Non-linear curve adjustments widen biological interpretation of relative growth analyses of the clam *Tivela mactroides* (Bivalvia, Veneridae)

Alexander Turra Corresp., [1] , **Guilherme N Corte** [1, 2] , **Antonia Cecília Z Amaral** [2] , **Leonardo Q Yokoyama** [1, 3] , **Márcia R Denadai** [2]

[1] Departamento de Oceanografia Biológica / Instituto Oceanográfico, Universidade de São Paulo, São Paulo, SP, Brasil

[2] Departamento de Biologia Animal / Instituto de Biologia, Universidade Estadual de Campinas, Campinas, SP, Brazil

[3] Departamento de Ciências do Mar / Instituto Saúde e Sociedade, Universidade Federal de São Paulo, Santos, SP, Brazil

Corresponding Author: Alexander Turra
Email address: turra@usp.br

Evaluation of relative (allometric) growth provides useful information to understand the development of organisms, as well as to aid in the management of fishery-exploited species. Usually, relative growth analyses use classical models such as the linear equation or the power function (allometric equation). However, these methods do not consider discontinuities in growth and may mask important biological information. As an alternative to overcome poor results and misleading interpretations, recent studies have suggested the use of more complex models, such as non-linear regressions, in conjunction with a model selection approach. Here, we tested differences in the performance of diverse models (simple linear regression, power function, and polynomial models) to assess the relative growth of the trigonal clam *Tivela mactroides*, an important fishing resource along the South American coast. Regressions were employed to relate parameters of the shell (length (*L*), width (*W*), height (*H*) and weight (*SW*)) among each other and with soft parts of the organism (dry weight (DW) and ash-free dry weight (*ASDW*)). Then, model selection was performed using the information theory and multi-model inference approach. The power function was more suitable to describe the relationships involving shell parameters and soft parts weight parameters (i.e. *L* vs. *SW*, *DW*, and *AFDW*, and *SW* vs. *DW*). However, it failed in unveiling changes in the morphometric relationships between shell parameters (i.e. *L* vs. *W* and *H*; *W* vs. *H*) over time, which were better described by polynomial functions. Linear models, in turn, were not selected for any relationship. Overall, our results show that more complex models (in this study polynomial functions) can unveil changes in growth related to modifications in environmental features or physiology. Therefore, we suggest that classical and more complex models should be combined in future studies of allometric growth of molluscs.

1   Non-linear curve adjustments widen biological interpretation of relative growth analysis of the

2   clam *Tivela mactroides* (Bivalvia, Veneridae)

4   Alexander Turra[1]*, Guilherme N. Corte[1,2], A. Cecília Z. Amaral[2], Leonardo Q. Yokoyama[1,3],

5   Márcia R. Denadai[2]

6   [1]Departamento de Oceanografia Biológica, Instituto Oceanográfico, Universidade de São Paulo, São Paulo, SP,

7   Brazil

8   [2]Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas, CP: 6109, CEP:

9   13083-970, Campinas, SP, Brazil

10   [3]Departamento de Ciências do Mar, Instituto Saúde e Sociedade, Universidade Federal de São Paulo, Santos, SP,

11   Brazil

12   *Email: turra@usp.br

13   Running head: Relative growth in *Tivela mactroides*

16   **ABSTRACT**

17   Evaluation of relative (allometric) growth provides useful information to understand the

18   development of organisms, as well as to aid in the management of fishery-exploited species.

19   Usually, relative growth analyses use classical models such as the linear equation or the power

20   function (allometric equation). However, these methods do not consider discontinuities in growth

21   and may mask important biological information. As an alternative to overcome poor results and

22   misleading interpretations, recent studies have suggested the use of more complex models, such

23   as non-linear regressions, in conjunction with a model selection approach. Here, we tested

24   differences in the performance of diverse models (simple linear regression, power function, and

25   polynomial models) to assess the relative growth of the trigonal clam *Tivela mactroides*, an

26   important fishing resource along the South American coast. Regressions were employed to relate

27   parameters of the shell (length (L), width (W), height (H) and weight (SW)) among each other

28   and with soft parts of the organism (dry weight (DW) and ash-free dry weight ($ASDW$)). Then,

29   model selection was performed using the information theory and multi-model inference

30   approach. The power function was more suitable to describe the relationships involving shell

31   parameters and soft parts weight parameters (i.e. L vs. SW, DW, and $AFDW$, and SW vs. DW).

32   However, it failed in unveiling changes in the morphometric relationships between shell

33   parameters (i.e. L vs. W and H; W vs. H) over time, which were better described by polynomial

34   functions. Linear models, in turn, were not selected for any relationship. Overall, our results

35   show that more complex models (in this study polynomial functions) can unveil changes in

36   growth related to modifications in environmental features or physiology. Therefore, we suggest

37   that classical and more complex models should be combined in future studies of allometric

38   growth of molluscs.

39

40

1. INTRODUCTION

42

43   Relative or allometric growth analysis allows a detailed evaluation of the proportionality

44   among the body parameters of individuals, and is useful to estimate the production and biomass

45   of a population from a single parameter such as length or width (Rainer 1985; Urban & Campos

46   1994; Vasconcelos et al. 2018). It also provides a better comprehension of modifications in life

47   strategies of species unraveling important steps in their development (Katsanevakis et al. 2006;

48   Rabaoui et al. 2007). Changes in growth rates are usually linked to changes in environmental

49   features (e.g. food availability), physiology (e.g. gonad maturation and spawning periods), or

50   biotic interactions (e.g. increase of competition or predation), and must be considered when

51   evaluating morphological modifications during the ontogeny of the individuals (Rabaoui et al.

52   2007; Caill-Milly et al. 2014). The analysis of allometric growth is therefore an important tool to

53   support exploitation and management of harvested species (e.g. improving the size-selectivity of

54   fishing gears) (Vasconcelos et al. 2018), and essential for the proposal of effective measures to

55   protect living resources (e.g., monitoring of stocks and limiting harvesting practices according to

56   size-based analyses of communities) (Robinson et al. 2010).

57   Traditionally, allometric growth analyses are performed using the linear equation and

58   power function (allometric equation) (e.g., Gaspar et al. 2001; 2002; MacCord & Amaral 2005;

59   Vasconcelos et al. 2018). While the former ($y = a + bx$) corresponds to an equivalent increase in

60   size of a body part y (dependent variable) and another body part x (independent variable; the

61   reference dimension), the power function (allometric equation) determines the relationship

62   between two parts of the body through an exponential equation $y = ax^b$, where b is a measure of

63   the constant difference in the growth rates of the body parts x and y (Katsanevakis et al. 2006).

64   However, the allometric exponent b is not necessarily constant and may exhibit breakpoints (i.e.

65   points of discontinuity in slope) for instance resulting from marked changes in the environment

66   or physiology (Katsanevakis et al. 2006). As an alternative to overcome poor and misleading

67   interpretation of results, more complex models that consider that nonlinearity and breakpoints

68   may exist in the relationship of body parts (e.g., polynomial functions such as quadratic or cubic

69   models) have been recommended (Hendriks et al. 2012; Katsanevakis et al. 2006). Preferably,

70   researchers should consider a set of pre-established models and use model selection methods,

71   such as the information theory and multi-model inference approach (Burnham & Anderson

72   2002b), to ascertain which better fits the data (Katsanevakis et al. 2006; Rabaoui et al. 2007).

73   Regarding economic important marine species, allometric growth analyses are relatively

74   common for fishes, but much scarcer for benthic invertebrates (Vasconcelos et al. 2018). For

75   bivalves, the growth and shape of the shell are normally influenced by both environmental (e.g.,

76   temperature, depth, currents, wave exposure, and sediment) and biological factors (predation,

77   growth, and burrowing abilities) (see revision by Gaspar et al. 2002). Therefore, variation in

78   these conditions may produce varying growth patterns of the shell and soft parts of the animals.

79   An evaluation of the allometric growth of the bivalve *Pinna nobilis*, for example, registered

80   significant variation in growth among five populations related to various environmental factors

81   (Rabaoui et al. 2007). Marked changes in bivalve allometric growth are also expected to be

82   associated with the maturity of individuals (i.e., the onset of reproduction), given that more

83   energy is allocated to soft parts (mainly to the development and maturation of gonads) than to

84   shell deposition (Bayne & Worrall 1980; Rabaoui et al. 2007). To better understand the

85   development of key species and provide critical information for fisheries stock assessment and

86   management, it is therefore essential that allometric growth studies are performed on a wider

87   diversity of organisms and use a more comprehensive set of statistical models. Only through this

88   approach, growth variation among species, and between and within populations (i.e., spatial and

89   temporal comparisons) can be unveiled.

90   In this study, we tested whether different models are equally adequate to estimate the

91   allometric growth of the trigonal clam *Tivela mactroides* (Born, 1778), an important fishing

92   resource in the Southeastern American coast (Denadai et al. 2005; Turra et al. 2016).

93   Specifically, we compared the suitability of models traditionally used in allometric growth

94   analyses (i.e., linear and power function models) with more complex models (i.e., polynomial

95   functions), and investigated whether alternative models may lead to a better interpretation of the

96   data and provide additional biological information about this species.

97

98   **2. MATERIALS AND METHODS**

99   *2.1.   Model species*

100   The trigonal clam *T. mactroides* is a widespread species found along the South America

101   coast, from Colombia to southeastern Brazil (Turra et al. 2014). This bivalve occurs from the

102   shallow subtidal to the upper intertidal zone (Denadai et al. 2005), and is a main feeding resource

103   for several species of fishes, sea-stars, and crabs (Turra et al. 2015a). Moreover, *T. mactroides* is

104   economically important and intensively exploited by fishermen and recreational harvesters in

105   many parts of South America (Turra et al. 2016).

106

107   *2.2.   Study area*

108   This work was performed at Caraguatatuba Bay, which is located in southeastern Brazil

109   (Fig. 1) and comprises several sandy beaches along a 16 km beach arch (Denadai et al. 2013).

110   Wave energy is moderate at Caraguatatuba Bay because of the shadowing effect of São

111   Sebastião Island (Denadai et al 2005), but beach characteristics vary in a north–south orientation.

112   The southernmost part has a wide intertidal ultradissipative terrace (800 m) with well-sorted fine

113   sand. The northern part has a more heterogeneous slope with low tide dissipative terrace and fine

114   poorly sorted sand (Denadai et al. 2005, Turra et al. 2014). The mean seawater temperature in

115   Caraguatatuba Bay ranges from 19 °C in winter to 26° C in summer (Corte et al. 2015). Salinity

116   is usually above 30 and significant variations only occur near the rivers that flow into the bay

117   (Amaral and Nallin 2011).

118

119   *2.3.   Sampling and laboratory procedures*

120   Field work was done following procedures described in Turra et al. (2015). Briefly, clams

121   were sampled monthly from January 2003 until October 2004 in two areas with high abundance

122   of *T. mactroides* (Denadai et al. 2005) (Fig. 1). The first southern area extended from Porto Novo

123   to Palmeiras; and the northern area from Indaiá to Centro beach (Fig. 1). Both areas had 2000 m

124   length and sampling was performed in the intertidal and subtidal zone of each area following

125   different procedures.

126   In the intertidal zone of each area, sampling was performed at eight randomly sorted

127   transects from 200 possibilities (i.e. the linear 2000 m length divided into 10-m intervals). Six or

128   seven samples (squares of 0.5 x 0.5 m) were excavated to a depth of 10 cm at regular intervals in

129   each transect. The number of samples collected at each transect depended on their length. A total

130   of 120 samples (30 m^2) were collected per month in the intertidal area.

131   In the subtidal zone, sampling was performed using a fishing boat at five different depths,

132   i.e., 400, 800, 1200, 1600 and 2000 m, from mean low water (MLW, 0.0 m). At each depth, one

133   50-m dredging was performed at three randomly sorted transects perpendicular to the coast.

134   Thus, 30 samples were dredged per month (2 areas x 5 depths x 3 transects). Samples were taken

135   using a rectangular dredge (70 x 25 cm) with 3.0 mm internal mesh size.

136   The sediment sampled at both intertidal and subtidal zones was washed with seawater

137   over a 3.0-mm-mesh sieve, using buckets. Clams from both zones were collected, counted and

138   measured for shell length to the nearest 0.01 mm with a digital caliper to examine the population

139   dynamics of *T. mactroides* at the study area as reported in Turra et al. (2014). Almost all the

140   individuals were returned alive to the sea after the measurements; however, approximately five

141   individuals from each of the 37 size classes identified in this population (from 3.0 to 39.0 mm; 1

142   mm intervals) where taken for morphometric analyses, totaling 187 individuals. These specimens

143   were maintained in clean, aerated seawater for 24 h to eliminate the feces. After this period, the

144   soft parts were separated from the shells and dried at 60°C to achieve a constant weight and

145   afterwards record the shell weight and the soft parts dry weight. Dry weight was used to avoid

146   discrepancy in the amount of water retained or fluctuation in soft-parts weight due to changes in

147   the physiological processes (Vasconcelos et al. 2008; 2018). Ash weight was obtained after

148   incinerating the dried soft parts in a muffle furnace at 550°C for 5 h. The ash-free dry weight

149   (organic content) was calculated by subtracting the ash weight from the dry weight. Thus, all

150   individuals had the shell length (*L*), height (*H*), and width (*W*) measured (Fig. 2), and the shell

151   weight (*SW*), soft parts dry weight (*DW*), and ash-free dry weight (*AFDW*) recorded.

152

153   *2.4.   Data analysis*

154   The allometric growth of *T. mactroides* was analyzed using models that relate the shell

155   length (independent variable) to the shell height, shell width, shell weight, soft parts dry weight,

156   and ash-free dry weight (*L* vs *H, W, SW, DW* and *AFDW*). The relationships between shell width

157   (independent variable) and shell height (W vs H), and between the soft parts dry weight

158   (independent variable) and the shell weight and ash-free dry weight were also evaluated (DW vs

159   SW and $AFDW$).

160   We used five models for the comparisons (Table 1): (1) simple linear regression ($y = bx$),

161   (2) second-order polynomial function ($y = bx+cx^2$), (3) third-order polynomial function ($y =$

162    $bx+cx^2+dx^3$), (4) fourth-order polynomial function ($y = bx+cx^2+dx^3+ex^4$), and (5) power function

163   (allometric equation, $y = ax^b$). The candidate models for allometric growth were fitted to raw

164   data and the fitted equations were compared based on the Kullback–Leibler (K-L) information

165   theory and multi-model inference (MMI) (Burnham & Anderson 2002). The Kullback–Leibler

166   (K-L) information theory can be interpreted as the distance from the approximating model to

167   full reality, and minimization of K-L distance is essential for model selection (Katsanevakis et

168   al. 2006). Multi-model inference, in turn, is a procedure where parameters are estimated from

169   several different models rather than from one *a priori* selected model (Burnham & Anderson

170   2002).

171   We used the small-sample bias-corrected form of the Akaike Information Criteria, AIC_c

172   (Hurvich & Tsai 1989) of the AIC (Burnham & Anderson 2002a) for the model selection,

173   according to the equation:

$$AIC_c = AIC + \frac{2k(k+1)}{n-k-1}$$

174

175   where AIC is given by:

$$AIC = n\left(\log\left(2\pi\frac{RSS}{n}\right)+1\right)+2k$$

176

177   where RSS is the residual sum of squares of the regression, n is the number of observations, and k

178   is the number of estimated parameters of the regression plus 1. The model with the smallest AIC_c

179   value ($AIC_{c,min}$) was selected as the 'best' among the tested models. The AIC_c differences

180   between adjusted functions, $\Delta_i = AIC_{c,i} - AIC_{c,min}$, were computed over all pairs of candidate

181   models. According to Burnham & Anderson (2002), models with $\Delta_i < 2$ have substantial support,

182   models with $4 < \Delta_i < 7$ have considerably less support, and models with $\Delta_i > 10$ essentially have

183   no support and can be ignored. In the present work, we considered that all values of $\Delta_i < 2$ have

184   substantial support for the model, and in the case of multiple models having $\Delta_i < 2$ we opted for

185   the simplest model (principle of parsimony), i.e. the model with fewer estimated parameters.

186

187   *2.5.   Field Study Permissions*

188   All activities complied with the license issued by the appropriate federal environmental

189   agency (Ministério do Meio Ambiente (MMA)—Instituto Chico Mendes de Conservação da

190   Biodiversidade (ICMBio) No. 19887-1; acronyms for, in English: Ministry of the

191   Environment—Chico Mendes Biodiversity Conservation Institute)

192

193   **3. RESULTS**

194   High determination coeficients ($r^2 > 0.842$) were obtained in all models fitted to the

195   relationships between the morphometric parameters of *T. mactroides* (Table 2). For most

196   relationships, more than one model was suitable since they had values of *Δi* ≤ 2 (Table 2). The

197   third-order polynomial suitably described all morphometric relationships excluding the *L/W*

198   relationship. Nevertheless, considering the parsimony principle, the traditional power function

199   was overall the most adequate model and better described five morphometric relationships

200   (*L/SW, L/DW, L/AFDW, SW/DW,* and *DW/AFDW*). The third-order polynomial model was the

201 best descriptor for two relationships (*L/H* and *W/H*), whereas the fourth-order polynomial was

202 selected as the best descriptor of the relationships *L/W*.

203 The relative growth between shell length and height was approximately isometric up to

204 20 mm L; above this size, shell length increased faster compared to shell height (Fig. 3). The

205 relative growth between shell length and width was always positive allometric (i.e., length

206 increased faster), but this relationship was stronger after reaching maturity (approximately 20

207 mm in L, Pietro 1980). The relationships between shell length and soft parts showed that the

208 increase in soft parts (*DW* and *AFDW*) was slow in young individuals (below 20 mm L);

209 followed by a rapid increase in soft parts weight was observed after reaching maturity. A similar

210 relationship was observed between shell length and shell weight. The allometric growth between

211 width and height oscillated during growth, mainly between 15 and 25 mm in shell width. The

212 shell weight increased continuously (practically linearly) with soft parts dry weight. Similar

213 relationship was established between ash-free dry weight and soft parts dry weight.

214

215 **4. DISCUSSION**

216 The usual approach when studying allometric growth in marine species is to *a priori*

217 adopt the classical linear or allometric model (power function), which may have implications in

218 the accuracy and precision of the estimated parameters (Katsanevakis et al. 2006; Rabaoui et al.

219 2007). When only these classical models are used, less informative conclusions may be reached

220 by smoothing the real growth pattern (Protopapas 2007; Rabaoui et al. 2007). In this study, we

221 used the information theory and multi-model inference approach (Burnham & Anderson 2002a)

222 to compare the suitability of classical (i.e., linear and power function models) and more complex

223 models (i.e., polynomial functions) to describe the allometric growth of *T. mactroides*. Our

224   results showed that classical models may adequately describe most morphometric relationships

225   of this species. However, their use alone may hide subtle changes in the allometric growth and

226   prevent a full understanding of growth patterns.

227   The power function (allometric equation) was the best model describing five of the eight

228   morphometric relationships analyzed (mainly relationships involving the weight parameters such

229   as shell weight, dry weight and ash-free dry weight). This function is commonly used in

230   morphometric analyses of bivalves (e.g., Clasing et al. 1994; Urban & Campos 1994; Gaspar et

231   al. 2001; Lomovasky et al. 2005), but is normally considered the weakest adjustment for many

232   morphometric relationships in some marine invertebrates (Katsanevakis 2007; Rabaoui et al.

233   2007; Garraffoni et al. 2010). A main drawback in the use of the power function is that it does

234   not consider breakpoints (i.e., marked changes in the allometric growth) and may hide major

235   indications of morphological variability among individuals of different sizes (Rabaoui et al.

236   2007). Our results show that the power function best characterized the allometric growth

237   between shell parameters and soft tissues, indicating that shell and somatic parts of *T. mactroides*

238   grow with a constant allometric exponent, whereas polynomial models better described

239   relationships between shell parameters. Likewise, Trussel (2000) found that changes in shell

240   morphology in *Littorina* snails were not related to soft tissue variations, and McKinney et al.

241   (2004) reported that allometric regression models best described changes in soft tissue content

242   with shell length for 10 different species, including the ribbed mussel *Geukensia demisa*, the blue

243   mussel *Mytilus edulis*, and the quahog *Mercenaria mercenaria*.

244   Several factors may influence the growth of soft tissue relative to shell parameters. Food

245   availability, for instance, can strongly affect growth, storage and utilization of body reserves;

246   thereby altering allometric relationships (McKinney et al. 2004). Similarly, temperature and

247   salinity may alter metabolic rates and determine net growth efficiency in bivalve species

248   (Resgalla Jr. et al. 2007, Xiao et al. 2014). The constant allometric growth of shell measurements

249   and weighings of *T. mactroides* at Caraguatatuba Bay is likely related to constant food supply to

250   the clams due to the presence of three rivers (i.e., Santo Antônio, Lagoa and Juqueriquerê – Fig.

251   1) that flow directly into the bay and provide a large amount of suspended organic material

252   (Corte 2015; Turra et al. 2015b). The absence of marked fluctuation in seawater temperature and

253   salinity at the study area (Amaral and Nallin 2011, Corte et al. 2015) probably also contributes to

254   the constant growth of soft tissues.

255   Although the power function was more precise to describe the morphometric relationship

256   between shell parameters and somatic parts, it was not enough to unveil changes in the

257   morphometric relationships between shell parameters. By adjusting polynomial functions, we

258   were able to detect differences in morphometric relationships of shell parameters over the

259   lifespan of *T. mactroides*. Changes in bivalves morphometric relationships are usually related to

260   the maintenance of an area/volume ratio that is physiologically suitable for the prevailing

261   environmental conditions (Gaspar et al. 2002; Rhoads & Pannella 1970). For instance, the shell

262   of the pill clam *Pisidium subtruncatum* (Malm 1855) change from a rounded and thin-shelled

263   form to an angular and thick-shelled form depending on the proportion of sand in the sediment

264   (Funk & Reckendorfer 2008), which enables the individuals to burrow easier in coarse

265   sediments. Similar modifications have also been observed in species that change their habits

266   from active burrowing juveniles to sedentary and deeper burrowing adults (Statzner & Holm

267   1982), such as the razor clam *Ensis macha* that shows an abrupt change in shell shape during

268   growth, from squarer to more elongated (Barón et al. 2004). This elongated form enables razor

269   clams to avoid predators by burrowing deeper with low energy requirements (Trueman 1967;

270   Urban 1994).

271   Modifications in the allometric relationships between shell parameters of *T. mactroides*

272   seem related to habitat changes and maturity of individuals. We observed that shell width and

273   height had a reduction in their proportional growth in relation to shell length when individuals

274   reached a length between 15 and 25 mm. This change is appropriate for the subtidal-intertidal

275   migration undertaken by this species (Denadai et al. 2005). The smallest individuals are usually

276   found in mud sediments in the subtidal level, where burrowing with a more-inflated shell is

277   easier. As individuals reach maturity, they passively migrate to firm intertidal sandy substrata

278   and their shell becomes longer and more compressed, potentially facilitating burrowing in this

279   type of sediment. Maturity is also a frequent cause of a distinct change in morphology, given that

280   more energy is allocated to the development of gonads than to shell growth (Bayne & Worrall

281   1980; Katsanevakis et al. 2006).

282   Besides providing further information for understanding the life history of species, the

283   knowledge of allometric growth has implications for economic exploitation of fishing resources.

284   In bivalves, the morphometric relationships between shell size and soft parts can help defining an

285   optimum size for exploitation. For *T. mactroides*, the analyses of allometric growth indicate that

286   more energy is invested in shell growth during early phases of the life cycle, thereby increasing

287   the protection and survival of juveniles. Only after reaching maturity, a faster increase in somatic

288   tissues was recorded. Thus, harvesting of *T. mactroides* should preferably target individuals with

289   shell length between 25-30 mm. This would ensure that individuals are already able to

290   reproduce, thus providing a better income to local harvesters since a higher meat yield (ratio

291   meat weight/shell weight) would be achieved.

292

5. CONCLUSIONS

294   Our results show that the classical power function is useful to evaluate the relative growth

295 of *Tivela mactroides*. Nevertheless, the use of this model alone may hide subtle changes in

296 morphology related to environmental or physiological processes such as habitat changes and

297 maturity of individuals. Only by applying more complex models, in the present case polynomial

298 models, we perceived subtle modifications in the allometric growth of *T. mactroides*. In this

299 regard, we reinforce the recommendation that allometric growth analyses should consider a set of

300 pre-established models including traditional and more complex models. Certainly, this would

301 improve allometric analyses and provide stronger and more informative conclusions.

302

6. ACKNOWLEDGEMENTS

304   We are grateful to all the staff who worked on the Biota / Fapesp Bentos-Marinho project

305 (Proc 1998 / 07090-3).

306

7. REFERENCES

308
309 Amaral ACZ, and Nallin SAH. 2011. Biodiversidade e ecossistemas bentônicos marinhos do
310   Litoral Norte de São Paulo, Sudeste do Brasil. Campinas, SP: UNICAMP/IB, 573 p.
311 Arrieche D, and Prieto A. 2006. Population parameters of the trigonal tivela *Tivela mactroides*
312   (Bivalvia: Veneridae) from Caicara Beach, Anzoátegui, Venezuela. *Ciencias Marinas*
313   32:285-296.
314 Barón PJ, Real LE, Ciocco NF, and Ré ME. 2004. Morphometry, growth and reproduction of an
315   Atlantic population of the razor clam *Ensis macha* (Molina, 1782). *2004* 68:7.
316   10.3989/scimar.2004.68n2211
317 Bayne BL, and Worrall CM. 1980. Growth and Production of Mussels *Mytilus edulis* from Two
318   Populations. *Marine Ecology Progress Series* 3:317-328.
319 Burnham K, and Anderson DR. 2002a. Information and likelihood theory: a basis for model
320   selection and inference. *Model selection and multimodel inference: a practical*
321   *information-theoretic approach* 2:49-97.

322 Burnham KP, and Anderson DR. 2002b. *Model selection and multimodel inference : a practical*
323   *information-theoretic approach*. New York: Springer
324 Caill-Milly N, Bru N, Barranger M, Gallon L, and D'Amico F. 2014. Morphological Trends of
325   Four Manila Clam Populations (*Venerupis philippinarum*) on the French Atlantic Coast:
326   Identified Spatial Patterns and Their Relationship to Environmental Variability. *Journal*
327   *of Shellfish Research* 33:355-372. 10.2983/035.033.0205
328 Clasing E, Brey T, Stead R, Navarro J, and Asencio G. 1994. Population dynamics of *Venus*
329   *antiqua* (Bivalvia: Veneracea) in the Bahía de Yaldad, Isla de Chiloé, Southern Chile.
330   *Journal of Experimental Marine Biology and Ecology* 177:171-186.
331   https://doi.org/10.1016/0022-0981(94)90235-6
332 Corte GN. 2015. Reproductive cycle and parasitism in the clam Anomalocardia brasiliana
333   (Bivalvia: Veneridae). *Invertebrate Reproduction & Development* 59:66-80.
334   10.1080/07924259.2015.1007215
335 Denadai MR, Amaral ACZ, and Turra A. 2005. Along- and across-shore components of the
336   spatial distribution of the clam Tivela mactroides (Born, 1778) (Bivalvia, Veneridae).
337   *Journal of Natural History* 39:3275-3295. 10.1080/00222930500126156
338 Denadai MR, Santos FB, Bessa E, Fernandez WS, Lorca L, and Turra A. 2013. Population
339   biology and diet of *Pomadasys corvinaeforrnis* (Perciformes: Pomadasyidae) in
340   Caraguatatuba Bay, Southeastern Brazil. *Revista de Biologia Tropical* 61:1947-1954.
341 Funk A, and Reckendorfer W. 2008. Environmental Heterogeneity and Morphological
342   Variability in *Pisidium subtruncatum* (Sphaeriidae, Bivalvia). *International Review of*
343   *Hydrobiology* 93:188-199. 10.1002/iroh.200710969
344 Garraffoni ARS, Yokoyama LQ, and Amaral ACZ. 2010. Allometry and population structure of
345   *Nicolea uspiana* (Polychaeta: Terebellidae). *Journal of the Marine Biological Association*
346   *of the United Kingdom* 90:877-883. 10.1017/s0025315409991354
347 Gaspar MB, Santos MN, and Vasconcelos P. 2001. Weight–length relationships of 25 bivalve
348   species (Mollusca: Bivalvia) from the Algarve coast (southern Portugal). *Journal of the*
349   *Marine Biological Association of the United Kingdom* 81:805-807.
350   10.1017/S0025315401004623
351 Gaspar MB, Santos MN, Vasconcelos P, and Monteiro CC. 2002. Shell morphometric
352   relationships of the most common bivalve species (Mollusca: Bivalvia) of the Algarve
353   coast (southern Portugal). *Hydrobiologia* 477:73-80. 10.1023/a:1021009031717
354 Hendriks IE, Basso L, Deudero S, Cabanellas-Reboredo M, and Álvarez E. 2012. Relative
355   Growth Rates of the Noble Pen Shell *Pinna nobilis* Throughout Ontogeny Around the
356   Balearic Islands (Western Mediterranean, Spain). *Journal of Shellfish Research* 31:749-
357   756. 10.2983/035.031.0319
358 Hurvich CM, and Tsai C-L. 1989. Regression and time series model selection in small samples.
359   *Biometrika* 76:297-307. 10.1093/biomet/76.2.297
360 Katsanevakis S. 2007. Growth and mortality rates of the fan mussel *Pinna nobilis* in Lake
361   Vouliagmeni (Korinthiakos Gulf, Greece): a generalized additive modelling approach.
362   *Marine Biology* 152:1319-1331. 10.1007/s00227-007-0781-2
363 Katsanevakis S, Thessalou-Legaki M, Karlou-Riga C, Lefkaditou E, Dimitriou E, and
364   Verriopoulos G. 2006. Information-theory approach to allometric growth of marine
365   organisms. *Marine Biology* 151:949-959. 10.1007/s00227-006-0529-4

366 Leontarakis PK, and Richardson CA. 2005. Growth of the smooth clam, Callista chione
367   (Linnaeus, 1758) (Bivalvia: Veneridae) from the Thracian Sea, northeastern
368   Mediterranean. *Journal of Molluscan Studies* 71:189-198.
369 Lomovasky BJ, Brey T, and Morriconi E. 2005. Population dynamics of the venerid bivalve
370   *Tawera gayi* (Hupé, 1854) in the Ushuaia Bay, Beagle Channel. *Journal of Applied*
371   *Ichthyology* 21:64-69. 10.1111/j.1439-0426.2004.00599.x
372 MacCord FS, and Amaral ACZ. 2005. Morphometric analyses of two species of Scolelepis
373   (Polychaeta: Spionidae). *Journal of the Marine Biological Association of the United*
374   *Kingdom* 85:829-834. 10.1017/S002531540501177X
375 McKinney RA, Glatt SM, and Williams SR. 2004 Allometric length-weight relationships for
376   benthic prey of aquatic wildlife in coastal marine habitats. *Wildlife Biology* 10:241-249.
377 Narchi W. 1972. Comparative study of the functional morphology of *Anomalocardia brasiliana*
378   (Gmelin, 1791) and *Tivela mactroides* (Born, 1778) (Bivalvia, Veneridae). *Bulletin of*
379   *Marine Science* 22:643-670.
380 Protopapas NK, S.; Thessalou-Legaki, M.; Verriopoulos, G. 2007. Relative growth of the semi-
381   terrestrial crab *Pachygrapsus marmoratus*: An information-theory approach. *Scientia*
382   *Marina* 71:383-394.
383 Rabaoui L, Tlig Zouari S, Katsanevakis S, and Ben Hassine OK. 2007. Comparison of absolute
384   and relative growth patterns among five Pinna nobilis populations along the Tunisian
385   coastline: an information theory approach. *Marine Biology* 152:537-548.
386   10.1007/s00227-007-0707-z
387 Rainer SF. 1985. Population dynamics and production of the bivalve *Abra alba* and implications
388   for fisheries production. *Marine Biology* 85:253-262. 10.1007/bf00393245
389 Resgalla Jr., Charrid, Brasil, Elisângela de Souza, & Salomão, Luis Carlos. (2007). The effect of
390   temperature and salinity on the physiological rates of the mussel *Perna perna* (Linnaeus
391   1758). *Brazilian Archives of Biology and Technology*, *50*(3), 543-556.
392 Rhoads DC, and Pannella G. 1970.Tthe use of molluscan shell growth patterns in ecology and
393   paleoecology. *Lethaia* 3:143-161. 10.1111/j.1502-3931.1970.tb01854.x
394 Robinson LA, Greenstreet SPR, Reiss H, Callaway R, Craeymeersch J, de Boois I, Degraer S,
395   Ehrich S, Fraser HM, Goffin A, Kröncke I, Jorgenson LL, Robertson MR, and Lancaster
396   J. 2010. Length–weight relationships of 216 North Sea benthic invertebrates and fish.
397   *Journal of the Marine Biological Association of the United Kingdom* 90:95-104.
398   10.1017/S0025315409991408
399 Statzner B, and Holm TF. 1982. Morphological adaptations of benthic invertebrates to stream
400   flow — An old question studied by means of a new technique (Laser Doppler
401   Anemometry). *Oecologia* 53:290-292. 10.1007/bf00389001
402 Trueman ER. 1967. The dynamics of burrowing in *Ensis* (Bivalvia). *Proceedings of the Royal*
403   *Society of London Series B Biological Sciences* 166:459-476.
404 Turra A, Fernandez WS, Bessa E, Santos FB, and Denadai MR. 2015a. Multi-species generalist
405   predation on the stochastic harvested clam *Tivela mactroides* (Mollusca, Bivalvia).
406   *Estuarine, Coastal and Shelf Science* 166:115-123.
407   https://doi.org/10.1016/j.ecss.2014.12.029
408 Turra A, Petracco M, Amaral ACZ, and Denadai MR. 2014. Temporal variation in life-history
409   traits of the clam *Tivela mactroides* (Bivalvia: Veneridae): Density-dependent processes
410   in sandy beaches. *Estuarine Coastal and Shelf Science* 150:157-164.
411   10.1016/j.ecss.2013.06.004

412   Turra A, Petracco M, Amaral ACZ, and Denadai MR. 2015b. Population biology and secondary
413   production of the harvested clam *Tivela mactroides* (Born, 1778) (Bivalvia, Veneridae) in
414   Southeastern Brazil. *Marine Ecology-an Evolutionary Perspective* 36:221-234.
415   10.1111/maec.12137
416   Turra A, Xavier LY, Pombo M, de Carvalho Paschoal C, and Denadai MR. 2016. Assessment of
417   recreational harvesting of the trigonal clam *Tivela mactroides*: Socioeconomic aspects
418   and environmental perception. *Fisheries Research* 174:58-67.
419   https://doi.org/10.1016/j.fishres.2015.08.026
420   Trussell, G. C. 2000. Predator-induced plasticity and morphological trade-offs in
421   latitudinallyseparated populations of Littorina obtusata. *Evolutionary Ecology Research*
422   2: 803-822.
423   Urban HJ. 1994. Adaptation of six infaunal bivalve species of Chile: coexistence resulting from
424   differences in morphology, burrowing depth and substrate preference. *Archive of fishery*
425   *and marine research* 42:183-193.
426   Urban HJ, and Campos B. 1994. Population-dynamics of the bivalves *Gari solida, Semele solida*
427   *and Protothaca thaca* from a small bay in chile at 36-degrees-S. *Marine Ecology*
428   *Progress Series* 115:93-102.
429   Xiao B, Li E, Du Z, Jiang R, Chen L, Yu N. Effects of temperature and salinity on metabolic rate
430   of the Asiatic clam *Corbicula fluminea* (Müller, 1774). *SpringerPlus*. 2014;3:455.
431   doi:10.1186/2193-1801-3-455.
432   Vasconcelos P, Lopes B, Castro M, and Gaspar MB. 2008. Comparison of indices for the
433   assessment of reproductive activity in *Hexaplex trunculus* (Gastropoda: Muricidae).
434   *Marine Biology Research* 4:392-399. 10.1080/17451000802020436
435   Vasconcelos P, Moura P, Pereira F, Pereira AM, and Gaspar MB. 2018. Morphometric
436   relationships and relative growth of 20 uncommon bivalve species from the Algarve coast
437   (southern Portugal). *Journal of the Marine Biological Association of the United*
438   *Kingdom*:98(3):463-474. https://doi.org/10.1017/S002531541600165X

Models and their respective equations and number of parameters estimated plus one (*k*). All models consider origin = 0.

1   Table 1. Models and their respective equations and number of parameters estimated plus one (k).

2   All models consider origin = 0.

Model	Equation	k
Simple regression (Ln)	$y = bx$	2
Second-order polynomial (Qd)	$y = bx+cx^2$	3
Third-order polynomial (Cb)	$y = bx+cx^2+dx^3$	4
Fourth-order polynomial (Qt)	$y = bx+cx^2+dx^3+ex^4$	5
Power-function (Pf)	$y = ax^b$	3

Tivela mactroides.

Summary and comparison among the determination coefficient (r²), standard error of the estimate (SE), residual sum of squares (RSS), Akaike information criteria corrected for small samples (*AIC_c*), and difference between *AICc* (*Δi*) of all models.

L, shell length; W, shell width; H, shell height; SW, shell weight; DW, soft parts dry weight; AFDW, ash-free dry weight. Ln, linear model; Qd, second-order polynomial model; Cub, third-order polynomial model; Qt, fourth-order polynomial model; Pf, power function. Most suitable model according to AICc and parsimony principle are highlighted in bold. When $\Delta_i < 2$, the model with the smallest number of parameters was selected.
1 Table 2. *Tivela mactroides*. Summary and comparison among the determination coefficient (r²), standard
2 error of the estimate (SE), residual sum of squares (RSS), Akaike information criteria corrected for small
3 samples (*AICc*), and difference between *AICc* (*Δi*) of all models. L, shell length; W, shell width; H, shell
4 height; SW, shell weight; DW, soft parts dry weight; AFDW, ash-free dry weight. Ln, linear model; Qd,
5 second-order polynomial model; Cub, third-order polynomial model; Qt, fourth-order polynomial model;
6 Pf, power function. Most suitable models according to AICc and parsimony principle are highlighted in
7 bold. When Δ$_i$ < 2, the model with the smallest number of parameters was selected.

Relation	Model	r²	SE	RSS	AICc	Δi
L/W	Ln	0.997	0.857	136.871	476.392	94.070
	Qd	0.998	0.753	104.985	428.861	46.539
	Cub	0.998	0.689	87.519	396.923	14.602
	Qt	**0.998**	**0.661**	**80.037**	**382.322**	**0.000**
	Pf	0.985	0.799	118.223	451.068	68.747
L/H	Ln	0.999	0.730	99.106	416.019	107.264
	Qd	0.999	0.574	61.111	327.669	18.914
	Cub	**0.999**	**0.546**	**55.005**	**310.073**	**1.318**
	Qt	0.999	0.543	54.005	308.755	0.000
	Pf	0.996	0.617	70.424	354.194	45.439
L/SW	Ln	0.861	1.730	556.922	738.824	464.003
	Qd	0.987	0.530	52.115	297.891	23.070
	Cub	0.989	0.499	45.964	276.496	1.675
	Qt	0.989	0.501	45.942	278.516	3.695
	Pf	**0.976**	**0.499**	**46.066**	**274.821**	**0.000**
L/DW	Ln	0.844	0.094	1.637	-342.574	250.325
	Qd	0.959	0.048	0.429	-586.848	6.052
	Cub	0.960	0.047	0.415	-591.088	1.811
	Qt	0.961	0.047	0.411	-590.689	2.210
	Pf	**0.918**	**0.047**	**0.415**	**-592.899**	**0.000**
L/AFDW	Ln	0.842	0.086	1.351	-374.856	251.689
	Qd	0.959	0.044	0.351	-619.540	7.004
	Cub	0.961	0.043	0.337	-624.709	1.836
	Qt	0.961	0.043	0.334	-624.112	2.433
	Pf	**0.918**	**0.043**	**0.338**	**-626.544**	**0.000**
W/H	Ln	0.999	0.835	62.982	331.243	20.198
	Qd	0.999	0.837	61.612	329.198	18.153
	Cub	**0.999**	**0.830**	**55.291**	**311.045**	**0.000**
	Qt	0.999	0.7651	107.127	436.837	125.792
	Pf	0.992	0.8365	129.446	468.027	156.982
DW/SW	Ln	0.962	0.047	0.399	-597.694	0.266
	Qd	0.962	0.047	0.395	-597.676	0.285
	Cub	0.963	0.046	0.393	-596.381	1.580
	Qt	0.963	0.047	0.391	-595.099	2.861
	Pf	**0.928**	**0.047**	**0.394**	**-597.961**	**0.000**
DW/AFDW	Ln	0.999	0.005	0.004	-1432.479	5.734
	Qd	0.999	0.005	0.004	-1434.282	3.932
	Cub	0.999	0.005	0.004	-1438.214	0.000
	Qt	0.999	0.005	0.004	-1436.168	2.045
	Pf	**0.999**	**0.005**	**0.004**	**-1437.069**	**1.145**

Figure 1

Map of the Caraguatatuba Bay, southeastern Brazil. Sampling areas are highlighted in grey.
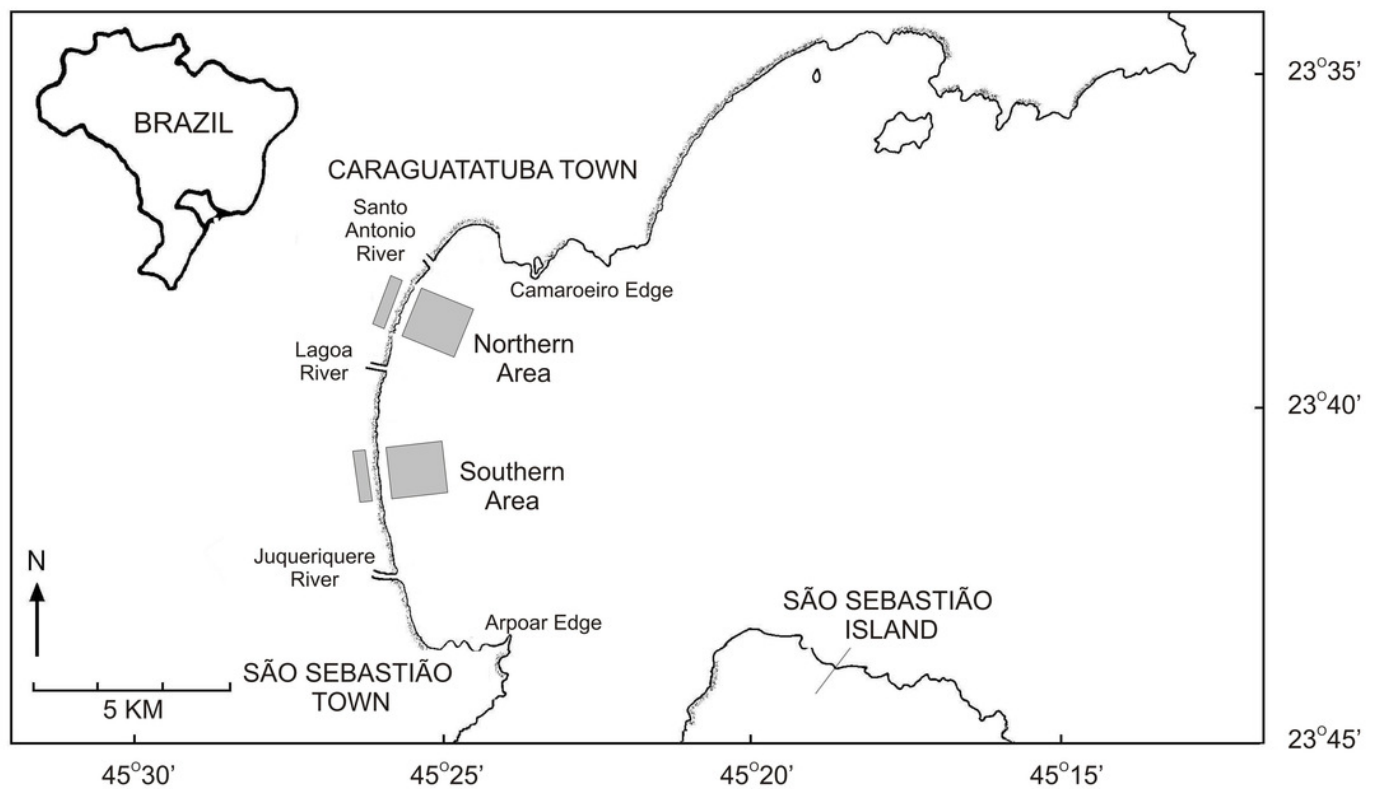
Figure 2

Tivela mactroides. Scheme indicating the measurements taken from the shells (shell length, L; height, H; and width, W). (A) frontal view. (B) lateral view.

Tivela mactroides
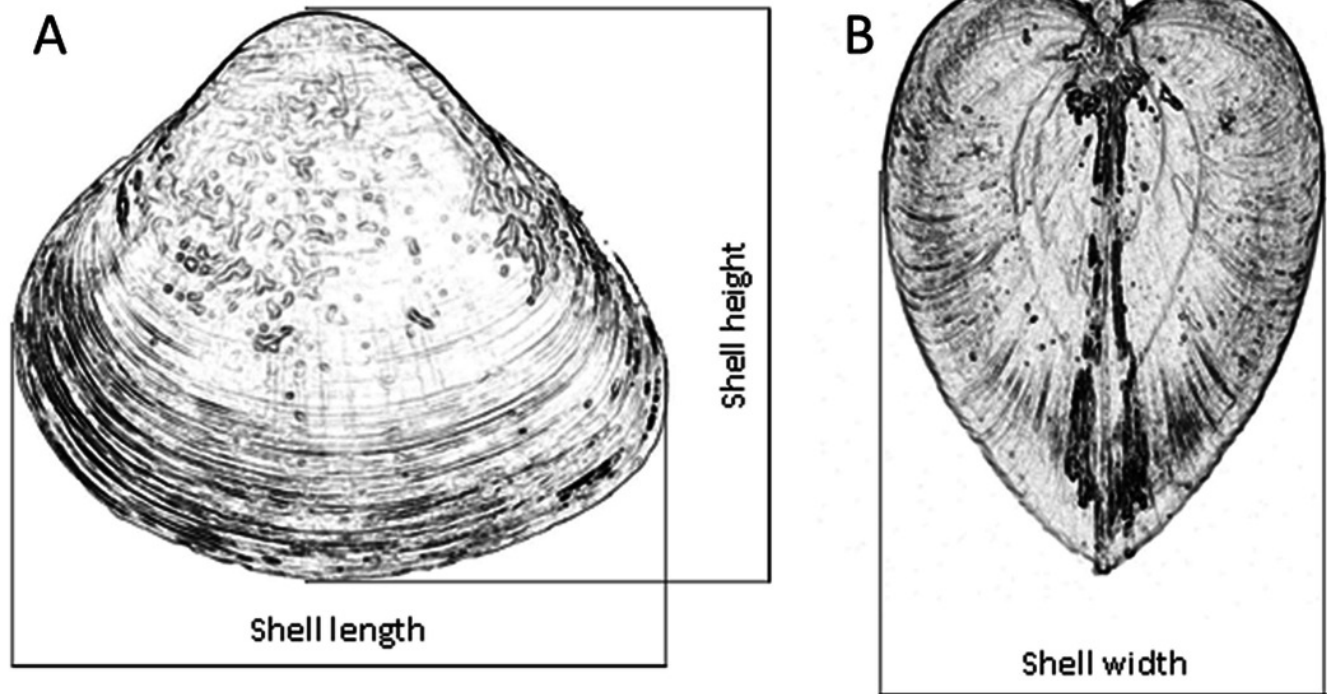
Figure 3

Tivela mactroides. Graphical representations of the allometric relationships.

Continuous lines represent the most suitable model describing the morphometric relationship. N: number of individuals analyzed. SE: standard error. AFDW: ash-free dry weight. (A) shell width ~ shell length. (B) shell height ~ shell length. (C) shell weigth ~ shell length. (D) dry weight ~ shell length. (E) ash free dry weigth ~ shell length. (F) shell heigth ~ shell width. (G) dry weigth ~ shell weigth. (H) ash free dry weigth ~ dry weigth.

$y = 0.414x + 0.031\ x^2 - 0.001x^3 + 0.00001x^4$
$N = 187;\ R^2 = 0.998$
$SE = 0.661;\ P < 0.001$

A

$y = 0.904x + 0.003\ x^2 - 0.0001x^3$
$N = 187;\ R^2 = 0.999$
$SE = 0.547;\ P < 0.001$

B

$y = 0.0005\ x^{2.712}$
$N = 187;\ R^2 = 0.976$
$SE = 0.499;\ P < 0.001$

C

$y = 0.00003\ x^{2.640}$
$N = 184;\ R^2 = 0.918$
$SE = 0.048;\ P < 0.001$

D

$y = 0.00003\ x^{2.682}$
$N = 183;\ R^2 = 0.918$
$SE = 0.043;\ P < 0.001$

E

$y = 1.517x + 0.011\ x^2 - 0.0003x^3$
$N = 187;\ R^2 = 0.998$
$SE = 0.830;\ P < 0.001$

F

$y = 0.055x^{0.949}$
$N = 184;\ R^2 = 0.922$
$SE = 0.046;\ P < 0.001$

G

$y = 0.909x^{1.009}$
$N = 183;\ R^2 = 0.999$
$SE = 0.004;\ P < 0.001$

H