, for a given age, various lengths may be present with different probability. This restriction, in his case, makes the age structure more rigid over time when it could be that, due to the type of population, let us assume species of relatively short longevity, the interannual differences in recruitment are manifested in a greater variability of the relative age structure of each cohort. Within this context, the gnomonic interval method can be interesting in this sense when it is calibrated with independent information on the duration of life stages. Often, the developmental stages observed within a gnomonic interval contain ecological elements in common, such as shared habitat, same predators, etc. In general, the importance of the methods to be applied representing biological processes, as faithfully as possible, is highlighted; of course, depending on the information available.

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