Natural mortality and life history stage duration for the jumbo squid (*Dosidicus gigas*) in the Gulf of California, Mexico, using the gnomonic time division

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The gnomonic-interval natural-mortality model (GIM) that provides an indicative vector of natural mortality (M) and of life history stage duration was applied to the jumbo squid (*Dosidicus gigas*) of the Gulf of California, Mexico. Estimate of M incorporated uncertainty because of fecundity variation. The variability in longevity and first stage duration were also explored for the estimations of M. We observed that M declines with age, independently of the duration of egg stage and of the longevity values and approached an asymptotic value for adult stage (M ≈ 5 per year). Compared with another iteroparous species, we found that jumbo squid which is assumed to be a semelparous species have relatively lower mortality rates during their early life stages and higher ones in their adult stages. The magnitude of the M values is greater when for its estimation the value of life spans is increased. A comparison of the G parameters (constant probability of death within each gnomonic interval) obtained with GIM for various species: jumbo squid (*Dosidicus gigas*), pink shrimp (*Farfantepenaeus duorarum*) and Pacific sardine (*Sardinops caeruleus*) reveals how differences in life-history strategy, fecundity and natural mortality might be related.
Key words: Natural mortality, duration of life history stages, semelparous species, iteroparous species.

Mortalidad natural y duración de los estadios del ciclo de vida del calamar gigante (*Dosidicus gigas*) en el Golfo de California, México, usando intervalos de tiempo gnomónico

El modelo de intervalos gnomónicos (GIM) que proporciona índices del vector de mortalidad natural (M) y de la duración de los estadios del ciclo de vida fue aplicado al calamar gigante (*Dosidicus gigas*) del Golfo de California, México. Las estimaciones del vector de M incorporaron incertidumbre debida a la variación de la fecundidad. La variabilidad en la longevidad y en la duración del primer estadio del ciclo de vida fue también explorada para las estimaciones de M. Se observó que M declina con la edad independientemente de la duración del estadio huevo y de los valores de longevidad y, se aproxima a un valor asintótico en el estadio adulto (M ≈ 5 por año). Comparados con otras especies iteróparas, nuestros resultados indican que el calamar gigante, que se asume como especie semélpara, tiene bajas tasas de mortalidad durante los estadios tempranos del ciclo de vida y altas en los estadios de adulto. La magnitud de los valores de M es mayor cuando para su estimación se incrementa el valor de longevidad. La comparación del parámetro G (la probabilidad de muerte se mantiene constante dentro de cada intervalo gnomónico) obtenido con GIM para varias especies: calamar gigante (*Dosidicus gigas*), camarón rosado (*Farfantepenaeus duorarum*) y sardina del Pacífico (*Sardinops caeruleus*), explica cómo las diferencias en la estrategia del ciclo de vida, la fecundidad y la mortalidad natural pueden ser relacionadas.
Palabras clave: Mortalidad natural, duración de los estadios del ciclo de vida, especie semélpara, especie iterópara.

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Introduction

The usual convention for describing the mortality factors affecting fishery stocks is that the total mortality rate (z) is the sum of constant rates of fishing (f) and natural (m) mortality. The natural mortality is a key parameter in fishery stock assessments because estimations of potential yield, optimum size to harvest and most refined methods for fishery stock assessment, all depend on having a reasonable estimate of the rate of death due to natural causes. Natural mortality includes all sources of mortality not related to fishing activities and is one of the most difficult parameters to quantify since it may vary due to age-specific predation including cannibalism, disease, spawning stress, starvation, senescence and inter or intra specific competition. The same species may have different natural mortality rates in different areas, depending on density of predators, competitors and environmental factors (Megrey, 1989; Sparre *et al.,* 1989). Uncertainty as to the value of *M* is often oversimplified by assuming that death due to natural causes is constant for all individuals in the population, and the conventional practice in stock assessment work for short-lived species such as penaeid shrimps and for most squid species of commercial importance, has been to assume a single indicative value for adult death rate: the constant natural mortality rate (Caddy, 1996). Although quite unrealistic for early life history stages, this assumption largely stems from the lack of a specific methodology for assessing natural mortality at age. This in turn stems from the difficulty of determining age with sufficient accuracy.

Direct estimates of *M* are difficult to obtain for most populations that have been harvested for many years and indirect methods are frequently used for its evaluation. The indirect methods most commonly used are correlations of *M* with other life history parameters such as growth rate, age at sexual maturity, environmental temperature and estimation of deaths due to predation (Beverton and Holt, 1959; Tanaka, 1960; Holt, 1965; Saville, 1977; Pauly, 1980; Hoening, 1983). Estimates of *M* has been obtained by applying a modified catch curve analysis, the assumption of this application is that in absence of fishing mortality f, the total mortality z is due entirely to natural causes z = m (Sinclair, 2001) and with a more traditional regression analysis of *z* as a function of *f*; the intercept of this regression is an estimate of *m* and the slope is an estimate of the catchability (Beverton and Holt, 1957; Paloheimo, 1961; Garrod, 1967; Ricker, 1975). Other approaches using tagging and telemetry have resulted in reliable direct estimates of *M* (Hearn *et al*., 1998; Frusher and Hoening, 2001; Hightower *et al*., 2001; Latour *et al.,* 2003; Pollock *et al*., 2004), however these methods are still inaccessible for most fishery scientists and no suitable to extensive migratory short-lived species.

Caddy (1991, 1996) developed a model that estimates a range of age specific *M* values for the invertebrates with short life spans. Fundamentally, the assumptions in the model are that the stock is under a stable condition and that its life span can be divided into intervals within which the probability of death from natural causes is assumed as constant. The assumption of "stable population replacement" is applied namely that beginning with the mean lifetime fecundity (mlf) of one female, a mortality vector should result in an average survival of at least one female and one male will survive. Assuming a 1:1 sex ratio, male and female mortality rates are assumed the same. The analogy developed in this model is between natural mortality processes at the cohort and the population level (Caddy, 1991). The method does not describe density-dependent effects. The natural mortality rate in the last intervals during and following the time at first maturity corresponds to the "constant *M* value of fishable adult stock" used in stock assessment (Vetter, 1988; Caddy, 1996). According to Caddy (1996), these *M* values can be used in stock assessment by assuming that the absolute or relative natural mortality rates estimated under unexploited conditions, also apply under exploitation. This methodology has been used for loliginid squid and shrimp (Royer *et al.,* 2002; Ramírez-Rodríguez and Arreguín-Sánchez, 2003). Martínez-Aguilar *et al.* (2005) used the Caddy (1996) method for species living longer than one year, incorporating uncertainty about fecundity. Martínez-Aguilar *et al.* (2005) were the first to notice that gnomonic intervals actually correspond closely to durations of successive life history stages. This modified

version also allows observed intervals to be incorporated in the procedure. The modified version of the gnomonic-interval natural-mortality method referred as GIM, was used to obtain indicative values for *M*-at-age for the long-lived Pacific sardine (*Sardinops caeruleus*) of the Gulf of California.

In this work, GIM is applied to the life history of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae), which supports an important fishery in the central region of the Gulf of California (Fig. 1). These new estimates of *M* for *D. gigas* are discussed in relation to previous estimates and the life history characteristics of the stock. Estimates of natural mortality rates for cephalopods are scarce and the existing ones are only for the adult stages. Natural mortality values have not been reported in the existing literature for early stages of the life cycle, neither for *D. gigas* nor for other squid species. Caddy (1996) reported indicative values for natural mortality vectors with age for short-lived invertebrate populations. The author mentioned that for semelparous species, like many squids, there is an almost instantaneous increase in adult death rate shortly following spawning in their adult stages. Previous estimates of *M* for this squid in the Gulf of California were based on indirect methods, mainly using the longevity of the species (Taylor, 1958; Allen, 1971; Pauly, 1980, 1987; Jensen, 1996). The range of reported *M* values is wide. The maximum estimates are 10 times greater than the minimum estimates (Table 1).

Material and methods

The life cycle of jumbo squid was divided into subunits of time, which increase as a constant proportion of the time elapsed from birth up to initiation of each subdivision, a strategy referred to as gnomonic (Caddy, 1996). Estimation of *M* for each gnomonic time interval (Δ_i) is referred to as *M*-at-age *i*, where $i = 1, 2, 3 \dots n$. The time elapsed (t_1), starting at time $t = 0$, during the first stage corresponds to the first gnomonic time interval (Δ_1). The duration of the second gnomonic interval was estimated as $\Delta_2 = \alpha \cdot t_{2-1}$, where α is a proportionality constant.

Table 1

Mortality natural estimates and longevity reported in the literature for the jumbo squid (*Dosidicus gigas*) of the Gulf of California

Mortality rates		Longevity		References
week $^{-1}$	1 year $^{-1}$	1 day	1 year	
0.01-0.03	0.6-1.56	487-1125	1.3-3	Erhardt *et al.* (1983)
0.01-0.04	0.48-1.8			Morales-Bojórquez *et al.* (1997)
0.1	4.8			Hernández-Herrera *et al.* (1998)
0.10	4.8			Morales-Bojórquez *et al.* (2001)
		365-730	1-2	Nigmatullin *et al.* (2001)
0.10	4.8			Morales-Bojórquez & Nevárez-Martínez (2002)
		243-730	0.7-2	Markaida-Aburto *et al.* (2003)
		456-365	1-1.3	Filauri (2005)
0.02-0.04	1.02-1.95			Nevárez-Martínez *et al.* (2006)

Successive gnomonic intervals are computed as $\Delta_i = (\alpha \cdot t_{i-1}) + t_{i-1}$, where $i \geq 3$ up to the *n-th* gnomonic interval. If the species has an annual life span, then $t_n = \sum_{i=1}^{n} \Delta_i$, is usually 365 days. Caddy (1991) suggested that each gnomonic time-interval should account for a constant proportion of the total lifetime mortality. Therefore, the product of M_i and Δ_i is assumed constant for all intervals and is defined as $G = M_i \cdot \Delta_i$, where *G* is the constant probability of death for each interval (Caddy, 1996). The natural mortality rate is $M = G/\theta_i - \theta_{i-1}$, where $\theta_i = \Delta_i/t_n$ represents the duration of a gnomonic interval as a proportion of a year for an annual organism. When the species lives longer than one year, t_n is modified to $t_l = \sum_{i=1}^{n} \Delta_i$, where t_l is total longevity (in days). Here θ_i was computed as $\theta_i = (\Delta_i/t_l)/365$ so that M_i estimates would have annual units.

The number of individuals (N_i) at the starting of each *i-th* interval is the number of survivors from the previous interval, except for the first for which it was assumed that hatched numbers are equivalent to mean lifetime fecundity (MLF) determined from individual fecundity estimates. Then, the N_1 of the first gnomonic time-interval is computed as $N_1 = MLF \cdot e^{-M_i \cdot \theta_i}$. Successive
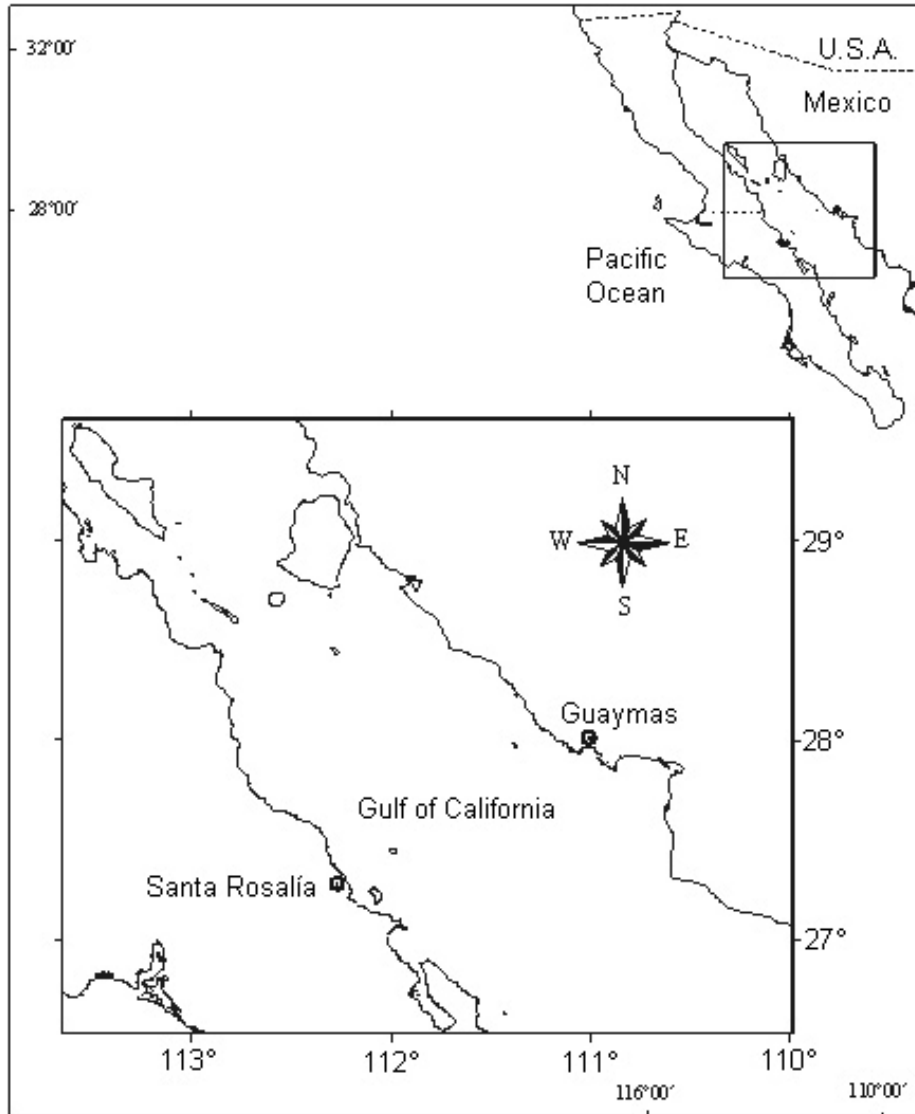
Fig. 1. The central region of the Gulf of California showing the fishing grounds of the jumbo squid.

values of N_i are computed as $N_i = N_{i-1} \cdot e^{-M_i \cdot \theta_i}$, where $i \geq 2$ up to the *n-th* gnomonic interval. The parameters α and G were calculated numerically using a Newton algorithm (Neter *et al.,* 1996). The α value was chosen such that the sum of gnomonic time-intervals was equal to the longevity (t_l). G value was chosen by iteration such that the number surviving to the last gnomonic time-interval (N_i) equaled two (Caddy, 1996). Daily survival rates for life stages (ς_i) were calculated as $\varsigma_i = \exp^{-\Pi_i} / \Delta_i$.

The number of gnomonic intervals was set at five based on the development stages that

reasonably describes the life cycle of jumbo squid: egg (egg masses are unknown); the mantle length (ML) at hatching averages 1.1 mm (Yatsu *et al.,* 1999), this is followed by four stages: paralarva (1-10 mm ML), juveniles (15-100 mm ML), subadults (150-300 mm ML) and adults (400-1 000 mm ML) (Nigmatullin *et al.,* 2001). During these life history stages, the morphology, food spectrum and ecological status of squid changes markedly. Observed duration for egg stage at 18 °C ranges between 6-9 days (Yatsu *et al.,* 1999). Nigmatullin *et al.* (2001) and Boyle and Rodhouse (2005) indicate that longevity of the

jumbo squid is about one year, but some huge specimens can live for up to 1.5 to 2 years. Since longevity is a parameter as difficult to quantify as M, for jumbo squid we tested 1, 1.2 y 1.5 years (365, 438 and 540 days) as longevity in the GIM based on older individuals in commercial catches from 2002 to 2005 (field data) obtained in Santa Rosalía fishing grounds (Fig. 1). We computed different vectors of M for a range of durations of the egg stage, with increments of 0.5 days for different longevity values.

Dosidicus gigas was assumed as monocyclic or semelparous, such that individual squid have only one reproductive season during their life. Reproduction occurs all year round with two spawning peaks during spring and summer (May-June, September-October). We utilized the potential fecundity (the maximum number of oocytes in the ovary prior to spawning) based on Markaida-Aburto (2001) data (Table 2) for estimation of MLF interval range which in turn was tested with the GIM. In our estimation of natural mortality for jumbo squid, we used values of MLF: 813 000; 16 387 656 and 25 887 000 eggs·female·year, which correspond to minimum, average, and maximum values. The spawning frequency was assumed once per lifetime.

We calculated standard deviations and coefficients of variation for our estimates, assuming that the main source of uncertainty and variability is on MLF with a uniform distribution, so that $\text{MLF} \approx \text{U}\left(\text{MLF}_{min}. \text{MLF}_{max}\right)$, where the lower and upper bounds were the smallest (MLF_{min}) and largest (MLF_{max}) values observed for MLF. We simulated 1 000 estimates of natural mortality for gnomonic time and estimated mean mortality rate $\left(\overline{\mu}_i\right)$. The standard error was represented by the standard deviation $\left(\sigma_i\right)$ for M_i. The coefficient of variation was $\text{CV}_i = \sigma_i / \overline{\mu}_i$ according to the bootstrap approach. The mean of the bootstrap analysis represents the mean of the original parameter estimated (in this case M for time-interval) (Deriso *et al.*, 1985), therefore the standard deviation of the bootstrap represents the standard error of estimated M. Our characterization of uncertainty was measured from standard error and mean in relation to M estimates.

Table 2
Mean lifetime fecundity (MLF) calculated from potential fecundity values reported for the jumbo squid (*Dosidicus gigas*) of the Gulf of California (Markaida-Aburto, 2001). *Calculated values by linear regression between average of potential fecundity at age reported and, the age (year)

Age (year)	Weight (kg)	Average fecundity (No. eggs)
0.3	0.39	813 000*
0.4	0.85	13 838 000*
0.5	1.54	10 231 355*
0.6	2.50	6 773 500
0.7	3.78	13 207 750
0.8	5.40	17 708 333
0.9	7.40	18 290 000
1.0	9.81	20 231 355*
1.1	12.66	22 231 355*
1.2	15.98	18 072 500
1.3	19.79	24 473 500
1.4	24.13	25 887 000

Results

The number of intervals (was set at five) into which the life history of jumbo squid was divided was an *a priori* decision. In this case, the knowledge of the life history allowed us to divide the lifespan into biologically realistic subunits of time (life history stages). Natural mortality vectors (M-vectors) estimated in this study, are based on the reported range of the egg stage duration combined with three different longevity values. Estimated M-vectors decreased with age during the early life history and approached the same asymptotic value for adult stage at $M \approx 5$ per year, independently of egg stage duration (from 6 to 9 days) and longevity (365, 438 and 540 days). The standard deviation of M_i also decreased with age. Nevertheless, the magnitude of M_i increased with a longer life span. M_i values for early intervals, from eggs to paralarva, were relatively high, ranging between 84 and 283 per year, for juvenile varied between 33 and 44 per year. M values have not been reported in the existing literature for early stages of the life cycle, neither for *D. gigas* nor for other squid species. M_i values from subadult to adult varied between 4.7 and 14 per year (Table 3). The values of M_i for adult ($M \approx 5$ per year) correspond to those phases

Table 3
Estimates of natural mortality vectors and duration of developmental stages for the jumbo
as a function of egg stage duration (bold numbers) and longevity of the jumbo squid (*Dosidicus gigas*).
Mean mortality rate for stage of development $\left(\overline{\mu}_i\right)$ and standard deviation (σ_i)

Stage of development longevity (days)	Duration (days) 365	μ_i per year	σ_i	Duration (days) 438	μ_i per year	σ_i	Duration (days) 540	μ_i per year	σ_i
Egg	**6.0**	191	10	**6.0**	229	12	**6.0**	283	14
Paralarva	11	107	6	12	119	6	12	136	7
Juvenile	30	38	2	34	41	2	38	44	2
Subadult	84	14	1	99	14	1	118	14	1
Adult	234	4.9	0.3	288	4.8	0.2	365	4.7	0.2
Egg	**6.5**	177	9	**6.5**	212	10.6	**6.5**	261	13.0
Paralarva	11	102	5	12	113	6	13	129	6
Juvenile	31	37	2	35	40	2	40	43	2
Subadult	85	14	1	100	14	1	120	14	1
Adult	232	5.0	0.2	285	4.8	0.2	361	4.7	0.2
Egg	**7.0**	164	8	**7.0**	196	10	**7.0**	242	12
Paralarva	12	97	5	13	108	5	14	123	6
Juvenile	32	36	2	36	38.5	2	41	41.6	2
Subadult	85	13	1	100	13.7	1	121	14.0	1
Adult	229	5.0	0.2	282	4.8	0.2	358	4.7	0.2
Egg	**7.5**	153	7	**7.5**	184	9	**7.5**	226	12
Paralarva	12	93	5	13	104	5	14	118	6
Juvenile	33	35	2	37	38	2	42	41	2
Subadult	86	13	1	101	14	1	122	14	1
Adult	227	5.1	0.2	280	4.9	0.2	355	4.8	0.2
Egg	**8.0**	143	8	**8.0**	172	9	**8.0**	212	11
Paralarva	13	89	5	14	100	5	15	114	6
Juvenile	33	34	2	37	37	2	43	40	2
Subadult	86	13	1	102	13	1	123	14	1
Adult	225	5.1	0.3	277	5.0	0.3	352	4.8	0.2
Egg	**8.5**	134	7	**8.5**	162	8	**8.5**	200	10
Paralarva	13	86	5	14	96	5	15	110	5
Juvenile	34	34	2	38	36	2	44	39	2
Subadult	87	13	1	102	13	1	124	14	1
Adult	222	5.1	0.3	275	5.0	0.3	349	4.9	0.2
Egg	**9.0**	128	6	**9.0**	153	7	**9.0**	188	10
Paralarva	14	84	4	15	93	5	16	105	6
Juvenile	35	33	2	39	35	2	45	38	2
Subadult	87	13	1	103	13	1	124	14	1
Adult	220	5.2	0.3	272	5.1	0.2	346	4.9	0.3

exploited by the artisanal fisheries. Estimated values for adult are in general terms, similar to those reported in the literature by independent methods (Table 1).

We found that the duration of the egg stage has an impact on consecutive M-at-age estimates. For example, the estimated time duration for paralarva stage using the extreme duration of egg stage (six and nine days), varied from 11 to 14 days and M ranged from 107 to 84 per year. For pelagic eggs Lo (1985) observed, in laboratory experiments, that developmental rate of eggs is temperature-dependent and that modifies the survival rate. The incubation time of the jumbo squid as a function of temperature have not been studied in the Gulf of California, therefore we used the reported times of egg development. Martínez-Aguilar *et al.* (2005) showed that the constant α (proportionality constant) is associated with the duration of life history stages and that it also is inversely related to the duration of the egg stages. We observed that for the jumbo squid the parameter α also is inversely related to egg stage duration (Fig. 2), whereas G (constant probability of death for each interval) varied with fecundity, but its range (2.6 to 3.3, average 3.1) is the same for all the natural mortality vectors. The relation between the development rate of eggs and temperature could be associated with the behavior of the constant α.

According to the concept of gnomonic intervals, the duration of development stages increases over the life cycle. The sum of the life
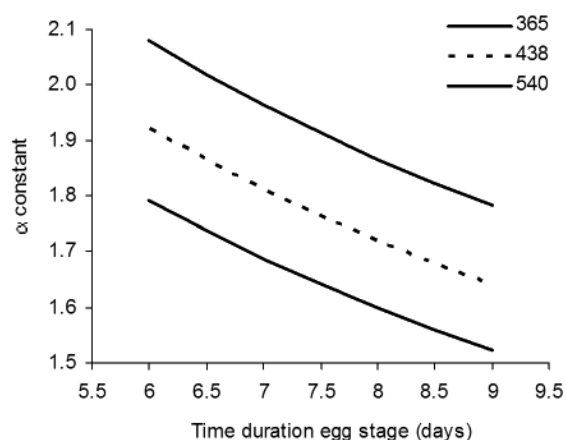
history stage duration estimated with GIM along the column (duration in days) of each vector is the total longevity (represented by 365, 438 and 540 days respectively), whereas values in adult stage correspond exclusively to the duration of this stage. As an example, using the vector of 6-days egg stage with longevity of 365 days, the duration estimated for adult stage was 234 days.

When M-at-age values were used to calculate daily population survival, we observed an inverse relationship between survival and duration at each development stage, except for the last stage. *Figure 3* shows an example for the paralarva in which daily survival is high when stage duration is short.
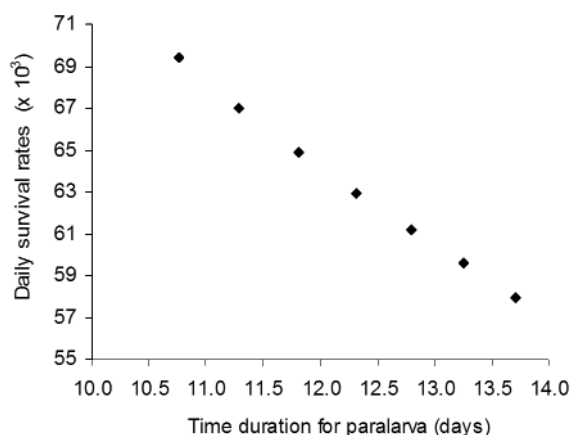

Fig. 3. Relationship between the daily survival rates with stage duration for paralarva of the jumbo squid (*Dosidicus gigas*).

Discussion

In the absence of direct measurements of natural mortality and independent observations of life history stage duration, we believe that the gnomonic model provides a reasonable starting point for estimating of the M-vector for jumbo squid, under explicit assumption for ideal conditions of stable population replacement. Although the jumbo squid show different size-at-maturity groups with different biological parameters (longevity, fecundity), and variable sexual proportion (Markaida-Aburto, 2001; Nigmatullin *et al.,* 2001), detailed information for such parameters at each size-at-maturity is absent, so that GIM analysis brings a general overview mainly focused on exploited stock of

Fig. 2. Relationship between value of the constant α and duration of the egg stage at different longevities.

jumbo squid. Under this context, an underlying assumption is that the exploited stock is mainly sustained by one single cohort, which has proved to be a reasonable analytical approach for modeling simulation and fishery management.

GIM can evaluate the impact of variations caused by fecundity and duration of development stages. The method does not make specific allowance for special factors such as cannibalism, which may be important for jumbo squid, however there is no reason to suppose that the size-specific risk of cannibalism in squids differs greatly from that due to other types of predation reason why it is not specified in the model (Caddy, 1996). Likewise, GIM does not identify patterns in natural mortality caused by strong environmental change, but GIM calculation is useful under average conditions.

Compared with another studies, the natural mortality rates we obtained ($M_i \approx 5$ year^{-1}) are on the higher side of the range estimated for *D. gigas* adults (Table 1). The M_i estimates for *D. gigas* using the GIM method seem to be in accordance with its life cycle characteristics: a high growth efficiency and short lifespan (Nigmatullin *et al.,* 2001). Calow (1987) found that high growth efficiency (efficient conversion of food energy into growth) in cephalopods is indicative of rapid accumulation of biomass into intermediate developmental stages. Compared with another iteroparous species, the rapid attainment of maximum body size suggests that jumbo squid have a relatively low mortality during early life stages (egg, paralarva and juvenile) and a higher mortality as adults. For example, egg stage mortality in Pacific sardine ranges from 318 to 117 per year while adult mortality ranges from 0.4 to 0.7 per year (Martínez-Aguilar *et al.,* 2005). In contrast, in jumbo squid egg stage mortality ranged from 229 to 153 per year, while adult mortality ranged from 4.8 to 5.1 per year (Table 4). For Boyle (2002) this indicates that a relatively high proportion of total production is retained in the adult fraction of squid population for breeding and subsequent death.

On the other hand, the increasing trend of M_i as life span increases can be explained by the variation in the growth rate. The growth rate for a 365-days lifetime is higher than a 540-days lifetime, because the organism must reach the

same length in less time. Rapid growth in early stages is usually assumed to be an advantage for individual survival, because exposure to predation is shorter. In our work, we also found that duration of the first stage (the egg) is inversely related to daily survival (ς_i). Houde (1987) reported that temperature has a significant effect on the daily mortality rate of fish pelagic-eggs by extending or shortening the development time. Duration of life stages obtained using the GIM method suggests this proportionally inverse relationship is a reasonable assumption for *D. gigas*.

A comparison of *G* parameter obtained with GIM for various species: jumbo squid (*D. gigas*) (G = 2.6-3.3), pink shrimp (*Farfantepenaeus duorarum*) (G = 1.64) (Ramírez-Rodríguez and Arreguín-Sánchez, 2003) and Pacific sardine (*Sardinops caeruleus*) (G = 1.3 constant value) (Martínez-Aguilar *et al.,* 2005) reveals how fecundity and natural mortality might be related under different life-history strategies (Table 4). For short-lived, annual species such as jumbo squid and pink shrimp, there is no overlapping of generations, so that population size depends largely on the strength of annual recruitment and even for pink shrimp there are changes in *G* value with those in MLF (Ramírez-Rodríguez and Arreguín Sánchez, 2003; Boyle and Rodhouse, 2005). In contrast, the Pacific sardine with a longer life cycle and whose recruitment represents the annual increment in number of the multi-annual-aged cohorts, inter-annual fluctuations in Δ (mean annual lifetime-fecundity) are of lesser relevance and *G* has a constant value. Nevertheless, for jumbo squid *G* value varied with fecundity, but its range is the same for all the natural mortality vectors. This can be caused by the presence of more than one cohort in the population. Morales-Bojórquez *et al*. (2001) mentioned that although they recognize a dominant cohort in the fishery of jumbo squid of the Gulf of California, the catchability analysis of the fishery suggest the presence of three cohorts.

Jones (1973) and Beyer (1989) discussed the importance of variations in fecundity as part of the population regulatory process and minimized the importance of density-dependent fecundity in the population regulation. Jones

Table 4
Instantaneous rates of natural mortality and the duration of development stages using the gnomonic-interval natural-mortality model (GIM) for pink shrimp (*Farfantepenaeus duorarum*) (Ramírez-Rodríguez and Arreguín-Sánchez, 2003) and Pacific sardine *(Sardinops caeruleus)* (Martínez-Aguilar *et al.,* 2005) and the estimates for jumbo squid (*Dosidicus gigas*) (this work). Mean lifetime fecundity (MLF), constant probability of death for each interval (G), mean annual lifetime-fecundity (δ) whish is the average of fecundity (eggs/female/year) at each age

Longevity (days)	Interval	Duration days	M_i per year	Duration days	M_i per year
Dosidicus gigas		$\alpha = 1.923$		$\alpha = 1.641$	
438		G $= 2.591 < 3.156 < 3.30$			
MLF:813 000 > 16 387 656 < 25 887 000					
	1. Egg	**6**	229	**9**	153
	2. Paralarva	12	119	15	93
	3. Juvenile	34	41	39	35
	4. Subadult	99	14	103	13
	5. Adult	288	4.8	272	5.1
Farfantepenaeus duorarum		$\alpha = 1.615$		$\alpha = 1.615$	
480		G = 1.775		G = 1.874	
MLF:		500 000		1 000 000	
	1. Egg	**1.5**	432	**1.5**	456
	2. Nauplius	2	267	2	282
	3. Protozoea	6	102	6	108
	4. Mysis (post-larvae)	17	39	17	41
	5. Juvenile	43	15	43	16
	6. Pre-adult	113	6	113	6
	7. Adult	296	2.2	296	2.3
Sardinops caeruleus		$\alpha = 1.286$		$\alpha = 1.050$	
2555		G = 1.298		G = 1.298	
δ: 646 763 > 855 748 < 1 090 678					
	1. Egg	**1.5**	318	**4**	117
	2. Vit. larvae	2	245	4.2	113
	3. Early larvae	4	106	9	55
	4. Late larvae	10	47	18	26
	5. Early juvenile	23	22	36	15
	6. Juvenile	53	7	74	7
	7. Prerecruit	120	4	152	4
	8. Early adult	275	2	311	1
	9. Adult	629	0.7	638	0.7
	10. Late Adult	1437	0.4	1309	0.4

(1973) demonstrated that very small changes in the daily instantaneous rate of mortality (z) in the egg stage, produce large changes in recruitment. Beyer (1989) suggested that large changes in fecundity can be compensated by small changes in mortality or survival rate. According to Rothschild (2000), we can accept that the positive effect of fecundity on regulatory processes occur in a relatively short time interval for the Pacific sardine but does not occur for

the pink shrimp and jumbo squid, because the population size depends largely on the strength of annual recruitment. We assumed the life cycle of jumbo squid to be semelparous or monocyclic for the GIM analysis. For coleoid cephalopods (except Nautiloidea) have been regarded as essentially semelparous, because they usually have short life cycles (<2-3 years in most cases), and no evidence of repeated cycles of gametogenesis have been reported.

We utilized the potential fecundity (the maximum number of oocytes in the ovary prior to spawning) for MLF estimates. There are few data for the fecundity (numbers of eggs spawned by individual females) for the jumbo squid and the more generalized approach has been to use the potential fecundity. This approach does not consider the number of eggs reaching full maturity which are successfully fertilized and spawned. Although the use of the potential fecundity could imply an overestimation on M, the fact that estimated values approach the same asymptotic value for adult stage and even this value agrees with independent estimations, indicates that M_i values and durations for developmental stages estimated with GIM method, adequately define the average conditions faced by jumbo squid in its life history and reflect a reasonable starting point providing plausible inputs for fishery stock assessment models.

Acknowledgments

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