

# Addressing caveats in current skate fisheries management: a comparative study on the morphometry and life history traits of commercially important skates blonde ray *Raja brachyura* and thornback ray *Raja clavata*.

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# Abstract

European skate fisheries management lacks species-specific measures due to data limitation and issues in species-specific reporting. Given these caveats, detailed information on commercially relevant skate stocks at species level is warranted. The morphometry and life-history parameters of 152 individuals (59 *Raja brachyura*, and 93 *R. clavata*) were determined for samples collected by observers within commercial fisheries, and two scientific surveys (December 2020 - August 2021) in the Southern North Sea and Eastern English Channel. The morphometry significantly differed between *R. brachyura* and *R. clavata*. Morphometric shape descriptor ratios were considered and proven more successful in species discrimination than linear morphometric measurements. Length-weight relationships indicated faster growth for *R. clavata*. Age was assessed by visual inspection of enhanced vertebral centra, allowing derivation of von Bertalanffy growth parameters. The macroscopic maturity was determined, and the relationship between body size and sexual development was ascertained in maturity ogives following logistic regression. Maturity assessment revealed interspecific and intersexual differences where male *R. clavata* matured at the smallest size ( $L_{50} = 654$  mm) and earliest age ( $A_{50} = 10.8$  yrs) while female *R. clavata* matured at the largest size ( $L_{50} = 839$  mm) and latest age ( $A_{50} = 11.5$  yrs). The morphometry of congeners *R. clavata* and *R. brachyura* significantly differs, which is reflected in the life history traits: length-weight relationships, growth, and reproductive biology. These interspecific differences once again highlight the need for species-specific data collection and management considerations of commercially relevant skate stocks in the Northeast Atlantic Region.

## Introduction

Skates (Chondrichthyes, Rajidae) of the genus *Raja*, are widely spread in Northeast (NE) Atlantic waters. They are oviparous and exhibit a K-selected reproductive strategy (MacArthur and Wilson 1967). In the NE Atlantic, skates are a long established and important fisheries resource, mainly landed as bycatch by bottom trawlers, and additionally targeted locally and seasonally by otter trawl and longline fisheries or by large-mesh trammel and tangle nets ((Ellis et al. 2010; STECF 2017; ICES 2020). For the Belgian fisheries, the beam trawl fleet targeting crustaceans and demersal fish species is the most important fishery. The fleet segments operate mainly in International Council for the Exploration of the Sea (ICES) divisions Central North Sea (4.b), Southern North Sea (4.c) and Eastern English Channel (7.d) (Flemish Government 2020). In 2019, the blonde ray (*Raja brachyura* Lafont 1873) was the most landed skate in Belgian ports, followed by the thornback ray (*Raja clavata* Linnaeus 1758) (Flemish Government 2020).

Aggregated landings of skates have roughly remained stable, yet relative contribution in abundance of certain species has changed (Dulvy et al. 2000; ICES 2020). The change in stock structure and density has been explained by the alteration of life-history characteristics due to long-term exploitation (Tanaka et al. 1990; Walker 1999). Over a century, *R. brachyura*, one of the commercially most valuable skate species, has sustained highly directed fishing pressures without substantial reduction in abundance, possibly attributed to the residence of females inshore, where less vulnerable to directed fisheries (Steven 1936; Gallagher 2000). On the contrary, *R. clavata* has declined in abundance and size distribution in the

North Sea (Dulvy et al. 2000). Additionally, Chevolut et al. (2006) noted near absence of mature individuals from *R. clavata* following a study on population structure, suggesting higher fishing pressure on the larger, often mature individuals. Various studies noted changes in life-history traits for *R. clavata*, an increased growth rate, and conversely a decrease in both length-at-maturity and age-at-maturity (Steven 1936; Nottage and Perkins 1983; Ryland and Ajayi 1984; Walker 1999; Ellis et al. 2010).

Despite the commercial or market value of certain skate species, the economic value of their total catch is small in comparison with other demersal species in the Belgian fishery (e.g., sole and plaice) (Crevits, 2020). As a result, skates have not been the focus in fisheries management. Currently, fisheries with skate landings are regulated under the European Common Fisheries Policy (CFP) through a Total Allowable Catch (TAC) system. Additional measures include listing of prohibited species or local size restrictive measures, such as the enforcement of the Belgian Minimum Landing Size (MLS) of 50 cm total length. Skates in bycatch fisheries are considered choke species under the European Landing Obligation (LO), which requires the landing of catches for quota and/or size-regulated species to reduce discarding, enforced for all TAC-regulated fish species since January 1<sup>st</sup>, 2019 (Uhlmann et al. 2019). Since 2019, skates are temporarily exempt from the LO under the exemption of high discard survival (EU Delegated Regulation 2019/2239).

Since different species of skate, exhibit different distributions with seasonal and ontological migrations, resulting in spatiotemporal dynamism, and in addition possess different life-history traits (Steven 1936; Walker et al. 1997; Hunter et al. 2005; Chevolut et al. 2006), the lack of species-specific management, could be considered as inadequate (STECF 2017). In addition, species-specific records (landings, discards) from data collection initiatives are often inaccurate, due to misidentification, misreporting and coding errors (STECF 2017; ICES 2020). Therefore, more robust protocols or techniques are to be provided to ensure correct species identification. To address the caveats in skate fisheries management, morphometric studies could be valuable (Serra-Pereira et al. 2010; McCully et al. 2012). Morphometric conversion factors are informative to correctly report the required measurement (depending on the country) of size (i.e., total length or disc width), when a specimen is damaged or sampled in a processed state upon arrival at the fish market. Length-weight relationships (LWR) are commonly used for biomass computation, and LWR parameter estimates provide information on growth pattern, condition, and morphometry of a species in a spatiotemporal setting (le Cren 1951; Froese 2006; McCully et al. 2012). Additionally, morphometric ratios were proven to aid in accurate species identification for six skate species in Portuguese waters (Serra-Pereira et al. 2010). However, this approach has yet not been undertaken in the Northern Part of the Northeast Atlantic region, where misreporting of skates still occurs due to incorrect species identification (STECF 2017)

Other key biological parameters have been addressed in many studies (Steven 1934, 1936; Holden 1972; Nottage and Perkins 1983; Ryland and Ajayi 1984; Fahy 1989; Walker 1999; Gallagher et al. 2004; Whittamore and McCarthy 2005; McCully et al. 2012). Age and growth studies are essential to understand the population dynamics of commercially exploited species as applied for quantitative stock assessments (Holden 1972; Ryland and Ajayi 1984). Age determination in cartilaginous fish is commonly

based on the observation of contrasting annual growth bands in the vertebral centra, however, no consensus has been made on the robustness of the findings of various age determination methods (Daiber F.C; Serra-Pereira et al. 2011). Growth is expressed as an increase in length or weight with increasing age, commonly modelled using the von Bertalanffy growth model (VBGM) (Serra-Pereira et al. 2008). Maturity studies are crucial to estimate the condition of the stock. Since skates exhibit well-marked sexual dimorphism in external characteristics, maturity studies mainly focus on macroscopic reproductive structures allowing allocation to maturity stages (Steven 1934; ICES 2020). Concordant with the K-selected reproductive strategy, skates reach sexual maturity at a late age, attain large sizes, and produce fairly low numbers of offspring, especially in comparison with teleost fishes (MacArthur and Wilson 1967; Walker 1999; Musick et al. 2005). Therefore, it is important that skates are given the opportunity to first reproduce before being caught by the fisheries. Only if the stock has sexually mature, reproducing individuals, there can be recruitment, which compensates for the loss of individuals from fishing mortality and natural mortality (Camp et al. 2020).

With this study we aim to indicate the necessity of a species-specific fisheries management of skates in the Northeast Atlantic region and provide additional tools for species identification, through a detailed assessment of the morphometry and life history traits of blonde ray and thornback ray. We hypothesise that *R. brachyura* and *R. clavata* possess significantly different morphometries and life-history characteristics.

## Materials And Methods

### Sample collection

Specimens of whole individuals (> 300 mm) of skate species *R. brachyura* and *R. clavata* were collected by seagoing observers. Specimens were hauled with a beam trawl aboard commercial beam trawlers, and during two scientific surveys aboard Research Vessel (RV) *Belgica*, and RV *Celtic Explorer* in the Southern North Sea (ICES area 4.c) and Eastern English Channel (ICES area 7.d) from November 2020 to August 2021 (Fig 1).

### Laboratory procedures

Detailed morphometric measurements of total length (TL), disc width (DW), disc length (DL), caudal length (CL), and total weight (TW) were recorded using the 'Smartfish' digital measuring board (ILVO, Clemaco Trading NV; d=1 mm), a calliper (Stanley; d=0.1mm) and a scale (Sartorius Combics 1; d=0.5 g) (Fig 2).

Individuals were dissected by opening of the ventral body cavity, after which the liver and the digestive tract were removed. The sexual maturity of the individuals was assessed by the macroscopic morphology of the reproductive tract, and on the presence of external maturity indicators in male individuals (i.e., clasper length, clasper calcification, presence of multiple rows of alar and/or malar thorns) following the ICES Maturity Scale for Oviparous Elasmobranchs from the ICES Workshop on Sexual Maturity Staging

of Elasmobranchs (ICES 2020). The clasper length was measured from the forward rim of the pelvic girdle to the tip of the clasper following Collenot (1969).

The age of all specimens was assessed by visual inspection of stained growth bands on the vertebral centra following the ILVO age reading protocol developed within the SUMARiS project (Interreg 2 Seas programme 2014-2020) (Fig. 3) (SUMARiS 2021). The vertebral column was removed by lateral sections along the dorsal surface of each individual. The vertebral column was cleaned by cooking in a water bath at 90°C for 30 minutes. A vertebral segment containing the ten most anterior vertebrae was extracted from each vertebral column, the neural arches were removed by scalpel to reveal the vertebral centrum. The vertebral centra were immersed in a 47°C pepsin-hydrochloric acid solution (500 ml water, 8 ml pepsin, 4 ml 25% hydrochloric acid) for 30 to 45 minutes depending on vertebral size, using a stir heating plate (IKA RT 10 Magnetic Stirrer, Labinco L80 Hotplate). The pepsin solution was drained, and the centra were immersed in an 80°C water bath for 30 to 45 minutes. The centra were air dried after immersion in ethanol (99.8%) for 5 to 10 minutes. For visualisation of the growth bands, the centra were etched in 5% EDTA solution (5g EDTA, 100 ml distilled water) for 5 to 10 minutes, stained in 0.01% crystal violet solution (2ml 0.5% crystal violet, 100 ml distilled water), and air dried. Using a stereomicroscope (light source, Zeiss KL 1500 LCD; microscope, Zeiss Stemi 2000-C) and a camera (Leica MC 171 HD), photomicrographs of ten vertebral centra per individual were taken and optimised for focus artefacts in SmartLab v1.2. The three most discernible centra per individual were independently read in SmartDots v2.3 through indication of the birth mark and growth bands by two operators, without prior knowledge of species, sex, size, maturity, and date of capture. Ages were verified by plotting against total length, outliers were re-examined through the previously mentioned age-reading procedure.

## Data analysis

The least squares method was used to adjust the linear relations between morphometric measurements for the officially reported size measurements per species:  $DW \sim a TL + b$ , with  $a$ , the slope of the regression line, and  $b$ , the intercept. Morphometric ratios (i.e., body shape descriptors) for disc shape (DL:DW), whole body shape (DW:TL), relative disc size (DL:TL), and relative tail size (CL:TL) were calculated per individual. Morphometric measurements of size and body shape descriptors were compared among species and sexes (unpaired t-test). Principal Component Analysis (PCA) was applied for: (1) morphometric measurements of size, with the variation of these measurements summarised in the alternative variable 'morphometry'; (2) body shape descriptors, with the variation in these descriptors summarised in the alternative variable 'shape'. Alternative variables were compared among species (unpaired t-tests). A flexible discriminant analysis (FDA) (Hastie et al. 1994) was applied to investigate which combination of morphometric ratios was adequate to discriminate species for: (1) all individuals; (2) landing-sized individuals (TL > 500 mm) and discards (TL < 500 mm); (3) immature versus mature individuals.

The LWR parameters were established per species by sex for the relationship between total weight (TW, in g) and total length (TL, in mm) using the log (base 10) transformation formula of le Cren (1951).

$$\log(TW) = \log(a) + b \log(TL)$$

$$TW = a TL^b$$

Where  $a$  is the initial growth coefficient, and  $b$  is the growth rate. Likelihood ratio tests (LRTs,  $\chi^2$  statistic) of the log transformed linear model were applied to investigate significance of predictors species and sex. Multiple R-squared was used to assess model fit.

Growth curves were fitted using the von Bertalanffy (1938) growth model per species by nonlinear regression:

$$L_t = L_\infty (1 - e^{-K(t-t_0)})$$

With  $L_t$ , the estimated length at age  $t$  (mm),  $L_\infty$ , the theoretical maximum length (mm),  $K$ , the Brody growth rate coefficient ( $\text{yr}^{-1}$ ), and  $t_0$ , the theoretical age at which total length equals zero (yrs). Model fit was visually assessed. Length-at-age data was compared among species and sexes by ANCOVAs (F-statistic).

Maturity ogives for length (proportion of mature individuals at any total length) and age (proportion of mature individuals at any age) were adjusted per species and sex by logistic regression in the Generalized Linear Models framework (McCullagh and Nelder 1989) with binomial maturity data (0, immature; 1, mature).

$$\log\left(\frac{p}{1-p}\right) = -a + b L + \varepsilon$$

$$L_{50} = \frac{-a}{b}$$

$$\log\left(\frac{p}{1-p}\right) = -a + b A + \varepsilon$$

$$A_{50} = \frac{-a}{b}$$

With  $p$ , the proportion of individuals in mature condition for total length ( $L$ , in mm) and age ( $A$ , in years). The size at which 50% of individuals are mature was defined as the mean size of maturity ( $L_{50}$ ), and the age at which 50% of individuals are mature was defined as the mean age of maturity ( $A_{50}$ ). LRTs ( $\chi^2$  statistic) were used to test for differences between species and sexes. To ascertain the relationship between body size and sexual development in male individuals, clasper lengths (in mm) were plotted to total length per species by maturity stage.

All analyses were performed in R STUDIO v1.4.1106 (RStudio Team, 2020) using the following main packages: car, dplyr, DescTools, emmeans, factoextra, FactoMineR, FSA, ggplot2, ggpubr, ggspatial, ggsignif, grid, mda, nlstools, rnatuarearth, stats, sf, vegan. Outliers were inspected by boxplots.

Assumptions of normality, homogeneity, and linearity were investigated by graphical examination of the residuals and variables. Autocorrelation was checked using a correlogram with Pearson correlation coefficients.

**Table 1.** Number of male (M) and female (F) specimens per species caught in the Eastern English Channel (7.d) and Southern North Sea (4.c) per trip for the period November 2020 to August 2021.

Trip	Area	<i>R. brachyura</i>		<i>R. clavata</i>		Total
		F	M	F	M	
November 2020	7.d	1	-	3	4	8
December 2020	7.d	23	23	39	31	116
	4.c	7	2	-	-	9
August 2021	4.c	2	1	8	8	19
Total		33	26	50	43	152
		59		93		

## Results

In total, 152 individuals of skates were caught and analysed in the present study. The catch composition represented in Table 2, included 59 individuals of *R. brachyura*, and 93 individuals of *R. clavata*.

### Morphometry

Linear relations between morphometric measurements disc width and total length are described in Table 2. Morphometric measurements of the disc were largest for *R. brachyura*, with statistical significance of disc length (unpaired t-test,  $t_{150} = 1.9762$ , p-value = 0.04996). Total length and caudal length were largest for *R. clavata*, but not significant among species (unpaired t-test, p-value > 0.05). Intersexual differences were not detected for neither species (unpaired t-test, p-value > 0.05). Morphometric measurements of size were strongly correlated for both species (Pearson  $r > 0.92$ ). Following PCA, the continuous variable 'morphometry' was established in which the morphometric variation of total length, disc length, disc width and caudal length was summarised, as the variable explained 97.27% of the morphometric variation. However, as visualised in Fig. 4, PC1 does not explain differences in the morphometric measurements between species, as the species are rather separated by the variation summarised in PC 2, which explained 2.43% of the morphometric variation. Consequently, the newly established variable 'morphometry' was found not to differ significantly between *R. brachyura* and *R. clavata* (unpaired t-test, p-value > 0.05).

Interspecific comparisons of morphometric shape descriptor ratios, however, were found to differ significantly among *R. brachyura* and *R. clavata* for 'whole body shape', 'relative disc size', 'relative tail size', and 'disc shape' (unpaired t-test, p-value < 0.0000000000000002), (Fig 4). Visually, this significant difference was supported by the separation of the variation in shape descriptor ratios across PC 1,

following PCA. Here, PC 1 explained 68.25% of the variation in morphometric ratios, mainly explained by the variation in 'relative tail size' and 'relative disc size'. This variation was summarised in alternative variable 'shape', which was found to differ significantly between *R. brachyura* and *R. clavata* (unpaired t-test,  $t_{150} = 14.913$ , p-value < 0.0000000000000002). PC 2 additionally explained 18.37% of the variation in morphometric measurements which consists of variation in 'disc shape' and 'whole body shape'. This result indicated a significantly different morphometry for the two *Raja* species under study. Following the FDA, in accordance with the PCA, a combination of the shape descriptor ratios for 'relative disc size' and 'relative tail size' was proven most accurate for species discrimination of all individuals (N = 152; misclassification 7.90%), discards (N = 40; misclassification 10.0%), and mature individuals (N = 20, no misclassification). For immature (N = 132, misidentification 8.33%), and landing-sized individuals (N = 112; misclassification 8.04%), correct identification increased when including 'disc shape' in the FDA.

**Table 2.** Linear relations between morphometric measurements disc width and total length per species. Linear relation described by the equation  $DW \sim a TL + b$  with  $a$ , the slope, and  $b$ , the intercept.

	$n$	Length range (mm)	$a$	$b$	$R^2$
<i>R. brachyura</i>	59	306 - 911	0.72262	-9.38127	0.99
<i>R. clavata</i>	93	332 - 906	0.66559	6.99057	0.96

## Life history traits

The length-weight relationships significantly differed among *R. brachyura* ( $a = 0.0000002$ ,  $b = 3.58468$ ) and *R. clavata* ( $a = 0.0000005$ ,  $b = 3.37734$ ) (Likelihood Ratio Test, p-value = 0.0004988), where the growth rates ( $b$ ) imply a greater increase in weight with an increase in size for *R. brachyura* in comparison with *R. clavata*. Intersexual differences in the LWR were detected between females and males of *R. clavata* (Likelihood Ratio Test, p-value = 0.007618) with females having a greater growth rate ( $b$ ) and a smaller initial growth coefficient ( $a$ ) (Fig. 5). Although not significantly different in *R. brachyura*, the LWR similarly indicate a greater growth rate ( $b$ ) and a smaller initial growth coefficient ( $a$ ) for females in comparison with males.

Growth band visibility on the vertebral centra differed among species, where bands on *R. clavata* were most discernible. The VBG models did not differ significantly between *R. brachyura* and *R. clavata* (Fig. 5). For *R. clavata*, length-at-age data differed significantly among sexes (ANCOVA,  $F = 5.8189$ , p-value = 0.0182).

The maturity stages followed a cascading alteration with increasing length. For *R. clavata*, consecutive maturity stages change at smaller lengths in males. No mature males of *R. brachyura* were assigned. Interspecifically, the succession of maturity stages occurred fastest in male individuals of *R. clavata* (600-700 mm TL), and slowest in female *R. brachyura* (800-900 mm TL). No active females (i.e., females



bearing egg capsules, ready to be deposited), nor spent males (i.e., males which show signs of recent copulation) were observed for neither species. For *R. brachyura*, 6.78% of the individuals (n=59) was mature, while for *R. clavata* a larger percentage of the individuals (17.20%, n=93) was determined sexually mature (Table 3).

The length-at-maturity (LRT, p-value = 0.004267) and age-at-maturity (LRT, p-value = 0.0401) significantly differed among the two species. Intersexual differences for length-at-maturity and age-at-maturity were additionally evident for *R. clavata* (LRT, p-value < 0.05), but could not be verified for *R. brachyura* due to a lack of mature males. Male *R. clavata* was found to mature at the smallest size and earliest age, while female *R. clavata* matured at the largest size and latest age (Table 3). However, this pattern could be an artefact of the reduced sample size in *R. brachyura*.

**Table 3.** Length at maturity ( $L_{50}$ ) and age at maturity ( $A_{50}$ ) estimates for *Raja brachyura* and *Raja clavata* in the Southern North Sea and Eastern English Channel by sex, following logistic regression (logit link, binomial error distribution) with binomial maturity data (0, immature; 1, mature).

Species	Sex	Number of mature individuals	$L_{50}$ (mm)	$A_{50}$ (mm)
<i>R. brachyura</i>	Female	4	827	11.1
<i>R. clavata</i>	Female	3	839	11.5
	Male	13	654	10.8

Clasper development was linear and rather slow in immature and developing individuals, upon maturation clasper length rapidly increased and leveled off, as apparent for *R. clavata* (Fig. 7). Interspecifically, we observed a more rapid sexual development for the average-sized *R. clavata* in comparison with larger-sized *R. brachyura*.

## Discussion

The present study provides the most recent morphometric, length-weight, growth, and maturity data for the commercially relevant species *R. brachyura* and *R. clavata* from the Eastern English Channel and Southern North Sea. In earlier studies, Serra-Pereira et al. (2010) and McCully et al. (2012) provided linear relations between morphometric measurements for these two focal species. As in this study, Serra-Pereira et al. (2010) considered the application of morphometric ratios for species identification through FDA, although no differentiation between landing-sized individuals, discards, immature and mature individuals was made there. Here, we additionally provide a visual comparison of the variation in body shape descriptors and summarised this variation in a single variable 'shape' which in turn was proven to differ significantly between the two species under study. Although size conversion factors obtained by linear relations typically differ between areas (Walker 1999), the linear regression parameters closely approximated the estimates provided by Serra-Pereira et al. (2010) and McCully et al. (2012) covering

respectively, Portuguese Waters, and the North Sea - Celtic Sea. As both the PCA and FDA indicated a highly different morphometry for the species under study, we recommend this morphometric approach to be applied for other Northeast Atlantic skates, which are commonly confused, such as small-eyed ray (*Raja microocellata*, Montagu 1818) and sandy ray (*Leucoraja circularis*, Couch 1838) which is relevant for the problematic reporting of these species. This approach, as proven valuable for congeneric species *R. brachyura* and *R. clavata* could be even more applicable for non-congeners as they differ even more in morphometric characteristics. Shape differences could, in addition to differences in coloration or patterns, aid in more accurate species reporting.

Studies on life history traits of skates typically focus on size and mass relationships, age and growth, or reproductive biology. The LWR parameters determined for the Eastern English Channel, were different from the most recent estimates by Serra-Pereira et al. (2010) and McCully et al. (2012). However, differences are in addition apparent between these studies, and in comparison, with earlier studies (Ryland and Ajayi 1984; Whittamore and McCarthy 2005). Since these studies cover different geographical regions and since LWR are influenced by many confounding factors, such as examined size range, season, habitat, degree of gonad development, and food availability, these estimates may not be entirely comparable (le Cren 1951; Jones et al. 1999; Froese 2006). The relationship between length and total eviscerated weight may therefore provide a better (i.e., more standardised) estimate for comparison among geographical areas, with the additional information on the examined size range, season, and maturity (Serra-Pereira et al. 2010). LWR estimates of growth rate were larger than 3, therefore these LWR relationships describe positive allometric growth and, a greater increment in weight with an increase in size, typically associated with the depressiform body shape of skates (Mahé et al. 2018). Allometric growth is typically described in fishes that change shape as they grow (Jones et al. 1999). Since LWR tend to differ among species with different body shapes, and following the results on morphometrics, the differences in LWR parameters may be explained by differences in the morphometry, translated in greater growth rates in females compared to males, and in the median-sized *R. clavata* compared with the larger-sized *R. brachyura*. These interspecific differences in the LWR estimates could immediately be linked to the difference in morphometry. As *R. brachyura* has a wider disc with a shorter tail, this species adds on more weight with an increase in size, in comparison with *R. clavata*, which is characterised by a longer tail and shorter disc.

Length-at-age data significantly differed between the focal species. Growth estimates of the VBGM revealed that the larger blonde ray, following Branstetter (1987), is the slowest growing species. The estimates obtained in this study, however, should be taken with caution, due to limited sample sizes. Currently, a standardised and widely adopted age-reading protocol for rays and skates is lacking. It should be noted that the ILVO age reading protocol has not been cross-validated, and that different age-reading methods have different flaws. For instance, Gallagher et al. (2004) noted that the use of whole centra for age estimation purposes is not ideal and that the vertebral centra of certain skate species provide poor resolution of growth increments near the nucleus, as was apparent during the age reading procedure for *R. brachyura* in this study. In addition, methods of age determination are commonly

dependent on interpretation by different readers, and although uncertainty may be minimised, disagreements in the resulting growth data can appear (Goldman 2005).

As the temporal coverage of this study does not cover the months April to July in which reproduction tends to peak for NE Atlantic skates (Holden 1972, 1975), no seasonal or general patterns in reproductive biology could be deduced. However, this could explain the absence of active females, and spent males, which in turn confirms the clearly delineated reproductive season for the NE Atlantic skates. The subsequent alteration of the maturity stages accompanies the life history characteristics and K-selected strategy of the focal species, according to the K/r-selected reproductive strategy theory by MacArthur and Wilson (1967). The larger-sized blonde ray matures more slowly, thus at larger lengths than the congeneric and smaller thornback rays, which are less K-selected. Given the close stock/recruitment relationship in elasmobranchs, protection of the reproductive potential is crucial (Holden 1974). The estimates of mean length-at-maturity, indicate that the current Belgian Regulation of an MLS of 50 cm is not sufficient to allow certain size classes of the skates under study to first reproduce before being landed. None of the collected skates below 500 mm total length were found to be sexually mature. Nevertheless, since ICES stock assessment advice for *R. brachyura*, and *R. clavata* are based upon survey data where solely individuals with a total length  $\geq 500$  mm were included, TAC settings should take this gap into account. Steven (1936), Nottage and Perkins (1983) and, Ryland and Ajayi (1984) suggested a decreased length-at-maturity for *R. clavata* over the long term. Here, the results also indicate a decrease in the length-at-maturity in comparison with Steven (1934), almost a century ago. This decrease however was not as apparent in comparison with more recent studies. Additionally, ICES noted in the Advice on fishing opportunities, catch, and effort for the Greater North Sea ecoregion (2019) that stock sizes of *R. brachyura* and *R. clavata* within the Southern North Sea and Eastern English Channel have increased over time (1988-2018).

## Conclusion

In conclusion, this study provided a comprehensive insight in the highly variable life history traits and highlighted the importance of gathering knowledge on interspecific and intersexual differences in commercially relevant species *R. clavata* and *R. brachyura* in the Northeast Atlantic. In addition, because of significantly different morphometries between the congeners, morphometric ratios were proven to serve as additional tools in the identification of skates, a caveat in current management. Finally, the results of this study prompt the development of a standardised, peer-reviewed age-reading protocol that lies at the basis of robust stock assessment and future management advice.

## Declarations

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## Conflicts of interest/Competing interests

Not applicable - The authors declare they have no conflict of interest.

## Availability of data and material

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

## Code availability

The code is available from the open access R packages: car, dplyr, DescTools, emmeans, factoextra, FactoMineR, FSA, ggplot2, ggpubr, ggspatial, ggsignif, grid, mda, nlstools, naturalearth, stats, sf, vegan.

## Ethics approval

As no live specimens were investigated during this research, no animal experiment permits were needed. The fish were sampled under commercial fishing practices by sea-going observers from ILVO (Flanders Research Institute for Agriculture, Fisheries and Food).

## Consent for publication

All authors provide consent to the publisher to publish this work, incl. all text, Figures and Tables.

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## Figures

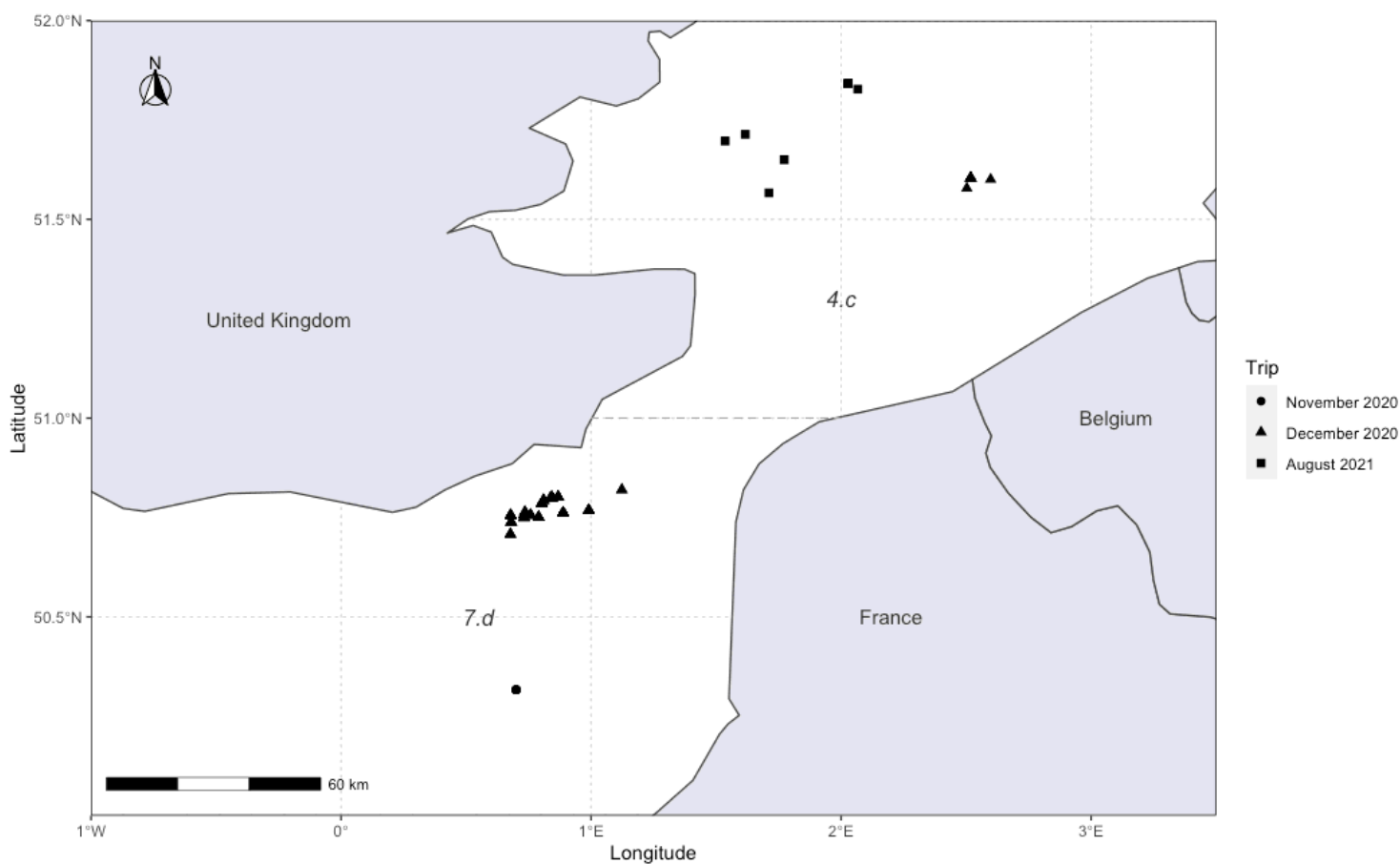
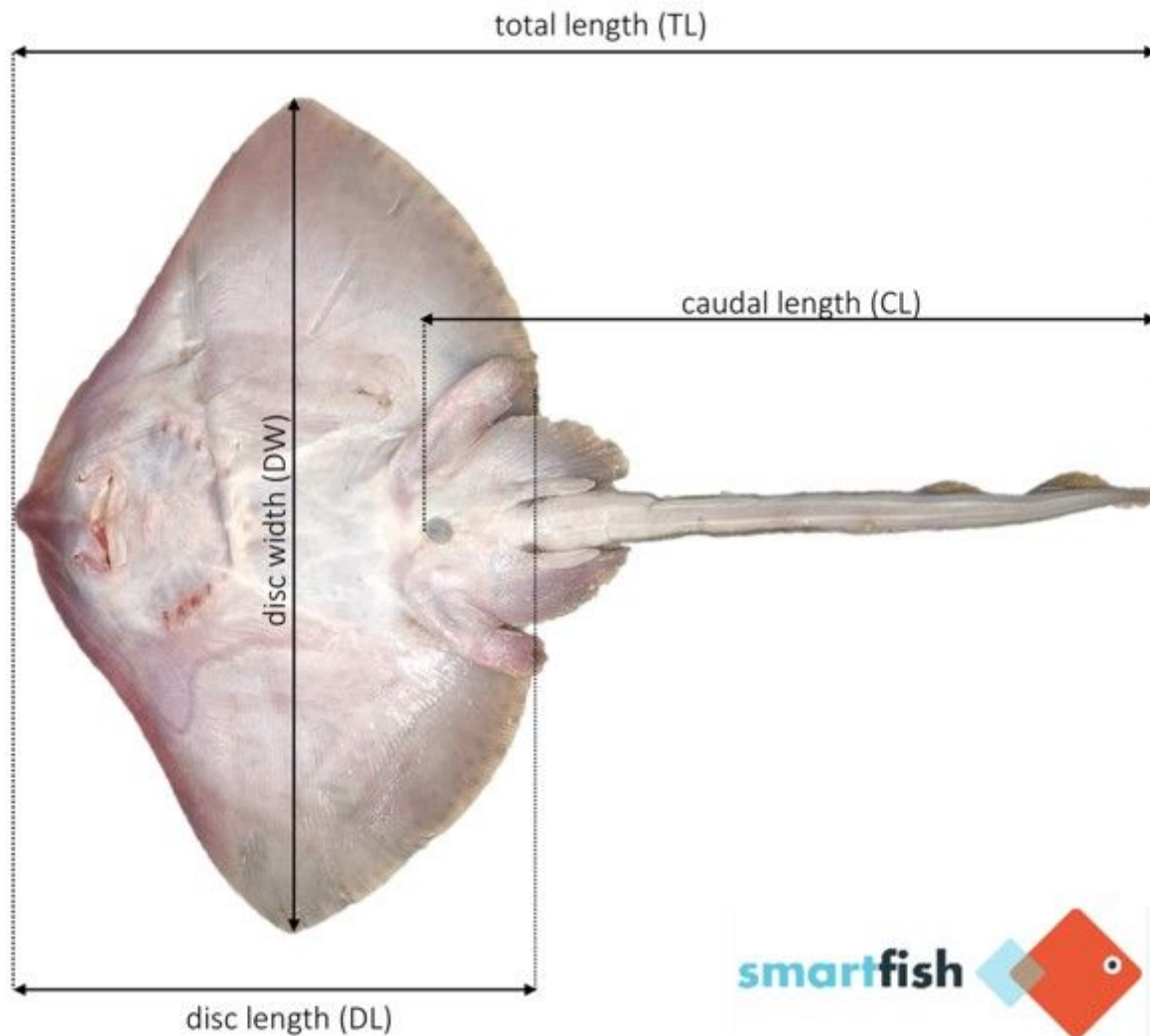


Figure 1

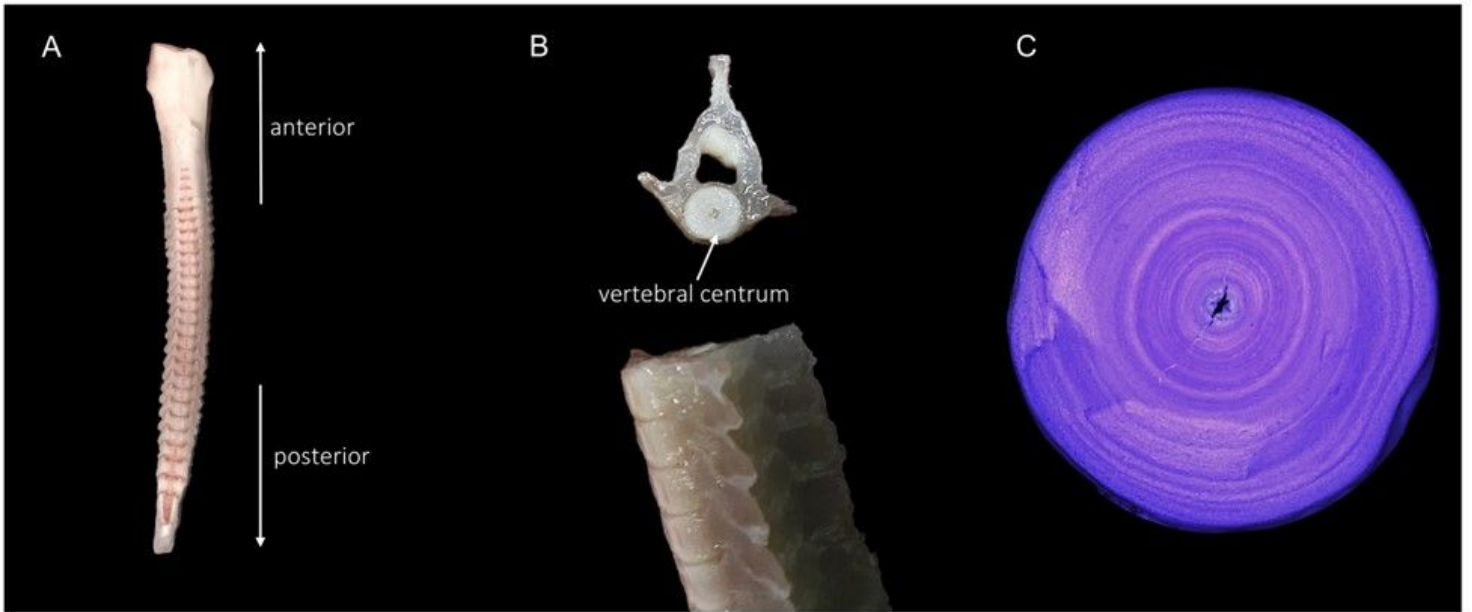
Sampling locations based on the end coordinates (longitude, latitude) per haul. With 7.d, ICES Area Eastern English Channel; 4.c, ICES Area Southern North Sea. Symbols indicate the hauling positions of the sampling trips per month (November 2020, December 2020, August 2021). Samples were obtained offshore the Belgian, English, and French coasts. Map created in Rstudio.



**Figure 2**

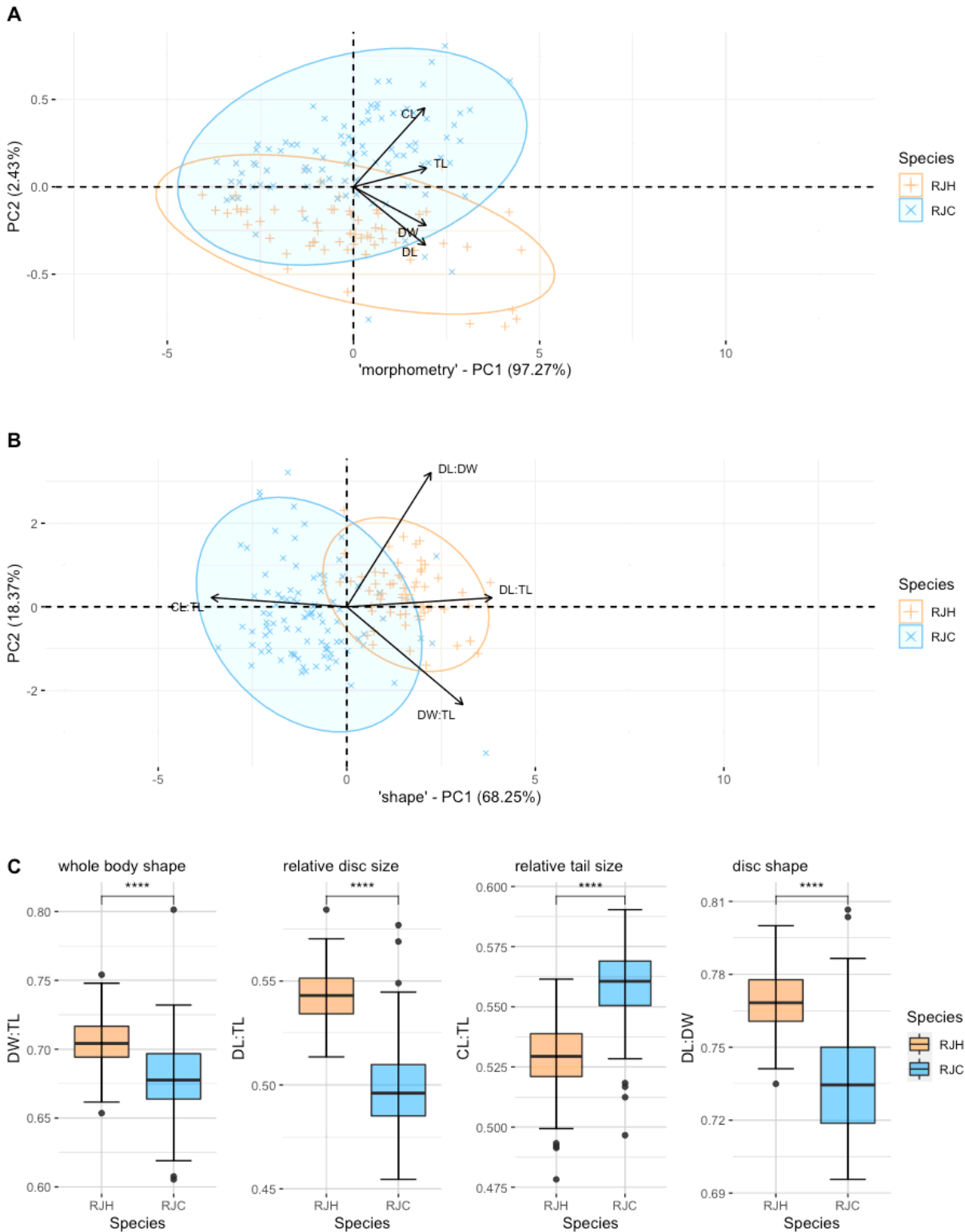
Morphometric measurements recorded on linear axes of each skate, indicated on blonde ray, *Raja brachyura*. With total length (TL), distance from tip of the snout to the end of the tail; disc width (DW), maximal distance between the tips of the pectoral fins; disc length (DL), distance from tip of the snout to the posterior edge of the disc formed by the pectoral fins; caudal length (CL), distance from anterior part of the cloacal opening to the tip of the tail.





**Figure 3**

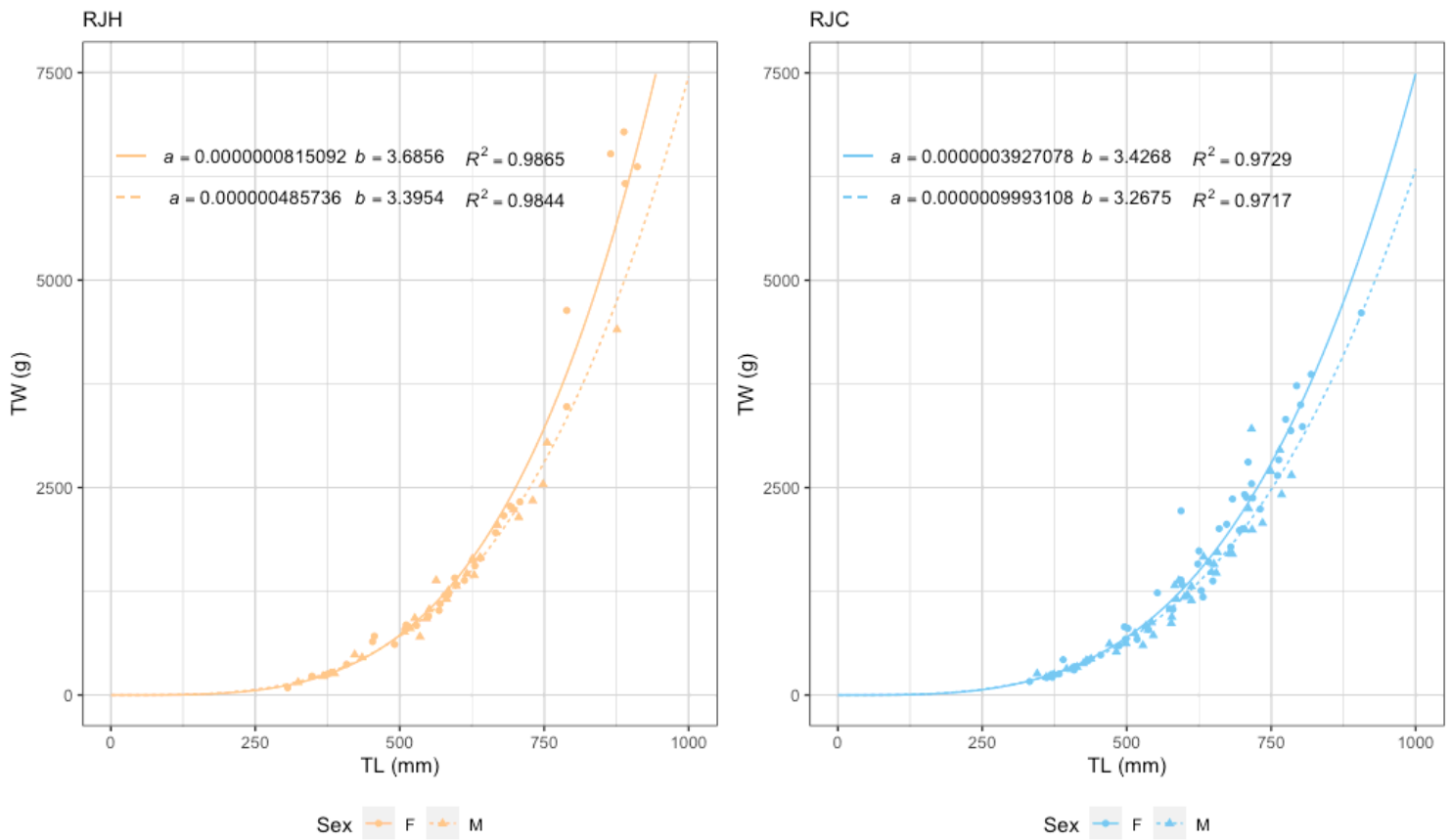
Age assessment procedure following the ILVO protocol for age assessment in chondrichthyan fish. With A, vertebral column of blonde ray, *Raja brachyura*; B, most anterior vertebra separated from the vertebral column with indication of the vertebral centrum; C, Photomicrograph of a vertebral centrum from *R. brachyura* etched in 5% EDTA, stained in 0.01% crystal violet, after focus correction in SmartLab.



**Figure 4**

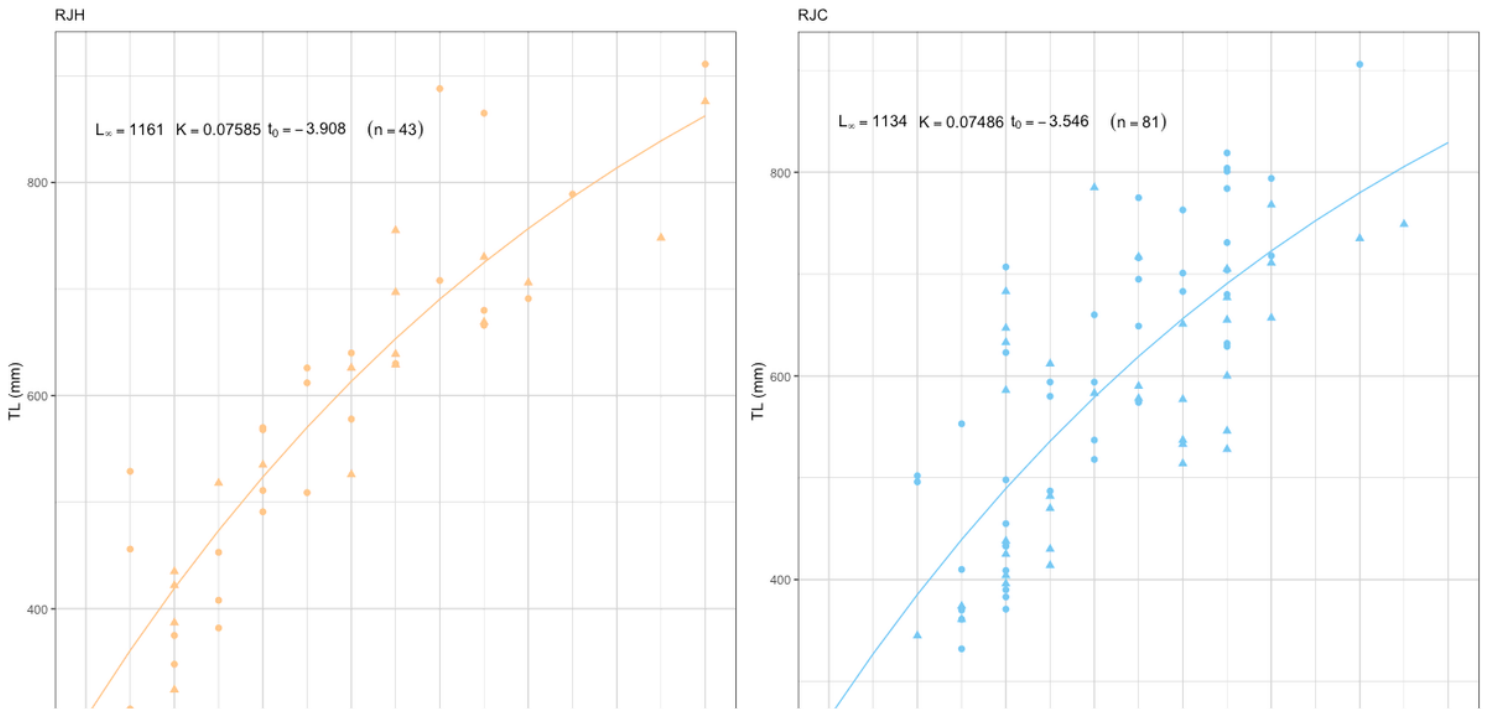
Variation in morphometry between species. A, Biplot of morphometric measurements of size following Principal Component Analysis (PCA); B, Biplot of morphometric shape descriptor ratios following PCA; C, Boxplots of morphometric shape descriptor ratios per species (statistical entries: maximum, third quartile, median, first quartile, minimum, outliers) with indication of statistical significance following unpaired t-

tests. Colors and symbols denote species identity (RJH, *Raja brachyura*; RJC, *R. clavata*). With TL, total length, DW, disc width, DL, disc length, CL, caudal length.



**Figure 5**

Length-weight relationship models of *Raja brachyura* (RJH) and *R. clavata* (RJC) by sex (F, female; M, male), following the equation  $TW = a TL^b$  estimated by the formula of Le Cren (1951). With TW, total weight in g; TL, total length in mm;  $a$ , initial growth coefficient/condition factor;  $b$ , growth rate;  $R^2$ , multiple R-squared to assess model fit.



**Figure 6**

length-at-age data for total length (mm) by species (RJH, *Raja brachyura*; RJC, *R. clavata*) per sex (symbols). With the von Bertalanffy growth model and parameters, estimated by nonlinear regression:  $L_t$ , the estimated total length at age  $t$  (mm);  $L_{\infty}$ , the theoretical maximum total length (mm);  $K$ , the Brody growth rate coefficient ( $\text{yr}^{-1}$ );  $t_0$ , the theoretical age at which total length equals zero (yrs). Ages based on visual inspection of the growth bands on stained vertebral centra.