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Reproductive maturity in the edible Chilean crab *Cancer edwardsii*: methodological and management considerations

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Size-at-maturity, often used by fisheries managers to specify reference points, was estimated for Cancer edwardsii*, the most intensely exploited brachyuran crab in Chile, using morphometric data and observation of the gonadal cycle. Sampling was conducted in Chiloé Island, the principal landing region. Several morphometric measurements of secondary sexual characters were recorded for both sexes. Their size-dependence was investigated in search of ontogenetic allometric changes. Six stages of maturity were established for females, and four for males, on the basis of macroscopic and histological observation of the reproductive system, allowing distinction between adults and juveniles. Females and males, on average, attained full development of secondary sexual characters at 106 and 118 mm carapace width (CW) respectively. The CW at which 50% of females and males have gonads of adult appearance was around 101 mm. Current minimum legal size is 120 mm CW, seemingly high enough for conservation purposes. This management control, however, is unlikely to provide effective protection due to the high proportion of crab of sub-legal size in the landings. Traps with escape vents could be introduced in this fishery in order to ensure its sustainability.*

Keywords: *Cancer edwardsii*, Chile, crab fishery, legal size, gonadal development, allometry, size at maturity

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INTRODUCTION

Size-at-maturity is widely used by managers as biological support for establishing legal size controls. The most common rationale behind the latter is that, in order to prevent recruitment overfishing individuals should be allowed to mate at least once before attaining legal size (Jamieson & Caddy, 1984; Myers & Mertz, 1998). One problem with the design of size-based strategies is that discrimination between juveniles and adults varies depending on the criteria applied.

In the case of decapod crustaceans size-at-maturity has been defined on the basis of four criteria (Waddy & Aiken, 2005): (1) physiological sexual maturity, which relates to the capacity of the gonads to produce gametes; (2) morphometrical sexual maturity, corresponding to the size at which individuals attain full development of secondary sexual traits; (3) behavioural sexual maturity, indicative of mating capacity; and (4) functional sexual maturity, at which the individuals effectively reproduce in nature.

Physiological maturity can be assessed through the macroscopic examination of the gonads (Cobo & Fransozo, 2005; Mura *et al.*, 2005) and/or the histological analysis of tissue from the ovaries, testis or vasa deferentia (Minagawa & Higuchi, 1997). Morphometrical maturity is usually detected through the statistical analysis of size-dependence in secondary sexual characters (Somerton, 1980; Hall *et al.*, 2006). Examples are the conspicuous changes that occur at the time of the puberty moult, such as the relative enlargement of the propodus of male chelae or the width of the female abdominal segments (Mura *et al.*, 2005). Behavioural sexual maturity can be established by the presence of sperm plugs (Tallack, 2007; Ungfors, 2007) and abdominal mobility (Fischer & Wolf, 2006) in the case of females, and by direct observation of mate or guarding behaviour (Orensanz *et al.*, 1995; Goshima *et al.*, 2000) or mating scars (Knuckey, 1996) in the case of males. Functional maturity is unequivocally evidenced in females by the presence of ovigerous masses (Wolff & Soto, 1992; Tallack, 2007).

Regardless of the criteria and methods used, size-at-maturity is usually expressed as the size at which 50% of the individuals are found to be mature, and eventually by an associated error term (Udupa, 1986; Roa *et al.*, 1999).

Chilean crab fisheries, which are entirely artisanal, are supported by eight species, namely *Cancer edwardsii* (Bell, 1835), *C. coronatus* Molina, 1782, *C. porteri* Rathbun, 1930, *C. setosus* (Molina, 1782) (Cancridae), *Homalaspis plana* (Milne Edwards, 1834) (Platyxanthidae), *Ovalipes trimaculatus* (De Haan, 1833) (Portunidae), *Taliepus dentatus* (Milne-Edwards, 1834) and *T. marginatus* (Bell, 1835) (Majidae). The principal target species is *C. edwardsii*, which represents almost 90% of the catch reported over the last five years (SERNAPSCA, 2002–2006). Chilean crab fisheries are concentrated in the southern regions, between 40°S and 48°S, where 72% of the catch is landed (SERNAPESCA, 2002–2006).

In 1990 the Chilean fisheries authority introduced a ban on the landing of ovigerous females and a minimum legal size of

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12 cm of carapace width (CW) for *C. edwardsii* all along the country's extended coastline, from approximately 18°S to 53°S. The rationale for this minimum legal size is not entirely clear because biological knowledge on this species is very scarce. Preliminary estimates are available only for morphometrical size-at-maturity (Pool *et al.*, 1998; Olguín *et al.*, 2006). Minimum legal size should be reconsidered, incorporating additional biological criteria.

In this study, we describe the gonadal development of females and males, macro-and microscopically, using visual inspection and histological techniques. Size-at-maturity was estimated for both sexes of *C. edwardsii* based on gonadal development and morphometry; functional maturity is estimated only for females.

MATERIALS AND METHODS

Individuals of *Cancer edwardsii* were obtained using commercial traps from October 2006 to May 2007 in two fishing areas: Bahia Ancud (41° 51′56″S 73° 50′4″W) and Isla Cochinos (41° 50′50″S 73° 48′27″W), both located at the north end of Chiloé island. Given that the two sites were close to each other (3 km) and that catches are landed in the same port (Ancud), data were pooled for analysis. The catch was stratified by size (5 mm intervals) for crabs in the range 75–135 mm CW; an additional stratum was defined for crabs >135 mm CW. A minimum of six individuals in each size-class were measured and dissected for visual inspection of the gonads. A total of 743 individuals were analysed, including 381 females and 362 males. Morphometrical measurements (besides CW) included the length, width and height of both chelipeds in males, and the length and width of the 5th and 6th abdominal segments in females (Figure 1).

Visual inspection of the reproductive system was standardized using photographs. Six and four stages of gonadal development were established by this method for females and males, respectively (Tables 1 & 2; Figures 2 & 3). The principal macroscopic character used to discriminate stages was the proportion of the cephalothoracic space occupied by the gonad. Additionally, colour and texture of the ovaries were considered for females, and the diameter of the *vasa deferentia* for males. Tissue from the ovary (N = 41 females) and the middle part of the *vasa deferentia* (N = 38 males) were fixed in buffered 5% formaldehyde solution, embedded in paraffin, sectioned, and stained with haematoxylin–eosin for microscopic description of each stage.

Stage of gonadal development was used to construct an index of maturity in order to estimate physiological size-at-maturity using criteria similar to Campbell & Eagles (1983). Full description of development stages is given in Tables 1 & 2. Females were considered mature when ovary stage was higher than Stage III (early development); the latter never has post-vitellogenic oocytes in histological analyses. Males were considered to be physiologically mature when they had attained Stage III, in which the testes are clearly distinguishable, the vasa deferentia are well developed and spermatophores occupy more than 50% of their lumen. The proportion of mature individuals (P_{mature}) as a function

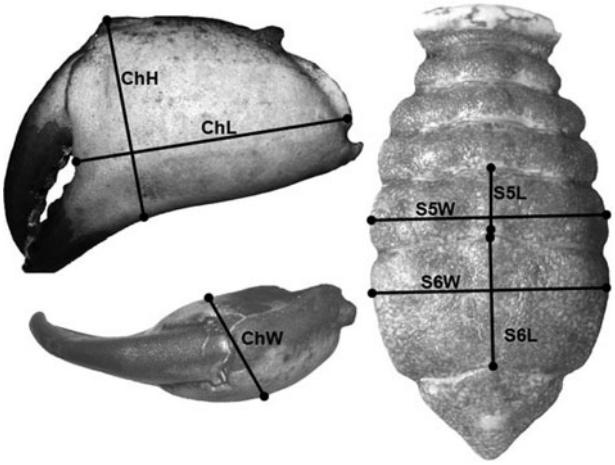

Fig. 1. Morphometric measurements of male cheliped and female abdomen. ChL, chela length; ChH, chela height; ChW, chela width; S5L, 5th abdominal somite length; S5W, 5th abdominal somite width; S6L, 6th abdominal somite length; S6W, 6th abdominal somite width.

Table 1. Maturity stages established for female *Cancer edwardsii* using visual inspection and histology of the ovary.

Ovary stages	Number	Diagnostic features
Immature	I	Ovary undetectable
Primordial	II	Ovary yellowish, covering up to 25% of the internal cavity, is difficult to distinguish from hepatopancreas
Early developing	III	Ovary orange or pale pink, covering 25–50% of the internal cavity and easily distinguished from the hepatopancreas
Late developing	IV	Ovary orange, beginning to swell and covering 50–75% of the internal cavity
Mature	V	Ovary fully developed, covering more than 75% of the internal cavity, including the gastric region. Colour ranging from orange to deep red
Recovering	VI	Ovary translucent but with several orange or red spots filling nearly 25% of the internal cavity. All females in this stage were brooding embryos

Table 2. Maturity stages established for male *Cancer edwardsii* using visual inspection of testes and histology of vasa deferentia.

Testes stages	Number	Characteristics
Immature	I	Testes not detectable
Primordial	II	Testes translucent, vasa deferentia as whitish filaments of constant diameter
Developing	III	Testes white or yellowish, testicular lobes more conspicuous than the vasa deferentia. The latter are white, diameter being slightly larger in the middle region
Mature	IV	Testes white-yellowish, testicular lobes less conspicuous than vasa deferentia. The latter are white and swollen; diameter of middle region three times that of other regions

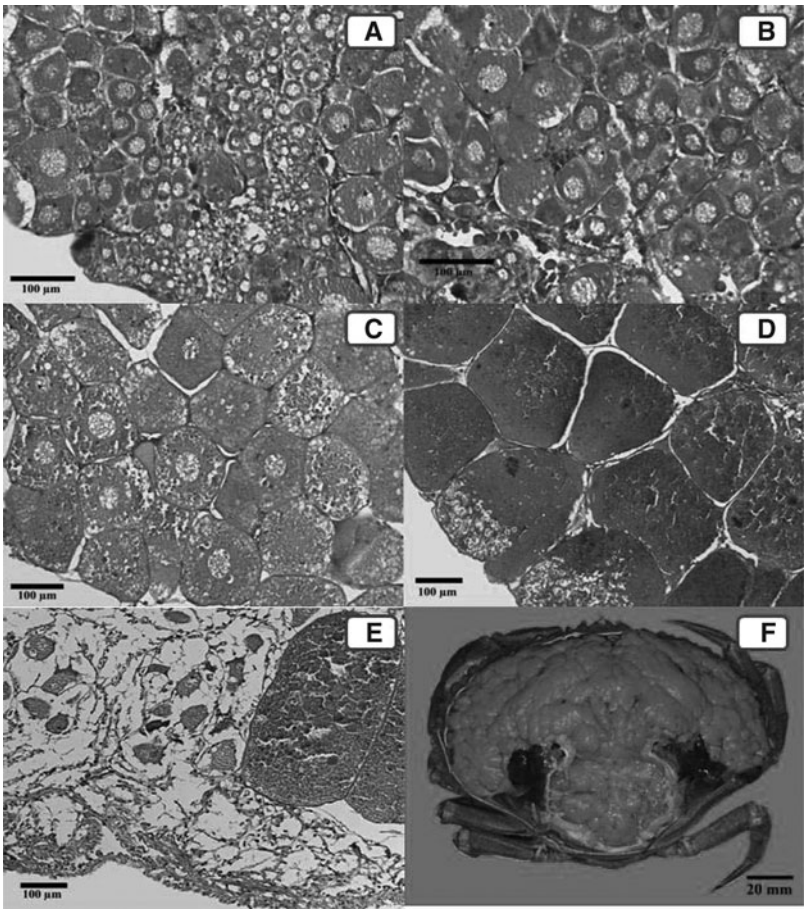

Fig. 2. Histological view of five macroscopic stages of ovary maturity. Gonad from first stage was undetectable. (A) Stage II primordial; (B) Stage III early development; (C) Stage IV late development; (D) Stage V mature; (E) Stage VI recovering; (F) macroscopic view of mature ovary (Stage V).

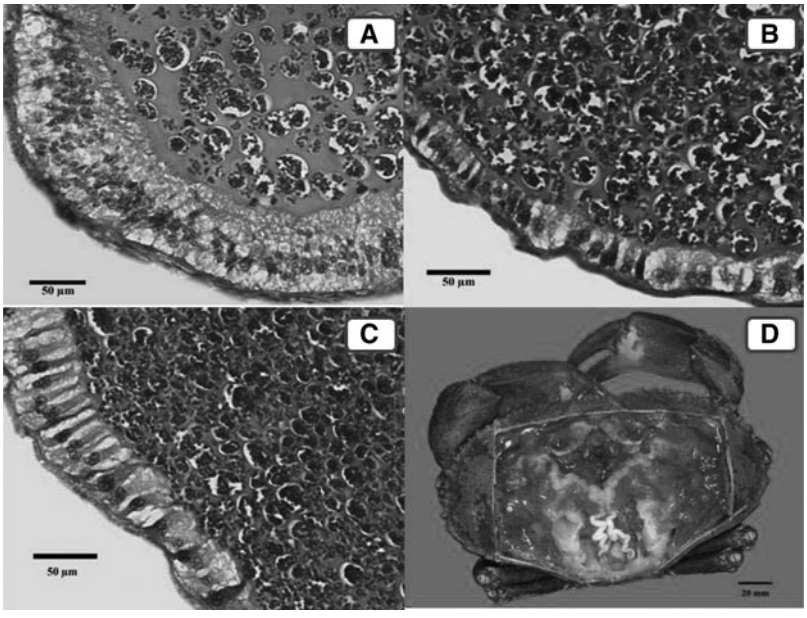

Fig. 3. Histological view of three macroscopic stages of the middle section of vasa deferentia. Tissue from first stage was undetectable. (A) Stage II primordial; (B) Stage III developing; (C) Stage IV mature; (D) macroscopic view of mature vasa deferentia. (Stage IV).

of size-class was modelled with a sigmoid function (Neter *et al.*, 1989):

$$P_{mature} = 1 - \left(\frac{1}{\left(1 + \frac{CW}{B_2}\right)^{B_1}} \right) \quad (1)$$

in which the asymptote is set to 1 because all individuals surviving through adulthood should eventually mature; B_1 is the regression coefficient and B_2 is the size at which 50% of the individuals have reached maturity. Parameters B_1 and B_2 were estimated by means of non-linear regression.

A piecewise linear regression model with a breakpoint was used to estimate morphometrical size-at-maturity. Parameters and their confidence limits were calculated by the least squares method using the Levenberg–Marquardt algorithm implemented in the STATISTICA software (Gill & Murray, 1978). The independent variable was size, expressed as CW, and the dependent variables were measurements taken on the right chelae or the abdominal segment (only females). We used measurements from the left chelae when the right chela was absent. We found no significant differences between the size of right and left chelae (chela length: $t_{1,569} = -0.33$, $P = 0.74$; chela width: $t_{1,569} = -0.34$, $P = 0.73$; chela height, $t_{1,569} = -0.12$, $P = 0.93$). The breakpoint is considered a morphometrical indicator of maturity (Somerton, 1980). For model selection (one versus two regression lines) we used the test proposed by Somerton (1980):

$$F = \frac{\frac{(RSS_1 - RSS_2)}{2}}{\frac{RSS_2}{(n-4)}} \quad (2)$$

where RSS_1 and RSS_2 are the residual sums of squares for models with one and two allometric phases respectively, and n is the number of data points. The statistic is distributed as F with 2 and $n-4$ degrees of freedom.

Functional size-at-maturity was analysed only for females, using the sigmoid model and the presence of a clutch as the indicator of maturity. For this purpose we used the proportion of ovigerous females relative to the total number of females within each size interval during the month with the highest prevalence of ovigerous females. This procedure assumes that the sampling period covered the brooding season of the whole female population, which in the study region occurs principally in late autumn and early winter (Pool *et al.*, 1998). Therefore, female functional size-at-maturity estimated here is only as a preliminary estimate.

RESULTS

Maturity stages

Six macroscopic stages were distinguished for females, based principally on ovary volume and colour (Table 1). In Stage I gonad tissue was undetectable, and therefore no histological analyses were conducted. In Stage II oocytes had large nuclei and conspicuous nucleoli; follicle cells were concentrated, principally in the periphery of the ovary lobules. Stage III presented oocytes in early vitellogenesis with follicular cells surrounding them; oocyte nuclei were easily visible in most cases. In Stage IV most oocytes were in late vitellogenesis, with round yolk granules distributed homogeneously; nuclei were not visible and follicular cells appeared flattened. Stage V was characterized by post-vitellogenic oocytes with large, lenticular yolk granules. Finally, Stage VI showed great diversity of cellular types: oogonia, follicular cells, and pre- and post-vitellogenic (remnant) oocytes (Figure 2).

The male reproductive system also showed conspicuous change during the course of development, and four maturity stages could be distinguished (Table 2). The aspect of the vasa deferentia changed from filamentous to highly convoluted, and the conduct thickened. Vasa deferentia and other parts of the male reproductive system were undetectable in Stage I, and therefore no histological analyses were conducted. Histological examination of vasa deferentia in Stage II showed nuclei of epithelial cells in a basal position, indicative of a juvenile stage (Johnson, 1980), with few spermatophores present. In Stage III the nuclei of epithelial cells became centric and many of them showed lobed nuclei; some spermatophores were surrounded by abundant seminal fluid (>50% of vasa deferentia lumen), spermatids inside spermatophores were small and peripherally located. Finally, Stage IV showed multinucleated cells close to the epithelial surface, spermatophores full of sperm, and seminal liquid occupying less than 20% of the vasa deferentia lumen (Figure 3).

Physiological size at maturity

The sigmoid curve fitted well the proportion of adults as a function of size, for both sexes (Table 3). No significant difference was detected in size at maturity (CW approximately 101 mm) between females and males based on observation of the gonads ($t = 6.35$, $P = 0.1$) (Figure 4).

Morphometrical size at maturity

A two-phase model fitted the relation between CW and male chelae height better than a one-phase model; this was not the case for other relations involving secondary sexual characters

Table 3. Estimated physiological size at maturity of *Cancer edwardsii* from the northern part of Chiloe Island.

	Estimated	Standard error	*t*	*P* value	CL + 95%	CL−95%
Females						
Size at maturity$_{50\%}$	101.52	1.64	61.74	<0.001	97.86	105.19
Parameter B_1	14.34	2.86	5.02	0.001	7.98	20.71
Males						
Size at maturity$_{50\%}$	101.59	2.15	47.31	<0.001	96.91	106.27
Parameter B_1	12.47	2.88	4.32	0.001	6.18	18.75

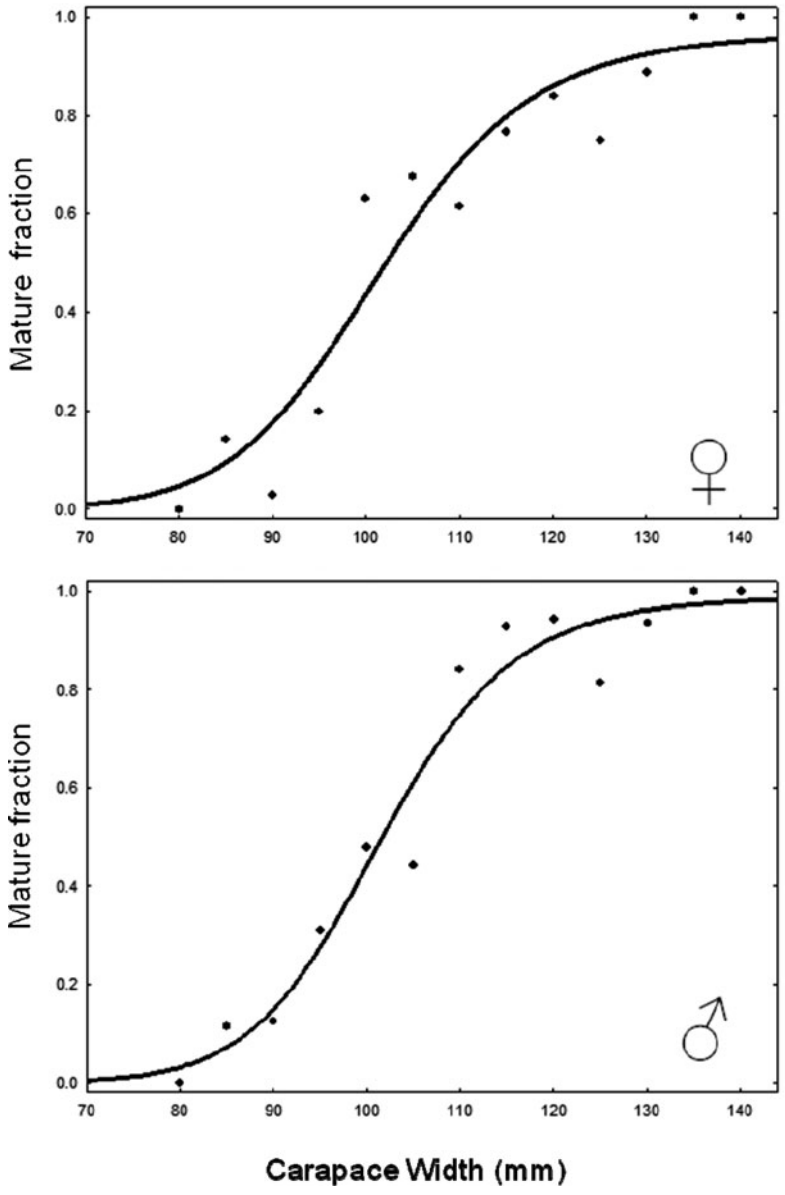

Fig. 4. Physiological size at maturity. Sigmoid function fitted to mature fraction as a function of size (CW). (A) Females (N = 279); (B) males (N = 288).

Table 4. Relation between body size and sexual secondary characters. Statistical comparison between one- and two-line regression models. RSS, residual sum of squares; CW, carapace width; ASW, abdominal segment width; ASL, abdominal segment length; PCA, principal component analysis.

	$RSS_{1\ phase}$	$RSS_{2\ phases}$	F	*P*
Females				
Ln CW versus Ln 5th ASW	0.688	0.687	0.405	0.959
Ln CW versus Ln 5th ASL	1.126	1.125	0.166	1.000
Ln CW versus Ln 6th ASW	1.004	1.003	0.279	0.993
Ln CW versus Ln 6th ASL	1.016	1.016	0.000	1.000
Ln CW versus PCA 1st factor	14.789	12.382	36.64	0.001
Males				
Ln CW versus Ln chela length	1.013	1.013	0.006	1.000
Ln CW versus Ln chela width	1.283	1.283	0.000	1.000
Ln CW versus Ln chela height	1.516	1.233	43.276	0.001
Ln CW versus PCA 1st factor	34.379	21.295	115.818	0.000

(Table 4). For that reason, all measurements of secondary sexual characters were integrated in a principal component analysis (PCA) for each sex. Although morphometric variables were highly correlated, PCA significantly improved the detection of allometric phases (Table 4; Figure 5), allowing the estimation of morphometrical size-at-maturity. Males reached morphometrical size-at-maturity at 118 mm CW ($CI_{95\%}$: 116–120) and females at 106 mm CW ($CI_{95\%}$: 102–109) (Table 5; Figure 5).

Functional size at maturity of females

The sigmoid model was fitted to the data (r = 0.67), but the slope was non-significant ($t = 2.66$, $P = 0.07$). Size at functional maturity was estimated to be 103.3 mm CW ($CI_{95\%}$: 77.9 mm, 128.6 mm).

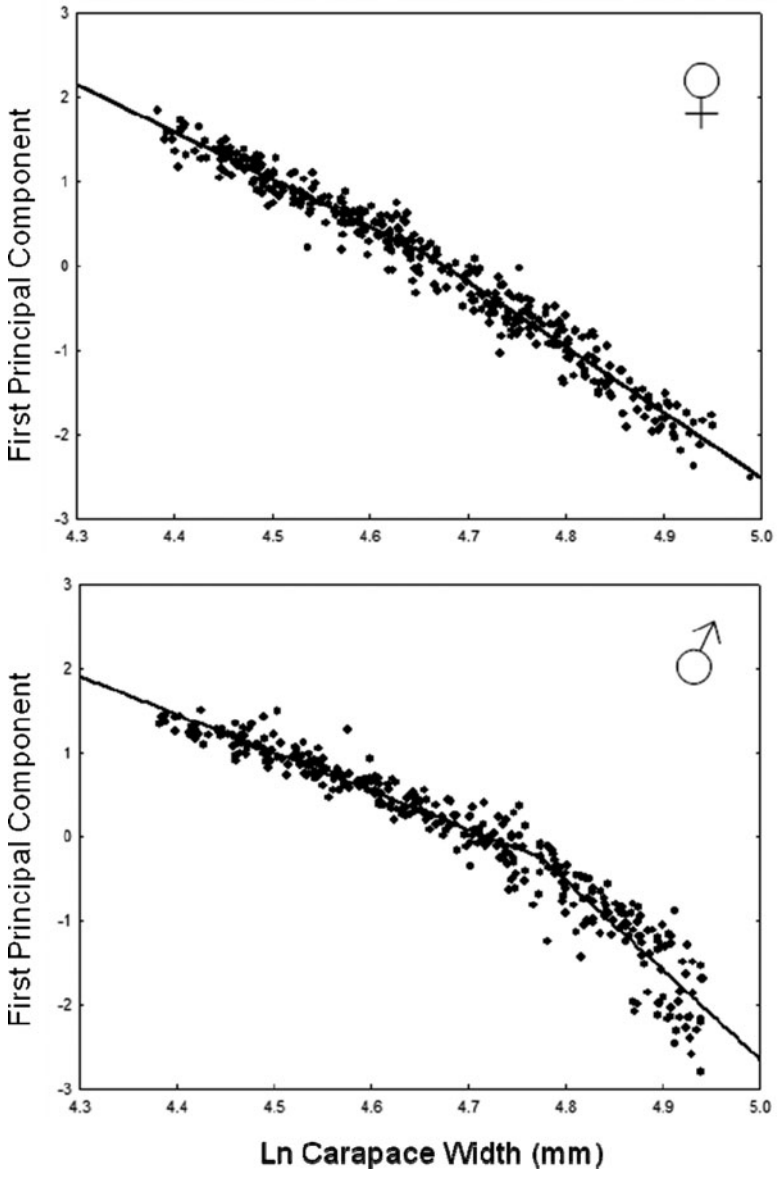

Fig. 5. Morphometric size at maturity. Piecewise linear regression. (A) Females (N = 381); (B) males (N =362).

Table 5. Estimated morphometric size at maturity for *Cancer edwardsii* from the northern part of Chiloe Island.

	Estimated	Standard error	*t*	*P* value	CL + 95%	CL−95%
Females						
Intercept	26.37	0.78	33.90	0.00	24.84	27.90
Slope I	−2.12	0.25	−8.53	0.00	−2.61	−1.63
Slope II	−5.63	0.17	−32.88	0.00	−5.97	−5.30
Breakpoint	4.66	0.02	271.47	0.00	4.63	4.69
Size at breakpoint	105.5				102.0	109.1
Males						
Intercept	21.50	0.68	31.63	0.00	20.17	22.84
Slope I	−4.56	0.15	−30.79	0.00	−4.85	−4.27
Slope II	−6.09	0.49	−12.32	0.00	−7.06	−5.12
Breakpoint	4.77	0.01	515.75	0.00	4.76	4.79
Size at breakpoint	118.4				116.3	120.6

DISCUSSION

The multivariate approach used here to estimate morphometric maturity might be helpful when bivariate allometries are not obvious. At least in the case of females, integrating measurements of multiple secondary sexual characters (e.g. length and width of the 5th and 6th abdominal segments) into the first factor of PCA was the only effective way to

detect allometric phases. Morphometric size-at-maturity was larger than physiological size-at-maturity in the Chilean commercial crab *Cancer edwardsii*; 95% confidence ranges overlap partially in the case of females. This implies that males and females are physiologically capable to reproduce before secondary sexual characters are fully expressed. The puberty moult (juvenile to adult transition) occurs within a size-range of 101–106 mm CW for females, and 101–118 mm CW for males. Whether individuals undergoing their puberty transition moult are effectively able to reproduce or not may depend on the size structure of the population, habitat quality, intensity of male–male competition, and female social interactions (Orensanz & Gallucci, 1988; Ennis *et al.*, 1990; Orensanz *et al.*, 1995; Wada *et al.*, 2000; Sainte-Marie *et al.*, 2002).

A sensible recommendation to fisheries managers is that minimum legal size should be larger than the size at which individuals become effectively reproductive. In this study we offer a preliminary estimate of functional maturity for *C. edwardsii* based on the size of ovigerous females (103 mm CW), but confidence intervals (78–129 mm) were wide. Otherwise, functional size at maturity, being dependent on ecological context, is a moving target (Orensanz *et al.*, 1995). In exploited populations, male–male competition may be relaxed when large male crabs are targeted and small males get the opportunity to mate. In addition, estimation of functional size at maturity is methodologically difficult for males (Goshima *et al.*, 2000), while for females it could be biased when traps are used for sampling, due to a well demonstrated reduction of foraging activity in ovigerous females (Howard, 1982).

Under a precautionary approach, morphometric size-at-maturity should be recommended as biological support to establish a minimum legal size. The rationale is that: (1) functional maturity may be contingent upon ecological conditions; (2) morphometrical maturity is normally attained after gonadal maturity (Hartnoll, 1982; Mura *et al.*, 2005; but see Tallack, 2007); and (3) accurate estimation of physiological and functional maturity usually present methodological difficulties (i.e. the requirement of a year-round sampling programme).

In the case of *C. edwardsii*, at least for males, the established minimum legal size (120 mm CW) would ensure that most individuals mate at least once before becoming available to the fishery. This size would be conservative in the case of females. However, in practice, scarcity of individuals larger than 120 mm CW (Olguín *et al.*, 2006) and poor enforcement by the fisheries authority render these regulations ineffective. A large fraction of the catch is below legal size: 20 to 71% for males and 70 to 93% for females at the main landing sites (Olguín *et al.*, 2006). More effective regulation is required to safeguard the reproductive potential of these harvested populations.

A 3S harvest strategy (size, sex and season) has been implemented in other cancrid species (Woll *et al.*, 2006). Seasonal closures could be implemented in the *C. edwardsii* fishery, but would not be necessarily effective in terms of improving the reproductive output of the harvested population (Shepherd, 1993; Arendse *et al.*, 2007). Considering that *C. edwarsii* is captured mainly with baited traps (Olguín *et al.*, 2006), control on gear selectivity appears to be a more suitable option for the *C. edwardsii*. Traps with escape vents to avoid capture of individuals under 100 mm CW could have better chances as an enforceable control. Trap designs with escape vents have been tested without success for *Cancer setosus* (Aguilar & Pizarro, 2006), but have shown good results in other cancrid crab fisheries (Ungfors, 2007). Experimental studies of trap design, coupled to research on crab reproductive ecology, should be a priority in management-oriented research for this valuable resource.

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