Article

Size at Sexual Maturity of Deep-Sea Unexploited Caribbean *Metanephrops binghami* (Boone, 1927) and Overexploited Mediterranean *Nephrops norvegicus* (Linnaeus, 1758) Using Morphometric and Gonadal Staging Approaches

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Abstract: The deep-sea Caribbean lobster (*Metanephrops binghami*) and the Norway lobster (*Nephrops norvegicus*) are Nephropidae species of high commercial interest. Although the first one still remains unexploited, the second is overexploited in the Mediterranean Sea. For effective fisheries management, size at sexual maturity is an essential indicator to protect immature individuals from exploitation. The estimation of this indicator can, however, be biased due to the difficulty of differentiating juveniles from adults by their size structure due to the natural process of molting. This study aims to estimate the size at sexual maturity of *M. binghami* and *N. norvegicus* females by comparing the effectiveness of the morphometric method versus the macroscopic evaluation of gonad maturity. Samples of *M. binghami* were collected from the Colombian Caribbean Sea in August and December 2009, March and May 2010, and August 2020 to May 2021. Samples of *N. norvegicus* were collected from the northwestern Mediterranean Sea from 2019 to 2022. Similar sizes at sexual maturity were found for *M. binghami* between the morphometric approach (ranging from 28.6 to 33.9 mm cephalothorax length, CL) and the gonadal staging approach (31.4 mm CL). Conversely, for *N. norvegicus*, the morphometric approach yielded higher measurements (between 27.2 and 30.4 mm CL) than the gonadal approach (26.0 mm CL). This discrepancy might stem from the intense fishing overexploitation conditions of *N. norvergicus*, leading to a physiological adaptation that enables earlier gonadal maturation at faster rates than morphometric adaptation. Further research is required to elucidate these discrepancies and the effect of overexploitation on physiological (i.e., mature gonads) and functional maturity (i.e., capacity to brood eggs at a larger size).

Keywords: deep-sea lobsters; management; morphometry; maturity; Nephropidae

Key Contribution: This research is the first comparative study on the morphological sexual maturity of Nephropidae species populations unexploited in the Colombian Caribbean and overexploited in the Mediterranean Sea.

1. Introduction

Deep-sea crustaceans are important constituents of demersal megafauna, holding substantial potential for global fisheries [1,2]. The deep-sea clawed Nephropidae species, the

Caribbean lobster *Metanephrops binghami* and the Norway lobster *Nephrops norvegicus*, are of high commercial interest [3]. *Nephrops norvegicus* inhabits the Mediterranean Sea and the Atlantic Ocean [3] and faces significant overexploitation, exceeding three times the maximum sustainable yield in the northwestern (NW) Mediterranean [4] (STECF 2022). Differently, *M. binghami* in the Colombian Caribbean Sea still remains, to date, unexploited [5].

Morphologically, both species are relatively small compared to other Nephropids such as *Homarus* spp. The mean cephalothorax length (CL) of *M. binghami* is approximately 34 mm [5], while that of *N. norvegicus* is around 30 mm [6]. Both lobsters show a very similar ecological niche and inhabit areas of soft sediments within self-made burrows, around which strong territorial behavior is associated [5,7]. Life trait similarities make *M. binghami* a valuable reference species to understand the effects of fishery management on exploited *N. norvegicus* stocks. The species establishes an unexploited baseline scenario for *N. norvegicus* stock recovery, given that the unexploited baseline was lost in Europe decades ago.

For effective fisheries management, size at sexual maturity is an essential indicator for protecting immature individuals from exploitation while ensuring sustainable harvesting that aligns with the reproductive capacity of populations [8,9]. *M. binghami* has been poorly studied in the Colombian Caribbean Sea, while *N. norvegicus* has traditionally been an object of fishery studies relating size and reproductive cycle, especially in the Mediterranean Sea. The estimation of its average CL at sexual maturity has been made through analyses of the different stages of gonadal maturity and associations with size classes [10–12]. However, the estimation of size at sexual maturity based on gonadal status can be biased due to possible visual errors in assigning maturity stages. In crustaceans, there is difficulty in differentiating juveniles from adults by size structure due to the natural process of molting to shed their exoskeleton in order to grow larger [13,14].

Other methods, such as morphometric analyses, could describe allometric growth changes linked to maturity aspects, being less affected by temporal and demographic fluctuations [15]. The change in growth at the beginning of sexual reproduction in crustaceans can be identified by analyzing morphometric relationships with the aim of differentiating juveniles and adults, and thus size at sexual maturity [16]. Consequently, it is expected that patterns of morphometric variation indicate differences in growth, as the shape of the body is related to structural changes in the ontogeny of organisms; this is very important for implementing efficient fishery management strategies [8].

In *Nephrops norvegicus*, size at sexual maturity onset in variable fishery pressure conditions can be attributed to reduced somatic growth, as energy is being used for the construction of gonads at smaller sizes [12,17–20]. In crustaceans, this process produces body changes that can be detected by discontinuities of growth at the onset of sexual maturity [18,19,21–23]. As a result, such discontinuities allow for analyzing morphometric relationships to differentiate juveniles from adults, and therefore to determine the size at sexual maturity [16]. In unexploited habitats, the size at maturity of *N. norvegicus* is unknown because unexploited areas in the Atlantic and Mediterranean are absent. In highly exploited fisheries, a decline in the onset of maturity is expected due to the selective removal of larger and more mature individuals from the populations [24]. This can lead to a shift in these populations toward smaller and younger individuals, which can result in a decline in the average size at sexual maturity. *N. norvegicus*, which has been overexploited for decades in NW Mediterranean fisheries, has had a decline in the size at maturity of females from around 30 mm CL to around 25.3 mm CL in the last 25 years [20]. Similarly, in the Irish Sea, a decline in female size at onset of maturity from 23.6 to 20.6 mm in two decades has been reported for *N. norvegicus* [25].

Here, the demographic analysis of the ecologically equivalent and unexploited Caribbean *M. binghami* has strategic value for European fishery management. The morphometric approach has been successfully used to establish a morphometric breakpoint for *M. binghami* [26] and *M. rubellus*, the latter in a partially exploited fishery in the Atlantic Sea off Sao Paulo, Brazil [19]. This study aimed to compare the effectiveness of the morphometric

approach with the gonadal macroscopic approach to estimate size at sexual maturity for females of unexploited *M. binghami* and overexploited *N. norvegicus*.

2. Materials and Methods

2.1. Data Collection for M. binghami and N. norvegicus

Samples of *M. binghami* were collected from the Colombian Caribbean Sea, between Punta Gallinas and the Gulf of Urabá (Figure 1A), in August and December 2009, March and May 2010, and from August 2020 to May 2021. Considering that Pérez et al. [26] reported the reproductive season for *M. binghami* to take place in October, the sampling encompassed both the reproductive and non-reproductive seasons, which enabled individuals from the entire size range to be evaluated. Sampling was carried out onboard a commercial bottom trawler, with an opening of 11.6 m at the footrope and a cod-end mesh size of 44.5 mm from knot to knot. A total of 87 fishing trawls were performed in depths ranging from 200 to 550 m, with at least two hauls per 100 m depth stratum. Each haul lasted 30 min and was conducted at an average speed of 2.5 knots. Size at sexual maturity was obtained for 490 females through visual gonadal stage classification, and for 199 females through the morphometric approach.
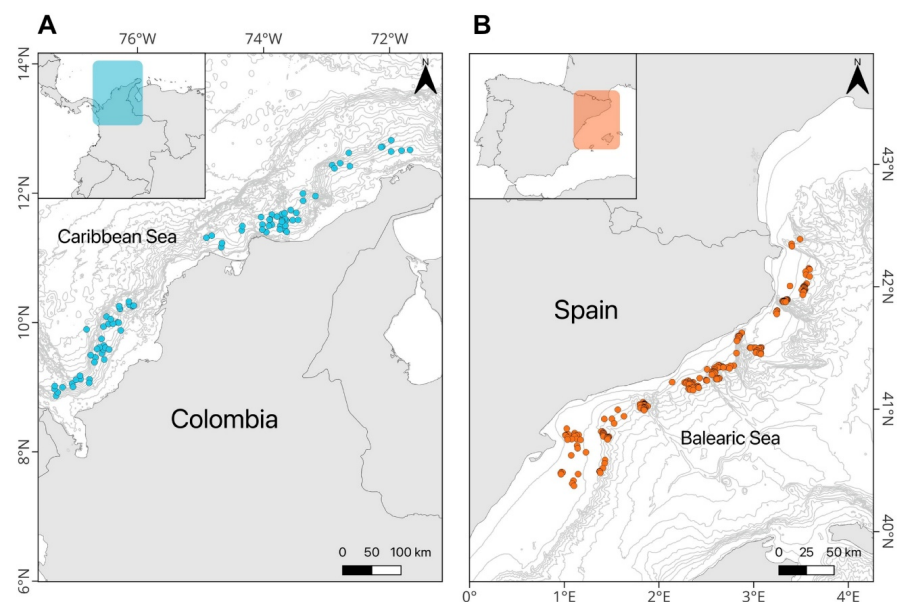

Figure 1. Sampling stations for *M. binghami* ((**A**), the Colombian Caribbean Sea) and *N. norvegicus* ((**B**), the NW Mediterranean Sea). Blue- and orange-colored dots are the trawl sampling events used to gather gonadal and morphometric data.

Samples of *N. norvegicus* were collected from deep-sea surveys in the northwestern Mediterranean Sea (Balearic Sea) along the Catalan coast (Figure 1B). ICATMAR [27] fishing monitoring program observers collected samples from 2019 to 2022, three times per month, on board bottom trawlers equipped with bottom-trawl nets with a cod-end mesh size of 40 mm squared. Surveys were carried out in slope areas where intensive fishing pressure has been occurring for decades [27]. A total of 197 fishing trawls were performed at 91 and 540 m on the Ebro Delta shelf and between 537 and 373 m on the slope off Blanes (see Figure 1B). The hauls lasted about 1.5 h at an average speed of 2.2 knots. Size at sexual maturity obtained by macroscopic examination of the color of the ovaries, based on Rotllant et al.'s [28] histological examination, was calculated for a total of 3433 females. A total of 116 females covering all size ranges were randomly selected for morphometric analyses. Given that the selective extraction of crustaceans in fisheries exploitation may modify size at sexual maturity, we compared the effectiveness of two methods to detect this change.

2.2. Morphometric Analysis Approach

For the morphometric approach to determine size at sexual maturity for females of *M. binghami* and *N. norvegicus*, all specimens were measured using seven body descriptors to the nearest 0.01 mm [29–31]: total length (TL); cephalothorax length (CL); first abdominal segment length (FSL); first abdominal segment width (FSW); first abdominal segment height (FSH); hepatic spine width (HSW); antennal spine width (ASW) (Figure 2).
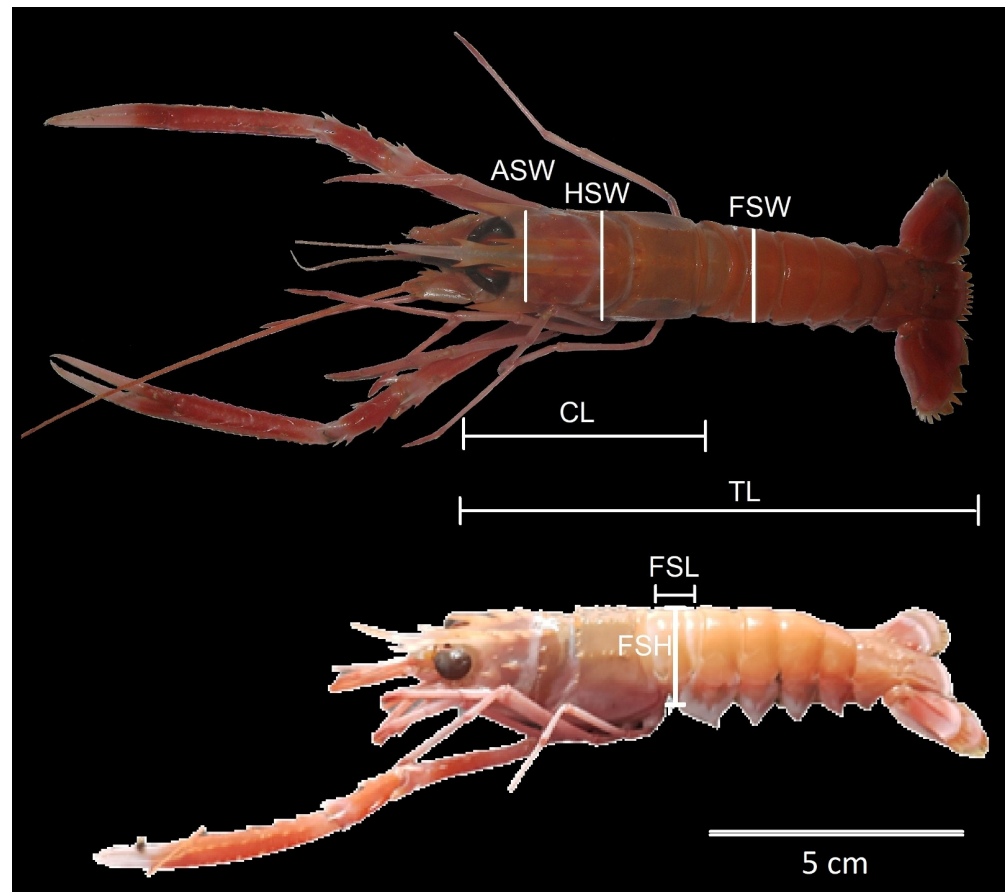

Figure 2. Morphometric measures of a female of *M. binghami*: total length (TL); cephalothorax length (CL); first abdominal segment length (FSL); first abdominal segment width (FSW); first abdominal segment height (FSH); hepatic spine width (HSW); and antennal spine width (ASW).

2.3. Data Analysis

The morphometric approach to distinguish juveniles and adults was conducted by means of a principal component analysis (PCA) with two allometric independent variables—TL, CL—and six dependent variables—CL, FSL, FSW, FSH, HSW, ASW—all transformed in a log base. The individuals were assigned to the juvenile and adult groups using a hierarchical cluster. Individuals from both groups were then assigned based on their weight on the two axes of the PCA [32]. Then, a discriminant analysis was performed to assign individuals to the juvenile or adult classes on the basis of the X and Y allometric variables. Size at 50% maturity ($L_{50\%}$) was estimated using a logistic regression, meaning the length at which a randomly chosen specimen had a 50% chance of being mature [31–34]. In the regression analysis, X (independent explanatory variable) and Y (the dependent response variable) had two alternative statuses (binomial): juveniles: 0; adults: 1. To evaluate differences in linear relationships between the juveniles and adults, an analysis of co-variance was performed (ANCOVA) [35].

2.4. Gonadal Maturity Analysis Approach

Size at sexual maturity was estimated via the classification of female stages of gonadal maturity based on the macroscopic examination of gonadal coloring. Maturity was evaluated only in female individuals of both species, as the maturity of males cannot be ascertained by the macroscopic inspection of gonads [28,36]. For *M. binghami*, we used five macroscopic stages, which were validated through histological observation [26]: 1, white, immature; 2, opaque, in development; 3, yellow, maturing; 4, green, mature; and finally, 5, ovigerous, carrying eggs on its pleopods. For *N. norvegicus*, we also used five maturity stages supported by previous histological analyses [37]: 1, white, immature, slender and thin ovaries; 2, resting, cream-yellowish; 3, beginning of maturation, small, light green; 4, big, thick, light green; and finally, 5, dark green, with advanced maturations in pre-spawning or spawning phases, also referred to as berried females.

The estimation of size at 50% maturity was carried out by equating the criteria defining maturity stages for both species. We defined mature females of *M. binghami* as those within stages 3 to 5, excluding stage 1 representing immature juvenile individuals and stage 2, representing individuals not yet mature, but in development. For *N. norvegicus*, mature individuals were defined from stage 2 to 5, with stage 1 representing immature juvenile individuals and those in development but not yet mature. The gonadal size at sexual maturity ($L_{50\%}$, CL and TL) was estimated using a logistic regression of the Bayesian Generalized Linear Model (GLM) (R package). We calculated the parameters *a* and *b* of the logistic function [16], where $P(L)$ is the mature female proportion. The size at 50% maturity was obtained by $L_{50\%} = (-a/b)$ [11].

$$P(L) = \frac{1}{1 + \exp(a + bL)} \tag{1}$$

3. Results

The total length (TL) of females of *M. binghami* ranged from 63.80 to 160.18 mm (122.87 ± standard deviation (SD) 22.97 mm) and the cephalothorax length (CL) ranged from 18.42 to 46.05 mm (35.25 ± 6.63 mm). *Nephrops norvegicus* females showed TL between 75.70 and 140.50 mm (103.46 ± 15.92 mm), and CL ranging from 22.26 to 44.36 mm (31.23 ± 5.13 mm). The morphometric relationships of *M. binghami* and *N. norvegicus* for both juveniles and adults were highly correlated between TL vs. CL, FSL, FSW, FSH, HSW, and ASW (Tables 1 and 2). The ANCOVA showed statistically significant differences between parameter *a* (intercept) of females for both species in all linear relationships, as well as in parameter *b* (slope) between TL vs. FSW and FSH, and CL vs. TL, FSW, FSH, and HSW for *M. binghami* (Figure 3; Table 1). In contrast, there was no significant difference in parameter *b* for *N. norvegicus* (Figure 3; Table 2) or *M. binghami* between TL vs. CL, FSL, HSW and ASW, or CL vs. FSL and ASW (Figure 3; Table 1). Juveniles were distinguished from adults for *M. binghami* and *N. norvegicus* (Figures 3 and 4; Tables 1 and 2) through morphometric relationships using discriminant functions.

The size at sexual maturity of *M. binghami*, as estimated by the morphometric relationships, varied between 110.49 and 118.56 mm $TL_{50\%}$ ($r^2 = 0.85$–0.96), and 28.60 and 33.89 mm $CL_{50\%}$ ($r^2 = 0.95$–1.00) (Table 3). In contrast, the size at sexual maturity of *N. norvegicus* estimated by morphometric relationships varied between 92.85 and 100.65 mm $TL_{50\%}$ ($r^2 = 0.87$–1.00), and 27.20 and 30.40 mm $CL_{50\%}$ ($r^2 = 0.869$–0.98) (Table 3).

The sexual maturity of females of *M. binghami* (N = 490; Figure 5) obtained by gonadal visual classification showed a majority of them in a mature condition, with 71.0% mature and 29.0% immature. The size at sexual maturity ($TL_{50\%}$) of females was 108.98 mm TL (95% CI = 106.10–111.60) and 31.40 mm CL (95% CI = 30.60–32.20) (Figure 5). The logistic model parameters for $TL_{50\%}$ were specified as $a = -15.06$ and $b = 0.14$, and for $CL_{50\%}$ as $a = -15.57$ and $b = 0.50$; $r^2 = 0.75$ in both cases.

Table 1. Parameters of morphometric relationships in females of *M. binghami*: total length (TL), cephalothorax length (CL), first abdominal segment length (FSL), first abdominal segment width (FSW), first abdominal segment height (FSH), hepatic spine width (HSW), and antennal spine width (ASW). N: number of specimens; r^2: determination coefficient. The numbers marked in bold denote significant differences from intercept and slope of morphometric relationships.

Relationship	Characteristic	N	N (%)	Intercept (*a*)	Slope (*b*)	r^2	*p* (ANCOVA)	
							Intercept	Slope
TL vs. CL	Juveniles	91	37.92	3.258	0.244	0.93	**0.000**	0.940
	Adults	149	62.08	2.062	0.271	0.83		
TL vs. FSL	Juveniles	72	36.18	0.263	0.017	0.82	**0.000**	0.148
	Adults	127	63.82	0.567	0.015	0.40		
TL vs. FSW	Juveniles	87	36.25	0.506	0.136	0.91	**0.000**	**0.034**
	Adults	153	63.75	1.177	0.142	0.76		
TL vs. FSH	Juveniles	83	34.58	0.126	0.112	0.81	**0.000**	**0.000**
	Adults	157	65.42	1.197	0.111	0.80		
TL vs. HSW	Juveniles	88	36.67	0.918	0.139	0.82	**0.000**	0.100
	Adults	152	63.33	0.742	0.154	0.65		
TL vs. ASW	Juveniles	101	42.08	1.029	0.140	0.89	**0.000**	0.975
	Adults	139	57.92	0.824	0.149	0.77		
CL vs. TL	Juveniles	91	37.92	4.926	3.406	0.93	**0.000**	0.038
	Adults	149	62.08	14.061	3.125	0.83		
CL vs. FSL	Juveniles	34	17.00	0.361	0.054	0.75	**0.000**	0.367
	Adults	166	83.00	0.501	0.053	0.65		
CL vs. FSW	Juveniles	68	27.87	−0.252	0.515	0.95	**0.000**	**0.032**
	Adults	176	72.13	1.198	0.494	0.73		
CL vs. FSH	Juveniles	90	36.89	−0.932	0.445	0.93	**0.000**	**0.000**
	Adults	154	63.11	2.086	0.366	0.69		
CL vs. HSW	Juveniles	108	44.44	−0.337	0.553	0.75	**0.000**	0.024
	Adults	135	55.56	0.190	0.550	0.83		
CL vs. ASW	Juveniles	92	37.86	−0.184	0.548	0.93	**0.000**	0.097
	Adults	151	62.14	0.750	0.521	0.85		

Table 2. Parameters of morphometric relationships in females of *N. norvegicus*: total length (TL), cephalothorax length (CL), first abdominal segment length (FSL), first abdominal segment width (FSW), first abdominal segment height (FSH), hepatic spine width (HSW), and antennal spine width (ASW). N: number of specimens; r^2: determination coefficient. The numbers marked in bold denote significant differences from intercept and slope of morphometric relationships.

Relationship	Characteristic	N	N (%)	Intercept (*a*)	Slope (*b*)	r^2	*p* (ANCOVA)	
							Intercept	Slope
TL vs. CL	Juveniles	38	32.48	1.972	0.271	0.86	**0.000**	0.965
	Adults	79	67.52	2.187	0.277	0.91		
TL vs. FSL	Juveniles	52	44.44	0.268	0.064	0.41	**0.000**	0.119
	Adults	65	55.56	0.900	0.059	0.72		
TL vs. FSW	Juveniles	41	35.04	−1.341	0.161	0.84	**0.000**	0.702
	Adults	76	64.96	−1.529	0.166	0.94		
TL vs. FSH	Juveniles	46	39.32	−0.729	0.141	0.63	**0.000**	0.527
	Adults	71	60.68	−3.797	0.177	0.81		
TL vs. HSW	Juveniles	55	47.01	1.968	0.110	0.61	**0.000**	0.210
	Adults	62	52.99	3.182	0.108	0.81		

Table 2. *Cont.*

Relationship	Characteristic	N	N (%)	Intercept (*a*)	Slope (*b*)	r^2	*p* (ANCOVA) Intercept	Slope
TL vs. ASW	Juveniles	34	29.06	0.680	0.043	0.22	**0.008**	0.598
	Adults	83	70.94	1.104	0.049	0.38		
CL vs. TL	Juveniles	38	32.48	7.194	3.111	0.86	**0.000**	0.382
	Adults	79	67.52	2.455	3.294	0.91		
CL vs. FSL	Juveniles	38	32.48	0.449	0.211	0.16	**0.000**	0.157
	Adults	79	67.52	0.272	0.218	0.71		
CL vs. FSW	Juveniles	38	32.48	−0.700	0.521	0.93	**0.000**	0.719
	Adults	79	67.52	−1.689	0.563	0.89		
CL vs. FSH	Juveniles	51	43.59	0.605	0.424	0.76	**0.000**	0.330
	Adults	66	56.41	−2.043	0.548	0.75		
CL vs. HSW	Juveniles	38	32.48	−0.216	0.460	0.65	**0.000**	0.612
	Adults	79	67.52	0.215	0.449	0.77		
CL vs. ASW	Juveniles	36	30.77	0.688	0.147	0.31	**0.009**	0.051
	Adults	81	69.23	0.934	0.171	0.40		

Table 3. Sizes at sexual maturity of *M. binghami* and *N. norvegicus* estimated by morphometric relationships using the discriminant functions method. C.I.: lower and upper confidence (95%); r^2: determination coefficient.

Species	Relationship	*a*	*b*	$L_{50\%}$	C.I. $L_{50\%}$	r^2
M. binghami	TL vs. CL	−33.812	0.298	113.54	111.40 to 115.80	0.89
	TL vs. FSL	−80.267	0.674	118.56	117.00 to 120.00	0.96
	TL vs. FSW	−33.103	0.297	112.05	109.70 to 114.00	0.89
	TL vs. FSH	−49.059	0.447	110.49	108.70 to 112.40	0.93
	TL vs. HSW	−25.682	0.229	112.33	110.00 to 114.40	0.85
	TL vs. ASW	−42.749	0.367	117.30	115.00 to 119.20	0.92
	CL vs. TL	−291.793	9.190	31.75	31.70 to 31.80	0.99
	CL vs. FSL	−3599.811	125.883	28.60	28.58 to 28.60	1.00
	CL vs. FSW	−67.876	2.305	29.45	29.40 to 29.45	0.95
	CL vs. FSH	−259.571	8.247	31.47	31.45 to 31.50	0.99
	CL vs. HSW	−103.206	3.046	33.89	33.89 to 33.90	0.97
	CL vs. ASW	−5405.663	170.208	31.76	31.75 to 31.80	1.00
N. norvegicus	TL vs. CL	−1850.197	19.523	94.77	94.80 to 94.80	1.00
	TL vs. FSL	−46.534	0.502	92.85	90.60 to 95.00	0.90
	TL vs. FSW	−106.388	1.088	97.82	97.80 to 97.80	0.97
	TL vs. FSH	−2297.428	23.819	96.45	96.50 to 96.50	1.00
	TL vs. HSW	−58.452	0.589	98.84	96.60 to 100.80	0.93
	TL vs. ASW	−37.089	0.369	100.65	98.20 to 103.10	0.87
	CL vs. TL	−83.222	2.893	28.77	28.80 to 28.80	0.95
	CL vs. FSL	−456.153	16.772	27.20	27.20 to 27.20	0.98
	CL vs. FSW	−162.028	5.541	29.24	29.20 to 29.20	0.97
	CL vs. FSH	−55.302	1.859	29.67	29.10 to 30.30	0.93
	CL vs. HSW	−42.464	1.431	29.44	28.70 to 30.20	0.90
	CL vs. ASW	−36.346	1.190	30.40	29.60 to 31.10	0.86

The sexual maturity obtained by gonadal visual classification for *N. norvegicus* females (N = 3433; Figure 5) indicated a nearly equal distribution, with 50.4% classified as mature and 49.6% as immature. The size at sexual maturity ($TL_{50\%}$) of females was 87.60 mm TL (95% CI = 87.00–88.10) and 26.03 mm CL (95% CI = 25.80–26.20) (Figure 5). The logistic model parameters for $TL_{50\%}$ were specified as *a* = −19.66 and *b* = 0.22, and for $CL_{50\%}$ as *a* = −17.81 and *b* = 0.69; r^2 = 0.60 in both cases (Figure 5).

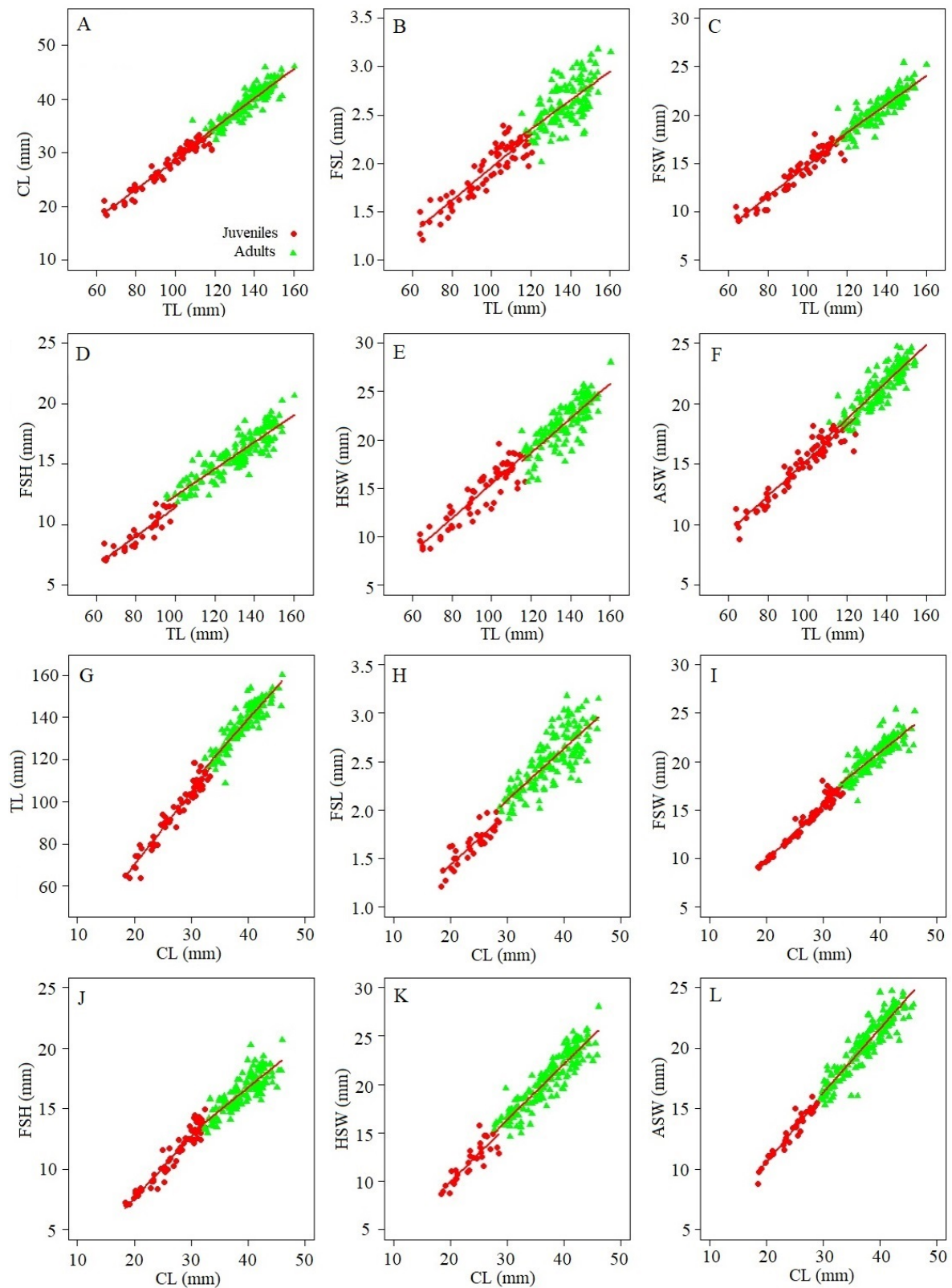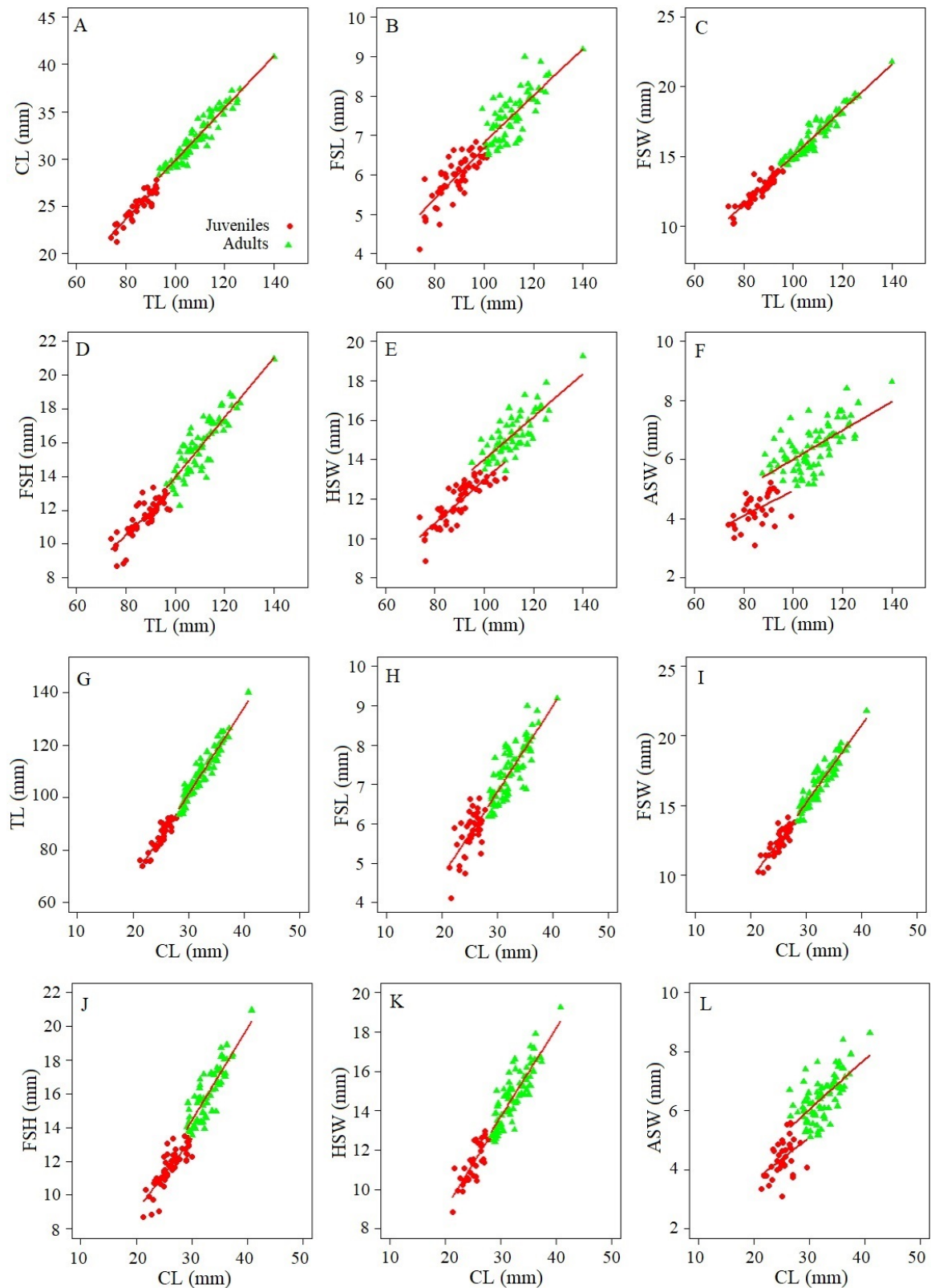**Figure 3.** Morphometric relationships using discriminant functions for juvenile and adult females of *M. binghami*. (**A**): TL vs. CL; (**B**): TL vs. FSL; (**C**): TL vs. FSW; (**D**): TL vs. FSH; (**E**): TL vs. HSW; (**F**): TL vs. ASW; (**G**): CL vs. TL; (**H**): CL vs. FSL; (**I**): CL vs. FSW; (**J**): CL vs. FSH; (**K**): CL vs. HSW; (**L**): CL vs. ASW.

Figure 4. Morphometric relationships using discriminant functions for juvenile and adult females of *N. norvegicus*. (**A**): TL vs. CL; (**B**): TL vs. FSL; (**C**): TL vs. FSW; (**D**): TL vs. FSH; (**E**): TL vs. HSW; (**F**): TL vs. ASW; (**G**): CL vs. TL; (**H**): CL vs. FSL; (**I**): CL vs. FSW; (**J**): CL vs. FSH; (**K**): CL vs. HSW; (**L**): CL vs. ASW.
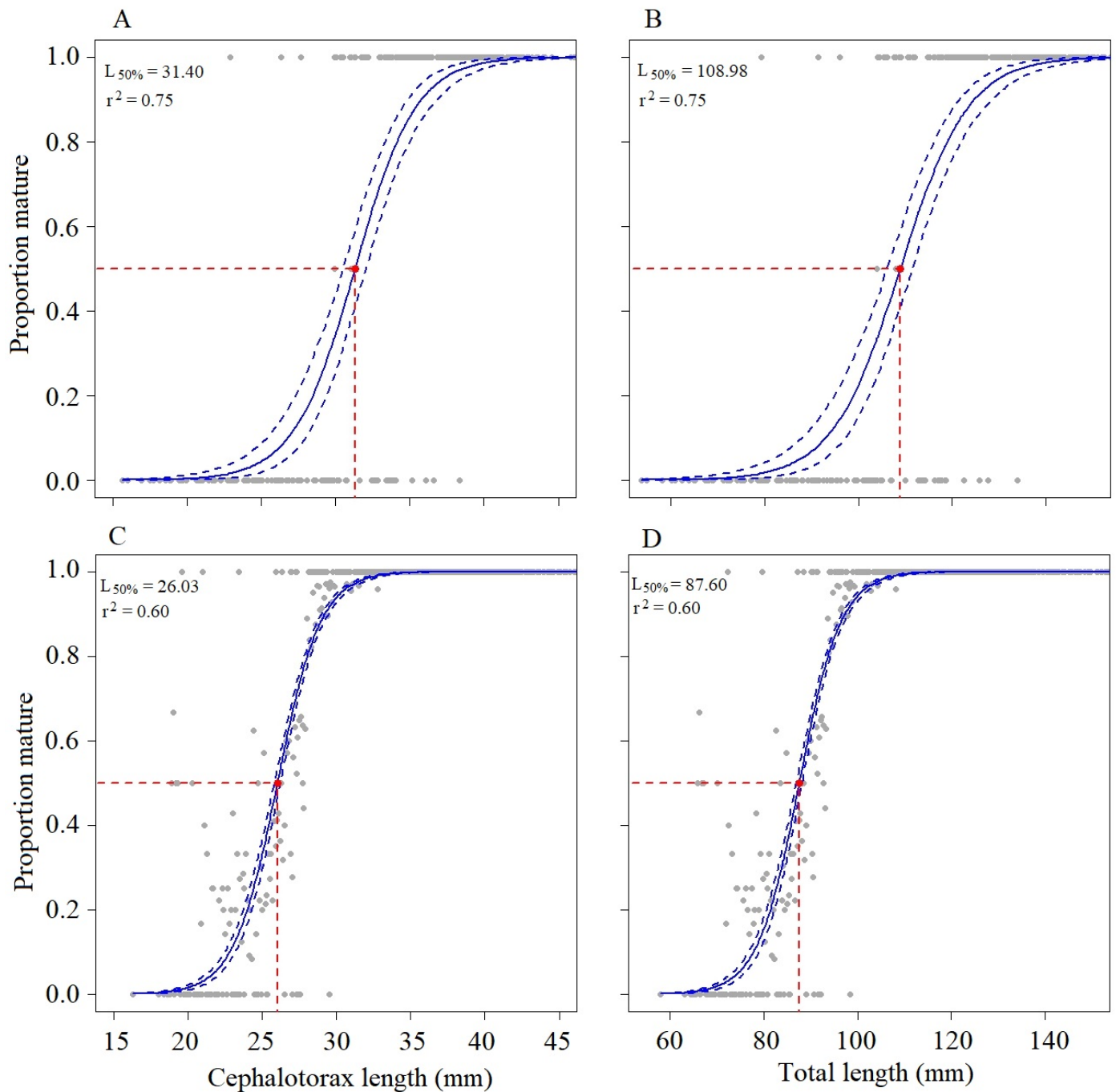
Figure 5. Size at maturity from the visual classification of gonadal maturity stages of females of *M. binghami* and *N. norvegicus*. Grey solid symbols indicate the points included in the estimation of size at sexual maturity. Red-dashed line represents length at which 50% of individuals reach maturity ($L_{50\%}$), red point. The blue line is the fitted logistic function and blue dotted line are the confidence intervals. (**A**): $CL_{50\%}$ *M. binghami*; (**B**): $TL_{50\%}$ *M. binghami*; (**C**): $CL_{50\%}$ *N. norvegicus*; (**D**): $TL_{50\%}$ *N. norvegicus*.

For the case of *M. binghami*, the sizes at maturity from the morphometric approach that were close to the size at sexual maturity estimated by maturity stages (108.98 mm TL and 31.40 mm CL) were TL vs. FSW (112.05 mm TL), HSW (110.49 mm TL), ASW (112.33 mm TL), CL vs. TL (31.75 mm CL), FSW (29.45 mm CL), FSH (31.47 mm CL), and ASW (31.76 mm CL) (Figure 6; Table 3). For the case of *N. norvegicus*, the sizes at maturity from the morphometric approach that were close to the size at sexual maturity estimated by maturity stages (87.60 mm TL and 26.03 mm CL) were TL vs. CL (94.77 mm TL), FSL

(92.85 mm TL), FSH (96.45 mm TL), CL vs. TL (28.77 mm CL), FSL (27.20 mm CL), and FSW (29.44 mm CL) (Figure 6; Table 3).
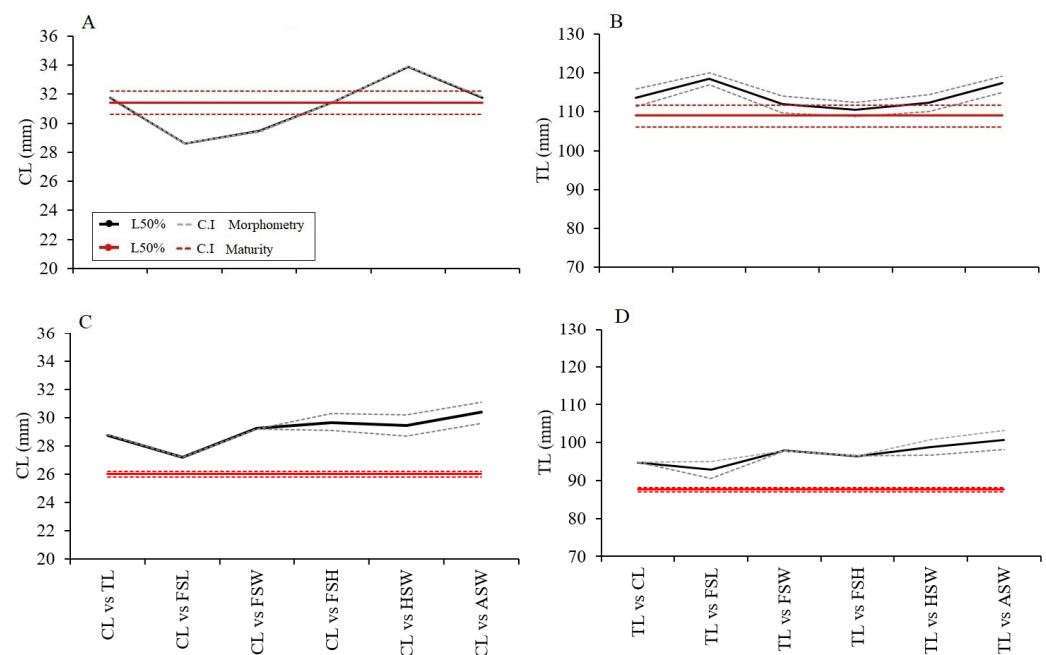
Figure 6. Comparison of sizes at sexual maturity estimated by morphometric and gonadal maturity for *M. binghami* and *N. norvegicus*. Dashed lines represent boundaries of 95% confidence intervals. (**A**): $CL_{50\%}$ *M. binghami*; (**B**): $TL_{50\%}$ *M. binghami*; (**C**): $CL_{50\%}$ *N. norvegicus*; (**D**): $TL_{50\%}$ *N. norvegicus*.

4. Discussion

In this study, we observed a discrepancy in the size at maturity between the visual gonadal approach and the morphometric approach for *N. norvegicus*. Specifically, the results from the morphometric approach indicated values between 27.20 and 30.40 mm CL, which were higher than those obtained through the gonadal visual approach (i.e., 26.03 mm CL). In contrast, when assessing the size at maturity of *M. binghami* using the morphometric approach, we found values between 28.60 and 33.89 mm CL, which were comparable to the value obtained through the gonadal visual approach (i.e., 31.40 mm of CL). Consequently, employing both methodologies as complementary techniques effectively estimated size at maturity in the unexploited species *M. binghami*. However, for the overexploited species, *N. norvegicus*, both methodologies are not complementary. Instead, they serve to highlight the overexploited condition of the population.

Intense fishery overexploitation may drive changes in size at sexual maturity because phenotypic traits are related to physiology, which could be more sensitive to contingent ecological factors [38,39]. In contrast, the phenotypic changes at the morphological level are more conservative. In fact, in crustaceans, physiological traits are capable of rapid local adaptation and divergent evolution [40]. Therefore, some studies suggest that size at maturity may respond faster than morphometric changes to the selective pressures of accrued mortality rates as a result of fishery overexploitation, reducing population density and at the same time impoverishing the food web due to sediment resuspension and removal by towed nets [41–43]. Morphometric changes may take longer to show modifications according to external fishery selective pressures, as they depend on the accumulation of genetic variations and the inheritance of favorable traits which are also influenced by a larger set of selective environmental forces [44]. In particular, *N. norvegicus* populations may be showing a selective response to overfishing conditions by accelerating the reproductive age in smaller size classes (i.e., a reduction in gonadal maturity size), while the ontogeny process imposes size conservation of the abdominal segments given their slowed-down

growth adjusted to a benthic lifestyle, the selective conditions (e.g., burrowing behavior) of which are invariant in the life history of the species today.

Nephrops norvegicus in Scottish waters show a larger CL size at the onset of maturity in females than that estimated from the gonadal maturity visual classification method [18]. Our results also confirm this observation for the deeper NW Mediterranean stock, and are in line with what has been reported in other decapod species. For example, the size at maturity of the crab *Portunus sanguinolentus* is smaller in heavily fished than less intensively harvested areas [45]. Also, the size at maturity of the crab *Sesarma rectum* is smaller in impacted mangrove areas [46]. However, for the latter species, the allometric growth of chelipeds was positive for both juveniles and adults, indicating no significant morphometric changes.

The size at maturity of crustacean species has been extensively studied in exploited marine environments with well-developed fisheries, e.g., *N. norvegicus* in the Mediterranean and North seas, based on gonadal maturity [6,12]. Nevertheless, the size of this species at their maturity in unexploited environments is information we will never attain, because unexploited grounds in the Atlantic and Mediterranean are missing. Therefore, it would be interesting to derive this knowledge with Nephropidae ecologically equivalent species such as *M. binghami* which inhabit unexploited continental margin areas of the Caribbean Sea [29].

In this study, using the gonadal maturity approach, the size at 50% maturity of *N. norvegicus* was 26.0, which differs slightly from that estimated by Vigo et al. [20], of 25.3 mm CL. It is important to note that the females analyzed in that study were collected in the same NW Mediterranean area at similar depths between 2019 and 2021 during the spawning season. Differently, here, we considered females collected from 2019 to 2022 across all the different seasons. Estimates of the onset maturity are known to vary seasonally, which may explain the slight difference in the present case.

Marković et al. [47] suggested that overfishing was the cause of the decreased size at 50% maturity (25.7 mm CL) observed for *N. norvegicus* in the South Adriatic Sea, the same size as the one found in the NW Mediterranean. Indeed, the abrupt decline in population abundances, which is observed in the NW Mediterranean Sea, caused by overfishing [4], can be followed by shifts in size and age at first maturity [48–50]. The current estimates of size at sexual maturity using the gonadal maturity of *N. norvegicus* (26.0 CL) confirm a decline in size at sexual maturity of about 4 mm CL in two decades, consistent with that reported by Vigo et al. [20], and probably linked to relatively high fishing pressure [12]. The size at sexual maturity of *N. norvegicus* found in this study through the morphometric approach showed a slowdown in somatic growth predominantly at 28.05 mm CL, which is closer to the size at maturity values reported more than 20 years ago of around 30 mm CL [12]. The overfishing effect of reducing size at maturity has also been suggested by Abelló et al. [19], who associated higher fishing pressures with smaller cephalothorax length in individuals from different areas subject to different exploitation levels in the Balearic Sea, Algarve, and the Adriatic. The size at maturity of *N. norvegicus* has also been observed to decline in the Western Irish Sea, from 23.6 mm CL in 1997 to 20.6 mm in 2016 [25]. According to the authors, the species has been overexploited in the past, though currently the population density is stable, but the stock abundance remains declining.

Identifying factors that drive the decline in the size at maturity of crustaceans is useful for understanding fishing and environmental impacts. Aside from fishing pressure, water warming has also been claimed to be responsible for the early maturity of crustaceans. For example, a study on the American lobster (*Homarus americanus*) shows that females living in warmer waters mature at smaller sizes [51]. Increasing water temperature may have been impacting the redistribution of *N. norvegicus* in the Balearic Sea [52], particularly after an abrupt warming from 2015 [53]. To our best knowledge, no studies of the direct effect of changes in water temperature on crustacean decapods' reproductive physiology or morphological changes have been reported. For the Caribbean Sea case, no reports are found on deep-sea water warming that may be impacting demersal communities.

This research is the first comparative study on the morphological sexual maturity of Nephropidae species populations in the Colombian Caribbean and Mediterranean Seas. The morphometric size at sexual maturity of *M. binghami* is similar to that obtained by gonadal maturity stages ($CL_{50\%}$ = 30.6 mm and $TL_{50\%}$ = 104.6 mm; Paramo and Saint-Paul [5]. In fact, Cusba and Paramo [29] estimated size at sexual maturity by morphometric measurements using the breakpoint approach [54] with similar results: the first abdominal segment height (FSH) in females resulted in $TL_{50\%}$ = 106.03 mm; taking FSH vs. CL as the morphometric variable resulted in $CL_{50\%}$ = 33.80 mm. Estimating the size at sexual maturity of *N. norvegicus* by the morphometric approach (CL vs. FSW, FSH, HSW, ASW and TL vs. FSW, FSH, HSW, ASW) resulted in similar results to those obtained by the gonadal approach in the Balearic Sea, Algarve, and Adriatic ($CL_{50\%}$ = 30 mm) [12]. The estimates of size at sexual maturity in this study obtained through morphometry indicate that the measurements of FSW, FSH, HSW, and ASW where the gonads are located are very similar to the estimates using gonadal stages. These morphological descriptors are the best variables for the determination of sexual maturity in both Nephropidae species. Furthermore, the size variability in the abdominal segment can be related to the beginning of sexual maturity, since at this life cycle stage, the onset of sexual maturity occurs, requiring a morphologically reproductive-compatible (i.e., a wider) abdomen for carrying and incubating eggs [29,55]. The relative abdomen growth in crustacean females may be related to the maternal care of eggs [56] in the form of a shelter–incubator chamber [57]. However, it is important to note that, for *N. norvegicus* females, there is still doubt on whether physiological maturity (i.e., the ability to produce mature gonads) or functional maturity (i.e., the ability to brood eggs at a larger size even if they already have mature gonads) occurs first, as presented in previous studies comparing morphometry and visual gonadal maturity [28,58]. This issue implies that abdominal widening can continue even after females are physiologically mature [18,28]. These discrepancies remain an open question that requires further research.

5. Conclusions

Estimating size at maturity of unexploited *M. binghami* and overexploited *N. norvegicus* can help us to understand the potential effects of fishery artificial selection on the physiological and morphological traits of commercially targeted species. In the NW Mediterranean, *N. norvegicus* seems to achieve a physiologically adapted gonadal maturation at smaller sizes (and age) under overexploitation regimes, not reflected by changes in morphology. In contrast, *M. binghami* shows similarity in the two traits in the unexploited demersal habitat of the Colombian Caribbean Sea. The value of our data will be incorporated within the Multi-Annual Management Plan for Mediterranean *N. norvegicus* Stocks [59], with the aim of identifying suitable demographic indicators of recovery. Estimating size at maturity from morphometric data is as an alternative to physiological-based methods; it has the advantage that data are easier and cheaper to obtain, and are less prone to temporal and seasonal biases [18,60].

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