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A review on the growth functions for large decapod crustaceans: progress and limitations for its use in fisheries stock assessment and management

Revisión de las funciones de crecimiento de los grandes crustáceos decápodos: avances y limitaciones para su uso en la evaluación y gestión de poblaciones pesqueras

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Abstract
The evaluation and management of crustacean fisheries are mainly based on models that use an annual period, even though since the 19th century, several authors have reported that, in the biology and growth of these species, the unit of time that should be used is the intermolt period, which varies according to the age of the organisms. In this paper we address the following two research questions: *i)* what is needed to know and thus to consider the molting schedules in large decapods populations' assessment and management?, and *ii)* what are the progress and limitations in using molting schedules in commercial decapods' age and growth and stock assessment models? We carried out a literature review primarily from 1948 to 2018, from which three theoretical-methodological proposals that consider molting schedules of lobsters (and large crustaceans) were chosen to examine in depth. Results show that despite we found considerable progress in using molting schedules in several high-income countries, many research teams on lobsters classify these species as difficult and expensive to age, and therefore, all their modeling efforts are length based with no consideration of growth based on molts. The progress we refer to was identified in thoroughly studied species, such as the American lobster (*Homarus americanus*) of Maine, USA, wherein some researchers have been able to cross schedule a molting-based growth with maturity, mortality, and recruitment to the fishery. Apparently, little is known on the trade-offs and implications of using this latter approach in these valuable species. We argue that unless fishery scientists and managers have a better understanding of the ecological, economic, and social implications of the stock assessment and management based on molting schedules for large decapod crustaceans in general, present efforts on these species' stock assessment and management elsewhere will continue to pay little or no consideration of crustacean growth processes.
Key words: age and growth, molting schedules, crustacean fisheries, stock assessment, unit step function.

Resumen
La evaluación y el manejo de las pesquerías de crustáceos se basan principalmente en métodos que usan los periodos anuales, a pesar de que desde el siglo XIX varios autores reportaron que en la biología y el crecimiento de estas especies, la unidad de tiempo que debería usarse es el periodo de la intermuda, que varía de acuerdo con la edad de los organismos. En este trabajo nos referimos a las dos preguntas de investigación siguientes: *i)* ¿Qué se necesita para conocer y así considerar los calendarios y periodos de muda en la evaluación y el manejo de grandes poblaciones de decápodos? y *ii)* ¿Cuáles son los avances y las limitaciones en el uso de los programas de muda en los modelos de evaluación de población y edad y crecimiento de los decápodos comerciales? Realizamos una revisión de la literatura, principalmente de 1948 a 2018, de donde se eligieron tres propuestas teórico-metodológicas que consideran los periodos de muda de langostas (y grandes crustáceos) para examinar en profundidad. Los resultados muestran que,

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a pesar de que encontramos un avance considerable en el uso de los programas de muda en varios países de altos ingresos, muchos equipos de investigación de langostas clasifican a estas especies como con alto grado de dificultad y de costos para determinar su edad y, por lo tanto, todos sus esfuerzos de modelado se basan en la longitud sin considerar el crecimiento basado en mudas. El progreso al que nos referimos se identificó en especies minuciosamente estudiadas, como la langosta americana (*Homarus americanus*) de Maine, EEUU, en donde algunos investigadores han podido empatar la programación de un crecimiento basado en la muda con la madurez, la mortalidad y el reclutamiento a la pesquería. Aparentemente se conoce muy poco acerca de las compensaciones e implicaciones del uso de esta aproximación en estas valiosas especies. Discutimos que, a menos que los científicos y administradores de pesquerías tengan una mejor comprensión de la ecología, la economía y las implicaciones sociales de la evaluación de *stocks* y el manejo basado en los periodos de muda para los grandes crustáceos decápodos en general, los esfuerzos actuales en la evaluación y la gestión de las poblaciones de estas especies en otros lugares seguirán prestando poca o ninguna consideración a los procesos de crecimiento de los crustáceos.

Palabras clave: edad y crecimiento, periodos de muda, pesquerías de crustáceos, evaluación de *stock*, función de unidad de paso.

Introduction

Several naturalists of the late XIX and early XX centuries acknowledged that in crustaceans' growth, the increase in carapace length during molting is a relatively discontinuous process, and that the difference between pre- and post-molt body size represents every individual's growth in size (Hiatt 1948, Bennet 1974). This fact implies that the "growth in body size of a crustacean is achieved in steps at successive moults" (Mauchline 1976: 79). Despite this knowledge being part of science more than a century ago, instead of using age and growth based on molt classes (see Bennet 1974: 818, Caddy 1987) or molt groups, most of the literature on marine crustacean stock assessments and management of the XX and XXI centuries, including yield-per-recruit models, have seldom considered the biological unit of the molting period. For instance, to provide advice to crustaceans' stock managers, most researchers have used methodologies with the rationale of age and growth for finfish species that are based on continuous functions with annual (or shorter) time schedules (Haist *et al*. 2009, Webber *et al*. 2018). Compared with results based on the frequency of molting and increase in size of large decapods (Kanaiwa *et al*. 2008), the latter procedures usually cause either an over estimation or underestimation of their final stock assessment results (see Saila *et al*. 1979). Given that many crustacean species, particularly decapods, are heavily fished due to their great economic significance (Cobb & Caddy 1989, Eddy *et al*. 2016), their management should be based on continuous research and monitoring that produce robust stock assessments results to avoid their overexploitation and collapse. In this paper we review the progress and underlying limitations of using stock assessment models that are based on growth functions that consider molting schedules in large decapod crustaceans. The paper addresses the following two research questions: *i)* what is needed to know and thus to consider the molting schedules in large decapods populations' assessment and management? and *ii)* what are the progress and limitations in using molting schedules in commercial decapods' age and growth and stock assessment models? Our review uses primarily the age, growth and the stock assessment and management of lobsters.

The paper is structured in four parts. After the introductory section, the second part presents a brief review on the age and growth of lobsters considering the biological unit of the molting period; the third part reviews three methodologies that used the lobsters' molting schedules to estimate their age and growth, which results either have been or could be further incorporated in stock assessment models, including when applicable, management strategies for lobsters. The last part addresses final remarks with main conclusions that attempt to respond the study's research questions.

Main attributes of the age and growth of lobsters

The biology of large decapod crustaceans including lobsters is a complex process. After hatching, most of the individuals of these species go through a series of stages, from larvae to a benthic stage. A conspicuous characteristic of crustacean biology is that the growth in size of these species occurs almost entirely at ecdysis (a process in which individuals molt their exoskeleton). Compared to the increase in size, the increase in weight of individuals is lagged, as it occurs gradually during the intermolt period. However, it has not been as intensively studied as the increase in length.

Once an individual reaches the form of a benthic life, usually after it suffered metamorphosis, there is a general growth pattern in lobsters that roughly could be divided into four stages (although some species might have its own particularities): *i)* the stage of juvenile's growth in which, compared with the growth of adults, the intermolt period is relatively higher in frequency; *ii)* the pre-adult growth stage, in which compared to the juvenile growth the intermolt period diminishes in frequency. Until this stage, the growth rate of both males and females is often of the same magnitude; *iii)* the adult female's growth in which, after attaining maturity, both, its molt frequency and increment in size diminish compared to the pre-adult stage; and *iv)* the adult male's growth, in which its molt frequency diminishes compared to the pre-adult stage and its increment in size is often greater than the adult female (see Sweat 1968, Saila *et al.* 1979, Hunt & Lyons 1986, Annala & Bycroft 1988, Forcucci *et al.* 1994, Comeau & Savoie 2001).

Similar to other species, there is variability associated with the individual growth of lobsters (including the time to reach metamorphosis). Age and growth vary both within a population and between spatially separated populations (Maxwell *et al.* 2009). It has been reported that environmental and biological factors can affect their growth rate, which influence intermolt periods and its increments (Cobb & Caddy 1989); among them are injury, temperature, maturation, and season (see Hunt & Lyons 1986, Forcucci *et al.* 1994, Arce & de León 2001, Comeau & Savoie 2001). Caddy (1986) found that a change in the slope is notable on the female's growth curve; particularly, for species that hold eggs under the abdomen for extended periods (Cobb & Caddy 1989).

Among the first studies that assessed crustaceans' growth using the intermolt period is the one proposed by Hiatt (1948), who had linearly fitted by eye a series of successive post-molt ('y') to pre-molt ('x') size of the lined shore crab *Pachygrapsus crassipes* Randall 1840. As a result, he obtained a figure which is called the Hiatt growth diagram where it is shown that an inverse relationship between size and molt frequency exists. Later on, Kurata (1962) (cited by Mauchline 1976), used Hiatt's data as well as his own data to estimate the crustacean's growth factor (*i.e.* the percentage increase in body or carapace size at each molt). Kurata (1962) reported that "growth factors decrease at successive molts in decapod and some other crustaceans (...). The decrease is usually logarithmic against body length" or molt number (Mauchline 1976: 81). The latter means that the duration of the intermolt period "increases logarithmically against increasing body length" (Mauchline 1976: 83). Among his results, Mauchline (1976) reported that the best way to represent the crustacean growth was by means of plotting the molt increment in % ('y') to the pre-molt length or individual's size ('x').

Among the most recent studies which have considered the occurrence of two molts per year in a size-structured stock assessment of the American lobster (*Homarus americanus* H. Milne Edwards 1837) are those of ASMFC (2006) and Kanaiwa *et al.* (2008 and references therein), yet Kanaiwa *et al.* (2008: 41) report that "[t]emporal trend in natural mortality and biased estimates of growth parameters posed the most serious problems" to their modeling results.

In the literature on age and growth of lobsters, several authors assume that there is an analogy between the intermolt growth scale and the growth in successive years of fish, frequently presented as a Ford-Walford diagram (*i.e.*, a plot of $L_{(t+\Delta t)}$ against $L_{(t)}$, see Sparre *et al.* 1989: 71-72) in which age classes could be identified. Based on this analogy, many studies on large decapods' stock assessment were carried out using solely length-frequency analysis (Caddy 2003). However, according to the analysis carried out by Mauchline (1976), a difference between those two approaches is that the crustaceans' intermolt period increases logarithmically and therefore, produces a logarithmic-time scale among the molt classes or cohorts, whereas the Ford-Walford diagram is linear, usually measured in terms of years or months (for short-lived species). Moreover, Caddy (2003: 78) reviewed published literature on molt frequency of 11 macrocrustacean species and reported that in each of the 11 species, its intermolt period follow a geometric progression as individual's size increases (*i.e.*, "a slowing of growth as a result of intermolts getting progressively longer with age"). Therefore, the analysis shown in Mauchline (1976) and Caddy (2003), specific for any decapod species, should be considered when analyzing whether any method based purely on length frequency analysis is appropriated in both, assessing the relative age classes and estimating the age and growth for lobsters and large decapods in general. Indeed, this literature's results are relevant because most often, length-frequency analysis' results together with the use of continuous growth functions for large decapods, are further utilized in stock assessments and in estimating the total allowable commercial catch (TACC, Haist *et al*. 2009, Weber *et al*. 2018), which are provided as advice to fishery managers.

Several direct and indirect methods have been used to estimate the age and growth of lobsters. The direct method is related with estimating individuals' growth in cages or laboratory conditions (Sweat 1968) and are useful to obtain data on juvenile stages. Among indirect methods are the following: *i)* the assessment of changes in the morphology of lobsters' setae along a year, known as setagenesis (Forcucci *et al*. 1994), *ii)* size increase derived from tag and recapture (Hunt & Lyons 1986), *iii)* a molecular approach based on the detection of neurolipofuscin to predict the chronological age or senescence among lobsters (Maxwell *et al*. 2009), and *iv)* the length-based frequency analysis to identify relative age classes. Given that the present paper is focused on two research questions dealing with the lobsters' molting schedule, in the following paragraphs, we consider only two methods which are related with our research questions, namely, the laboratory conditions and the tag-and-recapture method. In the latter method, researchers need to consider the selection of tags which are not lost at ecdysis. In this regard, among others, researchers on decapods recommend to use the so called "suture tag" (Bennet 1974) and "streamer" and "sphyrion" tags (Comeau & Savoie 2001).

Modeling approaches based on lobsters' molting schedules

Empirical growth formulas

In this section we review the comprehensive study of Saila *et al*. (1979), who estimated the age and growth of the New Zealand rock lobster *Jasus edwardsii* (Hutton 1875) and used their results to further assess this species' yield-per-recruit. In their estimations, these authors used both, conventional and empirical models. Moreover, at the end of this section, we review how this New Zealand rock lobster fishery is currently being assessed and managed.

With respect to using models to represent the age and growth of lobsters and other crustaceans, although the logistic, the Gompertz and the von Bertalanffy growth (VBG) functions have been used, the VBG formulae is the one that has been widely used by fishery biologists and other researchers because its parameters can be easily incorporated in the Beverton & Holt yield model (Cobb & Caddy 1989). Nevertheless, some authors have put considerable effort in estimating decapods' age and growth using the intermolt period, which approach primarily followed either the method of Hiatt (1948) or the one proposed by Mauchline (1976). These empirical growth formulas have been used primarily for lobsters and crabs (Bennet 1974, Mauchline 1976, Saila *et al*. 1979, Annala & Bycroft 1988, Comeau & Savoie 2001) and researchers had estimated, on one side, the molt frequency or intermolt period, and the increment in size, on the other. The latter procedure is also referred to in the literature as "the increment-frequency approach" (Caddy 1986: 2333). Considering the intermolt period in decapods' population dynamics has several advantages over any continuous growth function, including that in its resulting plots researchers can point out or locate the body size at which individuals' maturity occurs, spawning, as well as whether there is any change in growth on maturity, among others (Hiatt 1948, Mauchline 1976, Caddy 1986, 1987, Cobb & Caddy 1989). Despite these advantages, a literature review revealed that authors who had considered the intermolt period in these species, reported their resulting growth rate on a linear time-scale basis, such as growth rate per week, per month and per year; most often as age/year classes and not as molt classes (see Bennet 1974, Mauchline 1976, Saila *et al*. 1979, Hunt & Lyons 1986, Forcucci *et al*. 1994).

To estimate the age and growth of *J. edwardsii,* Saila *et al*. (1979) used two types of data: namely, observations of juveniles (12.5 to 42.5 CL) from laboratory conditions, and tag-and-recapture data (72.5 to 127.5 CL) for the period 1975-1977 from the Gisborne fishery in New Zealand. These authors adapted the empirical growth equation proposed by Bennet (1974) for the crab (*Cancer pagurus* Linnaeus

1758). In particular, instead of using linear regressions for estimating molt increments and molt frequency as related to pre-molt size as did Bennet (1974), Saila *et al.* (1979: 4) used exponential regressions, which they argued "provided better fits to the observations and because they were more realistic representations of the functional relationship between size and molt increment, or molt frequency as observed for *J. edwardsii*". These authors also assessed the yield-per-recruit for this species –which is usually expressed in terms of weight– and therefore, they used the weight/length relationships for *J. edwardsii* using the geometric mean (GM) functional regression (Ricker 1975) for males and females, as follows:

Males

$$\log_e W = -7.3611 + 2.92804 \log_e CL \qquad \text{eq. 1}$$

$$i.e.\ W = 0.0006353 CL^{2.92804}$$

(n = 198, r = 0.9991, standard error of functional regression = 0.00962); where W = weight (g) and CL = carapace length (mm).

Females

$$\log_e W = -7.32429 + 2.93201 \log_e CL \qquad \text{eq. 2}$$

$$i.e.\ W = 0.0006592 CL^{2.93201}$$

(n = 107, r = 0.9941, standard error of functional regression = 0.03110).

Thus, the fitted exponential regressions of percentage molt increment in weight (Wm) on pre-molt weight (Wp) in grams by sex are as follows:

Males

$$Wm = 53.3659\, e^{-0.00369\, Wp} \qquad \text{eq. 3}$$

r = 0.7714, n = 136

Females

$$Wm = 44.1905\, e^{-0.00456\, Wp} \qquad \text{eq. 4}$$

r = 0.7163, n = 79

To determine the molt frequency of *J. edwardsii,* a database with mark and recapture data was used. From this, authors used the "anniversary method" (Saila *et al.* 1979: 4) that involves estimating molt frequency by reference to the proportion of lobsters which have molted of the total caught one year after release. Molt frequencies were determined from tag recoveries occurring 330-390 days after release; data used in this analysis were grouped by sex into 5 mm class intervals. For the age and growth of the juvenile part of the population, the molt frequency was estimated from laboratory data in which the sexes were not separated. The results of fitting exponential regression lines to the data on molt frequency are described by sex as follows:

Males

$$A = 331.7819\, e^{-0.00323\, Wp} \qquad \text{eq. 5}$$

r = 0.8381, n = 81

where: A is the annual molt frequency (%) and Wp is the pre-molt weight (g) of the lobster.

Females

$$A = 363.9633\ ^{-0.00372\, Wp} \qquad \text{eq. 6}$$

r = -0.8737, n = 70

Interestingly, these authors based their growth's results as a weight-based model and not as an age-based model. Furthermore, because these authors had the ability to do so, Saila *et al.* used the results from equations *3* and *4* in an empirical yield-per-recruit model which they themselves devised. Lastly, these authors used the same growth-and-recapture data and estimated a continuous VBG curve for *J. edwardsii*, which in turn, was used in a Beverton & Holt yield-per-recruit model. Both results, the lobster's growth curves as well as the yield-per-recruit models were compared resulting that the two empirical formulas were considered more realistic for the lobster fishery than the conventional fishery science models.

This is an insightful example of the historical efforts on lobster assessment modeling using empirical formulas based on the molting schedule. However, it seems that a paradigm shift occurred among the fishery scientists of the New Zealand rock lobster fishery, because the biological meaning of the molting schedule for the stock assessment of this species was abandoned several years ago. In this regard, the most recent studies of *J. edwardsii* use Bayesian length structured stock assessment model with continuous growth function which do not consider the molting schedule (Haist *et al.* 2009). It is argued that: "Rock lobster assessment models (and invertebrate models in general) are typically length based because invertebrates are difficult and expensive to age, rendering the collection of age-based data infeasible" (Webber *et al.* 2018: 4). The results of the latter type of size-structured model are being used to manage this rock lobster fishery based on TACC.

"Gnomonic" time intervals as biological time units

Dr. John F. Caddy had shown particular interest on researching macrocrustaceans with emphasis on lobsters, and most of his publications on this topic show that he carried out comprehensive literature reviews authored by experts with similar interest to his. In this section we review the scientific contributions of our colleague John F. Caddy on age, growth and population dynamics for decapod crustaceans using molting schedules. We also review some examples of applied studies related to Caddy's theoretical propositions on decapods' fisheries research and management.

In 1986, Caddy (1986: 2330) argued that:

> *[w]e may look forward to the development of models that consider the nature of crustacean life histories, reflecting the need for cross-scheduling of growth and reproduction (...). Modelling life history processes in biological time units related to moult cycle duration, and cross-converting to real time for consideration of the fisheries component, should offer a notable simplification of the modelling process. The existence of several 'choices' for an individual crustacean at different points in the moulting/ reproduction cycles makes cohort models cumbersome and seems to require the adoption of a stochastic approach, for instance Markov-related processes, which better take into account complexities of biology and fishery-related processes.*

Particularly, Caddy (1986) referred to a "hierarchy of choices" that a crustacean species faces during its life cycle, that he represented in the following *Table* 1.

Table 1
Proposed hierarchy of choices for crustacean species

Hierarchy	*Choice*
I	Dies naturally in interval/ Does not die naturally
II	Molts/ Does not molt Captured/ Not captured
E	Discarded/ Retained Survives discarding/ Dies incidentally
III	Fertilized/ Not fertilized (eliminate for males)
E	As above
IV	Extrudes eggs/ Does not extrude eggs (eliminate for males)
E	As above
V	Releases larvae/ Does not release larvae (eliminate for males)
E	As above

Source: Adapted from Caddy (1986).

Where numbers I to V represent individuals' "physiological choices" and E represents the fishery-related processes in real time (Caddy 1986: 2338); with mortality rates being adjusted from real elapsed time. "The size at molting can thus be used in scheduling life history events into a number of intermolt periods, whose properties can then be defined on the basis of carapace lengths, rather than on any absolute instar number" (Caddy 1987: 44).

In the early XXI century, Caddy (2003: 74) was seeking for alternative approaches to modeling crustacean molt schedules; in particular, he was looking for an approach on how to divide a crustacean "life history into stanzas". He was aware that the molting processes are crustaceans' life events that clearly belong to a system of non-uniform time intervals and decided to carry out the following study. Drawing on published results on molt frequency of 11 data sets of different crustaceans' species,[1] which showed on average, that individuals show regular slowing trends in molting with size/age, doctor Caddy addressed the following research question "whether subdividing a life history into progressively longer intervals by a constant proportion between successive intermoult intervals is a useful way of modeling crustacean moulting schedules" (Caddy 2003: 73). His working hypothesis was that successive molt intervals follow a geometric progression, with intermolt duration a constant proportion of the time elapsed prior to each molt. The latter proposal of time division was referred to as "gnomonic" by Caddy (1996 cited by Caddy 2003) because those intervals, which follow a geometric growth, were analogous to the "gnomons" that represented geometric growth described by Thompson (1917). To statistically test his hypothesis, Caddy (2003) devised a mathematical model which followed a geometrical series and compared the 11 crustacean species' data on molt frequency to this model as follows. Assuming that an individual's first intermolt interval is given by:

$$\delta T_1 = ra$$

and that recursive relationships follow:

$$\delta T_i = ra^i \quad \text{and} \quad T_i = T_{i-1} + \delta T_i \qquad \text{eq. 7}$$

for: $i = 2, 3, \ldots, m$ intermolt (either observed in laboratory or estimated).

where the first intermolt interval δT_1 in the time series is the first interval –either observed or estimated, which may or may not correspond to the first interval in the life history of an individual–.

According to Caddy's working hypothesis, successive intermolt durations on average, follow a geometric progression, namely: $r, ra, ra^2, ra^3, ra^4, \ldots, ra^m$ (where m is not necessarily the last or terminal molt). In his study, sequences of intervals increasing proportionally in duration were generated for a range of values of a and r. In particular, the Excel spreadsheet software with the "Solver" routine was used, which was aimed at seeking values of these two parameters which minimized the difference between the observed intervals from the literature and those predicted by equation 7. In his results, Caddy (2003) reported that no intermolt series (n = 11) rejected the hypothesis at $p<0.005$, that successive intermolt intervals form a geometric or gnomonic series.

Several years later, doctor Caddy reported:

> *[o]ne of the concepts I learned from constructing a yield/recruit model for crustaceans, is that for slow-growing large crustaceans, annual data is not easily compatible where growth by moulting occurs after progressively longer intervals as life progresses. These non-uniform intervals are referred to from here on as gnomonic intervals. Converting the unit time to intermoult intervals seemed more logical, and in the long run, it eventually became clear that gnomonic intervals are biological time units that I used later for life history modeling and formulating natural mortality rates for other organisms (Caddy, no date, online Crustacean studies)*[2].

In our literature review we found that in the current stock assessment of the American lobster (*Homarus americanus*) in Maine, USA, a "growth transition matrix is determined outside the framework based on size-specific molting frequency and molting increment defined in ASMFC (2000)" (Chen *et al.* 2005: 649). In particular, these authors use a size-structured stock assessment model for *H. americanus* (Hogdon *et al.* 2022) considering

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[1] Crustacean species were *Homarus americanus* (four data sets or 4DS), *Panulirus argus* (1DS), *Pachygrapsus crassipes* (2DS), *Caprella okaida* (2DS), and *Cancer polydon* (2DS) (Caddy 2003, p. 74).

[2] Caddy JF. (no date) Crustacean studies. Online: https://sites.google.com/view/john-caddy-fisheries-science/fisheries-science/crustacean-studies.

a major and a minor molt per year. The latter is related to recruitment because, for a given fishing year, Chen *et al.* (2005) take into consideration that lobsters recruitment occurs in summer and autumn, which are associated with major and minor molting events respectively. Therefore, the biological meaningful proposal of cross scheduling of growth, maturity, and mortality in crustaceans posed by Caddy (1986, 1987) and Cobb & Caddy (1989), among others, is currently being considered in the stock assessment and management of *H. americanus* in Maine (ASMFC 2006, Chen *et al.* 2005, Kanaiwa *et al.* 2008). Yet, Chen *et al.* (2005: 659) argue that "[f]or an important fishery like the American lobster fishery, it is certainly inappropriate for its assessment to solely depend on one type of model" suggesting that for this and other valuable fisheries elsewhere, "[a] multiple modelling approach with an incorporation of comparative study of different models is more appropriate."

The theoretical proposition of using molting schedules to model age and growth of large crustaceans, suggested by Hiatt (1948) and supported my many authors, until the work of Caddy (2003), motivated exploring possible representations of discontinuous growth functions of lobster individuals using a time varying unit step function.

A growth function for crustaceans to simultaneously model the increment in size and the duration of the intermolt period

This section contains a review of the study of Arce *et al.* (1991) who used published data from the Florida Keys to estimate the age and growth of the lobster *Panulirus argus* (Latreille 1804). In contrast to the first insightful studies on age and growth for decapods which provided separate estimates of molt frequency and size increment at molt, the original contribution of Arce *et al.* (1991) was that they proposed a growth equation applied to lobsters (but useful to most crustaceans) which considers their two growth components in the same formulae, namely the unit step function. In particular, Dr. Arce learnt about this integrated approach when she was taking her graduate course on simulation modeling delivered by doctor Seijo at CINVESTAV-Mérida. Doctor Seijo, in one of his classes stated that: "taking into account that the growth of lobsters is achieved in steps at successive molts, I consider that the unit step function seems suitable to model this type of discontinuous growth". This statement was the seed of their joint publication of Arce *et al.* (1991). Although in their 1991 publication, these authors did not address converting size to weight in lobsters, this review adds this aspect.

In the systems theory, the unit step function or Heaviside function is frequently used to represent inputs, step by step, and based on their performance, researchers can assess the system's general behavior (Manetsch & Park 1982).

Considering a period involving t_0 and t, this unit step function is 0 for negative values of t, and one (1) for positive values of t. Thus, it is defined by:

$$u_1 (t - t_0) = 1 \text{ for } t \geq t_0 \qquad \text{eq. 8}$$
$$= 0 \text{ for } t < t_0$$

Where: t_0 is the time at the start of the step and is ≥0 (Fig. 1).

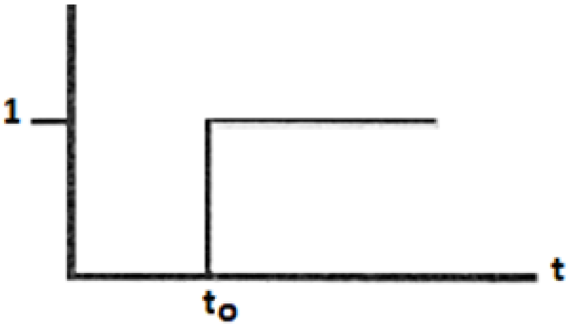

Fig. 1. Graphic representation of the unit step function.

In using this function to estimate the age and growth of *P. argus*, the step (or jump) in *figure 1* represents the increment in body size at molt whereas *t* is related with the duration of the intermolt period. To use this model, researchers need to have (or collect) data of both, the duration of the intermolt period and the increment in size of lobsters. In its applied form involving a series of steps (*i.e.,* a series of unit step functions). *Figure 1* also includes a coefficient α, which represents the size (or jump) of each of the modeled steps (see further explanation below).

Arce *et al.* (1991) obtained the needed growth data for *P. argus* from laboratory conditions (from 6.1 mm to 43 mm carapace length, CL) published by Sweat (1968), and from tag-and-recapture data (for size 43 to 101 mm CL) published by Hunt & Lyons (1986). In this regard, the growth equation for *P. argus* started considering the average of lobsters' CL once they had suffered metamorphosis and became a post larvae or the first benthic stage known as *puerulus*:

$Ave\ l_0 = 6.1$ mm Carapace Length, CL (Sweat 1968),

and the time needed to reach this benthic stage (obtained from the literature), $t_0 = 38.6$ weeks (larval drift = 9 months, Lyons *et al.* 1981).

If $\alpha_0 = Ave\ l_0$ eq. 9

Then $\alpha_0 u_1 (t - t_0)$ eq. 10

Therefore, the first increment in size (CL) of *P. argus* is represented by *equation 10*.

To include the notation of the molt (m) in the equations, Arce *et al.* (1991) defined:

$\alpha_m = l_m - l_{m-1}$ eq. 11

at time: $t_m = t_0 + \sum_{i=1}^{m} \lambda_i$ eq. 12

Where: λ_i is the intermolt period *i* and *m* is the total number of molts.

Once the data on the duration of the inter-molt period *i* and its increment in size of lobsters are obtained, the final growth function in size for *P. argus* will be a sum of unit step functions as follows:

$L_t = \sum_{m=0}^{n} [\ \alpha_m \cdot u_1\ (t - t_m)]$ to all $t \geq t_m$ eq. 13

Where: α_m is the increment in size (*i.e.* the step in *figure 1*) which occurs in molt *m,* as defined in *equation 11.*

In contrast to what were reported by Arce *et al.* (1991), in this review we ordered the pairs of data of the growth components of *P. argus* (molt increment and intermolt period) from laboratory conditions only as reported by Sweat (1968). This latter author reported this species' growth from the first benthic stage (or transparent *puerulus*) to subadults. Here we used his data until molt number 16 (Table 2).

Table 2

Data of the two components of *Panulirus argus*' growth, molt increments and intermolt periods

**Molt number*	*Molt increment, α_m (mm of CL)*	*Intermolt period, λ_i (Weeks)*	*t_m (Weeks)*
0 (Metamorphosis)	6.1 (CL at metamorphosis)	**38.6 (t_0)	38.6 (t_0)
1	0.2	1.16	39.73
2	0.5	3.84	43.53
3	0.8	3.43	47.0
4	1.0	3.76	50.76
5	2.5	4.07	54.83
6	2.2	4.29	59.12
7	2.1	4.89	64.01
8	1.4	5.69	69.7
9	2.4	4.73	74.43
10	1.8	4.93	79.36
11	4.5	5.03	84.39
12	2.8	4.74	89.13
13	2.7	7.03	96.16
14	5.4	6.69	102.85
15	1.1	8.51	111.36
16	5.5	10.5	121.86

Source: data from Sweat (1968: 26, Table 3) which corresponding intermolt periods were in days but we converted them into weeks.

* Relative molt number could also be used.

** t_0, larval drift proposed by Lyons *et al.* (1981).

The growth equation of *P. argus* which using a series of unit step functions models its observed molt increments and intermolt periods is the following:

$$L_t = \sum_{m=0}^{16} [\, \alpha_m \cdot u_1 \,(t - t_m)] \text{ to all } t \geq t_m \qquad \text{eq.14}$$

Solving for Lt, we obtained $43_{121.86}$, meaning that from *pueruli* or the first benthic stage (average length of 6.1 mm CL), *P. argus* reaches a carapace length of 43 mm in 121.86 weeks (Table 2), which is represented graphically in *figure 2*:

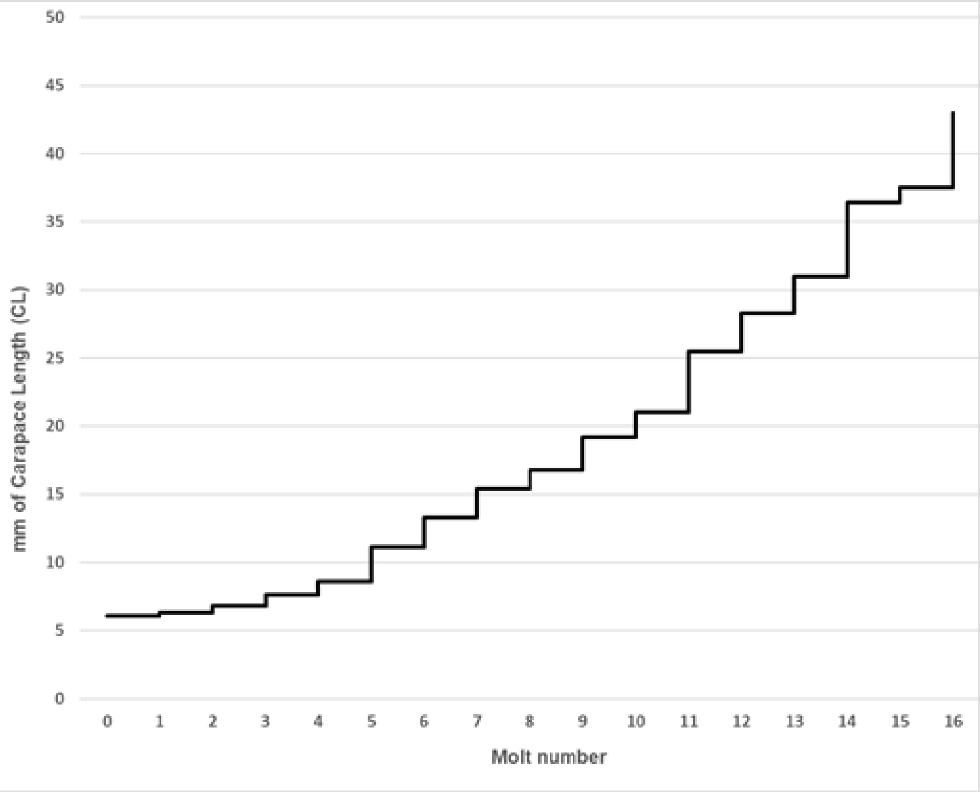

Fig. 2. Spiny lobster (*Panulirus argus*) growth model. Source: own elaboration using data on molt increments and intermolt periods from Sweat (1968: 26).

Here, in contrast to previous growth functions for lobsters, the original contribution of Arce *et al*. (1991) was that they could model the growth of spiny lobster using the two components of growth in a series of units' steps functions.

Again, as it was reported by Saila *et al*. (1979), if researchers want to further carry out any yield-per-recruit assessment for lobsters, in this case for *P. argus*, it would be based on the weight of individuals, and therefore, the weight/length relationships for this species are needed too. This requires developing a unit step-based function for the weight-length relationship. Nevertheless, most experts on age and growth of decapods know that in these species an individual's increase in weight occurs gradually during the intermolt period; in other words, the increase in weight of this species is lagged.

For purposes of the present study, the following unit step-based function for the weight of lobster *P. argus* is proposed:

$$W_t = \sum_{m=0}^{n} \beta_m [\, \alpha_m \cdot u_1 \,(t - t_m)] \textit{ for all } t \geq t_m \qquad \text{eq. 15}$$

Where: β_m is the weight reached at each molt *m*

This proposed growth model in weight could further be used in simulation models to carry out a stock assessment of the spiny lobster *P. argus*. The only data needed are intermolt periods duration and its corresponding size/weight increments, which could be obtained from carefully planned tag-and-recapture studies and from laboratory conditions.

To date, our literature review revealed that, in none of the countries comprising the regions of the Western Central Atlantic and the Pacific Coasts wherein spiny lobsters (*P. argus, Panulirus interruptus* J. W. Randall 1840, *Panulirus gracilis* Streets 1871, and *Panulirus penicillatus* Olivier 1791) are geographically distributed, researchers have carried out efforts on population assessments using age and growth models which consider the intermolt period. In the case of Mexico, the stock assessment of the two most important lobster species (*P. argus* and *P. interruptus*) are based on length-frequency data (Ríos-Lara & Salas 2009, Vega *et al.* 2021). With respect to the management of these two species, it was noteworthy that the lobster (*P. interruptus)* fishery, which received the certification of sustainable fishery by the Marine Stewardship Council (MSC 2016)[3] and contributes with approximately 68% of the catches of lobster at a national level, is in the Fishing National Chart (Carta Nacional Pesquera) but has its management plan unpublished (DOF 2018). In contrast, the lobster (*P. argus*) whose catches represent the second place in the total catch of lobsters at a national level, are not considered for management in the Fishing National Chart but has its management plan published (DOF 2014).

Final considerations

In this paper we carried out a review on the progress accomplished to date on the age and growth of decapods, primarily on lobsters, using molting schedules and their application on stock assessment and management. This section contains final remarks and considerations that try to respond our two research questions:

i) What is needed to know and thus to consider the molting schedules in large decapods populations' assessment and management? A straightforward response to this question is that there are at least three essential interrelated things which are needed. First, those scholars interested in addressing age and growth and stock assessment and management of lobsters (and large decapods in general), using the molting schedules that provide biological meaning to their modeling efforts (Chen *et al.* 2005, Kanaiwa *et al.* 2008), need to promote gatherings such as workshops and conferences to discuss the usefulness and implication of their modeling results to the robust management of these species. Are those research efforts worth of pursuing them? What would be the trade-offs in terms of the financial resources needed to obtain data on molting schedules and their use in stock assessment *vis á vis* simply using crustaceans' length data to carry out its assessment? If these scholarly initiatives were successful, it is expected that young researchers will become interested in developing this topic further. We argue that unless fishery scientists and managers have a better understanding of the ecological, economic, and social implications of the stock assessment and management based on molting schedules for lobster species (and large crustaceans in general), present efforts on large decapods' stock assessment and management elsewhere will continue to be based upon length (and weight). Put it differently, literature on comparison of conventional methods (*i.e.*, based on length-frequency analysis and continuous growth functions) *versus* alternative methods (*i.e.* those that use *ad hoc* or empirical formulas based on molting periods) is scarce (except for instance, Saila *et al.* 1979); therefore, researchers who use conventional stock assessment methods for lobsters are not able to identify any serious error/bias in their estimations. Hence, there is no need to embrace the complex yet expensive approach based on molting schedules.

The second thing that is required to pursue this approach further is scientists to conduct research projects aimed at generating data of the two components of large decapods growth (*i.e.* molting periods and increments in size/weight). This could be accomplished in research projects using both, laboratory conditions and tag-and-recapture studies.

Our literature review found that mark and recapture studies, which are expensive, have been carried out primarily by researchers from countries with high income that are able to invest from moderate to high financial resources in fisheries assessment and management of

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[3] Marine Stewardship Council (MSC) 2016.http://www.msc.org

lobsters and species alike such as Canada, the USA, Australia and New Zealand; therefore, several of their research teams on lobsters and large crustaceans, do have these types of data. In contrast, researchers from countries with middle and low incomes such as Cuba, Ecuador (Galapagos Islands) and Mexico, among others, have also carried out this type of studies but their research efforts are smaller in coverage than the former, either in number of tagged animals or in geographic areas (see Cruz-Izquierdo 1999, Martínez *et al.* 2001,[4] Lozano-Álvarez *et al.* 1991, Ramírez-Estévez *et al.* 2010). Yet, except for a couple of cases, our literature review revealed that even researchers from high income countries who carry out tag-and-recapture studies of lobsters, put aside the analysis of molting schedules and use the length-based frequency analysis to assess the stock's age and growth (using a continuous growth function) (Haist *et al.* 2009, Webber *et al.* 2018) and, based on those results, they further estimate the yield per recruit using the Beverton & Holt model (see Miller & Breen 2010). In this regard, a detected gap in knowledge has to do with fishery scientists lacking the capability to do *ad hoc* modeling that could use molting schedules in any of the ways proposed by Saila *et al.* (1979), Arce *et al.* (1991), and Caddy (2003). Thus, the third thing that is needed to fill up this gap in knowledge, is to recruit/invite researchers with expertise on simulation models for them to be able of incorporating the required age and growth assessment based on molting periods into *ad hoc* yield models other than the Beverton & Holt. Alternatively, some current fishery scientists could be interested in getting a proper training to do the needed simulation exercise for large crustaceans.

To do more progress on this topic, we suggest that collaborative work, like the work that FAO and the Western Central Atlantic Fishery Commission (WECAFC), did in the region on spiny lobster's stock assessment and management from 1998 to 2002 (FAO 2001). These efforts were aimed at having a better stock assessment and possibly, a better aligned management of the lobster *P. argus* in the WECAF region. These efforts were organized in a series of workshop format and were led by doctor S. Cochrane and mister B. Chakalall, and included scholars by many of countries of the WECAFC region which coasts are inhabited by this species.

With respect to our second research question, *ii)* what are the progress and limitations in using molting schedules in commercial decapods' age and growth and stock assessment models?

Drawing on studies of crustacean growth, physiology, and behavior (Hiatt 1948, Sweat 1968, Aiken 1980, Hunt & Lyons 1986, among many others), the progress in scientific knowledge shows evidence that the basis of any biologically meaningful population dynamics and stock assessment modeling in decapods, requires having data to cross schedule of growth, maturity, and mortality. In fact, the core of a robust stock assessment and yield-per-recruit in these species is first and foremost having a biologically meaningful estimation of the decapods' discrete growth patterns. We found that considerable progress has been made since 1979 (Saila *et al.* 1979) to 2008 (Kanaiwa *et al.* 2008) in using molting periods to assess the rock lobster of New Zealand and the American lobster, respectively. The latter progress is biologically integrated since researchers have been able to cross-scheduling of growth, maturity, and mortality, which is being applied particularly in the stock assessment and management of the American lobster (*H. americanus*) in Maine, USA (ASMFC 2000, 2006, Chen *et al.* 2005, Kanaiwa *et al.* 2008).

Among the limitations in using the analyzed approach, apart from lacking financial resources to carry out the required tag-and recapture studies mentioned in previous paragraphs, in most cases, even when they collected data on tagging, these are not analyzed in terms of molting schedules but in age classes using annual scales or in length-based growth matrix which use continuous growth functions (*i.e.*, Haist *et al.* 2008). Perhaps, their data base of tagging results needs to be revisited by scholars who are willing to explore the molting schedules in depth. These re-analyses are needed for experts to discuss and argue about the tradeoffs and purpose of conducting tagging studies.

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[4] Martínez CE, V Toral, G Edgar. 2001. Estado de conservación y aspectos de biología poblacional de *Scyllarides astori* (Scyllaridae: Decapoda) en las islas Galápagos. Informe final. World Wildlife Fundation. Ecuador. 25p.

Lastly, another limitation seems to be that improving the assessment and management of lobsters and large decapods in general, is not a pressing issue for many governments. Despite warnings that many fisheries are being overexploited worldwide (FAO 2002) and regionally (Arreguín-Sánchez & Huitrón 2011, Bravo *et al*. 2022), and that spiny lobsters' stocks in the Caribbean, one of the most valuable resources (Cochrane & Chakalall 2001, Sosa-Cordero *et al*. 2008) have been steadily declining since several decades ago (Ehrhardt *et al*. 2011, Alzugaray & Puga 2012), currently, there are no calls at any level (national, regional or global) to collaborate around improving the assessment and management of large crustaceans. Hence, as it happens in many other fields of knowledge, we suggest that the leadership needs to be taken by scholars interested in doing more scientific progress on any biologically meaningful stock assessment for decapod crustaceans.

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