Relative growth of the semi-terrestrial crab *Pachygrapsus marmoratus*: an information-theory approach

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SUMMARY: The patterns of allometric growth of the grapsid crab *Pachygrapsus marmoratus* were investigated with an information-theoretic approach. This approach is beneficial, more robust, and may reveal more information than the classical approaches (e.g. hypothesis testing). No differentiation in allometric growth was detected between right and left chelar propods in either sex. Significant sexual differentiation in the allometric growth of chelar propods, abdominal somites and telson was found. It was shown that the allometry of chelar propodus width may be used to identify puberty in males, as there is a marked breakpoint at a carapace width of ~16.0 mm. For females, puberty was identified by the breakpoint in the allometry of the third and fourth abdominal somites at a carapace width of ~16.5 mm. In many cases (e.g. in chelar propods of males, or in most abdominal somites and the telson in females) the classic allometric equation $\log Y = \log a + b \log X$ has no essential support and non-linear allometric models between the log-transformed morphometric characters have to be used.

Keywords: AIC, allometry, breakpoint, crab, growth, information-theory.

RESUMEN: CRECIMIENTO RELATIVO DEL CANGREJO SEMITERRESTRE *PACHYGRAPSUS MARMORATUS*: UN ENFOQUE A PARTIR DE LA TEORÍA DE LA INFORMACIÓN. – Los patrones de crecimiento alométrico del cangrejo grápsido *Pachygrapsus marmoratus*, fueron investigados mediante un enfoque a partir de la teoría de la información. Esta aproximación es más robusta, completa, y puede revelar más información que los estudios clásicos (como la comprobación de hipótesis). No se detectó diferenciación en el crecimiento alométrico en los quelípedos derecho e izquierdo en ambos sexos. Sí se halló una diferenciación sexual importante entre el crecimiento alométrico de quelípedos, segmentos abdominales y telson. Se demostró que la alometría del ancho de los quelípedos puede utilizarse para identificar la pubertad en los machos, ya que hay un marcado punto de rotura en una anchura de caparazón de ~16.0 mm. En las hembras, la pubertad se identifica por el punto de rotura en la alometría de los segmentos abdominales tercero y cuarto con un ancho de caparazón de ~16.5 mm. En muchos casos (por ejemplo en los quelípedos de los machos o en la mayoría de los segmentos y el telson en las hembras) la ecuación alométrica clásica $\log Y = \log a + b \log X$ no tiene esencialmente ninguna base y deben utilizarse modelos alométricos no lineales entre los caracteres morfométricos trasformados logarítmicamente.

Palabras clave: AIC, alometría, cangrejo, crecimiento, punto de rotura, teoría de la información.

INTRODUCTION

Growth in animals is often accompanied by changes in proportion as well as in size, i.e. some body parts grow at a different rate than others. This phenomenon is called relative or allometric growth. One of the consequences of crustaceans having an exoskeleton is that growth proceeds in steps by a series of moults (or ecdyses), which separate the stages (or instars). Usually the change in shape in

crustaceans is progressive, but sometimes particularly marked changes occur at a single moult, which in extreme cases are regarded as a metamorphosis (Hartnoll, 1985). Using the allometric equation (Huxley, 1932) is the most extensively used method for analysing relative growth during ontogeny. The relationship between the size of a body part Y relative to another body part X, usually carapace width or length, has the form $Y = aX^b$, where the exponent b is a measure of the difference in the growth rates of the two body parts. To estimate the coefficients of the allometric equation, the data are usually log-transformed and a linear regression is fitted to the equation $\log Y = \log a + b \log X$ (L model), where the allometric exponent b is the slope of the resulting linear equation. Logarithmic transformation is generally appropriate because morphological data tend to have log-normal structure, as they are non-negative, with positively-skewed distributions and variances that increase with the mean (Jolicoeur, 1990; Ebert and Russell, 1994).

However, the classic allometric equation frequently fails to adequately fit the data and more complex models of the form $\log Y = f(\log X)$ should be used. The reason might be due either to the existence of non-linearity (i.e. f is non-linear) or the existence of breakpoints (i.e. f and/or its first derivative f' are not continuous functions). The existence of breakpoints in allometric data has been recognized since the allometric equation was first proposed (Huxley, 1932). These breakpoints are usually identified visually, when data are obviously separated, and then linear regression analysis is done on both sides of the selected breakpoint. Estimating breakpoints visually is not, however, an accurate method and using segmented regression models has been proposed to be a better alternative (Somerton, 1983; Shea and Vecchione, 2002).

The patterns of relative growth vary greatly among different crab families (Hartnoll, 1983). For example, in logarithmic plots of the chelae of male crabs against carapace length or width, three distinct segments were present in majid crabs (Hartnoll, 1963), a change in slope but no discontinuity was found for *Portunus pelagicus* (Hall *et al.*, 2006), while gradual changes in b that appeared to follow a smooth, curvilinear trend were demonstrated for *Chaceon bicolor* (Hall *et al.*, 2006).

One approach to study relative growth, followed quite often by many researchers, is to fit more than one model to the data and then use a criterion, like minimizing the residual sum of squares or maximizing the adjusted R^2, to select the 'best' model. When the models are nested, a statistical hypothesis testing approach is often used with an F test or with a likelihood ratio test when the probability distribution of the error structure is specified. However, there are several practical pitfalls and theoretical problems with such an approach (Burnham and Anderson, 2002). During the past twenty years, modern statistical science has been moving away from traditional formal methodologies based on statistical hypothesis testing. In particular, hypothesis testing for model selection using traditional approaches (such as forward, backward, and stepwise selection) is often poor and of limited value (Akaike, 1981) and it has been suggested that it will be used less and less in the years ahead (Burnham and Anderson, 2002). Hypotheses testing schemes are based on arbitrary a levels (commonly 0.05 or 0.01), multiple testing is challenging, and tests between models that are not nested are problematic. The adjusted coefficient of multiple determination (R^2) that is often used in model selection was found to be a very poor approach (McQuarrie and Tsai, 1998).

Model selection based on information theory is a relatively new paradigm in the biological sciences and is quite different from the usual methods based on null hypothesis testing. Information theory has been increasingly proposed to be a better and advantageous alternative for model selection (Burnham and Anderson, 2002), e.g. in studies of fish growth (Katsanevakis, 2006) or aquatic respiration (Katsanevakis *et al.*, 2007b). Katsanevakis *et al.* (2007a) recommended the information theory approach as a more accurate, robust and enlightening way to study allometric growth of marine organisms. They demonstrated that using the classical allometric model when it is not supported by the data, might lead to characteristic pitfalls, data misinterpretation, and loss of valuable biological information.

In the present study, the relative growth of the grapsid crab *Pachygrapsus marmoratus* (Fabricius, 1787) was studied, following the information-theory approach proposed by Katsanevakis *et al.* (2007a), accounting possible breakpoints and non-linearity in the equations relating log-transformed morphometric data. The pattern of relative growth was investigated for various somatic parts of this grapsid crab and the potential pitfalls of using the classic allometric equation were emphasized.

MATERIALS AND METHODS

Test species – Morphometric measurements

The family Grapsidae is one of the richest among Decapoda, in terms of intertidal species. *Pachygrapsus marmoratus* is the most common grapsid crab in the intertidal belt of rocky shores throughout the Mediterranean Sea, Black Sea and northeastern Atlantic from Brittany to Morocco including the Canary Islands, the Azores and Madeira (Ingle, 1980; Cannicci *et al.*, 1999; Flores and Paula, 2001, 2002). *P. marmoratus* has a semi-terrestrial life-style and is an omnivorous species that actively searches for food, relying on the intertidal community throughout its post-larval life (Cannicci *et al.*, 2002).

A total of 85 *P. marmoratus* individuals was collected by hand from rocky shores of the Saronikos Gulf (37°30'N-37°55'N; 23°E-24°E) from January to November 2005. The following somatic parts of each crab were measured: maximum carapace length (*CL*), maximum carapace width (*CW*; excluding the lateral spines), maximum length (*LPL*) and width (*LPW*) of the propodus of the left chela, maximum length (*RPL*) and width (*RPW*) of the propodus of the right chela, and maximum width of the six abdominal somites and the telson (S_1 to S_7; S_7 corresponding to the telson). A vernier caliper with 0.1 mm accuracy was used for lengths >14 mm and an Image Analysis system, comprising of a stereoscope (Wild M8), a Sony camera (Hyper HAD) and the software ImagePro plus v3.0.1, for lengths <14 mm.

Data analysis

The allometric growth of *CL, LPL, LPW, RPL, RPW*, S_i (i = 1 to 7) in relation to *CW* was investigated separately for males and females. In larger crabs, sex was identified from the abdominal shape, while in smaller crabs, pleopods were examined under a dissecting microscope.

Five candidate models for the relationship $\log Y = f(\log X)$ were fitted to the log-transformed data (logarithms with base 10), as proposed by Katsanevakis *et al.* (2007a), with non-linear least squares with iterations: linear (L), quadratic (Q), cubic (C), broken-stick (BS), and two-segment (TS) (Table 1). In the current context, the allometric exponent *b* is generalized to mean the first derivative of *f*, i.e. $b = f'(X)$. Hereafter, $X = CW$, while *Y* is any of the other measured body parts.

The L model is the classical allometric equation, assuming that allometry does not change as body size increases ($b = a_2$). The Q and C models assume that a non-linearity exists in the relationship of log *Y* and log *X* and that *b* changes continuously with increasing body size ($b = a_2 + 2a_3 \log CW$ and $b = a_2 + 2a_3 \log CW + 3a_4 (\log CW)^2$ respectively). The BS and TS models assume a marked morphological change at a specific size of $CW = a_4$; the BS represents two straight line segments with different slopes that intersect at $CW = a_4$, while the TS represents two straight line segments that do not intersect; thus, there is a point of discontinuity at $CW = a_4$, and their slope (i.e. *b*) may or may not be equal.

TABLE 1. – The candidate models used for relative growth investigation. The variable *Y* was one of *LPL, LPW, RPL, RPW*, S_i (i = 1 to 7). The sign function is defined as $sign(x) = \begin{cases} -1, & x < 0 \\ 0, & x = 0 \\ +1, & x > 0 \end{cases}$ ·

Name of Model	Abbr.	Equation
Linear	L	$\log Y = a_1 + a_2 \log CW$
Quadratic	Q	$\log Y = a_1 + a_2 \log CW + a_3 (\log CW)^2$
Cubic	C	$\log Y = a_1 + a_2 \log CW + a_3 (\log CW)^2 + a_4 (\log CW)^3$
Broken-Stick	BS	$\log Y = a_1 + \left(a_2 + \dfrac{a_3}{2}(\text{sign}(CW - a_4) + 1) \right) \cdot (\log CW - \log a_4)$
Two-Segment	TS	$\log Y = \left(a_1 + \dfrac{a_5}{2}(\text{sign}(CW - a_4) + 1) \right) + \left(a_2 + \dfrac{a_3}{2}(\text{sign}(CW - a_4) + 1) \right) \cdot (\log CW - \log a_4)$

Model selection – Multi-model inference (MMI)

According to the information theory approach, data analysis is assumed to be the integrated process of *a priori* specification of a set of candidate models (based on the science of the problem), model selection based on the principle of parsimony according to Akaike Information Criterion AIC (Akaike, 1973), and the estimation of parameters and their precision. The principle of parcimony implies selecting a model with the smallest possible number of parameters to adequately represent the data, a bias versus variance trade off. Furthermore, rather than estimating parameters from only the 'best' model, parameters can be estimated from several or even all the models considered. This procedure is termed multi-model inference (MMI) and has several theoretical and practical advantages (Burnham and Anderson, 2002). Further details on using information theory to study allometric growth may be found in Katsanevakis *et al.* (2007a), while a thorough presentation of information theory, the philosophical principles behind it and many related issues are given in Burnham and Anderson (2002).

In the current context, the small-sample, bias-corrected form AIC_c (Hurvich and Tsai, 1989) of the AIC (Akaike, 1973; Burnham and Anderson, 2002) was used for model selection. The model with the smallest AIC_c value $(AIC_{c,min})$ was selected as the 'best' one out of the models tested. The AIC_c differences $\Delta_i = AIC_{c,i} - AIC_{c,min}$ were computed over all candidate models. According to Burnham and Anderson (2002), models with $\Delta_i > 10$ have essentially no support and could be omitted from further consideration, models with $\Delta_i < 2$ have substantial support, while there is considerably less support for models with $4 < \Delta_i < 7$. The 'Akaike weight' w_i of each model was calculated to quantify the plausibility of each model given the data and the set of five models. This is considered to be the weight of evidence in favour of model i which is actually the best model of the available set of models (e.g. Akaike, 1983; Buckland *et al.*, 1997; Burnham and Anderson, 2002). 'Average' models were estimated by averaging the predicted response variable across models, using the corresponding w_i's as weights (Burnham and Anderson, 2002). Absolute residuals were plotted against log CW for the linear and average model, as a diagnostic tool to check model assumptions and especially to check for curvature in the pattern of residuals; the display was enhanced by

a smoothing spline curve (with 4 degrees of freedom) fitted to the residuals.

Confidence intervals (95%) of the model parameters (CI_{boot}), were estimated with non-parametric bootstrap (Efron and Tibshirani, 1993), with bootstrap sample size $B = 2000$, by resampling biometric data for the individual crabs in the original data set and fitting the respective model by non-linear least squares to each sample.

RESULTS

The CW of male and female *P. marmoratus* respectively ranged between 3.5 to 39.4 mm and 4.3 to 34.9 mm. No significant differences were found in comparison tests between left and right chelar propodus lengths and widths in males (paired t-tests; p = 0.15 for lengths and p = 0.18 for widths) or females (p = 0.18 for lengths and p = 0.23 for widths). Therefore, there was no asymmetry between left and right chelar propodus in either males or females. Consequently, data for left and right chelar propods were combined. For chelar propodus length (PL) and width (PW), the models were fitted to the pooled data. The regression parameters describing the allometry of the various somatic parts in relation to CW are given in Table 2. The AIC_c differences and the 'Akaike weights of evidence' for the five models and for each biometric variable are given in Table 3.

In females, L was the best model for the growth of PL, while for PW there was almost equal support for the L and TS models (Table 3). There was also some support for other models for both PL and PW. Based on the L model, the CI_{boot} for the allometric exponent $b = a_2$ was (1.005, 1.031) and (1.002, 1.041) for PL and PW respectively. This indicates that the growth of female chelar propods may be considered slightly positive allometric.

In males, the best model for PL growth was the Q model. There was also substantial support for the C model and some support for other models (Table 3). For the growth of PW in males, the best model was the TS model, with some support for the BS (Table 3); total w_i for the two models was 97%, i.e. with strong evidence of the existence of a breakpoint in the allometric growth of PW; the breakpoint was quite marked (Fig. 1) at $CW \approx 16$ mm. It is worth mentioning, that there was no support for the linear model (which was best for females), which indicates sub-

TABLE 2. – The parameters a_i and the residual sum of squares RSS of the regression equations between the logarithms of the measured biometric variables Y in relation to CW. Model abbreviations as in Table 1.

Model	Param.	CL	PL	PW	S1	S2	S3	S4	S5	S6	S7
Females											
L	a_1	-0.077	-0.230	-0.551	-0.386	-0.442	-0.519	-0.743	-0.930	-1.087	-1.186
	a_2	1.019	1.018	1.023	1.022	1.099	1.240	1.427	1.555	1.638	1.579
	RSS	0.0057	0.0219	0.0532	0.0140	0.0378	0.0447	0.0658	0.0858	0.1095	0.1405
Q	a_1	-0.077	-0.234	-0.527	-0.419	-0.434	-0.415	-0.650	-0.840	-1.049	-0.969
	a_2	1.020	1.025	0.976	1.087	1.082	1.033	1.244	1.375	1.561	1.147
	a_3	0.000	-0.003	0.0216	-0.030	0.008	0.095	0.058	0.083	0.035	0.199
	RSS	0.0057	0.0219	0.0530	0.0139	0.0377	0.0433	0.0647	0.0848	0.1093	0.1344
C	a_1	0.243	-0.223	-0.385	-0.379	-0.113	0.370	0.511	0.963	1.206	1.613
	a_2	0.077	0.993	0.552	0.971	0.137	-1.276	-2.174	-3.933	-5.074	-6.452
	a_3	0.885	0.027	0.425	0.079	0.895	2.262	3.293	5.065	6.264	7.332
	a_4	-0.267	-0.009	-0.123	-0.033	-0.268	-0.655	-0.969	-1.505	-1.881	-2.155
	RSS	0.0050	0.0219	0.0528	0.0139	0.0370	0.0390	0.0554	0.0623	0.0742	0.0884
BS	a_1	0.766	1.056	0.890	1.090	0.664	0.681	0.503	0.416	0.301	0.146
	a_2	0.948	1.021	1.017	1.027	1.066	1.121	1.226	1.268	1.318	1.067
	a_3	0.081	-0.014	0.176	-0.225	0.053	0.182	0.254	0.359	0.387	0.633
	a_4	6.8	18.3	25.8	27.7	10.3	9.7	7.8	7.7	7.4	7.6
	RSS	0.0053	0.0219	0.0521	0.0133	0.0374	0.0408	0.0610	0.0760	0.0995	0.1121
TS	a_1	0.834	1.095	0.821	0.958	0.926	0.943	0.939	0.900	0.848	0.647
	a_2	0.927	1.025	1.032	1.018	1.060	1.116	1.284	1.397	1.491	1.356
	a_3	0.085	0.005	0.204	-0.123	-0.096	0.040	0.002	-0.050	-0.120	-0.002
	a_4	8.1	19.9	21.7	20.8	18.3	16.5	16.5	16.5	16.5	16.5
	a_5	0.019	-0.005	-0.028	0.017	0.040	0.071	0.091	0.110	0.115	0.142
	RSS	0.0050	0.0217	0.0496	0.0126	0.0323	0.0319	0.0457	0.0564	0.0754	0.0903
Males											
L	a_1	-0.062	-0.309	-0.670	-0.320	-0.294	-0.287	-0.418	-0.529	-0.619	-0.714
	a_2	1.013	1.117	1.163	0.921	0.914	0.944	0.989	1.006	1.006	0.941
	RSS	0.0043	0.0763	0.1257	0.0141	0.0104	0.0094	0.0140	0.0168	0.0213	0.0380
Q	a_1	-0.110	-0.115	-0.421	-0.393	-0.392	-0.388	-0.524	-0.620	-0.696	-0.807
	a_2	1.112	0.721	0.654	1.071	1.115	1.150	1.205	1.193	1.164	1.133
	a_3	-0.046	0.184	0.236	-0.069	-0.093	-0.095	-0.100	-0.087	-0.073	-0.089
	RSS	0.0038	0.0621	0.1022	0.0132	0.0086	0.0076	0.0120	0.0153	0.0202	0.0364
C	a_1	0.052	-0.309	-0.441	-0.297	-0.323	-0.287	-0.305	-0.575	-0.653	-0.586
	a_2	0.611	1.321	0.717	0.771	0.901	0.838	0.527	1.051	1.029	0.446
	a_3	0.434	-0.391	0.176	0.220	0.113	0.205	0.551	0.050	0.057	0.571
	a_4	-0.145	0.174	0.018	-0.088	-0.062	-0.0912	-0.198	-0.041	-0.040	-0.201
	RSS	0.0035	0.0610	0.1022	0.0130	0.0086	0.0074	0.0113	0.0153	0.0202	0.0357
BS	a_1	1.381	0.950	0.495	0.955	0.944	1.036	0.970	0.858	0.789	0.620
	a_2	1.023	1.027	0.978	0.938	0.939	0.963	1.011	1.026	1.022	0.967
	a_3	-0.136	0.216	0.328	-0.138	-0.149	-0.187	-0.215	-0.150	-0.153	-0.277
	a_4	26.3	14.3	11.1	23.8	22	24.7	24.8	23.4	24.7	25.4
	RSS	0.0032	0.0621	0.0955	0.0125	0.0080	0.0066	0.0103	0.0147	0.0194	0.0327
TS	a_1	1.350	0.999	0.656	1.029	1.042	1.050	0.882	0.461	0.380	0.592
	a_2	1.018	1.016	0.985	0.939	0.934	0.967	1.002	1.201	1.229	0.941
	a_3	-0.150	0.205	0.261	0.023	0.066	-0.067	-0.192	-0.199	-0.211	-0.400
	a_4	24.7	16.1	16.0	28.5	28.2	25.4	20.5	8.6	8.6	24.6
	a_5	0.009	0.021	0.0623	-0.024	-0.031	-0.019	0.020	-0.049	-0.065	0.038
	RSS	0.0029	0.0608	0.0874	0.0116	0.0066	0.0059	0.0098	0.0130	0.0161	0.0271

stantial sexual differentiation in the relative growth of chelar propods. The generalized allometric exponent for the growth of *PL* in males was an increasing function of the crab size (Fig. 1). The generalized allometric exponent for the growth of *PW* in males, based on the TS model, was initially $b_{PW} = 0.985$, with CI_{boot} = (0.893, 1.070). Then, after the breakpoint, it increased to $b_{PW} = 1.246$, with $CI_{boot} = (1.153, 1.322)$. From the smoothing spline fit of the residuals, it is clear that in males, both for *PW* and *PL*, the assumption of linearity is more or less violated as the residuals of the L model do not have a random distribution around zero but show evident curvature (Fig. 1). The situation clearly improved with the average model,

TABLE 3. – Values of the AIC$_c$ differences (Δ_i) and of the 'Akaike weights' w_i for the five models of the measured biometric variables.

Model\\Y	CL	PL	PW	S1	S2	S3	S4	S5	S6	S7
FEMALES										
AIC$_c$ differences, Δ_i										
L	2.2	0.0	0.0	0.0	0.6	9.8	11.2	14.0	15.0	18.8
Q	4.5	2.2	1.9	1.8	2.9	10.5	12.7	15.8	17.3	18.9
C	0.0	4.4	3.8	4.3	4.4	7.7	7.2	2.5	0.0	0.0
BS	3.3	4.2	2.5	2.0	4.9	10.0	12.1	12.7	15.0	12.1
TS	2.4	5.7	0.1	1.8	0.0	0.0	0.0	0.0	3.4	3.7
Akaike Weights, w_i (%)										
L	17	61	36	44	35	1	0	0	0	0
Q	5	21	14	17	11	1	0	0	0	0
C	52	7	6	5	5	2	3	22	84	86
BS	10	7	10	16	4	1	0	0	0	0
TS	15	4	34	18	46	96	97	78	15	14
MALES										
AIC$_c$ differences, Δ_i										
L	8.8	13.3	19.9	0.0	8.3	8.7	5.7	1.1	2.0	4.0
Q	6.7	0.0	6.9	0.3	4.2	3.5	2.7	0.3	2.7	5.0
C	5.1	1.0	9.2	2.7	6.7	5.5	3.3	2.9	5.3	7.0
BS	1.5	2.3	4.2	1.3	4.1	1.4	0.0	1.6	3.9	3.8
TS	0.0	3.1	0.0	1.6	0.0	0.0	1.0	0.0	0.0	0.0
Akaike Weights, w_i (%)										
L	1	0	0	32	1	1	3	18	20	10
Q	2	47	3	28	9	10	13	28	14	6
C	5	28	1	8	3	4	9	7	4	2
BS	29	15	11	17	10	29	47	14	8	11
TS	63	10	86	14	77	57	28	32	54	72

with the smoothing spline fit of the residuals much closer to the horizontal axis.

The sexual differentiation in growth patterns of chelar propods is demonstrated in Figure 1, in which the 'average' models and the corresponding generalized allometric exponents are plotted. Initially there were no differences in the size of the chelar propods between males and females, but as the crabs grew larger, males attained significantly larger propods. The allometric exponent was initially near unity for both sexes, but for males it soon increased at a greater rate compared to females (Fig. 1B).

Female abdominal somites showed a variety of allometric growth patterns (Table 3). For S_1 the L model was the best, and the Q, TS and BS models also had substantial support. For abdominal somites S_2, S_3, S_4, and S_5, the TS was the best model; for S_3 and S_4 in particular, no other competing model had substantial support. The breakpoint for somite S_3 and S_4 was at $CW = a_4 \approx 16.5$ mm. For somites S_6 and S_7, the C model was the best with much less support for TS and essentially no support for any other model. The variation of the growth pattern among the seven abdominal somites of the females is demonstrated in Figure 2, where log S_i and the allometric exponents are plotted against log CW, based

on the 'average' models. The residual plots of the average models were much improved in relation to those of the linear models in most cases; two examples (for S_4 and S_6) are given in Figure 2 (E-H).

In females, the corresponding allometric exponent and its CI$_{boot}$ were estimated using the L model for the growth of S_1 (Table 4). The two b values for each line segment of the TS model were estimated for the growth of each of S_2, S_3, S_4, and S_5, (Table 4). The change of the allometric exponent b at the breakpoint was not significant in any of the cases (Table 4, Fig. 2). The generalized allometric exponent for the growth of somites S_6 and S_7 has a maximum at an intermediate size (Fig. 2). The maximum value of b and its value for the smallest and greatest measured CW of our dataset were estimated (Table 4). The allometric growth of S_6 and S_7 was initially negative allometric, then it gradually became positive allometric and finally isometric. The differences in the growth pattern of the abdominal somites cause a morphological change in the abdominal shape during the ontogeny of *P. marmoratus* females (Fig. 3).

The best model for the growth of male abdominal somites was the TS in most cases, except for S_1 where it was the L model (as in females) and for S_4 where it was the BS model. In most cases, models
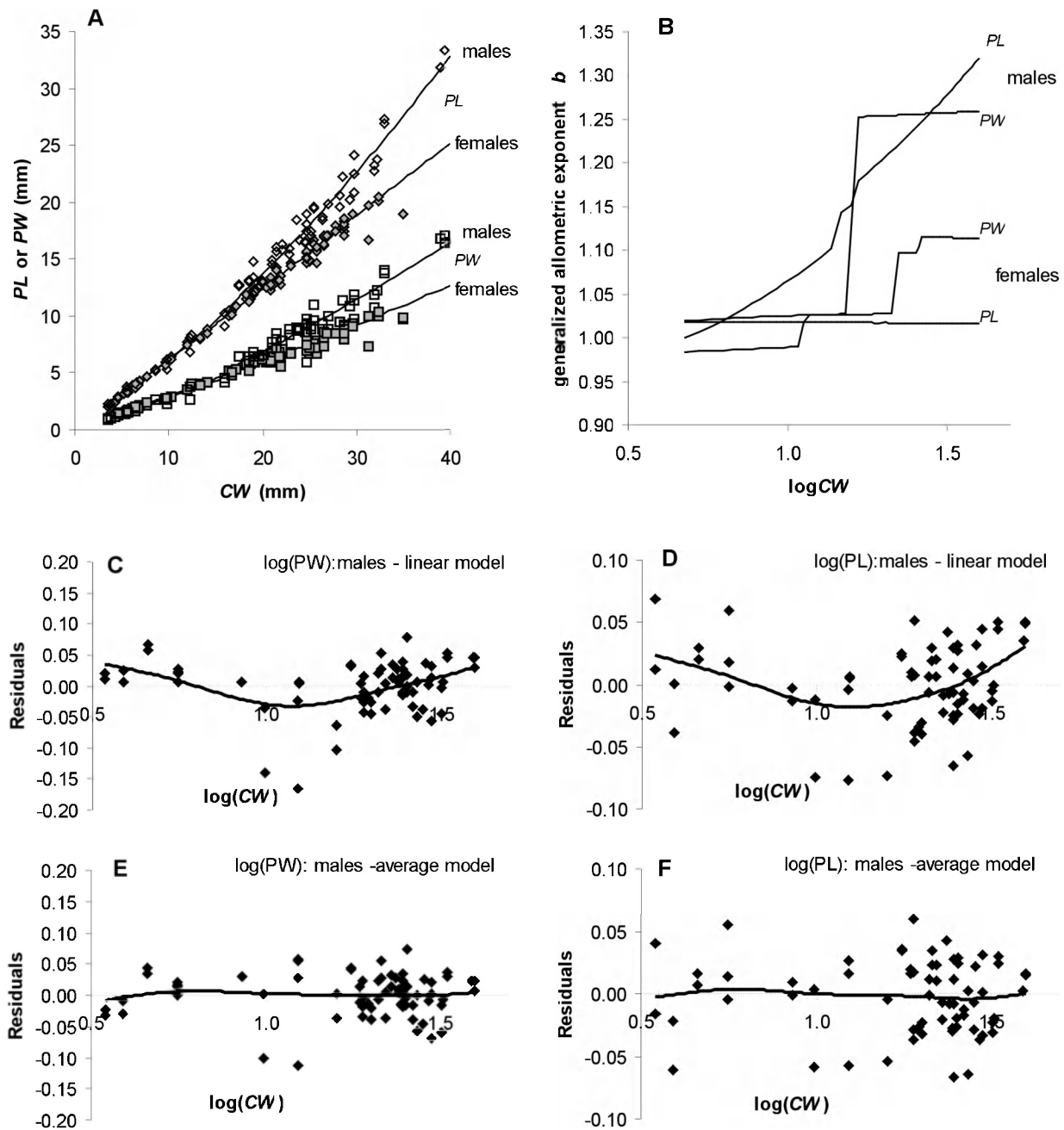
Fig. 1. – (A) The relative growth patterns of chelar propods (*PL* and *PW* in relation to *CW*) in male and female *P. marmoratus*; the datapoints and the 'average' models are given in absolute scales. (B) The generalized allometric exponent *b* for the relative growth of *PL* and *PW*, calculated as the slope of the corresponding 'average' models. (C-F) Residual plots against log *CW* for the linear (C, D) and the average (E, F) models for log *PW* (C, E) and log *PL* (D, F) in males, with a smoothing spline fitted to the residuals.

other than the best ones were also substantially supported by the data (Table 3). The *b* values and the corresponding confidence intervals were estimated based on the best model (Table 4). The corresponding plots based on the 'average' models are given in Figura 4. Growth of the abdominal somites of the male *P. marmoratus* was either isometric or negative allometric (Table 4, Fig. 4).

The overall outcome of the differences in the relative growth of abdominal somites between males and females is that at small sizes there was no morphological sexual differentiation of the abdomen, but at larger sizes there was substantial differentiation with the abdomen of the females becoming relatively larger and more rounded, while that of the males remained lance-shaped (Fig. 3).
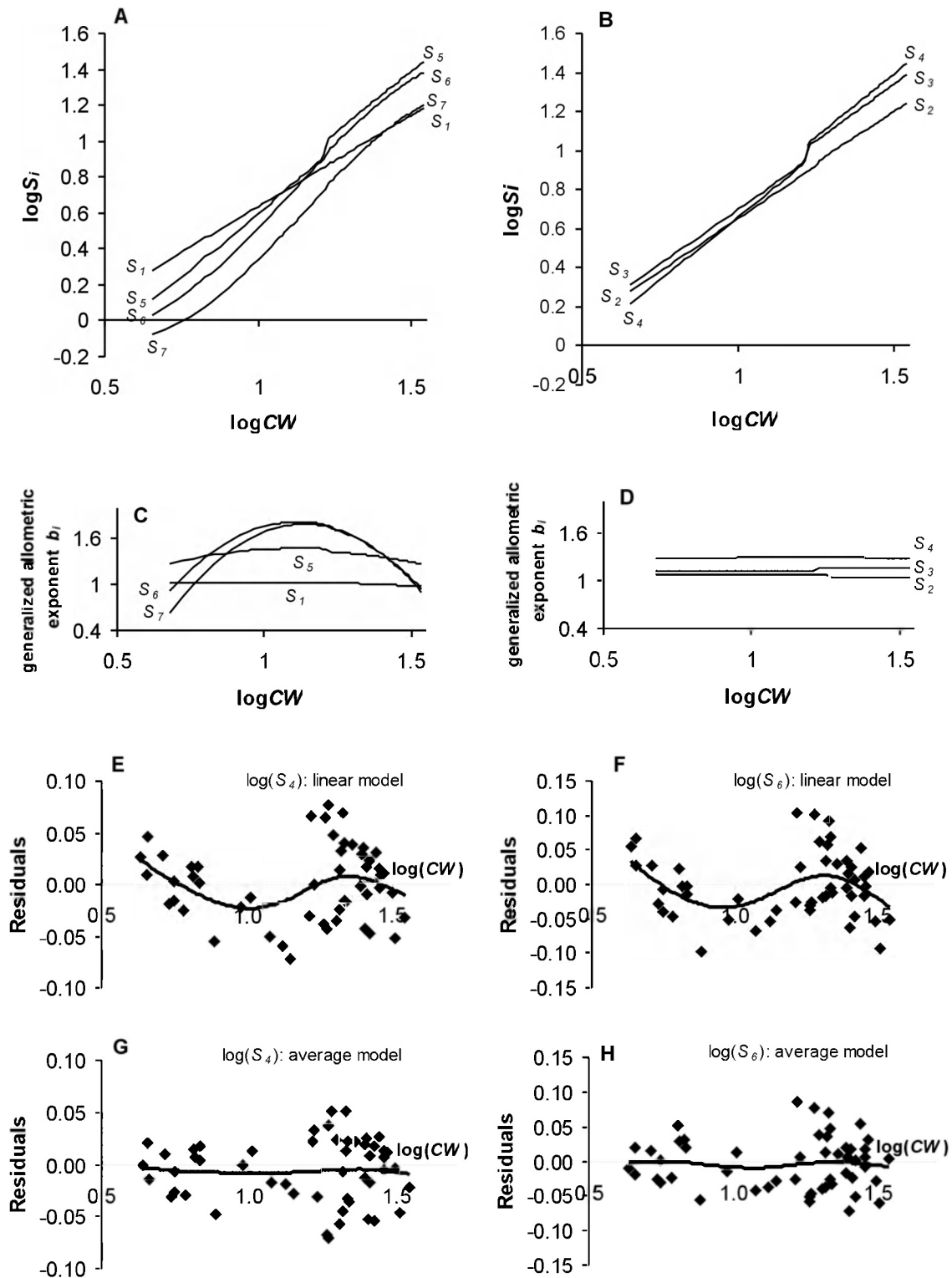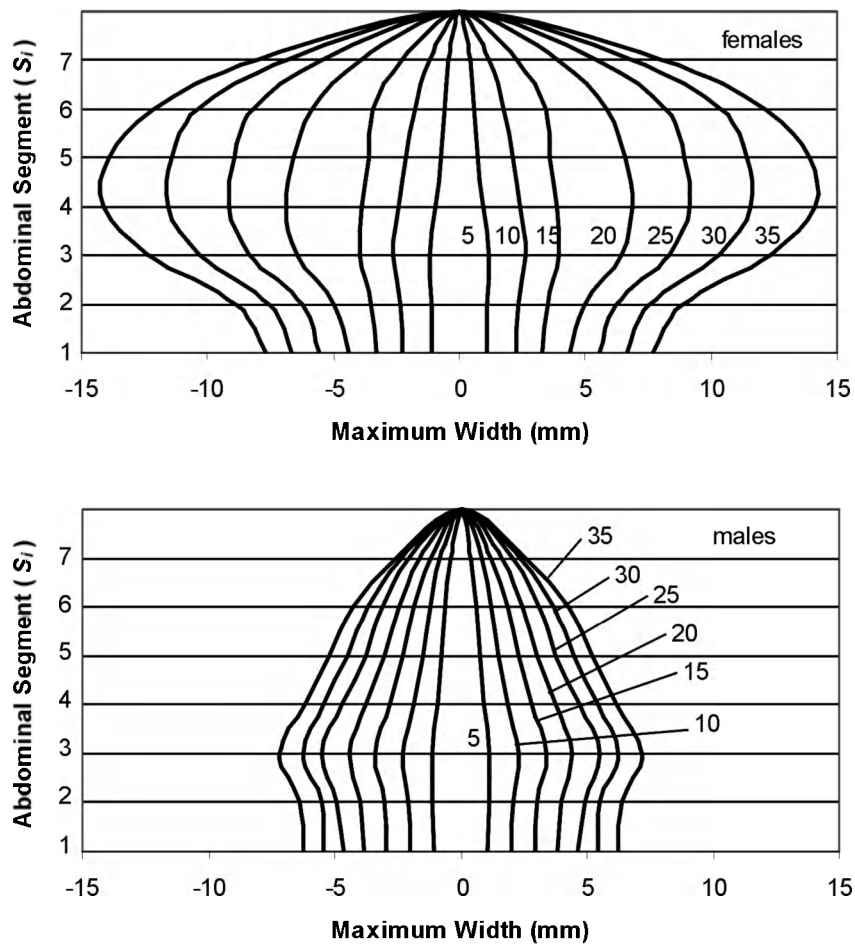
Abdomen Somites: Females

FIG. 2. – (A, B) The relative growth patterns of the width of abdominal somites (S_i) of female *P. marmoratus* according to the corresponding 'average' models; the Akaike weights w_i were used for the weighted averages; somites S_2, S_3 and S_4 were separated for clarity. (C, D) The generalized allometric exponent b for the relative growth of each S_i of female *P. marmoratus*, calculated as the slope of the corresponding 'average' models between log S_i and log CW. (E-H) Residual plots against log CW for the linear (E, F) and the average (G, H) models for log S_4 (C, E) and log S_6 (D, F) in females, with a smoothing spline fitted to the residuals.

TABLE 4. – The allometric exponents b_i and their 95% bootstrap confidence intervals for the growth of the abdominal somites S_i in females and males, according to the corresponding 'best' models. +: positive allometry, -: negative allometry, =: isometry.

| | | Females | | | Males | |
	b	CI_{boot}	Allometry	b	CI_{boot}	Allometry
S_1	1.022	1.006, 1.039	+	0.92	0.893, 0.943	−
S_2	b_1=1.060	1.021, 1.095	+	b_1=0.934	0.909, 0.949	−
	b_2=0.964	0.765, 1.149	=	b_2=1.000	0.588, 1.266	=
S_3	b_1=1.116	1.083, 1.163	+	b_1=0.967	0.947, 0.981	−
	b_2=1.157	1.023, 1.315	+	b_2=0.900	0.668, 1.014	=
S_4	b_1=1.284	1.236, 1.348	+	b_1=1.011	0.982, 1.038	=
	b_2=1.286	1.136, 1.446	+	b_2=0.796	0.603, 0.916	−
S_5	b_1=1.397	1.316, 1.459	+	b_1=1.201	0.925, 1.330	=
	b_2=1.347	1.188, 1.539	+	b_2=1.002	0.925, 1.041	=
S_6	b_{low}=0.618	0.217, 0.951	−	b_1=1.229	0.908, 1.391	=
	b_{max}=1.879	1.779, 1.987	+	b_2=1.018	0.934, 1.057	=
	b_{high}=0.818	0.397, 1.230	=			
S_7	b_{low}=0.269	-0.162, 0.589	−	b_1=0.941	0.891, 0.985	−
	b_{max}=1.863	1.775, 1.970	+	b_2=0.541	0.245, 0.775	−
	b_{high}=0.786	0.281, 1.266	=			

FIG. 3. – The morphological sexual differentiation of the abdomen of *P. marmoratus*; The S_i's are given for seven different sizes of *CW* (from 5 to 35 mm) for each sex.
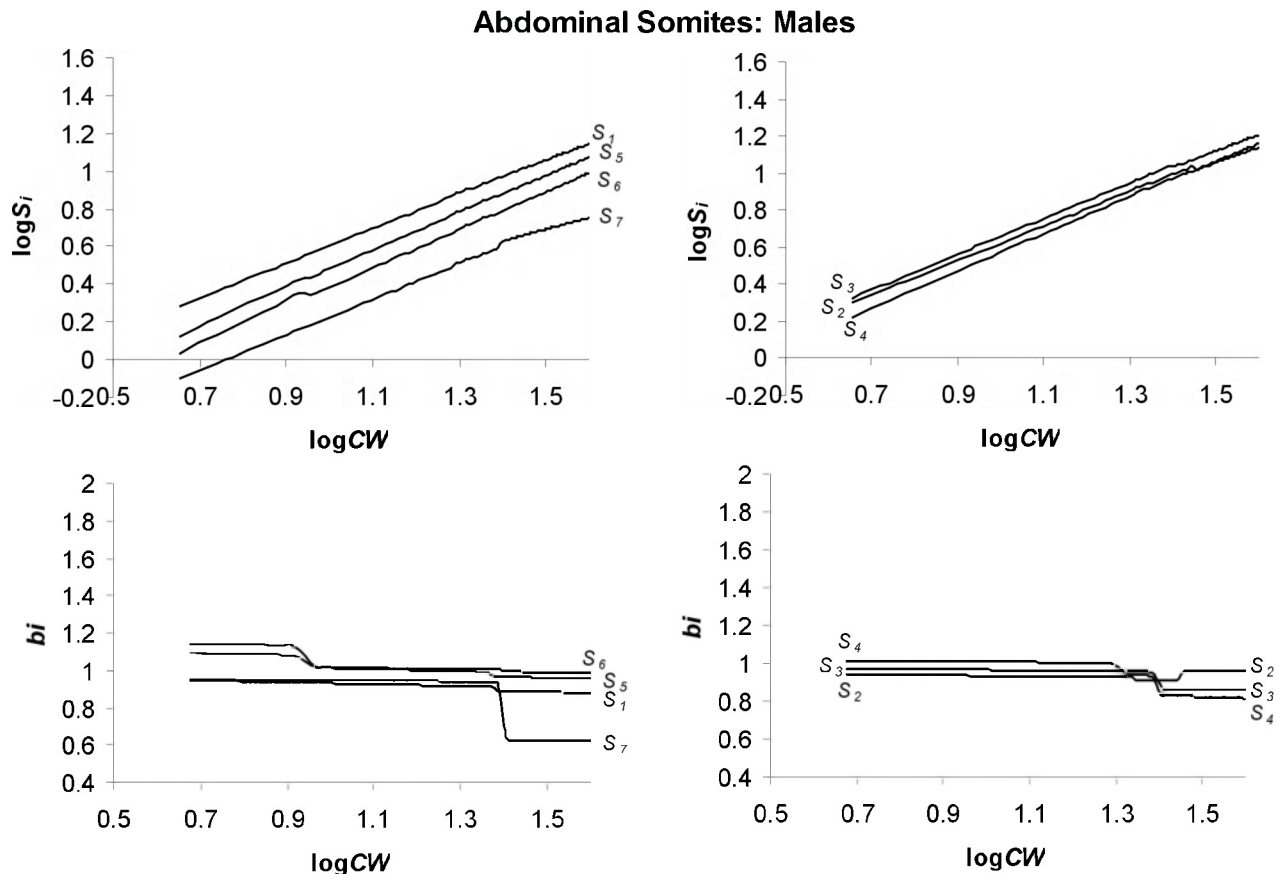
Abdominal Somites: Males

FIG. 4. – (Top) the relative growth patterns of the width of abdominal somites (S_i) of male *P. marmoratus* according to the corresponding 'average' models; the Akaike weights w_i were used for the weighted averages; somites S_2, S_3 and S_4 were separated for clarity. (Bottom) the allometric exponent b for the relative growth of each S_i of male *P. marmoratus*, calculated as the slope of the corresponding 'average' models between log S_i and log CW. The scales of the axes were kept the same with the corresponding plots in Figure 2 for comparison.

DISCUSSION

The information theory approach frees the analyst from the limiting concept that the proper approximating model is somehow 'given'. When a model is 'picked' in some way, independent of the data, and used to approximate the data as a basis for inference, both the uncertainty associated with model selection and the benefits of selecting a parsimonious model are ignored. This strategy incurs substantial costs in terms of reliable inferences because model selection uncertainty is assumed to be zero. When the data support evidence for more than one model, model-averaging the predicted response variable across models is advantageous for reaching a robust inference that is not dependant on a single model (Burnham and Anderson, 2002; Katsanevakis, 2006; Katsanevakis *et al.*, 2007a).

In allometric growth studies, it is a common practice to 'pick' the simple linear model (for log-transformed data) or sometimes to investigate for

breakpoints using a version of the broken-stick or the two-segment model; examples of model selection and multi-model inference are rare (e.g. Hall *et al.*, 2006; Katsanevakis *et al.*, 2007a). Had we not followed an information-theoretic approach in this study, a large part of information would have been lost. We found that the relative growth pattern in *P. marmoratus* varies substantially among somatic parts and between sexes; some parts grow according to the classic allometric equation in relation to a reference dimension, others exhibit a non-linear change of their generalized allometric exponent during ontogeny, while in others there is a discontinuity in f and/or b at a breakpoint. In many cases, the simple linear model had no support (e.g. in the chelar propod of males or in the abdominal somites S_3, S_4, S_5, S_6, and S_7 in females). Using the linear model when there is strong non-linearity would cause 'smoothing' of the true picture; e.g. the abdominal somites S_6 and S_7 initially grow isometrically, then positive allometrically and then again isometrically,

but with the linear model, an 'average' positive allometry would be concluded throughout ontogeny, which is only a rough approximation. Thus, a set of candidate models including the simple linear model, models that assume a continuous change in allometry, and models that assume discontinuity at breakpoints should be considered in allometric growth studies. An information-theoretic approach is recommended to account for model uncertainty, while null hypothesis testing should be avoided.

Three kinds of maturity can be distinguished in crustaceans: physiological maturity (mature gonads), functional maturity (ability to mate) and morphometric maturity (possession of morphometric characteristics that are distinct from those of immature individuals) (Hall *et al.*, 2006). The attainment of morphometric maturity is often identified by a breakpoint in the allometric data, i.e. f and/or its first derivative f' change markedly at a certain body size corresponding to the pubertal moult (i.e. the moult to maturity). Physiological, functional and morphometric maturity are not necessarily simultaneous. Functional and physiological maturity are prerequisites for a crab to reproduce, while mating may also depend on morphometric maturity (mostly in males), although this is not always necessary. In non-competitive environments, physiologically mature but morphometrically immature male *Chionoecetes opilio* mate successfully (Sainte-Marie and Lovrich, 1994).

In *P. marmoratus*, a sexual dimorphism in the chelae was evident in larger specimens, with males having significantly larger chelar propods than females, although these differences are not of the same magnitude as in many other crab species. Similar results were found for other grapsid species, e.g. *Hemigrapsus oregonensis* (Olmsted and Baumberger, 1923), *Plagusia dentipes* (Tsuchida and Watanabe, 1997), *Pachygrapsus transversus* (Flores and Negreiros-Fransozo, 1999). The breakpoint in the allometric growth of *PW* in males was marked (Fig. 1) at a *CW* ~16 mm, and thus the breakpoint of the *PW* may be used as an indicator of morphometric maturity in males, which represents the pubertal moult. It is worth mentioning that Flores and Negreiros-Fransozo (1999) found no inflection points in the chelar dimensions of the congeneric *P. transversus* males, using Somerton's techniques (Somerton, 1983), and consequently, chelar relative growth could not offer any clues for male morphological maturity in that species. It can be

suggested that in *P. marmoratus*, large chelae seem to be advantageous for larger males, since, in the Mediterranean, these individuals have been observed to have territories that do not overlap and which they share with small males and females (Cannici *et al.*, 1999).

The data of this study supported the existence of a breakpoint in the allometry of the third and fourth abdominal somites in females (S_3 and S_4) at a *CW* ~16.5 mm, according to the TS model. For S_3 and S_4 only the TS model, out of the set of candidate models, was substantially supported by the data (Table 3). The TS with the same breakpoint was the best model for S_5 as well, but there was also support for the C model. The generalized allometric exponent for the relative growth of S_3 and S_4 did not change at the breakpoint but there was a marked discontinuity in f. It should be noted that both in males and females the breakpoints were found to occur at similar sizes (*CW* of ~ 16.0 and 16.5 mm respectively). This breakpoint in females may also be an indicator of morphometric maturity, which represents the pubertal moult. However, Flores and Negreiros- Fransozo (1999) observed that young *P. transversus* females may, after breeding, moult from a morphotype of rounded abdomen to a morphotype with ogival abdomen. Therefore, for this species two separate regression lines differentiate young and resting individuals from potentially reproductive females and not immature from mature females. This phenomenon of abdomen degradation has also been reported for *P. marmoratus* (Vernet-Cornubert, 1958). So far, the existence and/or importance of the above mentioned abdomen degradation is not known for different *P. marmoratus* populations. Further studies are needed in order to check this hypothesis and also to combine morphological analysis with physiological and functional maturity data.

A gradual increase is observed (Fig. 2) in the generalized allometric exponents of the relative growth equations of the abdominal somites in females, with $b_{S1} < b_{S2} < b_{S3} < b_{S4} < b_{S5}$ during ontogeny (where b_{Si} is the generalized allometric exponent of the growth of somite S_i), while b_{S6} and b_{S7} are also $> b_{S5}$ in the middle size range. Furthermore, the allometric exponent of S_5 has an intermediate form between the approximately constant b type of abdomen somites $S_1 - S_5$ and the parabolic type of b through ontogeny of S_6 and S_7. Such a smooth change of b from each abdominal somite to the next is anticipated, as consecutive somites are bonded

together with joints, and thus the growth of each somite restricts the growth rate of the adjacent ones.

In conclusion, relative growth patterns, as demonstrated in the present study, can diverge in different ways from the classical linear model, the main outcome of which is the definition of the allometric exponent and the type of allometry. Marked discontinuities of the allometric exponent can not be detected using the linear model, and thus using it can give misleading results. Such changes in the growth trajectories of morphological characters during ontogeny are a potentially useful source of information as they may be caused by marked events in the life history of the species or fast ecological change; therefore, they should not be overlooked. The attainment of morphometric maturity in crabs is identified by finding breakpoints in the allometry of certain body parts at the puberty moult, usually chelae in male crabs and abdominal segments in females (Somerton 1981; Hall *et al.* 2006). The present study revealed the possibility of gradual changes in the generalized allometric exponent, which may follow a smooth, curvilinear trend (e.g. in female abdominal somites S_6 and S_7). This growth pattern could not be detected by the classic allometric model or models incorporating discontinuities. The information-theoretic approach proved to be quite effective in deciding on the most appropriate model from among a set of biologically meaningful candidate models and provided more information than the classic approach.

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