An approach to estimate natural mortality-at-length for unexploited stocks with an application to the Venus clam, *Chione californiensis* (Mollusca: Veneridae) in the Gulf of California, México

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Natural mortality estimates constitute one of the most challenging problems in fisheries science. Most methods are empirical and involve estimation based on exploited ages. Tagging experiments or consumption data can also yield such estimates. However, these approaches can be expensive or complex to apply continually. In this paper, we propose an approach to estimate natural mortality-at-length based on data from unexploited stocks (virgin stocks or stocks during closed seasons). The approach is based on a transition matrix in which growth probabilities are based on the von Bertalanffy equation and elements of the survival matrix are given by $e^{-M\Delta t}$. The input data required are vectors of length-frequency distributions representing the stock abundance at different times. The solution is found by applying a least squares algorithm. The approach is illustrated by applying the method to data on the Venus clam *Chione californiensis* during the closed season (approximately eight months). Natural mortality-at-length tends to decrease with length. This tendency was observed every month, but its parameters (intercept and slope) showed a seasonal pattern. Natural mortality-at-length and at-time is explained in terms of the dynamics of the life cycle. Density-dependent effects are also indicated.

Key words: Natural mortality-at-length, projection matrix, Venus clam, Chione californiensis.

Enfoque para estimar la mortalidad natural por longitud en stocks vírgenes y su aplicación a la almeja Venus *Chione californiensis* (Mollusca: Veneridae) en el Golfo de California, México

La estimación de mortalidad natural es uno de los grandes retos en las ciencias pesqueras. La mayor parte de los métodos son empíricos y se basan sólo en edades sometidas a explotación. Experimentos de marcado o datos de consumo pueden ser útiles también para estas estimaciones sin embargo, suelen ser costosos o complejos para ser usados de manera cotidiana. En este trabajo se propone un procedimiento para estimar la tasa instantánea de mortalidad natural por clase de longitud aplicado a datos de poblaciones no explotadas. El procedimiento se basa en el uso de la matriz de transición donde las probabilidades de crecimiento se basan en la ecuación de von Bertalanffy y los elementos de la matriz de supervivencia se calculan como $e^{-M\omega}$. Los datos de entrada corresponden a vectores de distribuciones de frecuencia de longitudes representando la abundancia de la población en diferentes tiempos. La estimación se obtiene mediante la aplicación de un algoritmo de mínimos cuadrados. La aplicación del método se ilustra con datos de la almeja *Chione californiensis* que corresponden a un periodo de veda de aproximadamente ocho meses. La mortalidad natural muestra un patrón decreciente con la longitud. Este patrón se repite cada mes pero sus parámetros (ordenada y pendiente) muestran un patrón estacional. La mortalidad natural por clase de talla se interpreta en términos de la dinámica del ciclo de vida incluyendo efectos densodependientes. **Palabras clave**: Mortalidad natural por clase de longitud, matriz de proyección, almeja, *Chione californiensis*.

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Introduction

Estimation of natural mortality rate (M) is one of the greatest challenges for biologists and modelers in fisheries science because of the extreme difficulties associated with the estimation of M in field experiments. A number of empirical methods have been developed based on different assumptions. Most methods (Table 1) provide an estimate of M that is constant over both time and age. Some methods estimate the mortality caused by predation and assume that predation is the predominant or unique cause of natural mortality. A few approaches estimate M as a function of age.

Table 1	
Some models and approaches proposed in literature to estimate natural mortality rat	е

Model equation	Comments	References
Z = M + qE	Z = total mortality rate, q = catchability coefficient, E = fishing effort	Silliman (1943), Paloheimo (1980)
$M = (1.521/((Tm_{50})^{0.72}) - 0.155)$	Tm_{50} = age of massive maturation	Rikhter & Effanov (1976)
ln(M) = -0.0152-0.279 ln(L\infty)+0.6543 ln (K)+0.463 ln(T)	Fish populations. L_{∞} and K are parameters of the von Bertalanffy growth equation. $T = annual$ average temperature in the habitat	Pauly (1980)
$Y = aZ^2+bZ+c$, and $M = (-b+((b2-4ac)^{1/2}))/2a$	Z = total mortality rate, $Y =$ yield, a, b and c constants	Csirke & Caddy (1983)
Ln(M) = a + b ln(Tm)	Tm = longevity age a = 1.46, b = -1.01 (fish) a = 1.23, b = -0.832 (molluscs)	Hoenig (1983), Alagaraja (1984)
"reciprocal model" $[M_t - A] \cdot t = [M_{t+\Delta} - A] \cdot (t+\Delta)$	A = asymptotic mortality; Δ indicates time interval	Caddy (1990)
$0.01 = 1^{*} \exp - M^{*} (4.6/K)$	K = von Bertalanffy growth coefficient	Chávez (1995)
"gnomonic model" Uses gnomonic periods along the life-history, and as a condition Mi $\Delta i = G$, being G = constant for all gnomonic periods.	Model solved numerically once gnomonic periods and their duration were defined	Caddy (1996)
$Log(M) = 4.355 \cdot 0.083 \log(W_{\infty}) + 6.39$ $(W_{\infty}/L_{\infty}^{3}) + 0.627 \log(K) \cdot 1190.43 (1/T+273)$	Fish populations. W_{∞} , L_{∞} and K are parameters of the von Bertalanffy growth equation. $T =$ water temperature (°C)	Brey (1999) (modified from Pauly, 1980)
$M = 0.082^{*}0.925^{*}(P/B)$	Unexploited benthic invertebrates	Brey (1999)
log(P/B) = 1.672+0.993* log(1/ Amax)-0.035*log(Mmax)-300.447*1/ (T+273)	Benthic invertebrates Amax = Maximum age (y-1) Mmax = Max. individual body mass, P/B = production/biomass ratio. T = Bottom water temperature	Brey (1999)
$c_{ij}(B_i, B_j) = v_{ij}a_{ij}B_iB_j/(v_{ij} + v'_{ij} + a_{ij}B_j)$	is consumption rate (= predation mortality), is the rate of effective search for prey type i by predator j,, are prey vulnerability parameters, B is the stock biomass	Walters <i>et al.</i> (1997)
$M_{i} = M_{0,i} + (M_{\max,j} \cdot B_{j})/(b_{j} + B_{j})$	$M_{0,i}$ = natural mortality not accounting for predation; $M_{max,i}$ is the maximum level of predation when j-predator abundance (B _j), becomes very large; and b _j is the predator abundance level at which the rate of predation is maximized	Arreguín-Sánchez (2000)

It is recognized that natural mortality generally varies with age and time. A pattern of age variation in natural mortality that is accepted for many species is that *M* is higher during the early stages of life history and decreases rapidly towards an asymptotic value for adults and older individuals. Caddy (1990) indicated that the simplest model of variation in M with age is an inverse relationship between M and age. More recently, Caddy (1996) proposed an algorithm to estimate natural mortality for invertebrates based on the durations of different life history stages and the mean lifetime fecundity. These stages are termed gnomonic intervals. Martínez-Aguilar et al. (2005) presented a modified version of Caddy's method of gnomonic intervals. They extended the method to long-lived species by incorporating independent data for life stages duration and by including uncertainty in the mean annual fecundity.

Models based on consumption can provide estimates of predation mortality for the entire population (Walters *et al.*, 1997; Arreguín-Sánchez, 2000) and can even address size-specific predation mortality (Beyer & Lassen, 1994; Beyer, 1998; Beyer *et al.*, 1999). However, the amount of information on stomach contents can be substantial. Therefore, if consumption models are viewed as generalized methods for estimating M, their requirements for data gathering and data processing must also be considered.

The need to estimate a natural mortality variable is an important issue in the context of current management, particularly if management is based on risk analysis. In stock assessment we usually apply a constant value of *M* in structured models to estimate available stock biomass in the immediate past. In this case, the assumption of a constant *M* value is not restrictive because most fisheries harvest adult stages of the stock and these stages correspond to the asymptotic value of M-at-age. This assumption becomes important if the stock assessment models are used for prediction or to evaluate management scenarios. The assumption of constant natural mortality is restrictive in this case because the number of pre recruits must be estimated accurately. These individuals will be recruited to the stock in subsequent years and will affect the projected yields significantly. A related consideration is that management may require estimates of the numbers of individuals surviving after exploitation. Information about juveniles and mature adults is important to prevent recruitment overfishing or growth overfishing. These examples illustrate the need and importance of estimating M-atlength and M-at-age. In this paper, an approach to this estimation problem will be presented.

Materials and methods

Estimating natural mortality from field observations requires information on unexploited stocks. For fisheries studies, this information can only be collected during closed seasons or in closed areas. This study includes an example based on data from the Venus clam stock (Chione californiensis) in La Paz Bay, México. Samples of stock density (Fig. 1) were collected on the beach from July 1988 through September 1989 during closed seasons. A transect-based sampling design was used, and density (number of individuals per 20 cm³) and size (total length with a precision of 0.01 mm) of clams were recorded (García-Domínguez et al., 1994). Venus clam stock was exploited during two periods: September-October 1988 and February-April 1989.

Natural mortality, *M*, was estimated with an iterative process based on the transition matrix adapted from Arreguín-Sánchez (1996) and Arreguín-Sánchez & Pitcher (1999). This procedure computes *M* values that can vary with length (and time) and is described by the relationship:

$$N(\ell, t + \Delta t) = \sum_{k} [G(\ell, k) \bullet S(k)] \bullet N(k, t) \quad \text{Ec. 1}$$

Where: N = vectors of stock densities expressed as length-frequency distributions, and k and ℓ = successive length classes, G = growth matrix whose elements represent growth probabilities per length class according to von Bertalanffy growth equation (Shepherd, 1987); S = survival matrix whose elements represent survival for length class k and are given by $S(k) = \exp(-M)\Delta t$ (in the absence of fishing); and t represents time. Because the Venus clam is a relatively short-lived species, age is measured in months and Δt represents the amount of time between successive samples. If $\Delta t \neq 1$ month, its value is represented as a proportion relative to the unit time interval of one month. Growth estimates obtained by Wright *et al.* (2000) were used with parameter values of L_∞ = 48.2 mm, K = 0.735 year⁻¹ and to = -0.64 years. The fitting process used was a single least squares algorithm:

$$MIN \sum_{\ell=i}^{n} \left(N_{obs}(\ell, t + \Delta t) - N_{est}(\ell, t + \Delta t) \right)^2 \qquad \text{Ec. 2}$$

Where: $N_{obs}(\ell, t + \Delta t)$ = observed stock density at length ℓ and time $\mathbf{t} + \Delta \mathbf{t}$, and $N_{est}(\ell, t + \Delta t)$ = estimated stock density at length ℓ and time $\mathbf{t} + \Delta \mathbf{t}$.

All parameters except for $S(k) = \exp(-M)\Delta t$ were known. A numerical solution for equations (1) and (2) was found with the Newton-Raphson algorithm. The solution to these equations provided estimates of M-at-length. The pattern of variation of these estimates was then analyzed and interpreted in terms of the population biology of the stock.



Fig. 1. Length-frequency distributions of the Venus clam (*Chione californiensis*) from La Paz Bay, used as a case study to illustrate the method to estimate natural mortality-at-length.

Results

Equations (1) and (2) were applied to a set of 13 samples. Each pair of length-frequency distributions representing stock density yields a vector of M-at-length that is represented as a function whose form is defined in agreement with the general trend. For our study we selected the functional form $M = a\ell^{-b}$ (Fig. 2). Parameters of the M-at-length function are shown in *table 2*. Regression analyses showed that the variance explained by the model was at least 84% for all of the analyzed cases.



Fig. 2. Natural mortality-at-length pattern for the Venus clam *Chione californiensis*, estimated with the transition matrix method. This pattern represents the annual average. For estimates on a monthly basis, see *table 2*.

Slopes varied from -0.0109 to -0.3268. The highest values occurred during summer and coincided with the peak of the spawning period (García-Domínguez & Levy-Pérez, 1995). The lowest values were found during autumn, immediately after the spawning peak. Values of the slope measured the decrease rate of individuals' numbers over time. High values during spawning season suggest high mortality rates at a time when the abundance of early stages was high. Slopes trend over time suggest an oscillatory pattern, although it is more evident for the intercepts (Fig. 3). The intercept represents the mortality at t = 0, i.e., M₀, mortality associated with the earliest larval stage. This oscillation can provide an index to the seasonal changes in M_0 .

Weighted average values for natural mortality-at-length were obtained for each sample. A plot of these values against time is shown in *figure*



Fig.3.Seasonaloscillations of the parameters of the natural mortality-at-length functions for Venus clam *Chione californiensis*. The intercept represents M_0 value, whereas the slope indicates the rate at which individuals' numbers decrease with age.

4. The plot shows an oscillatory pattern, with the highest values during the peak-spawning time. A global weighted average value (per length and time) of natural mortality was estimated as $M_{ww} = 0.247 \text{ month}^{-1}$. These weighted average values represent individuals between 4 and 63 mm in total length.



Fig. 4. Seasonal oscillation of the monthly average natural mortality for the Venus clam *Chione californiensis*.

Discussion

This paper proposes an approach to natural mortality-at-length estimation, based on data for unexploited stocks. The algorithm based on the projection matrix appears to offer a powerful tool, but results will always depend on the sampling data that represent stock abundance. If an unexploited stock can be sampled through the year, time patterns of natural mortality can also be determined. Such information is of importance for detailed studies on population dynamics and to explore management decisions based on structured models.

Mortality-at-length pattern for this case study of the Venus clam exhibits the expected inverse relationship between natural mortality and length. As suggested by Gulland (1983) and Caddy (1990, 1996), the higher mortalities at early stages decline with age and approach an asymptotic value for adult individuals.

The study found an oscillatory pattern of variation in natural mortality, which suggests strong seasonal variation. The highest values of natural mortality occurred at the time of peak spawning. This result makes biological sense because survival at the early stages tends to be low for most species. In particular, low survival at the early stages appears appropriate in this case study in the light of larval drift and settlement. Seasonal oscillations found for the Venus clam also suggest density-dependent effects on the survival of early stages. In most clam species, strong competition for space occurs during settlement (see McLachlan et al., 1996). Therefore, high mortality rates are expected during the time of peak-spawning.

Most of the available methods to estimate natural mortality are largely empirical. Although some of these methods have provided a useful first approach, they have at least two problems. The first problem is the assumption that natural mortality is constant over age and time. The second problem is that such estimates are usually applied to (and estimated for) adult individuals (or those who appear well represented in catches). In each case, these values are then extrapolated over the life history. The approach suggested here provides a tool to fit field data to obtain an M-vector that could represent a biologically meaningful function.

In our case study, the M-at-length pattern was described by an inverse relationship. This pattern can be considered common in nature and appropriate for the Venus clam. However, the projection matrix algorithm could also identify other patterns if they are present in the field data. No particular pattern is assumed by the method. The main constraint on the algorithm application proposed here to estimate M-at-length is that the estimated values depend directly on the validity of the sampling design. Because the estimation procedure is a numerical method based directly on field data, estimates will be biased if the samples are biased.

Table 2Parameters of M-at-length function for the Venus clamChione californiensis. The variable ts indicates the sampledate at time t in equation 1 taken as a proportion of the year,starting January 1st; R^2 is the coefficient of determination

ts	$Log_{10}(a)$	Slope (-b)	R^2
0.79	0.0430	0.0109	0.854
0.84	0.2634	0.0759	0.840
0.87	0.6555	0.1388	0.853
0.96	0.3605	0.0786	0.854
0.02	0.6234	0.1362	0.854
0.08	0.6234	0.1362	0.854
0.26	0.1022	0.2720	0.853
0.30	0.2208	0.0525	0.854
0.46	0.0586	0.0163	0.851
0.55	1.7172	0.2896	0.850
0.59	2.1618	0.3268	0.849
0.65	1.2856	0.2545	0.853
All	0.6763	0.1288	0.853

The potential applications of the method proposed here are also limited because unexploited periods generally do not exist for commercially exploited stocks. If information on unexploited periods does not exist or is not available, other approaches should be considered. In contrast, if data from unexploited periods are available, the method can provide improved estimates of natural mortality-at-length and natural mortalityat-age.

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