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Lengths at maturity and conversion factors for skates (Rajidae) around the British Isles, with an analysis of data in the literature

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Biological data on skates (Rajidae) from around the British Isles were collected between 1992 and 2010. The relationship between total length and weight for nine species (*Amblyraja radiata*, *Dipturus batis*-complex, *Leucoraja fullonica*, *L. naevus*, *Raja brachyura*, *R. clavata*, *R. microocellata*, *R. montagui*, and *R. undulata*) are provided for each sex and ICES ecoregion (when significantly different). Conversion factors for disc width to total length are provided. The lengths at first maturity and of the largest immature skates are reported for each sex, and the lengths at 50% maturity are estimated. Spatial differences in the length at maturity of *R. clavata* (females only) and *L. naevus* (both sexes) were observed. The lengths at maturity are discussed in relation to the results of earlier studies, and methodological differences are considered to have influenced reputed decreases in the length at maturity. A more standardized approach to collecting and reporting maturity information is required if potential spatial differences and temporal changes are to be investigated.

Keywords: Batoidea, length–weight, life history, Rajiformes, reproductive biology.

Introduction

Skates (Rajidae) are vulnerable to overfishing because they are long-lived, slow-growing, late to mature, have protracted breeding cycles, and produce few young, which, coupled with their generally large size, morphology, and aggregating nature renders them susceptible to capture in many fisheries (Ellis *et al.*, 2010). Although the issue is now widely recognized by fisheries managers, it should also be noted that concerns over skate stocks in northern Europe were expressed early in the 20th century. For example, Howell (1921), and Steven (1932) both held concerns over localized and regional declines in skate stocks, and about the accompanying lack of both biological and ecological knowledge of the various species. By the 1970s, Holden (1977) questioned whether elasmobranch fisheries were sustainable, given the species' biology and susceptibility to capture, and suggested that skate stocks had not been replacing themselves for 15–20 years. This insightful work provided the catalyst for increased biological studies on elasmobranchs, with the importance of key life-history parameters recognized as essential for fisheries assessment and management, and ultimately the sustainable exploitation of elasmobranchs.

Species that attain and mature at a large body size are typically less resilient to overexploitation (Holden, 1977; Brander, 1981), because such characteristics are often associated with slow rates of population growth. Hence, the depletion of some larger species of skate may allow smaller sympatric species, which may grow faster and mature earlier, to increase in relative terms. Dulvy and Reynolds (2002) reported that extirpated skates tended to have a large body size, as seen in the extirpation of the common skate complex *Dipturus batis* from the Irish Sea (Brander, 1981; *Dipturus batis* is now recognized as two species, *Dipturus* cf. *intermedia* and *Dipturus* cf. *flossada*; Iglésias *et al.*, 2010), and white skate *Rostroraja alba* from the English Channel (Rogers and Ellis, 2000; Ellis *et al.*, 2010). The barndoor skate *Dipturus laevis* was also thought to have declined dramatically in the Northwest Atlantic (Casey and Myers, 1998), although more recent investigations into the life-history parameters of this species have shown that it may be more resilient to overfishing than previously thought (e.g. Gedamke *et al.*, 2009).

Improved biological knowledge, including length–weight and total length–disc width conversion factors, are needed to support the assessment and management of skate fisheries. Such conversion factors are required to estimate the weights of fish measured in market sampling and on board commercial fishing vessels. Additionally, weight-at-size conversion factors can be used in recreational fisheries, if anglers are to return fish alive (Kohler *et al.*, 1995). Similarly, total length-disc width conversions are needed when a specimen has a damaged tail or is sampled in a state already processed for market. The ICES Working Group on Elasmobranch Fishes (WGEF) collated a variety of conversion factors for elasmobranchs (ICES, 2007), although data for some factors were limited for several of the skates in UK waters.

Length at maturity is another key biological parameter given that it is fundamental to the application of demographic and other assessment models, and can be used in helping to inform on size restrictions (Caddy and Mahon, 1995). Examination of the spatial differences in life-history parameters can also be used to better ascertain potential stock boundaries (Pawson and Ellis, 2005), and knowledge of temporal changes in such parameters can help inform on potential fishing impacts.

Overexploitation of fish can lead to density-dependent changes in certain life-history characteristics (Fahy, 1989a), and in some elasmobranch populations, density-dependent regulation can be achieved by compensatory increases in fecundity and growth rate, and a reduced length at maturity (Ellis and Keable, 2008). Reduced size at maturity, potentially in response to fishing pressure and decreases in population size, have been discussed for several elasmobranchs, including spurdog, *Squalus acanthias*, and yellownose skate, *Dipturus chilensis* (Sosebee, 2005; Paesch and Oddone, 2008). However, because of the sporadic nature of many biological studies of elasmobranchs, and because sources of biological material and methods are often different between disparate studies, relating observed temporal differences in life-history parameters to the effects of overexploitation can be problematic (Ellis and Keable, 2008).

The present study provides information on the length–weight and total length–disc width relationships for the main skate species found over the continental shelf of the British Isles, including starry ray, *Amblyraja radiata*, the *Dipturus batis*-complex, shagreen ray, *Leucoraja fullonica,* cuckoo ray, *Leucoraja naevus*, blonde ray, *Raja brachyura*, thornback ray, *Raja clavata*, small-eyed ray, *Raja microocellata*, spotted ray, *Raja montagui*, and undulate ray, *Raja undulata*. The observed lengths at first maturity and largest immature fish found are given, and the lengths at 50% maturity (L_{50}) are estimated.

Material and methods

Field studies and biological sampling

Skates were caught during groundfish surveys in the North Sea, English Channel, Irish Sea, Bristol Channel, and Celtic Sea during bottom trawl surveys by RVs "Corystes", "Cirolana", and "CEFAS Endeavour". Data collection started on some surveys in 1992, but >80% of the records were collected after 2000. Additional data on the length at maturity of *R. clavata* were collected from commercial fishing vessels during a UK Fishery Science Partnership (FSP) project collecting information on this species in the southern North Sea (Ellis *et al.*, 2008). Additional data on total length–disc width and length at maturity were also available for *R. undulata*, *R. brachyura*, and the *Dipturus batis*-complex from ongoing field studies on skate discard survival. The surveys used in the study are summarized in Table S1.

Total length (L) was measured from the tip of the snout to the end of the tail (unless damaged) and rounded down to the cm below, and total weight (W) was recorded to the nearest 1 g (juveniles) or 5 g (larger individuals). At the start of the period, data on disc width (D) were also collected, but in recent years this information has only been collected for larger fish and/or less abundant species.

Maturity scale

All skate were classified as immature (A), maturing (B), mature (C), or active (D), according to the maturity key given in Table 1. Only fish at Stages C and D are considered to be mature (i.e. capable of reproducing). Male maturity was usually assigned based on clasper state. For specimens where the external observation of clasper state was felt to be inconclusive (e.g. for fish that may or may not have reached Stage C), those fish were dissected and the internal reproductive organs examined to gauge maturity more accurately.

Female maturity was assigned based on examination of internal reproductive organs. In recent years, however, females of either <40 cm (*R. montagui* and *L. naevus*), <45 cm (*R. clavata*), or <55 cm (*L. fullonica*, *R. brachyura*, *R. microocellata*, and *R. undulata*) are not usually examined if alive, and are assumed to be immature (based on preliminary observations of the data shown here). Different states of egg-case formation were not recorded because very few active females were observed during surveys, either because the surveys were conducted outside the main spawning season and/or away from the spawning grounds.

Quantitative data to validate the maturity stage information (e.g. clasper length for males, oviducal gland width for females) were not collected owing to time constraints. Similarly, although estimates of fecundity are needed for many species of skate, there is currently no resource to allow for the collection, preservation, and subsequent laboratory examination of skate ovaries, and this was not undertaken.

Data analysis

Maturity data and length–weight data were collated by species, sex, and ICES ecoregion. Generalized linear models (GLMs) were used to investigate the length–weight relationship and the proportion of fish mature at length. To maximize wider utility of these data, sex was always disaggregated in these analyses, and potential spatial differences (by ecoregion) were examined for the three most abundant species (*L. naevus*, *R. clavata*, and *R. montagui*).

Initially, a sex-disaggregated length–weight relationship:

$$W = aL^b$$

was fitted for each species, combining both ecoregions. The function was log-transformed so that a linear regression could be fitted. To investigate whether this relationship varied between ecoregion, a GLM was used to fit the length–weight relationship with ecoregion as an interaction. The errors were assumed to be Gaussian. The fitted parameters (a and b), sample size, length range, and significant differences between parameter values were returned for each ecoregion (Table 2, Supplementary Table S2). The sample sizes included in Table 2 cannot be used to examine the sex ratio, because some studies (e.g. tagging programmes) only provided maturity information for male skate.

The linear relationship between total length and disc width was calculated according to the equation

$$D = aL + b$$

(Table 3). Data were not separated into ecoregions, because data for most species (except *A. radiata*) were for the Celtic Seas ecoregion.

Table 1. Maturity scale used for skates in the present study.

Maturity stage	Males	Females
A (Immature)	Claspers undeveloped, shorter than extreme tips of posterior margin of pelvic fin. Testes small and thread-shaped.	Ovaries small, gelatinous, or granulated, but with no differentiated follicles visible. Oviducts small and thread-shaped, width of oviducal gland not much greater than the width of oviduct.
B (Maturing)	Claspers longer than posterior margin of pelvic fin, their tips more structured, but claspers soft and flexible and cartilaginous elements not hardened. Testes enlarged, sperm ducts beginning to meander.	Ovaries enlarged and with more transparent walls. Follicles differentiated in various small sizes (ca. <5 mm). Oviducts small and thread-shaped, width of oviducal gland greater than width of the oviduct, but not hardened.
C (Mature)	Claspers longer than posterior margin of pelvic fin, cartilaginous elements hardened, and claspers stiff. Testes enlarged, sperm ducts meandering and tightly filled with sperm.	Ovaries large with enlarged follicles (ca. >5 mm), with some very large, yolk-filled follicles (ca. 10 mm) also present. Uteri enlarged and wide, oviducal gland fully-formed and hard.
D (Active)	Clasper reddish and swollen, sperm present in clasper groove, or flowing if pressure exerted on cloaca.	Egg-capsules beginning to form in oviducal gland, partially visible in uteri, or egg-capsules fully-formed and hardened and in oviducts/uteri, or egg-case being exuded from cloaca.

The relationship between the proportion of fish mature at length was also investigated (Table 4, Supplementary Table S3) through a GLM model where the error distribution and link function were binomial (Crawley, 2007). The numbers of mature and immature fish at length were used to model the proportion of mature fish using a logistic model as a function of length, x, as:

$$p = e^{a+bx}/1 + e^{a+bx}$$

Therefore, $\ln(p/q) = a + bx$,
where p is the proportion of mature fish, and $q = 1 - p$, the proportion of immature fish. This gives a linear predictor, $a + bx$, for the logit transformation of p, $\ln(p/q)$. A linear regression was not used because as data analyses were weighted by sample size, there may have been non-constant binomial variance, and linear regression can predict values outside the range 0–1.

Additionally, analyses were examined in relation to overdispersion where, in general, the residual scaled deviance should be roughly equal to the residual degrees of freedom. Data were separated by sex and then into mature and immature skates, with one dataset for combined ecoregions, and a second dataset that kept them separate to identify any potential significant differences in the length at maturity between ecoregions.

Initially, a GLM was used to fit the mature and immature numbers against length, with ecoregion not considered as a factor. A function was written to fit the GLM on subsets of the data, i.e. by species and sex. The function returned the parameters of the fit and their significance, the Akaike information criterion (AIC), the log-likelihood, the number of observations, and the estimated L_{50} (Supplementary Table S3). Subsequently, another GLM function was written that used ecoregion as an interaction with length. This was analysed for three species (*R. clavata*, *R. montagui*, and *L. naevus*), because there were sufficient data for both ecoregions. Where the interaction was significant, two b parameters were produced (one for each ecoregion), though the intercept parameter (a) was not fitted separately for each ecoregion, thus yielding different relationships between the proportion mature at length for each ecoregion. The significance level was set at 0.05. Model fitting was carried out in the statistical environment R v.2-13.2 (R Development Core Team, 2011).

Results

Length–weight and total length–disc width relationships

Total weight and total length were strongly correlated for all species ($r^2 \geq 0.95$). The constants required for the conversion of these measurements are listed in Table 2. The results of the GLM, using ecoregion as a factor, indicated that there was a significant difference in weight at a given length for *R. clavata*, with fish from the Celtic Seas ecoregion significantly heavier than in the North Sea ecoregion. No significant spatial differences in the length–weight relationship were observed in *R. montagui* and *L. naevus*.

Total length and disc width were also highly correlated for all species ($r^2 \geq 0.94$), and the constants required for the conversion of these measurements are given in Table 3.

Table 2. Length–weight relationships and length at maturity for skates (Rajidae) around the British Isles for each sex and ICES ecoregion, where significantly different (marked in bold).

Species	Ecoregion	Number of fish used in length–weight calculation (length range)		Total weight and total length ($W = aL^b$)						Number of fish used for maturity studies (number of mature fish)		First maturity		Largest immature		50% mature (L_{50})	
				Male			Female										
		Male	Female	a	b	r^2	a	b	r^2	Male	Female	Male	Female	Male	Female	Male	Female
A. radiata	North Sea	426 (8–49)	446 (8–49)	0.008 4	3.004	0.96	0.011 4	2.915	0.95	426 (181)	446 (148)	30	32	44	46	36.2	38.4
D. batis-complex	Combined	30 (20–118)	32 (19–135)	0.004 1	3.123	0.95	0.002 6	3.222	0.99	30 (2)	32 (2)	115	125	98	97	–	–
L. fullonica	Combined	17 (21–96)	17 (24–70)	0.001 4	3.317	0.99	0.003 6	3.075	0.98	17 (2)	17 (0)	75	–	82	–	–	–
L. naevus	Combined	943 (11–72)	948 (10–69)	0.004 1	3.105	0.99	0.003 5	3.147	0.99	944 (128)	948 (75)	48	45	64	65	56.4	59.4
	Celtic Seas	834 (11–72)	819 (10–69)	0.004 1	3.105	0.99	0.003 6	3.147	0.99	835 (100)	819 (61)	49	51	64	65	**57.3**	**59.8**
	North Sea	109 (17–63)	129 (15–62)	0.003 2	3.161	0.99	0.003 0	3.183	0.97	109 (28)	129 (14)	48	45	57	58	**50.8**	**53.6**
R. brachyura	Combined	357 (13–100)	386 (12–102)	0.002 7	3.256	0.99	0.002 6	3.271	0.99	359 (25)	387 (17)	55	60	91	93	78.0	83.4
R. clavata	Combined	3 123 (10–94)	3 073 (10–98)	0.004 6	3.082	0.99	0.003 7	3.148	0.99	5 917 (1 119)	3 229 (206)	47	47	88	90	66.6	76.6
	Celtic Seas	2 427 (10–89)	2 368 (10–98)	**0.004 2**	**3.106**	0.99	**0.003 6**	**3.162**	0.99	2 427 (276)	2 368 (107)	56	47	76	90	–	**78.2**
	North Sea	696 (13–94)	705 (13–92)	**0.006 1**	**3.003**	0.99	**0.004 6**	**3.090**	0.99	3 490 (843)	861 (99)	47	57	88	82	–	**73.7**
R. microocellata	Combined	703 (13–80)	733 (12–85)	0.003 2	3.195	0.99	0.002 8	3.248	0.99	705 (65)	733 (26)	66	73	74	83	68.9	77.9
R. montagui	Combined	1 900 (10–67)	1 775 (10–76)	0.004 2	3.100	0.99	0.003 1	3.194	0.99	1 911 (310)	1 775 (84)	40	49	66	70	50.9	62.5
R. undulata	Combined	58 (22–89)	33 (17–60)	0.003 5	3.162	0.99	0.004 3	3.112	0.99	85 (28)	34 (1)	80	79	88	83	82.3	NA

Table 3. Relationship between total length (*L*) and disc width (*D*) for nine species of skate, where $D = aL + b$, and sample size (*n*), length range examined, and correlation coefficient.

Species	*n*	Length range (cm)	*a*	*b*	r^2
Raja brachyura	401	12–105	0.712 5	−0.328 8	0.99
Raja clavata	1 962	11–96	0.657 2	0.909 5	0.98
Raja microocellata	477	12–83	0.719 3	−0.900 8	0.99
Raja montagui	1 141	10–69	0.660 5	0.284 1	0.99
Leucoraja naevus	596	10–67	0.584 0	−1.005 0	0.99
Amblyraja radiata	486	8–49	0.659 2	0.087 3	0.94
Raja undulata	331	35–100	0.564 8	4.713 0	0.97
Leucoraja fullonica	25	24–96	0.623 9	−2.644 0	0.99
Dipturus batis-complex	37	44–130	0.677 1	3.268 7	0.97

Table 4. GLM results from fitting the proportion of fish mature to length, with ecoregion as an interaction, and significance level set at 0.05.

Species	Sex	*a*	*b* (combined)	*b* (CS)	*b* (NS)	*p*-value	L_{50} (combined)	L_{50} (CS)	L_{50} (NS)	AIC	*n*
R. clavata	M	−23.096	0.349	NA	NA	0.17	66.161	NA	NA	234.390	5 917
	F	−19.161		0.245	0.260	0.00		78.17	73.67	168.095	3 229
R. montagui	M	−16.976	0.334	NA	NA	0.39	50.818	NA	NA	182.142	1 911
	F	−14.202	0.227	NA	NA	0.91	62.490	NA	NA	125.636	1 775
L. naevus	M	−18.668		0.326	0.367	0.00		57.34	50.81	90.823	944
	F	−22.193		0.371	0.414	0.00		59.80	53.62	84.707	948

NA = the interaction was not significant and results were combined across ecoregions (CS = Celtic Seas ecoregion, NS = North Sea ecoregion).
AIC = Akaike information criterion, which measures the goodness-of-fit.
n = number of observations.

Length at maturity

Maturity data were analysed for the seven most commonly caught species of skate (Tables 2 and 4, Figures 1–3), and descriptive notes are provided for the less frequent species.

Raja brachyura

This was one of the larger skate species routinely sampled during surveys and, although fish of up to 108 cm total length were caught, data were limited for large fish. The lengths at first maturity were 55 cm and 60 cm for males and females, and L_{50} was reached at 78.2 cm and 85.6 cm, respectively (Figure 1a and b). The largest immature *R. brachyura* were 91 cm (male) and 93 cm (female). There were insufficient data to investigate spatial differences in length at maturity.

Raja clavata

Across all areas, female *R. clavata* first matured at 47 cm and L_{50} was estimated at 75.1 cm. First maturity in males was also 47 cm, although L_{50} was attained at a smaller length (66.5 cm). The largest immature female and male measured 90 and 88 cm, respectively. The GLM indicated a significant difference in the length at maturity of females between the two ecoregions, and L_{50} for females from the North Sea was 4.5 cm less than in the Celtic Seas (Figure 1c and d; Table 4).

Raja microocellata

The smallest mature male and female observed were 66 cm and 73 cm, respectively, with L_{50} at 69.0 cm (males) and 77.1 cm (females; Figure 1e and f). The largest immature fish were 74 cm (male) and 83 cm (female). Only a few *R. microocellata* were caught in the North Sea ecoregion, and sample sizes of mature fish (especially females) were small.

Raja montagui

The smallest mature male and female observed were 40 cm and 49 cm, respectively, and, whereas L_{50} for males was 50.3 cm, that for females was only reached at 64.0 cm (Figure 2a and b). The largest immature males and females were 66 cm and 70 cm, respectively. There were no significant differences in length at maturity between ecoregions. The outlying points for male maturity (Figure 2b) resulted from low sample sizes at certain lengths.

Leucoraja naevus

Males and females first matured at 48 cm and 45 cm, respectively, and L_{50} was at 56.3 cm and 59.4 cm (Figure 2c and d). The largest immature males and females were 64 cm and 65 cm. The GLM highlighted a significant difference in the L_{50} for both males and females between ecoregions, with female and male *L. naevus* in the North Sea being 6.2–6.5 cm less than in the Celtic Seas (Table 4).

Amblyraja radiata

This was the smallest species sampled in the study, and was only captured in the North Sea. The largest fish were 49 cm long, and length at first maturity was ~30 cm and 32 cm for males and females. The L_{50} values for males and females were 36.2 cm and 38.2 cm, respectively (Figure 2e and f). The largest immature fish were 44 cm (male) and 46 cm (female).

Raja undulata

Data were limited for this species, so the data provided here should be viewed as preliminary. The lengths at first maturity were broadly similar in both sexes (80 cm and 79 cm in males and females, respectively). L_{50} was estimated at 83 cm for males (Figure 3), but no reliable estimate of this parameter was possible

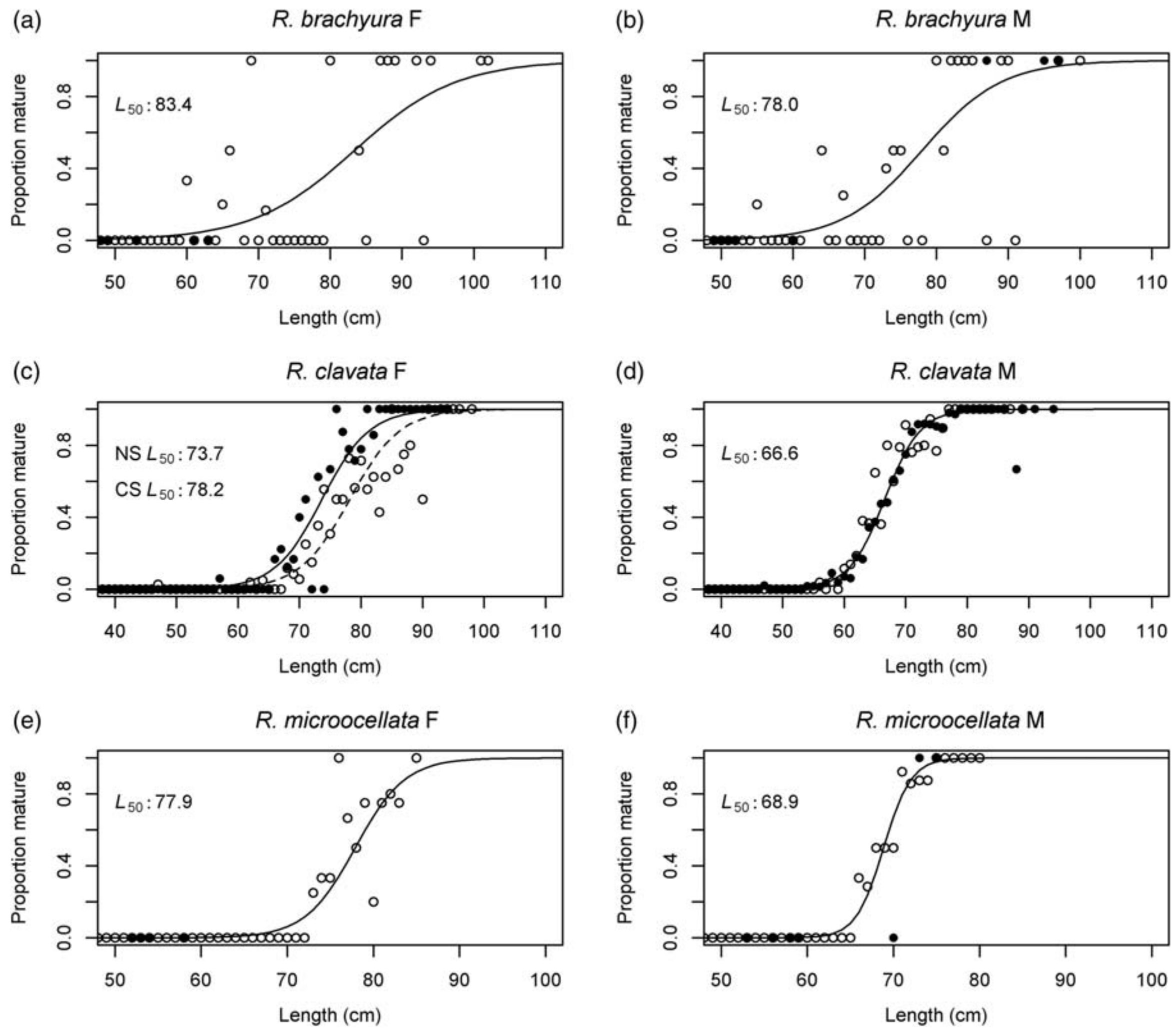

Figure 1. Proportion of mature (a) female and (b) male *R. brachyura*, (c) female and (d) male *R. clavata*, and (e) female and (f) male *R. microocellata*. Data from Celtic Seas ecoregion (open symbols) and North Sea ecoregion (filled symbols) were combined when fitting the GLM (solid line) in all plots apart from female *R. clavata*, (c), where ecoregion was found to be a significant factor [Celtic Sea (CS, open symbols dashed line) and North Sea (NS, filled symbols and solid line)].

for females, given the small overall sample size ($n = 45$) and very low numbers of mature fish.

Other species

Limited data were available for *L. fullonica* and the *Dipturus batis*-complex and, given uncertainty in their general biology, only qualitative information on their maturity status can be provided. There were 34 records of *L. fullonica* in the database (all but three of which were from the Celtic Sea), 17 males (21–96 cm) and 17 females (24–70 cm). All 17 females were immature, but two of the larger males (75 and 96 cm) were mature (Stage C); the largest immature male was 82 cm.

There were 62 records of the *D. batis*-complex, and all but one of these were from the Celtic Sea; samples are most likely to refer to *D.* cf. *flossada* (Griffiths *et al.*, 2010). There were 32 females (length range 19–135 cm), of which only two were mature (a fish 125 cm long at maturity Stage C, and a 135 cm fish at Stage D), and all the others (up to 97 cm) were immature. Of the 30 males (length range 20–118 cm), the two largest (115–118 cm) were mature (Stage C), and the others (up to 98 cm) were immature.

Discussion

Length–weight and total length–disc width conversion factors

The present study provides the most recent length–weight data for the species around the British Isles, with large sample sizes, and these data are also categorized according to sex and ecoregion (if significant differences were observed). In earlier studies, Holden (1977) provided length–weight relationships for *R. brachyura*, *R. clavata*, *R. montagui*, and *L. naevus*, and Ryland and Ajayi (1984) gave length–weight relationships for *R. clavata*, *R. microocellata*, and *R. montagui*. Length–weight relationships for all these species and for *R. undulata* were reported for the Bay of Biscay, English Channel, and Celtic Sea by Dorel (1986), but data were combined for both sexes and, with the exception of *R. undulata*, the sample sizes were smaller than in this study. More recently, Coull *et al.* (1989) provided length–weight information for *R. clavata*, *R. montagui*, and *L. naevus* in Scottish waters, but data were limited by sample size and/or size range of fish examined. Other conversion factors (including gutted-weight and wing-weight relationships) were given by Bedford *et al.*

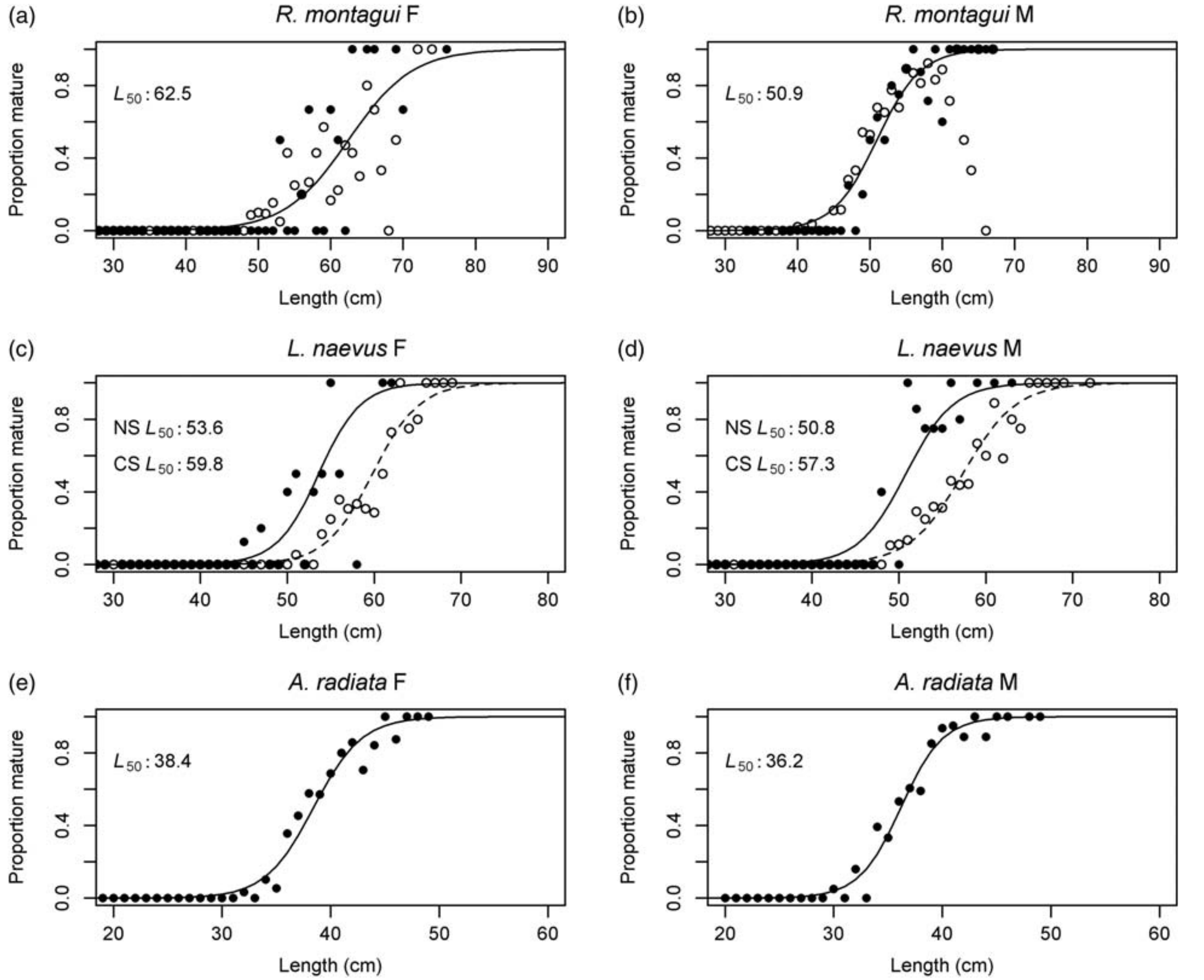

Figure 2. Proportion of mature (a) female and (b) male *R. montagui*, (c) female and (d) male *L. naevus*, and (e) female and (f) male *A. radiata*. Data from Celtic Seas ecoregion (open symbols) and North Sea ecoregion (filled symbols) were combined when fitting the GLM (solid line) in all plots apart from female and male *L. naevus*, (c and d), where ecoregion was found to be a significant factor [Celtic Sea (CS, open symbols dashed line) and North Sea (NS, filled symbols and solid line)].

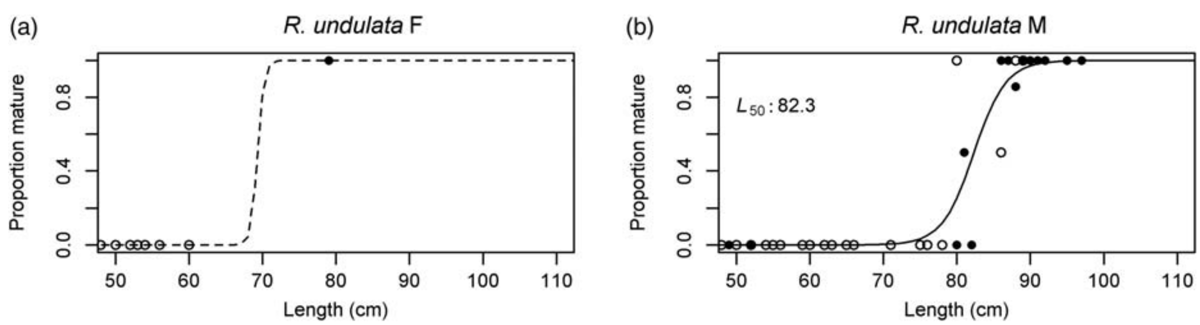

Figure 3. Proportion of mature (a) female and (b) male *R. undulata*. Celtic Seas ecoregion (open symbols) and North Sea ecoregion (filled symbols) were combined when fitting the GLM (solid line). For female *R. undulata*, (a), the GLM algorithm did not converge due to lack of data and no reliable estimate of L_{50} can be given. The dashed line in (a) is therefore only a guide.

(1986) for *R. clavata*, *R. brachyura*, *R. montagui*, *A. radiata*, and *L. naevus*.

The length–weight relationships for the three most abundant species (*R. clavata*, *R. montagui*, and *L. naevus*) were compared by ecoregion, but significant spatial differences in this relationship were only observed for *R. clavata*. This may be due to the smaller sample size (especially for larger fish) in the North Sea. However, most data for the North Sea ecoregion were collected during July

Table 5. Summary table for earlier estimates of length at maturity for *Raja clavata*, with values estimated from the disc width (using the relationship in Table 3) denoted by an asterisk. Values in square brackets indicate approximate lengths at maturity.

Area (and ICES Division)	Sex	*n*	Length range examined (cm)	Length (cm) at First maturity	Length (cm) at 50% maturity (L_{50})	Source
Plymouth (VIIe)	M	–	17–92*	74.7*	76.2–82.3*	Steven (1934)
	F	–	17–129*	97.5*	99–105*	
Irish waters (VIIb)	M	386	39–83	56–64*		Fitzmaurice (1974)
	F	331	40–88	67.8–75.5*		
Solway Firth (VIIa)	M	271	18.4–101.6	61.8	–	Nottage and Perkins (1983)
	F		32.5–102.1	62.4	–	
Bristol Channel (VIIf)	M	1 019	13–99.0	60.5	–	Ryland and Ajayi (1984)
	F	1 124		59.5	–	
English Channel (VIId-e)	M	960	10–101	80	–	Dorel (1986)
	F			95	–	
Bay of Biscay (VIII)	M	23	11–98	80	–	Dorel (1986)
	F			95	–	
North Sea (IV)	M	41	ca. 20–90		67.9	Walker (1999)
	F	52			77.1	
Irish waters (VIIa)	M	165	ca. 17–92	61	65.7	Gallagher *et al.* (2005)
	F	90		58	71.8	
North Wales (VIIa)	M	54	ca. 27–78	–	58.8	Whittamore and McCarthy (2005)
	F	135	ca. 18–92	–	70.5	
Portugal (IX)	M	906	12.5–105.0	59.0	67.6	Serra-Pereira *et al.* (2011)
	F	861	13.8–96.5	69.9	78.4	
Tunisia	M	–	–	[75]		Capapé (1976)
	F	–	–	[85]		
Southern France	M	120	15.4–76.2	62.5		Capapé *et al.* (2007)*
	F	137	15.4–103.6	80.8		
Sicily	M	712	–	57–59		Cannizzaro *et al.* (1995)
	F	763	–	77–79		
Adriatic Sea	M	–	–	[55–60]		Jardas (1973)
	F	–	–	[80–85]		
	M	183	12–95	47	59.3	Krstulović Šifner *et al.* (2009)
	F	181		47.5	61.2	
Black Sea	M	52	34–95	–	64.0	Demirhan *et al.* (2005)
	F			–	66.7	
	M	99	14.3–92.0	68.0	71.8	Saglam and Ak (2011)
	F	131	15.6–93.0	72.0	74.6	

and August, which is after the main spawning season (Holden, 1975), whereas data for the Celtic Seas ecoregion mostly originated from surveys in either March or from September to December, and so temporal factors may also have influenced this result.

There were close relationships between total length and disc width for all species. Although there are no national or EC minimum or maximum size limits for rajids, local bylaws in some English and Welsh inshore waters provide a minimum landing size (MLS) of 40–45 cm disc width for skates, and these are enforced by Inshore Fisheries Conservation Authorities (IFCAs). On average, a disc width of 40–45 cm equated to estimated total lengths of 61.0–68.7 cm, although there were species-specific differences in the total length-disc width relationship. For example, *L. naevus* has a narrower disc than the other species studied, and a disc width of 40–45 cm would correspond to an estimated length of 70.2–78.8 cm, beyond the maximum length of the species. In contrast, *R. brachyura* at 40–45 cm disc width are ~56.6–63.6 cm long. Hence, if generic minimum landing sizes were implemented for all species of skate, this would result in increased discarding of some species and may not benefit larger skate species, such as the *D. batis*-complex, *R. undulata*, or *R. brachyura*, which mature at a much larger size. In fact, the only species that attained L_{50} by 41 cm disc width (lengths estimated from Table 3 and compared with L_{50} as given in Table 2) were *A. radiata*, *L. naevus*, and male *R. montagui*.

Length at maturity

The lengths at maturity for selected species of skate around the British Isles, as reported in previous studies, are summarized in Tables 5 and 6. The L_{50} values for most of the species examined tended only to show subtle differences from values reported in earlier studies.

Only preliminary maturity estimates are available for *R. brachyura*, as few mature fish were caught. *R. brachyura* and *R. montagui* can be confused, and so it is possible that some of the smaller mature fish may have resulted from occasional misidentifications. The current analysis however gives increased weight to larger sample sizes at each length, and so potential outlying data points will not unduly influence the ogive and estimates of L_{50} if based on low sample sizes. Although the current estimates

Table 6. Summary table for the length (cm) at maturity for skate species around the British Isles from earlier studies. Values in square brackets indicate approximate lengths at maturity.

Species	Area	Sex	*n*	Length range examined (cm)	Length (cm) at		Source
					First maturity	50% maturity (L_{50})	
A. radiata	North Sea	M	273	ca. 10–54	–	39.6	Walker (1999)
		F	323		–	39.5	
L. naevus	North Sea	M	51	ca. 30–65	–	55.0	Walker (1999)
		F	62		–	55.0	
	Celtic Sea	Combined	276	13–70	60	–	Dorel (1986)
		F	–	–	–	[59]	Du Buit (1976)
	Irish waters	M	353	ca. 13–70	52	56.9	Gallagher *et al.* (2005)
		F	191		49	56.2	
R. brachyura	English Channel	Combined	100	17–105	100	–	Dorel (1986)
	Irish waters	M	123	ca. 15–103	75	81.9	Gallagher *et al.* (2005)
		F	61		81	83.6	
R. microocellata	Bristol Channel	M	1218	14–90.6	58.0	–	Ryland and Ajayi (1984)
		F	1374		57.5	–	
	English Channel	Combined	97	15–87	70	–	Dorel (1986)
R. montagui	Irish waters	M	274	ca. 17–67	48	53.7	Gallagher *et al.* (2005)
		F	175		52	57.4	
	North Sea	M	87	ca. 25–70	–	56.7	Walker (1999)
		F	80		–	62.2	
	English Channel	Combined	81	ca. 12–70	60 (Male) 65 (Female)	–	Dorel (1986)
	Bristol Channel	M	986	12–72.9	56.2	–	Ryland and Ajayi (1984)
		F	1019		57.3	–	

compared well with previously reported values (Gallagher *et al.*, 2005), dedicated studies to better elucidate the length at maturity for this species are required, particularly in the case of large females.

More data were available for *Raja clavata* (Table 5 and references therein). The present study indicated that there were significant spatial differences in the L_{50} value of female *R. clavata*, although this was not apparent in males. The results of the present study for *R. clavata*, which is based on a large sample size and included samples from several areas of abundance (e.g. southern North Sea, Bristol Channel, and Irish Sea), were broadly comparable with several earlier studies (Walker, 1999; Gallagher *et al.*, 2005), but are less than reported by Steven (1934), as discussed further below.

There has been no previous estimate of the L_{50} value for *R. microocellata*, although Ryland and Ajayi (1984) reported the length at first maturity, which for both sexes was lower than recorded here.

The L_{50} for male *R. montagui* was lower than reported previously in the North Sea (Walker, 1999) and Irish Sea (Gallagher *et al.*, 2005), but for females, the present estimate was higher than reported previously in the Irish Sea (Gallagher *et al.*, 2005) and on par with that reported by Walker (1999). The occasional outlying data points for male *R. montagui* from the Celtic Sea were based on very small sample sizes for certain 1 cm length groups. The ogive, however, was more influenced by the larger sample sizes (and 100% maturity) at intervening length groups and from North Sea samples.

The L_{50} values for male and female *L. naevus* were larger in the Celtic Seas than in the North Sea, which may be due to there being different stocks in the two areas, although other investigations to confirm this (e.g. tagging and genetic studies) are required. The L_{50} values in the North Sea were 50.8 cm and 53.6 cm for males and females respectively, slightly less than reported by Walker (1999). Within the Celtic Seas ecoregion, the L_{50} for males and females were 57.3 cm and 59.8 cm, respectively, and these values compare well with the estimate of Du Buit (1976) for the species in the Celtic Sea, but are marginally higher than those reported by Gallagher *et al.* (2005) for the Irish Sea.

Male and female *A. radiata* appeared to have a marginally smaller L_{50} than reported by Walker (1999), but length at maturity in the North Sea is very different from that reported for the same species in the Northwest Atlantic (Templeman, 1987).

Data for *R. undulata* were limited, because few mature fish have been sampled in existing surveys (Ellis *et al.*, 2012), although estimates are available for populations around the Portuguese coast (Moura *et al.*, 2007).

It is uncertain whether the differences in length at maturity noted for various species above are attributable to *bona fide* spatial or temporal differences, or simply reflect subtle differences in sampling (e.g. maturity staging, sample sizes).

It has been suggested that there may have been temporal changes, with a reduced L_{50} in recent times. Steven (1934) suggested that L_{50} was at 66–70 cm and 51–55 cm disc width for females and males, respectively. Converted to length, these maturity estimates are far higher than observed in all subsequent studies (Fitzmaurice, 1974; Nottage and Perkins, 1983; Ryland and Ajayi, 1984; Walker, 1999), leading to some authors questioning whether the length at maturity has decreased over time as a result of fishing pressure (Nottage and Perkins, 1983; Whittamore and McCarthy, 2005). However, Fries *et al.* (1895) stated that a male *R. clavata* "rather more than 60 cm long" had fully-developed claspers, and a fish of that length would likely be smaller than the estimated length of about 75 cm suggested by Steven (1934), who reported that males matured at 51–55 cm disc width.

The L_{50} for *R. clavata* in the present study was larger than reported by Whittamore and McCarthy (2005), probably the result of methodological differences. In recent years, several studies have combined fish at Stage B (maturing) with later maturity stages when estimating the proportion mature (e.g. Whittamore and McCarthy, 2005; Krstulović Šifner *et al.*, 2009). Similarly, Demirhan *et al.* (2005) included females with ovaries containing "eggs greater than 0.5 mm" as mature. That these studies reported lower lengths at maturity than earlier works and the present study would appear to be due to the inclusion of fish that were not fully mature in the proportion mature at length. A more robust and standardized approach to reporting the proportion mature is therefore required.

Some earlier studies on skate maturity have failed to identify clearly either the maturity scale used, or to what the length at maturity referred (i.e. first or 50% maturity). The adoption of standardized maturity scales, as proposed by the Workshop on Sexual Maturity Staging of Elasmobranchs (WKMSEL) (ICES, 2010) could rectify such disparities in future. For comparative purposes, all reports of skate maturity should consistently state the lengths at first and 50% maturity (L_{50}) and the largest immature fish. Although most recent studies on skate maturity have provided information on total sample size, this often includes a disproportionate number of juveniles, and there is rarely an indication of either the number of mature fish observed or the number of fish examined over the length range spanning first to 100% maturity. If published life-history information and maturity data are to be used in stock assessments, it is important that reliable estimates (based on appropriate sample sizes, size ranges and methods) can be identified.

It is often suggested that overexploitation can lead to a reduction in the length at maturity and maximum size. Although it is difficult to ascertain whether the length at maturity for *R. clavata* has decreased, given that the only "evidence" is inferred from the work of Steven (1934), there is little indication of a reduced maximum length. The maximum size of *R. clavata* reported here (98 cm) was similar to that reported by Nottage and Perkins (1983): 102 cm, Ryland and Ajayi (1984): 99 cm, and Fahy (1989b): 101 cm. Although one early published study reported a maximum length of ca. 120 cm (Holt, 1910) (length estimated from disc width), a discard observer trip in 2009 reported one *R. clavata* of 130 cm (Lockley, 2009). Hence, there is little indication of a decrease in the maximum length of *R. clavata* over recent time.

Future studies in the UK

Ongoing fishery-independent surveys, including several that are internationally coordinated, catch relatively high numbers of some of the more widespread skate species (as shown in Table 2), although data are limited for species with patchy distributions. Additionally, catch rates for larger fish and species can also be low in such surveys. In recent years, some skate species, including *R. brachyura*, *R. clavata*, and *R. undulata*, have been subject of more dedicated field surveys. For example, in 2007 and 2008, a UK FSP project used inshore fishing vessels with commercial gears to tag and release *R. clavata* in the Greater Thames Estuary (Ellis *et al.*, 2008). That study provided additional length and maturity information for 2887 fish. Similarly, recent studies on the survival of discarded skates in southwest England have provided more information on larger *R. brachyura* and *R. undulata*. These results highlight the potential value of dedicated surveys for some of the larger-bodied elasmobranchs that can be locally abundant in certain areas, because sample sizes of mature fish in commercial gears and on commercial fishing grounds can be greater than taken in existing groundfish surveys. Dedicated surveys may also be required if detailed information is to be collected for offshore species (e.g. *L. circularis* and *L. fullonica*), given the low catch rates of these species in existing groundfish surveys, and limited information on their movements and life history.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of this manuscript in the form of length–weight relationships and GLM fitting results for proportion of fish mature by length.

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