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Estimating growth of the Florida spiny lobster, *Panulirus argus*, from molt frequency and size increment data derived from tag and recapture experiments

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ABSTRACT

Molting schedules and growth per molt of *Panulirus argus* were deduced by gender from size at tag and recapture of 3481 females and 3330 males released off the Florida coast during 1967–2003. Functional relationships were estimated for the intermolt period from premolt carapace length (CL) and for growth increment from premolt and postmolt CL. Starting at 5 mm CL stepwise growth functions were derived by repeatedly applying these two functions in succession. Growth curves were simulated for each sex to 30 years maximum age. At maximum age females reach a CL of 151 mm and males reach 220 mm. Significant slowdown of growth is expressed by an abrupt change in the intermolt period at the onset of maturity, while there is no evidence of a change in slope of the postmolt and premolt functions at that time. The segmented growth characterizations differ very significantly from all of the von Bertalanffy-type functions estimated for the species from indirect ageing procedures.

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1. Introduction

The process of determining age and growth of exploitable aquatic species is fundamental for determining lifespan, age at recruitment and first capture, age at first maturity, and cohort identification. In stock assessment work age and growth are the bases for yield per recruit estimation, age length keys to estimate catch at age matrices used in sequential population analyses, definition of management bench marks, etc. Age determination in crustaceans is conspicuously difficult because molting of the exoskeleton means that no discontinuities in the seasonal growth (annuli) comparable to those in finfish hard parts are available for age reading. Most of the Caribbean spiny lobster, *Panulirus argus*, age and growth estimates available in the scientific literature are from indirect methods based on size modal progression (FAO, 2001). These methods identify groups of individuals of approximately similar size in a size frequency distribution under the assumption that such groupings should represent animals of a given age. Several problems associated with such methods exist when applied to size frequencies of the Caribbean spiny lobster: (1) minimum size regulations approximately set at the size of first maturity and differential gear-type selectivities and availability of the youngest individuals to the gear types affect definition of the size distributions of the youngest ages, (2) slowdown of growth with the onset of maturity at ages 2 or 3 creates significant overlap of size–age distributions at older ages; therefore, precluding separation of the age groups through most of the mature life span of the species, which may exceeds 20 years, and (3) protracted seasonal reproduction and seasonal differences in growth generate temporally clustered mixes of individual size progressions making identification of cohorts very difficult. For these reasons the applicability of these methods to study growth is defined as quite limited among spiny lobsters (Sheehy et al., 1998; Phillips et al., 1992; Maxwell et al., 2007).

Direct ageing of *P. cygnus* and *P. argus* has been accomplished by using a molecular approach that consistently finds the neuronal accumulation of insoluble autofluorescent lysosomotropic compounds (lipofuscin) as a predictor of chronological age or senescence among crustaceans (Sheehy et al., 1998; Fonseca and Sheehy, 2007; Maxwell et al., 2007). The method, however, poses a particular challenge in that it requires calibration of the lipofuscin accumulation in individuals of known age. Sheehy et al. (1998) highlighted the pitfalls in extrapolation of laboratory-derived information on growth to the natural environment regarding *P. cygnus*. Maxwell et al. (2007) performed the ageing analysis based on individual Florida spiny lobsters kept under laboratory conditions for over 4 years starting from post-larval age and the analyses remain to be tested for wild populations of *P. argus*. This is particularly important given that changing environmental conditions and other

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density dependent factors have effects on growth (Phillips et al., 1992).

While fish species grow continuously towards an asymptotic size, crustacean growth is the product of two distinct but discrete biological processes: (1) molting frequency or its corollary the molting probability, and (2) growth per molt. These two seemingly separated processes are correlated to age in that intermolt periods increase with age while growth per molt decreases with age and more conspicuously so starting at the age or size of first maturity. Therefore, crustacean growth is characterized by segmented or piecewise growth that may or may not be modeled by standard size at age models adopted for fish and some mollusk species (e.g. von Bertalanffy growth function). Crustacean segmented growth can be studied by either direct observation of animals in captivity or by means of tagging experiments. Muller et al. (1997) report segmented growth trends for tagged male and female *P. argus* in Florida following Fogarty and Idoine's (1988) logistic regression procedure to estimate probability of an individual molting. In this paper, new segmented growth functions for males and females of *P. argus* in the Florida fishery are developed from a vast tagging database.

2. Materials and methods

Data were provided by the Florida Marine Conservation Commission consisting in capture–recapture information generated from several spiny lobster tagging studies carried by the State of Florida, and by the University of Florida. The integrated database consists of 3481 females and 3330 males recovered from tagged individuals released throughout the Florida Keys between 1967 and 2003. Female lobsters ranged in size from 32 to 111.7 mm carapace length (CL) while males ranged between 35 and 118 mm CL. Each individual record consisted of size at the time of tagging and release, days at large and size at recapture. Additional information on capture–recapture location and injury status was recorded. Details of the protocols of the tagging experiments are found in Hunt and Lyons (1986) and Muller et al. (1997).

Additionally, data on intermolt period at size corresponding to the first 17 intermolt events of 169 post-larval lobsters captured in the Florida Keys and successfully kept in the laboratory by Sweat (1968) were added to the intermolt information estimated from the tagging data. According to Sweat (1968) the laboratory data was consistent with the growth obtained in the laboratory by Lewis et al. (1952). The 169 post-larval lobsters ranged from an average size of 8 mm CL corresponding to the first post-larval stage at the start of the experiment to an average of 50 mm CL at the end of the 17th molting event. Incorporation of these data was necessary such that a regression range covering from the first post-larval event to sizes well above the size of first maturity are available for fitting non-linear intermolt period-premolt size functions.

Sample sizes in the combined 1967–2003 tagging data varied widely within size groups with large proportion of samples falling between 70, 80, and 90 mm CL categories for sexes combined. Significantly fewer lobsters were tagged and recaptured in size categories below 70 mm CL and above 100 mm CL (Fig. 1). Therefore, the tag-recapture data is the outcome of an unbalanced sample design that may have an impact, especially regarding the larger or older individuals closer to asymptotic sizes.

Also, due to the very high fishing intensity exerted in the areas where the tagged lobsters were released, a large and significant number of the tag returns show extremely short times at large; therefore, preventing the observation of growth (Fig. 2). In Fig. 2 the frequency of recaptured female and male lobsters from all tagging experiments plotted as a function of time at large show that most

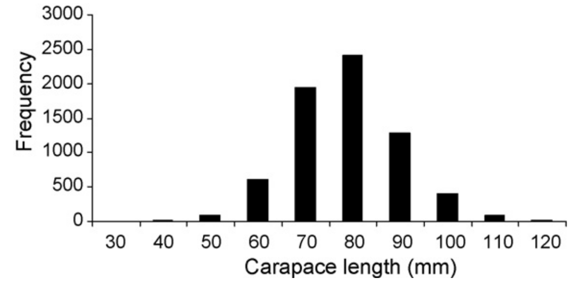

Fig. 1. Size frequency distribution of male and female *Panulirus argus* recaptures from all tagging experiments between 1967 and 2003.

tags (97–98%) were recaptured before 120 days at large while 96% of them were recaptured before 100 days at large.

Under the condition of short times at large measurement error plays a significant role on growth estimation. This initial measurement error was analyzed separately by sex by grouping length at recapture minus length at release for all tag returned within 5 days of tag release. The error distribution centers significantly about 0 mm for either sex (Fig. 3). The error does not appear to propagate 2 mm above or below 0 mm CL. The distributions are very approximately similar between sexes. This finding is similar to that of Hunt and Lyons (1986) regarding measurement errors. Consequently, only those recaptured individuals showing a CL increment larger than 2 mm were considered in the analyses of growth.

Intermolt periods were estimated separately by sex and by 10 mm CL intervals starting with a size category <40 mm CL and then every 10 mm above 40 mm CL until the largest individuals tagged in each sex. Intermolt periods were estimated following an algorithm that functionally follows Munro's (1974) procedure (Fig. 4). The procedure estimates intermolt periods from tagging studies by assuming that if at the time of tagging, individuals of the same size or in a given size group are uniformly randomly dis-

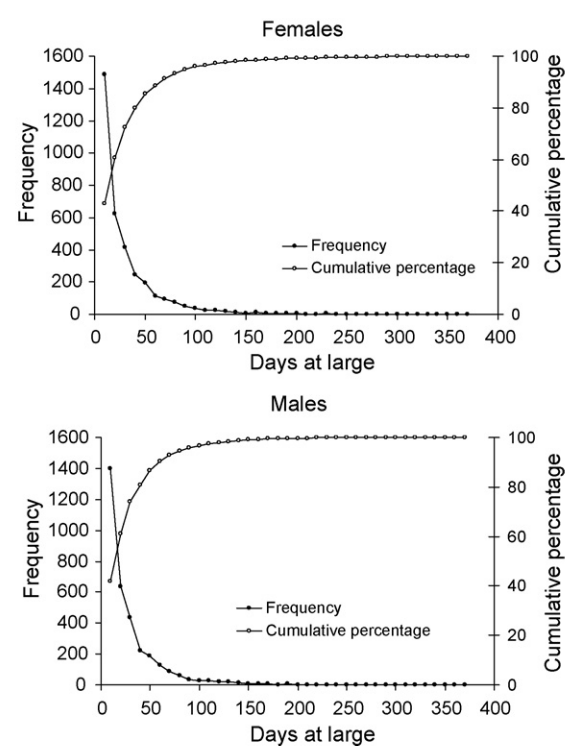

Fig. 2. Frequency and cumulative percentage of males and females recaptured after given times at large from all tagging experiments.

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