Natural mortality of three commercial penaeid shrimps (*Litopenaeus vannamei, L. stylirostris* and *Farfantepenaeus californiensis*) of the Gulf of California using gnomonic time divisions

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Summary: The estimation of natural mortality (M) is critical for stock assessment and fisheries management. The shrimp fishery is the most valuable one in Mexico and along the Pacific Coast of Mexico, and exploitation primarily targets three species: white (*Litopenaeus vannamei*), blue (*L. stylirostris*), and brown (*Farfantepenaeus californiensis*). It is a sequential fishery, so an appropriate estimate of M for different life stages is required for management purposes. Typically, M is estimated from the exploited stock, which is usually composed of adults, assuming a constant value for M, and this estimate is used for studies of population dynamics, stock assessments and determinations of the status of a fishery. In this study, we estimate M-at-age (i.e. life stage) for each species using the gnomonic time division model. The gnomonic intervals correspond to the actual life stages reported in the literature, whose duration was used for model fitting. The gnomonic model showed that M declines sharply in early life stages but declines to an asymptotic value after reaching maturity, and the model provided biologically consistent estimates of M at each life stage for the three shrimp species. Such estimates may be used with confidence to model the dynamics of sequential shrimp fisheries.

Keywords: Gulf of California; natural mortality; sequential fishery; penaeid shrimps; gnomonic intervals.

Mortalidad natural de tres camarones peneidos comerciales (*Lithopenaeus vannamei, L. stylirostris* y *Farfantepenaeus californiensis*) del Golfo de California usando intervalos de tiempo gnomónicos

Resumen: La estimación de mortalidad natural (M) es crítica para la evaluación de stocks y el manejo de las pesquerías. La pesquería de camarón es la de mayor valor en México y a lo largo de la costa del Pacífico de México, y la explotación tiene primariamente a tres especies como objetivo: blanco (*Litopenaeus vannamei*), azul (*L. stylirostris*) y café (*Farfantepenaeus californiensis*). Se trata de una pesquería secuencial, de tal suerte que para su manejo se requiere de una apropiada estimación de M para los diferentes estadios de vida. Típicamente M es estimada de stocks explotados, los cuales están usualmente compuestos de organismos adultos, se supone un valor de M constante y esta estimación es usada para estudios de dinámica de poblaciones, evaluación de stocks y determinación del estado de las pesquerías. En este estudio estimamos M-a-edad (p.ej. estadios de vida) para cada especie usando el modelo de intervalos de tiempo gnomónicos. La duración de los intervalos gnomónicos corresponde a los estadios de vida reportados en literatura, cuya duración fue usada para ajustar el modelo. El modelo de intervalos gnomónicos mostró que M declina rápidamente en estadios tempranos de vida, cambiando hacia un valor asintótico después de alcanzar la madurez. El modelo provée estimaciones de M biológicamente consistentes para cada estadio de vida para las tres especies. Estas estimaciones pueden ser usadas con confianza para modelar la dinámica de pesquerías secuenciales del camarón.

Palabras clave: Golfo de California; mortalidad natural; pesquería secuencial; camarones peneidos; intervalos gnomónicos.

INTRODUCTION

Natural mortality, *M*, is a critical parameter in studies of population dynamics and in the modelling of the fish stocks for the development and implementation of management programmes. Biased estimates of *M* affect the assessment analysis of resources, which can have severe consequences (Caddy 1991, Ramírez-Rodríguez and Arreguín-Sánchez 2003).

There is biological evidence showing a typical *M*-at-age trajectory in penaeid shrimps; there is an early, steep drop over a short time period, which includes the early life stages (eggs and larvae), rapidly converging on an *M*-value asymptote for ages approaching maturity (Caddy 1991, 1996, Ramírez-Rodríguez and Arreguín-Sánchez 2003). The existence of an asymptote gives rise to the conventional assumption of a constant *M* for stock assessment purposes. This happens for two main reasons: many fisheries target adult individuals and it is difficult to estimate variable mortality based on field data from harvested stocks. Although this assumption would reasonably apply to individuals of the same age and area (Caddy 1996), other conditions may lead to errors. Such critical cases are the sequential fisheries, particularly those of penaeid shrimps in tropical waters, in which the harvesting may occur throughout most of the life history of the species.

The Mexican Pacific shrimp fishery is the most important fishery in Mexico. It is primarily based on three shrimp species: white (*Litopenaeus vannamei* Boone, 1931), blue (*L. stylirostris* Stimpson, 1874), and brown (*Farfantepenaeus californiensis* Holmes, 1900). The last two species comprise 80% of the landings (INP 2012). Three fleets typically exploit these shrimps: the estuarine or inshore fleet, which targets mainly juveniles, comprises fishermen who built barriers across the estuarine channels called *tapos* to prevent juvenile shrimps from escaping to offshore ground. They catch them using *atarrayas* or throwing nets from land or in small boats or canoes (typically 5 m long) with no engine, or outboard engines typically of 15-45 hp. The coastal fleet, which targets late-stage juveniles and pre-adults, uses a boat or *panga* (typically 7 m long) equipped with one trawling net. Finally, the offshore or industrial fleet targets adults and uses vessels (typically 18 to 23 m long) equipped with two trawling nets with a 30- to 40-day autonomy at sea. The sequential nature of this fishery imposes the need for proper *M*-at-age estimations to assess stocks and inform management.

Estimates of *M* for Mexican Pacific penaeid shrimps are mainly based on the exploited component of the offshore stock, which is mainly comprised of adults, so there are few estimates for the juveniles, and almost no estimates for very young stages (Table 1). The extreme variations in the *M* interval values reported in the literature for the three species range from $M_{postlarvae} = 46.8$ year^{-1} to $M_{adults} = 0.78$ year^{-1} in white shrimp, $M_{preadults} = 6.34$ year^{-1} to $M_{adults} = 0.48$ year^{-1} in blue shrimp, and $M_{preadults} = 8.5$ year^{-1} to $M_{adults} = 0.24$ in brown shrimp. With the exception of the estimate by García-Borbón (2009) (which was not included in the above ranges), who used the gnomonic model, these estimates were obtained through empirical methods assuming a constant *M* with age and time (Table 1).

The assumption of a constant *M*-value can be addressed by applying the gnomonic interval model proposed by Caddy (1991, 1996) and later expanded and improved by Martínez-Aguilar et al. (2005). The gnomonic model has been applied to short-lived species such as squids, *Loligo forbesi* and *L. vulgaris* of the English Channel (Royer et al. 2002) and *Dosidicus gigas* of the Gulf of California (Martínez-Aguilar et al. 2010), and to penaeid shrimps, *Farfantepenaeus duorarum* and *F. californiensis* of the Gulf of Mexico and the Gulf of California, respectively (Ramírez-Rodríguez and Arreguín-Sánchez 2003, García-Borbón 2009). Additionally, the model has been applied to some fish species, including the pacific sardine *Sardinops caeruleus* (Martínez-Aguilar et al. 2005) and the red grouper *Epinephelus morio*, of the Gulf of Mexico (Giménez-Hurtado et al. 2009).

Given the importance of the Mexican Pacific shrimp fishery and the sequential exploitation of the stocks, the objective of this study was to estimate the variation in natural mortality by life history stage in the three most important commercial penaeid shrimp species: white (*L. vannamei*), blue (*L. stylirostris*), and brown (*F. californiensis*).

MATERIALS AND METHODS

Determination of the gnomonic intervals

In this study, the gnomonic interval model (Caddy 1996, Martínez-Aguilar et al. 2005) was used to calculate the natural mortality values, *M*, for each life history stage in three penaeid shrimp species of the southern Gulf of California. The estimation of *M* for each gnomonic time interval requires the definition of the number of developmental stages during the life span of a species (Table 1); the duration of the first stage, which corresponds to the first gnomonic time interval, in this case the egg stage (Table 3); the mean lifetime fecundity (MLF) of each species (Table 2); and the individual durations of the life stages, which are used to calibrate the estimates (Table 4). The gnomonic model is based on the following assumptions (Caddy 1991, 1996): 1) stable population conditions; 2) 1:1 sex ratio and equal male and female mortality rates; 3) steady-state population replacement, i.e. that beginning with one female of MLF, a realistic mortality vector should result in an average survival of at least one female and since sex ratios are not considered, one survivor also from the males in the cohort (Caddy 1991); 4) the life history of a species can be subdivided into gnomonic time intervals in which the total deaths due to natural mortality in each are assumed constant, and the durations of the intervals increase proportionally with age; and 5) the estimated *M* values initially decline steeply from the egg stage to early maturity but then remain nearly constant.

Table 1. – Natural mortality estimates for the white (*L. vannamei*), blue (*L. stylirostris*) and brown (*F. californiensis*) shrimps in the Mexican Pacific.

Life history stage interval	Natural mortality M (year⁻¹)	Method	Locality
L. vannamei			
Egg			
Nauplius			
Protozoea			
Mysis			
Post-larvae	46.8 [a]	Subtraction between incoming inshore post-larvae and the commercial capture [a]	Huizache Caimanero lagoon, Sinaloa [a]
Juvenile	21.32 [a]	Juvenile tagging [a]	Huizache-Caimanero lagoon, Sinaloa [a,b]
	3.24-25.32 [b]	Ricker (1975) [b]	
Pre-adult	6.6-8.4 [c]	Ricker (1975) [c]	Topolobampo, Sinaloa [c]
Adult	1.92-4.98 [d]	Pauly (1980) [d]	Golfo de Tehuantepec [d,e]
	1.92 [e]	Ricker (1958) [f]	Mazatlán, Sinaloa [f]
	0.78-2.52 [f]		
L. stylirostris			
Egg			
Nauplius			
Protozoea			
Mysis			
Post-larvae			
Juvenile			
Pre-adult	6.34 [c]	Ricker (1975) [c]	North of Sonora [c]
	0.96-10.08 [c]		Bahía Magdalena [c]
Adult	2.4 [c1], 0.48-6.72 [c2]	Ricker (1975) [c1,c2]	Topolobampo, Sinaloa [c2]
	0.75-1.98 [f]	Beverton and Holt (1959) [g,h,j,l]	South of Sonora [g]
	1.56 [g]	Silliman (1943) [i]	North of Sonora [c1,h,k,l]
	3.3 [h]	Ricker (1958) [k]	Mazatlán, Sinaloa [f,i,j]
	0.96 [i,j]		
	0.72 [k]		
	0.99-1.45 [l]		
F. californiensis			
Egg	1559.5 [m]	Gnomonic model [m]	Bahía Magdalena [m]
Nauplius	553 [m]	Gnomonic model [m]	Bahía Magdalena [m]
Protozoea	106.8 [m]	Gnomonic model [m]	Bahía Magdalena [m]
Mysis			
Post-larvae	47.6 [m]	Gnomonic model [m]	Bahía Magdalena [m]
Juvenile	13.6 [m]	Gnomonic model [m]	Bahía Magdalena [m]
Pre-adult	7.8-8.5 [c]	Ricker (1975) [c]	Topolobampo, Sinaloa [c]
	8.1 [m]	Gnomonic model [m]	Bahía Magdalena [m]
Adult	2.38 [c1], 3.72 [c2]	Pauly (1980) [d,o1]	Golfo de Tehuantepec [d,e]
	2.28-3.6 [d]	Ricker (1958) [f,k]	Mazatlán, Sinaloa [f,i]
	2.28 [e]	Silliman (1943) [i]	North of Sonora [c1,k,l]
	0.24-1.93 [f]	Ricker (1975) [c1,c2,l]	Topolobampo, Sinaloa [c2]
	1.2 [g]	Gnomonic model [m]	Coastline of Sonora [n1,n2,n3]
	1.32 [i]	Rikhter and Efanov (1976) [n1,o2]	Bahía Magdalena [m,o1,o2]
	1.08-3 [k]	Pauly (1980) [n2]	
	2.23-2.36 [l]	Jensen (1996) [n3]	
	2.7 [m]		
	2.11 [n1], 2.72 [n2], 2.82 [n3]		
	1.22 [o1], 2.13 [o2]		

[a] Edwards (1977); [b] Sepúlveda-Medina (1981); [c1,2] Sepúlveda-Medina (1999); [d] Ramos-Cruz et al. (2006); [e] Rodríguez de la Cruz and Chávez (1994); [f] Jacquemin (1976); [g] Rodríguez de la Cruz (1976); [h] García de Quevedo (1990); [i] Lluch (1974); [j] Sáenz-Martínez and Lluch-Belda (1990); [k] García-Gómez (1976); [l] Ross-Terrazas (1988); [m] García-Borbón (2009); [n1,2,3] López-Martínez (2000); [o1,2] García-Borbón (2007).

The first data input is the time duration of the first gnomonic interval, $\Delta_1 = t_{1-0}$, which represents the egg stage after the moment of hatching (t_0). The duration of the second gnomonic stage is $\Delta_2 = \alpha * t_{2-1}$, where is the proportionality constant, and t_{2-1} is the duration of the interval. Successive gnomonic intervals are calculated as $\Delta_i = (\alpha * t_{i-1}) + t_{i-1}$, where $i \geq 3$ until the ith gnomonic interval. The typical lifespan of the penaeid shrimp is a year, so $t_n = \sum_{i=1}^{n} \Delta_i = 365$ days. Martínez-Aguilar et al. (2005) also proposed the inclusion of the durations of the observed life stages as auxiliary information to fit estimates of M-at-age or M_i to real data. This information is grouped to gradually obtain the best fit for the number and duration of the life stages estimated in the model, and the groupings are based on the biological characteristics of the life history stages, such as the respective habitats and predators. Therefore, the individuals that are grouped inside a gnomonic interval are assumed to be subject to the same biological and ecological conditions, which results in the same natural death rate. In our case, the duration of each life stage for each shrimp species is based on information reported in the literature (Tables 2 and 3).

According to Caddy (1996), each gnomonic interval has a constant proportion of the overall natural death rate (this could alternatively be expressed as a consequence of assuming that there is an equal risk of natural selection occurring in each life history stage),

Table 2. – Fecundity (average number of eggs per female) estimations reported in the literature for the white (*L. vannamei*), blue (*L. stylirostris*), and brown (*F. californiensis*) shrimps in the Mexican Pacific.

Species	Fecundity	Total length (mm)
L. vannamei	Minimum = 80000 [a]	TL$_{50}$ = 140 [b]
	Average = 265000 [a]	TL$_{MAX}$ = 210 [a,c]
	Maximum = 450000 [a]	
L. stylirostris	Minimum = 60000 [d]	TL$_{50}$ = 170 [e]
	Average = 350000 [d]	TL$_{MAX}$ = 240 [f]
	Maximum = 650000 [d]	
F. californiensis	Minimum = 100000 [e]	TL$_{50}$ = 117 [e]
	Average = 550000 [e]	TL$_{MAX}$ = 240 [g]
	Maximum = 1000000 [e]	

[a] Hernández-Covarrubias et al. (2012); [b] Sepúlveda-Medina (1991); [c] Chávez (1973); [d] Hernández-Covarrubias et al. (2003); [e] García-Gómez (1976); [f] Castro-Ortiz and Sánchez-Rojas (1976); [g] Chávez and Rodríguez de la Cruz (1971).

Table 3. – Duration of the egg stage reported for the white (*L. vannamei*), blue (*L. stylirostris*), and brown (*F. californiensis*) shrimps in the Mexican Pacific.

Species	Egg stage duration (hours)	(hours/24hrs)
L. vannamei [a,b,c]	10	0.4167
	13	0.5417
	16	0.6667
L. stylirostris [d,e]	13	0.5417
	14	0.5833
	15	0.6250
F. californiensis [f,g,h]	13	0.5417
	14	0.5833
	15	0.6250

[a] Andrade-Vizcaíno (2010); [b] Torres-Acuña (2008); [c] Kitani (1986a); [d] Kitani (1986b); [e] Prahl and Gardeazábal (1977); [f] Kitani and Alvarado (1982); [g] Schafer (1971); [h] Rodríguez de la Cruz (1976).

Table 4. – Gnomonic division of the life history for the white (*L. vannamei*), blue (*L. stylirostris*), and brown (*F. californiensis*) shrimps, showing correspondence with the observed information.

#Interval	Stage	Time (days) Initial	Final	Duration	Length (mm)	Reference
L. stylirostris						
1	Egg	0	0.58	0.58	0.36	Kitani (1986b)
2	Nauplius	0.58	1.5	0.92	0.48	Kitani (1986b)
3	Protozoea + Mysis	8.5	22	13.5	1-4	Kitani (1986b)
4	Post-larvae	15	36	21	5-25	Kitani (1986b), Renfro (1964)
5	Juvenile	36	82.08	46.08	25-90	Castro-Ortiz and Sánchez-Rojas (1976)
6	Pre-adult	82.08	161.65	79.57	90-160	Renfro (1964)
7	Adult	161.65	411	249.35	160-244	García-Gómez (1976), Alcántara-Razo (2005)
F. californiensis						
1	Egg	0	0.58	0.58	0	Kitani and Alvarado (1982)
2	Nauplius	0.58	2.4	1.82	0.6	Kitani and Alvarado (1982)
3	Protozoea + Mysis	9.4	19	9.6	2.7-5	Kitani and Alvarado (1982)
4	Post-larvae	12	32	20	5-25	Kitani and Alvarado (1982), Garduño-Argueta (1976)
5	Juvenile	32	90	58	20-80	Chávez and Rodríguez de la Cruz (1971)
6	Pre-adult	90	165	75	80-130	Chávez and Rodríguez de la Cruz (1971)
7	Adult	165	565	400	130-242	Chávez and Rodríguez (1971), Olguín-Palacios (1967), Rodríguez de la Cruz (1981), Sepúlveda-Medina (1991)
L. vannamei						
1	Egg	0	0.54	0.54	0.28	Andrade-Vizcaíno (2010)
2	Nauplius	0.54	2.75	2.21	0.6	Andrade-Vizcaíno (2010)
3	Protozoea + Mysis	10.75	20	9.25	2.7-4.5	Andrade-Vizcaíno (2010)
4	Post-larvae	12	25	13	6-25	Garduño-Argueta (1976)
5	Juvenile	25	79.04	54.04	25-90	Gutiérrez (1980)
6	Pre-adult	79.04	152	72.96	90-140	Lluch (1974), Gutiérrez (1980)
7	Adult	152	365	213	140-200	Lluch (1974), Gutiérrez (1980)

so the product of M_i and Δ_i is a constant for all of the intervals, $G=(M_i * \Delta_i)$, where G is the constant proportion of the mortality for each interval. The natural mortality rate is estimated as $M_i=G/ \theta_i - \theta_{i-1}$, where $\theta = \Delta_i/t_n$ and represents the duration of the gnomonic interval on an annual basis.

The number of individuals (N_i) at the beginning of each gnomonic interval is the number of survivors from the previous interval according to the relationship

$$N_{i+1} = N_i * e^{(-M_i * \theta_i)}$$

where $i \geq 2$. This is the case, except for the first interval, in which the number of hatching eggs is assumed to be similar to the MLF, such that

$$N_1 = MLF * e^{(-M_i * \theta_i)}.$$

Thus, the parameters α and G are calculated using

Newton's algorithm (Martínez-Aguilar et al. 2005), in which the values are selected when the sum of the life stage durations is equal (t_n*G). Under the assumption of "stable population replacement", N_i in the last gnomonic interval is equal to two (i.e. a 50% sex ratio is assumed, with identical mortalities at stage for males and females).

Variability in the estimation of M_i

The estimation of M_i in the gnomonic model assumes initial stability, at least for the cohort for which M is estimated. However, natural variability implies changes in both fecundity and the duration of the first life stage, which are the model input parameters, so the variability in the estimation of M_i is explored using changes in fecundity and the duration of the first life stage. The ranges of variation in fecundity and life stage duration are shown in Tables 2 and 3, respectively.
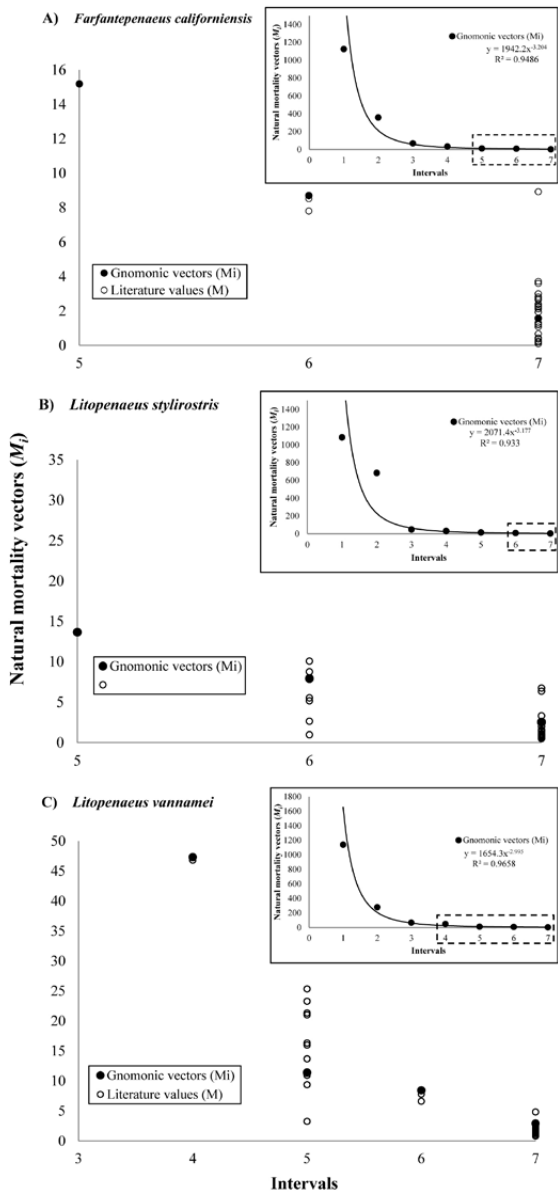
Fig. 1. – Natural mortality vectors estimated for brown (*F. californiensis*) (A), blue (*L. stylirostris*) (B), and white (*L. vannamei*) shrimps (C) with the gnomonic model are shown in solid black circles. Independent estimations from the literature are shown in solid white circles.

RESULTS

Estimation of the natural mortality by gnomonic intervals, M_i

Fitting the gnomonic model to the observed data resulted in seven intervals for the three penaeid shrimp species; each interval has its own characteristics related to development and habitat. The first three intervals are planktonic, but they are differentiated by the intrinsic characteristics of the larval development. The remaining four gnomonic intervals are benthic. The first two of these intervals, the post-larvae and juvenile stages, are differentiated by their characteristics and behaviour, according to the life history stage and habitat; both are present in estuarine and coastal waters. The

next two intervals, the pre-adult and adult life stages, inhabit the continental shelf and are differentiated by their behaviour and distribution, as adults commonly inhabit deeper waters and zones further from the continental shelf than pre-adults. The differences in the estimates of M_i can be explained by differences in the stages of development, such as behaviour, habitat use, vulnerability to predation and specific predators.

The longest-lived and most fecund species was the brown shrimp (565 days, MLF=550000 eggs) followed by the blue shrimp (411 days, MLF=350000 eggs) and the white shrimp (365 days, MLF=265000). The estimates of   for the different developmental stages and species are shown in Table 5; they fit most of the *M* values reported in the literature (Fig. 1A, B, C). In some cases, however, the reported value for adult brown shrimp is *M*=8.9 (Fig. 1A), which is a clear overestimation.

Variability in M_i

Based on the data reported in the literature, the variability in M_i associated with the variation in the duration of the egg stage was analysed (Table 3). Because the duration of the first gnomonic interval, the egg stage, is measured in hours, we considered steps of 0.5 hours within the range observed in the literature and fit these with the durations of the other stages, resulting in estimations of a mean value, standard deviation and coefficient of determination for M_i (Table 6).

DISCUSSION

Obtaining realistic estimates of the natural mortality of species with short lifespans, such as penaeid shrimp, represents a challenge for the fishery biologist. The white (*L. vannamei*), blue (*L. stylirostris*), and brown (*F. californiensis*) shrimps considered in this study are no exception. Though they have been intensively studied because of their commercial importance, there are still many aspects of their biology that are unknown, especially the early life stages, including their instantaneous rates of natural mortality. Independent estimates of *M* have been calculated in previous studies, but the majority of the literature is concentrated on the pre-adult and adult stages. The empirical equations used to estimate natural mortality were developed for adult stages and assume a constant *M*, and even when some authors have calculated *M* for juveniles, these estimates have usually been consistent with the biology of the species.

The gnomonic model obtains M_i estimates that better represent the biological reality than other models because it differentiates realistic life stages that correspond to different behaviours and habitats used by species throughout their life histories. Furthermore, Martínez-Aguilar et al. (2005) also proposed an algorithm that allows for calibration of the life stages.

The M_i values estimated for the three penaeid species were different, and this may be the result of their different life histories. The blue shrimp showed the lowest M_i values in four of the seven intervals (Table 5), and the least variation among the interspecific stages was observed in

Table 5. – Estimation of the natural mortality for the gnomonic intervals (M_i) using the mean duration of the first life stage (egg stage) for the species of white (*L. vannamei*), blue (*L. stylirostris*), and brown (*F. californiensis*) shrimps, using the gnomonic model; MLF, mean lifetime fecundity ; G, constant probability of death for each interval; α, is a proportionality constant.

Longevity, (days)	Intervals*	Stage	Gnomonic intervals (days)	Mortality at age (M_i)	Number of individuals (N_i)
P. vannamei (MLF = 265000; G = 1.684)					
α = 4.027	1	Egg	0.54	1138.87	49147
365	2	Nauplius	2.21	278.28	9115
	3	Protozoea + Mysis	9.25	66.49	1690
	4	Post-larvae	13.00	47.31	314
	5	Juvenile	54.04	11.38	58
	6	Pre-adult	72.96	8.43	11
	7	Adult	213.00	2.89	2
P. stylirostris (MLF = 350000; G = 1.724)					
α = 4.027	1	Egg	0.58	1085.34	62382
411	2	Nauplius	0.92	684.24	11119
	3	Protozoea + Mysis	13.50	46.63	1982
	4	Post-larvae	21.00	29.98	353
	5	Juvenile	46.08	13.66	63
	6	Pre-adult	79.57	7.91	11
	7	Adult	249.35	2.52	2
F. californiensis (MFL = 550000; G = 1.789)					
α = 4.027	1	Egg	0.58	1125.97	91900
565	2	Nauplius	1.82	358.83	15356
	3	Protozoea + Mysis	9.60	68.03	2566
	4	Post-larvae	20.00	32.65	429
	5	Juvenile	58.00	11.26	72
	6	Pre-adult	75.00	8.71	12
	7	Adult	400.00	1.63	2

Table 6. – Variation due to different egg duration stages for the white (*L. vannamei*), blue (*L. stylirostris*), and brown (*F. californiensis*) shrimps using the gnomonic model; n, number of different egg duration stages used in the estimation; SD, standard deviation; CV, coefficient of variation.

Gnomonic intervals	*F. californiensis* (n=5)			*L. stylirostris* (n=5)			*L. vannamei* (n=13)		
	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
1 Egg	1724.35	103.65	0.06	1212.71	62.71	0.051	884.25	520.64	0.589
2 Nauplius	550.59	10.29	0.018	761.37	25.29	0.033	240.46	95.85	0.399
3 Protozoea + Mysis	104.24	0.1	0.001	51.89	0.062	0.001	57.35	22.77	0.397
4 Post-larvae	50.03	0.05	0.001	33.36	0.04	0.001	40.81	16.2	0.397
5 Juvenile	23.27	0.02	0.001	15.2	0.018	0.001	9.82	3.89	0.396
6 Pre-adult	13.34	0.01	0.001	8.8	0.011	0.001	7.27	2.88	0.396
7 Adult	2.41	0	0.001	2.81	0.003	0.001	2.49	0.98	0.394

the egg and pre-adult stages (coefficient of variation [CV] = 2.5% and 4.86%, respectively; for others, CV ranged from 11% to 48.8%). The low variation in the egg stage is probably associated with its short stage duration (hours), and the pre-adult stage shrimp inhabit the continental shelf, so that stage is probably associated with relative low densities and, consequently, relative low vulnerability to predation as individuals are widely dispersed prior to their subsequent reproductive aggregation. From the nauplius to the adult stages, the CV of each M_i between species diminishes and continues to decrease with the duration of the stage until the pre-adult stage (Fig. 2). We hypothesize that this tendency suggests a similar pattern of behaviour between species in relation to their habitats, in which they share similar life conditions as they age. The pattern probably only changes for the adult and egg stages because reproductive processes and conditions are different between species, an aspect that is known in the literature (Magallón and Jaquemin 1976).

White shrimp showed the lowest M_i values of the larval mean range values ($\overline{M}_{1-4}$ =382.73 year^{-1}) as this species is probably less vulnerable to predation as a result of its rapid larval development in inshore habitats in contrast with the other two species. On the other hand, the brown shrimp lives in the offshore habitat throughout its lifecycle and showed a medium mean larval mean range value ($\overline{M}_{1-4}$ =396.37 year^{-1}), which is probably associated with its life history as most of its metamorphosis occurs in the water column, where it is exposed to higher predation. Blue shrimp showed the highest M_i values for the mean larval stage ($\overline{M}_{1-4}$=461.54 year^{-1}); this is due to the second interval, or nauplius stage, which had an estimated value of M_i=684 year^{-1}, almost double the values of the other species (white shrimp, M_4=278 year^{-1} and brown shrimp, M_4=358 year^{-1}). Blue shrimp showed a
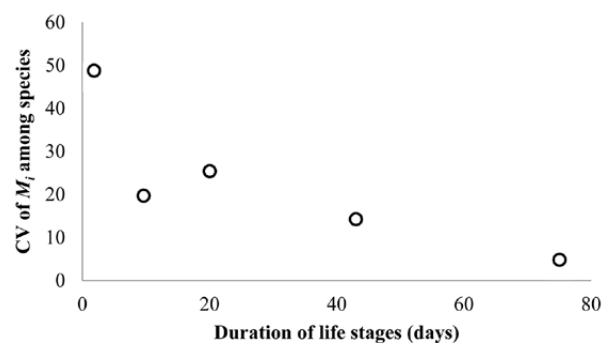

Fig. 2. – Decrement in the coefficient variation (CV) of the natural mortality at age (M_i) among the brown (*F. californiensis*), blue (*L. stylirostris*) and white (*L. vannamei*) shrimps in relation to the duration of their life stages (not including egg and pre-adult stage).

shorter duration and smaller size at this stage than the other two species (Table 4).

The blue shrimp is the dominant species in captures from the coastal zones, including the mouths of bays and estuaries (Rodríguez de la Cruz 1976, INP 2013). These zones are mostly exposed to environmental factors that contribute to higher larval mortality, including wave action and coastal currents that move larvae away from more favourable zones (Dahlberg 1979, Rumrill 1990). Furthermore, these zones serve as transit areas for the predators of penaeids. Local studies have reported predator species such as swimming crabs of the genus *Callinectes* and fishes, such as the snooks *Centropomus robalito* and *C. nigrescens*; the flounder *Cyclopsetta panamensi*; the catfish *Ariopsis seemani*; the snappers *Lutjanus argentiventris* and *L. novemfasciatus*; and the milkfish *Chanos chanos* (Sepúlveda-Medina 1981, Amezcua and Portillo 2010).

Previous shrimp stock assessment studies have primarily focused on the intervals most vulnerable to the offshore trawling fishery: pre-adults and adults. The gnomonic estimated values for both stages showed low variability among the shrimp species, possibly due to the convergence of all the species in the same zone during their migration to deeper marine waters (García and Le Reste 1986).

Globally, the M values reported for the adult penaeid stock varied between M=1.2 and 5.4 year^{-1} (García and Le Reste 1986), encompassing the estimated values from the gnomonic model. The M values reported in the literature for adult Mexican Pacific shrimps ranged from 0.09 to 8.92 year^{-1}. Caddy (1996) observed that low adult values, such as M_i=0.2-0.5 year^{-1}, are possible but imply extremely high mortality in the egg and larval phases. Similarly, in accordance with Gracia (1997), the author found that adult M values higher than 5 are excessive and incompatible with an annual species. Thus, the magnitudes of the M_i values estimated with the gnomonic model in this study appear to be reasonable and compatible with the life histories of the three shrimp species.

The gnomonic model as proposed by Caddy (1996) and improved by Martínez-Aguilar et al. (2005) appears to provide biologically reasonable estimates of natural mortality during all life history stages. Fitting the estimates with independent data allowed for the identification of key life stages. Additionally, though some of the independent estimates of M for some life stages appear to be biologically inconsistent, they do not greatly affect the final estimation (even when included in the fitting process) because the pattern of the duration of time between life stages is governed by the properties of the gnomonic model, where parameter maintains the proportionality between the duration of the different life stages. The duration of the first life stage is most critical as an input for the gnomonic model because it affects parameter α.

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