Age, Growth and Maturity of the Commercial Ray Species from the Irish Sea

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Abstract

The age, growth and maturity of 1 554 individuals (268 *Raja brachyura*, 258 *R. clavata*, 468 *R. montagui* and 560 *Leucoraja naevus*) of the main commercial ray species from the Irish Sea were determined from samples taken from commercial and research trawls between 1997 and 1998. Sagittal sections of vertebral centra stained using crystal violet enhanced the underlying band patterns of each species, allowing the derivation of age and von Bertalanffy growth parameters. Age estimates were relatively low for each species, with a maximum age of 7 yr recorded for *R. montagui* and 8 yr for each other species. Growth rate parameters ranged between $K = 0.093$ ($L_\infty = 139.500$ and $t_0 = -1.841$) for female *R. clavata* and $K = 0.304$ ($L_\infty = 72.400$ and $t_0 = -0.924$) for male *R. montagui*, and were notably higher for both the smaller growing *R. montagui* and *R. naevus*. Morphological assessment of maturity, revealed that; male *R. montagui* matured at the smallest size (53.651cm) and earliest age (3.410 yrs), male and female *R. clavata* matured at the greatest age (6.130 yrs) and female *R. brachyura* matured at the largest size (83.560 cm). In each species, an abrupt increase in clasper size in males and nidamental gland width in females was closely associated with the onset of maturity. Age, growth and maturity are discussed for each species with respect to previous studies and observed trends in the fishery.

Key words: age, fishery, growth, Irish Sea, maturity, rays, vertebrae

Introduction

The Irish Sea ray fishery is an important, long established resource, with rays considered as 'prime fish' at U.K. fish markets since the early-1900s (Steven, 1936). Although 11 species have been recorded in these waters, only the blonde ray, *Raja brachyura*, the thornback ray, *R. clavata,* the spotted ray, *R. montagui*, and the cuckoo ray, *Leucoraja naevus* are of commercial importance (Fahy, 1989). These are landed as a mixed species assemblage, by size grade, from both a by-catch, and a seasonally directed bottom trawl fishery (Holden, 1977; Fahy, 1989). U.K. landings have declined, over the last 10 yrs, owing largely to reductions in fleet size (Brander, 1988; Corlett, 1990). Conversely, Irish landings have increased in recent decades and annual ray landings consistently constitute over 10% of the total demersal landings in the Irish Sea (Fahy, 1989, Gallagher, 2000).

Unlike many of the commercially exploited teleost species that have shown major declines as a result of long-term intensive exploitation in the Irish Sea (Armstrong and Briggs, 1993; Anon., 1999a) the aggregated landings of rays, although variable, have remained relatively stable over the past 60 years (Brander, 1988; Fahy, 1989, 1991; Dulvy *et al.*, 2000). Nonetheless, changes in the relative abundance of certain species are evident, with the virtual disappearance of the large common and long-nosed skates, *R. batis* and *R. oxyrhincus*, (Brander, 1981; Holden, 1977; Dulvy *et al.,* 2000) and the reduction in both the abundance and size distribution of the moderately sized thornback ray (Holden, 1974; Fahy, 1989; Dulvy *et al.*, 2000). Furthermore, evidence suggests that the small spotted and cuckoo rays have increased in abundance (Holden, 1977; Fahy, 1989; Dulvy *et al.*, 2000). This phenomenon has also been observed in the North Sea ray fishery, and it has been suggested that smaller more resilient, less *k*-selected species, have a more selective survival advantage relative to the larger species (Walker and Hislop, 1998). It has also previously been reported that changes in stock structures and densities, through long-term exploitation, can alter life history traits of elasmobranchs (Tanaka *et al.,* 1990; Officer *et al.,* 1996). Walker (1999) noted this for the thornback ray in the North Sea, where the growth rate had increased and the age-at-maturity had decreased over a thirty-year period.

Historical evidence also suggests that similar changes in the growth and maturity of rays from the Irish Sea have occurred. Particularly rapid growth has been recorded for the two smaller commercial species, the spotted and cuckoo rays (Fahy, 1989), with growth rates almost double those reported in previous studies for the spotted ray (Holden, 1972; Ryland and Ajayi, 1984). In addition,

maturity estimates also indicate that both the size- and age-at-maturity have also decreased for the thornback ray over a sixty-year period (Stevens, 1936; Williams *et al.,* 1965; Nottage and Perkins, 1983; Ryland and Ajayi, 1984).

Difficulties often arise for elasmobranchs when comparing species-specific growth and maturity estimates between studies (Cailliet, 1990; Cailliet *et al.*, 1990; Tanaka *et al*., 1990). Differing methodologies together with inadequate or incomplete sample sizes or ranges prevent the true comparison of estimates and present difficulties in determining whether observed differences are biological or methodological (Stevens, 1936; Williams *et al*., 1965; Nottage and Perkins, 1983; Ryland and Ajayi, 1984; Fahy, 1989). These difficulties are also evident when previous growth and maturity studies of the Irish Sea ray species (Tables 1 and 2) are examined (Stevens, 1936; Williams *et al*., 1965; Nottage and Perkins, 1983; Ryland and Ajayi, 1984; Fahy, 1989). In particular, the most recent growth estimates derived for the commercial ray species (Fahy, 1989), which strongly suggested rapid growth for the smaller species are confounded by restricted sampling, as samples were collected from the commercial landings only and no enhancement techniques were used to resolve bands for age assessment purposes. Furthermore, the significance of the various maturity estimates is difficult to

ascertain, as differing maturity indices and limited sample sizes are evident (Stevens, 1936; Williams *et al.,* 1965; Nottage and Perkins, 1983; Ryland and Ajayi, 1984).

Holden and Vince's (1973) tetracycline tag-recapture study of the thornback ray in the southern North Sea was the first to validate annual band formation in the vertebral centra of elasmobranchs. Although it was suggested, that the opaque bands form from July to November, and that November marked the changeover from opaque to translucent band formation, there were uncertainties about these assumptions. This was largely due to the poor temporal range of the samples collected owing to the seasonal nature of the fishery along with the fact that connective tissue obscured the visualisation of bands forming at the periphery of the vertebral centrum. Although it is recommended that the temporal nature of band formation should be established for differing stocks of a given species to determine the rate and timing of growth band deposition (Cailliet, 1990) this has not yet been determined for Irish ray species.

This study focuses on the derivation of comprehensive age, growth and maturity estimates for each of the Irish Sea commercial ray species and discusses the findings in relation to previous studies and the current status of the fishery at the species level.

TABLE 1.   von Bertalanffy growth parameters for Irish Sea ray species (L_∞ = theoretical maximum length, K = Brody growth coefficient and t_0 = theoretical age at which length is zero). (* Denotes range of growth rate parameters derived by Fahy (1991)).

Species	Sex	L_∞	K	t_0	References
R. brachyura	F	118.4	0.19	-0.8	Holden (1972)
R. brachyura*	F	120.0–144.3	0.19–0.29	-0.31–+0.15	Fahy (1991)
R. brachyura	M	115	0.19	-0.18	Holden (1972)
R. brachyura*	M	116.7–119.4	0.24–0.26	-0.31–+0.15	Fahy (1991)
R. clavata	both	139.2	0.09	-2.63	Ryland and Ajayi (1984)
R. clavata	both	105	0.22	0.45	Brander and Palmer (1985)
R. clavata	F	127.3	0.1	-2.5	Taylor and Holden (1964)
R. clavata	F	107	0.13	-0.6	Holden (1972)
R. clavata*	F	107.8–120	0.15–0.26	-1.01-+0.05	Fahy (1991)
R. clavata	M	88.3	0.22	-1.3	Taylor and Holden (1964)
R. clavata	M	85.6	0.21	-0.6	Holden (1972)
R. clavata*	M	96.8–104.3	0.19–0.24	-1.36–+0.32	Fahy (1991)
R. montagui	both	97.8	0.15	-1.72	Ryland and Ajayi (1984)
R. montagui	F	72.8	0.18	-0.37	Holden (1972)
R. montagui	F	74	0.24	-2.72	Fahy (1991)
R. montagui	M	68.7	0.19	0.56	Holden (1972)
R. montagui	M	68.2	0.33	-1.87	Fahy (1991)
R. naevus	F	73.1	0.23	-2.47	Fahy (1991)
R. naevus	M	69.9	0.33	-1.12	Fahy (1991)

TABLE 2. Size (total length (cm)) and age-at-maturity (yr) estimates for Irish Sea ray species. (* Denotes total length estimates based on conversion of disc-width, using conversion factors calculated in this study.)

Species	Sex	Length-at-maturity (cm)	Age-at-maturity (yr)	Study
R.clavata	both	60	5	Ryland and Ajayi (1984)
R.clavata	F	90–97*	9	Steven (1936)
R.clavata	F	71*		Williams *et al.*, (1965)
R.clavata	F	65		Nottage and Perkins (1983)
R.clavata	M	72*	7	Steven (1936)
R.clavata	M	62*		Williams *et al.*, (1965)
R.clavata	M	60		Nottage and Perkins (1983)
R. montagui	both	60	5	Ryland and Ajayi (1984)

Methods

Specimens were collected from commercial landings and research surveys from the Irish Sea (from ICES Statistical Division VIIa) between 1996 and 1998 as follows: 127 male and 141 female blonde rays, 165 male and 93 female thornback rays, 274 male and 194 female spotted rays and 351 male and 209 female cuckoo rays. Species, sex, total length (cm), disc width, ungutted and gutted weight (g) maturity status, clasper length (cm) in males, and nidamental gland width (mm) in females, were recorded.

Age and Growth

A vertebral segment containing approximately 10 vertebrae was extracted, from each sample collected, immediately posterior to the scapular origin of the vertebral column. Tissue was removed by immersing the segments in hot water (circa. 70–85°C). Segments were subsequently air-dried and then immersed in a 5% solution of trypsin (hog pancreatin) at 35–40°C for 24 hours, to remove the neural and haemal arches, and the connective tissue from the vertebral fascia. Following this process, centra were washed for 30 minutes in running water.

In order to fully appraise the effectiveness of each enhancement technique examined, a sample of centra from each species was processed in a variety of forms (e.g. whole, whole scraped and etched, sagittal sections). An extensive range of enhancement techniques, described in Gallagher (2000), was applied to each centrum preparation. The most effective technique was a modification of the crystal violet staining technique described by Schwartz (1983). Sagittal sections were prepared from the two largest centra from each specimen. Sections were etched by immersion in an acid alcohol (IMS) solution (5%) for 15 minutes, and were subsequently washed for 15 minutes in running water. Sections were then placed in a 0.005% solution of crystal violet for 36 hours, and checked every 12 hours for stain uptake. Stained sections were then washed in running water for 2 minutes. Over-stained sections were de-stained for 2–4 minutes in an alcohol solution (70%).

For age reading purposes a growth increment or 'band' on a sagittal section was defined as a heavily stained opaque band appearing at relatively regular intervals along the *corpus calcareum*, and separated by a translucent band. As the intermedialia was often over-stained or ground away, the majority of band counts were derived from counts of the heavily stained bands on the *corpus calcareum*. The birth or hatching mark (age zero) was defined as the first mark after the change in the angle of the *corpus calcareum*. All age readings were made from the focus towards the distal edge on a single axis exhibiting greatest resolution. Band counts were corroborated with readings made along the remaining three axes.

Prepared centra were viewed on three separate occasions independently under a dissecting microscope using both transmitted and reflected light, without prior knowledge of species, sex, size, maturity and date of capture. A sub-sample of centra was read by a second and third reader independently, on three separate occasions. Each of the two readers used the same criteria as the primary reader to count bands. Coefficient of variation (*V*), which describes the standard deviation as a percentage of the mean and the index of precision (*D*) (Chang, 1982) were determined for reader estimates of age.

Bands forming at the edge of stained sagittal sections were characterised as belonging to one of the three following stages of formation (Yudin and Cailliet, 1990):

Grade 1. Centrum: Opaque band forming at the marginal edge

Grade 2. Centrum: Narrow, translucent band forming at the edge

Grade 3. Centrum: Translucent band well formed on the marginal edge

For each species, length and age data were logged, and analyses of covariance (ANCOVA) were carried out to establish whether significant differences existed in the length and age estimates between the sexes of each species. The von Bertalanffy (1938) growth model was fitted to the data using nonlinear regression. Fishparm (Prager *et al.*, 1987), which implements Marquardt's algorithm for nonlinear, least squares, parameter estimation (Marquardt, 1963), was chosen to fit the growth curves to the data sets, and also calculated standard error and goodness of fit (r^2).

Maturity

Maturity of each individual was assessed using a modification of Stehmann's (1987) maturity scale for elasmobranchs (Table 3). The logistic model (Fishparm (Prager *et al.*, 1987)) was used to estimate the length and age at which 50% of each species examined attained maturity. Males and females assessed as stage 3 and 4, respectively, in the maturity index were deemed mature for the analysis.

Clasper length (cm) and total length (cm) were plotted for males and nidamental gland width (mm) was also plotted against total length (cm) for females to ascertain the relationship between body size and sexual development.

Results

Age and Growth

Crystal violet staining of sagittal sections proved to be the most effective enhancement technique for all species in the study and had a number of distinct advantages over the other techniques tested. Principal amongst these was a single stage in the staining protocol. As a result the effects of altering the stain concentration or the immersion time could be readily ascertained and the desired intensity of staining carefully controlled. In addition de-staining of over-stained sections was accomplished, using alcohol.

Each species had a similar band morphology, with opaque bands appearing as relatively thick regularly spaced dark coloured bands along each sagittal sections axis, separated by narrower lighter coloured translucent bands (Fig. 1).

For each species opaque band formation was generally associated with the mid-summer autumn growth phase (June–October). This was evident for the blonde ray (Fig. 2), with opaque band formation (Grade 1) being dominant from July to September (100%) and for the thornback ray (Fig. 3), where band formation (Grade 1) also developed

during the summer–autumn growth cycle (June 10%, August 70%). However, a discontinuity in the cycle of band formation was evident in the thornback ray, with translucent band formation (Grade 2) being dominant in September (67%), and opaque band formation (Grade 1) being dominant in November (78%). It is probable that this discontinuity was due to a combination of a small sample size in September, and interpretational difficulties at the distal margins. For the spotted ray (Fig. 4) opaque band formation (Grade 1) became more discernible from July (14%) to October (100%). A similar trend was also apparent for the cuckoo ray (13% in July, 80% in September) (Fig. 5). Opaque band formation may be complete at an earlier stage in the cuckoo ray than the spotted ray, as all the spotted rays examined were forming an opaque band in October, whereas the formation of translucent bands (Grade 2) had commenced in the cuckoo ray (43%).

The autumn–winter transition (October–November) generally marked the changeover from opaque to translucent band formation for each species. This was particularly apparent for the two smaller sized spotted (Fig. 4) and cuckoo ray species (Fig. 5). Opaque band formation (Grade 1) dominated both the spotted and cuckoo rays sampled in October (100% and 57%, respectively). However, the transition to translucent band formation occurred for both species in November with forming translucent bands (Grade 2) being evident in equal proportions (38%) to fully formed bands (Grade 3) for the spotted ray, and forming bands dominating the cuckoo rays sampled (73%). The trend of translucent band formation became more evident with the proportions of forming (Grade 2) and fully formed (Grade 3) translucent bands increasing further in December for both species (Fig. 4 and 5), whereas opaque band formation was not evident. For the blonde ray (Fig. 2) the changeover from opaque to translucent band formation was also evident from October to November with a drop in the proportion of opaque bands (Grade 1, 69% to 13%) and an increase in the proportion of forming translucent bands (Grade 2, 31% to 87%). Unfortunately no samples were examined in December to assess whether this trend continued. Due to limited sample sizes, a clear trend is not as discernible for the thornback ray from October to November. However the proportion of opaque bands dropped (Grade 1, 78% to 25%) and translucent forming bands increased (Grade 2, 22% to 75%) from November to December.

For each species fully developed translucent bands (Grade 3) were more evident towards the end of spring and entering summer. This was evident in the May–June samples for both the cuckoo (May 93%, June 85%) and the spotted rays (May 50%, June 80%). Although fully formed

TABLE 3.   Maturity indices (modification of Stehmann's scale 1987) used in the assessment of maturity of *Raja brachyura, R. clavata, R. montagui, R. naevus.*

Male	Female
1. Juvenile	**1. Juvenile**
Claspers less than the length of the pelvic fins. Testis undeveloped, thread or leaf-like. Spermatophoric area present as leaf-like zone within the testis. Sperm duct undeveloped. Kidneys evident.	Ovaries leaf-like, thin. No obvious eggs present in opaque zone within ovary with gelatinous or granular appearance. Nidamental glands undeveled, present as opaque bulge in oviduct. Oviduct small and thread-like.
2. Adolescent, Maturing	**2. Adolescent, Maturing**
Claspers longer than tips of pelvic fins. Clasper tips (glans) already structured but skeleton still flexible. Testis swollen with developing spermatophoric spheres. Sperm ducts with obvious structure and uniform size throughout. Kidneys slightly obscured by developing sperm duct.	Ovaries containing small eggs. Nidamental gland small and developing, cream in colour with obvious white ends. Oviducts small and thread-like.
3. Adult, Mature	**3. Adult, Developing**
Claspers rigid and much longer than pelvic fins, glans structure fully formed. Testis swollen with developing spermatophoric spheres. Sperm ducts with obvious structure, separated into two distinct sections and filled with flowing sperm. Sperm duct obscuring at least half of kidneys**.**	Ovaries containing developing eggs some of which are very large. Nidamental gland fully developed, uniformly white**.** Ovary walls thickened.
4. Adult, Running	**4. Adult, Mature**
Glans clasper often dilated, its structure reddened and swollen. Sperm flowing on pressure from cloaca and/or present in clasper groove or glans. Testis swollen with developing spermatophoric spheres. Sperm duct with obvious structure, separated into two distinct regions. Sperm duct obscuring majority of kidneys.	Ovaries containing large eggs. Large eggs present in fallopian tubes, or already passing through to nidamental gland. Nidamental gland fully developed. Egg cases if present, only partially extruded. Oviducts developed, walls thick and venous.
	5. Adult, Laying
	Ovaries containing large eggs. Nidamental glands fully developed, uniformly white. Fully formed eggs present. Oviducts developed, wall thick and venous or may appear stretched (following extrusion).
	6. Adult, Resting
	Ovaries containing a variety of eggs in different stages of development. No extremely large eggs present. Nidamental glands fully developed. No eggs present in fallopian tubes or oviducts. Oviducts venous and stretched.

translucent bands (Grade 3) were apparent for the two remaining species, the fact that they never dominated the monthly thornback ray or blonde ray samples is probably due to the difficulties of distinguishing between forming (Grade 2) and fully formed translucent bands (Grade 3), particularly in larger specimens.

For each species no distinct trends in precision among readers were evident indicating each of the readers were equally able to resolve bands (Table 4). The lowest coefficient of variation was evident for reader one's assessment of male thornback ray (0.055) whereas the highest evident was for reader three's readings of female thornback ray (0.154).

ANCOVAs revealed that the differences in the length-at-age data were only significant between the sexes for the blonde ray (Table 5). There was however a number of distinct trends evident in the derived growth data. Male growth rates were higher than females for each species (Fig. 6–9, Table 6), and a notable divergence in the shape of the growth curves is apparent between the sexes for the thornback ray (Fig. 7). Growth rates were also lower for the two larger sized species, the blonde (male, $K = 0.145$; female, $K = 0.129$) and thornback rays (male, $K = 0.135$; female, $K = 0.093$) compared to the smaller spotted (male, $K = 0.304$; female, $K = 0.256$) and cuckoo (male, $K = 0.294$; female, $K = 0.197$) rays. However overestimations of L_{∞} relative to maximum observed sizes were apparent
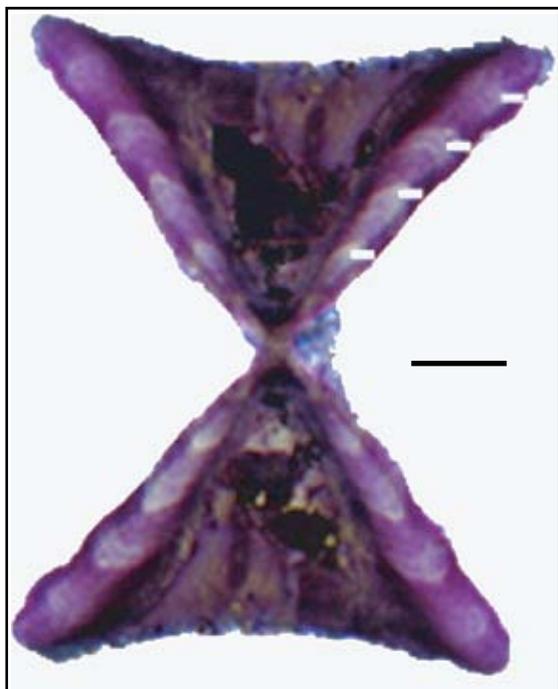
Fig. 1.   Photomicrograph of a centrum in longitudinal sec-
tion, etched in 5% EDTA and stained in 0.005%
crystal violet, from a spotted ray, *Raja montagui*,
specimen estimated to be in its 5th year. White bars
denote the position of enumerated bands. Scale bar
= 0.65 mm.

for both larger species (blonde, male L_∞ = 145.8 max. obs.
size =109 (note: size here in after refers to total length in
cm), female L_∞ = 154.7 max. obs. size = 108; (thornback,
male L_∞ = 106.5 max. obs. size =90, female L_∞ = 139.5
max. obs. size = 104). The limited sample sizes in the
larger size-classes for both these species have contributed
to an overestimation of length at age resulting in somewhat
lower growth rate estimates. The comprehensive sample
sizes/ranges evident for both smaller species (Fig. 8 and
9) yielded more comparable maximum observed sizes
and L_∞ estimates (spotted, male L_∞ = 72.4 max. obs. size
=75, female L_∞ = 78.4 max. obs. size = 77; cuckoo, male
L_∞ = 74.57 max. obs. size =71, female L_∞ = 83.92 max.
obs. size = 70).

Maturity

With the exception of the cuckoo ray (females =
56.16, males = 56.87) females of all species matured at a
larger size than males (Fig. 10 to 17, Table 7). In addition,
with the exception of the thornback ray (both sexes 6.13
yrs), all females matured at a later age than males (Fig. 9
to 16, Table 7). Male spotted ray matured at the earliest

age (3.41 yrs) and at the smallest size (53.65 cm), whilst
the thornback ray matured at the latest age (6.13 yrs, both
sexes), and the blonde ray at the largest size (females =
83.56 females).

For each species a very gradual increase in the size of
claspers in males and nidamental gland width in females
relative to body size was evident prior to maturity (Fig.
18–25). However at the onset of maturity (50% maturity
estimates (Table 7) denoted by an arrow) a distinct in-
crease in both clasper size and nidamental gland width was
clearly evident for all species examined. For each species
the overall shapes of the distributions of clasper size and
nidamental gland width relative to increasing body size
were similar, and this similarity was particularly evident
for both smaller species where sample sizes were larger
(Fig. 22–25).

Discussion

The modification of the crystal violet staining tech-
nique initially investigated by Schwartz (1983) proved
very effective. Owing to the simplicity and versatil-
ity of the single-stage staining process the desired stain
intensity could readily be ascertained and over-stained
sections could be de-stained effectively using alcohol.
Preliminary trials using this technique also showed
potential for a variety of other elasmobranch species
(common skate; *Raja batis*, shagreen ray; *R. fullonica*,
Arctic skate; *R. hyperborea*, small eyed ray; *R. microocel-
lata*, long nosed skate; *R. oxyrhincus*, Norwegian skate;
R. nidarosiensis, Richardson's ray; *Bathyraja richardsoni*,
blue shark; *Prionace glauca*, lesser spotted dogfish; *Scyl-
iorhinus canicula*, greater spotted dogfish; *S. stellaris* and
the blackmouth catshark; *Galeus melastomus*).

The temporal range of samples examined allowed
both the rate and timing of band formation to be derived
using centrum edge analysis. For each species, annual
band pair formation, and in addition, opaque band forma-
tion associated with the summer-autumn growth phase
was evident. This confirms Holden and Vince's (1973)
observation on the rate and timing of band formation for
the thornback ray in the southern North Sea, and compares
with band formation processes for several other elasmo-
branch species (Brandstetter, 1987; Martin and Cailliet,
1988; Zeiner and Wolf, 1993).

Growth and maturity estimates revealed that the
larger rays (blonde and thornback rays) reached matu-
rity at larger sizes and later ages, and displayed slower
growth than both smaller rays (spotted and cuckoo rays).
Overall, growth estimates agreed most closely with those
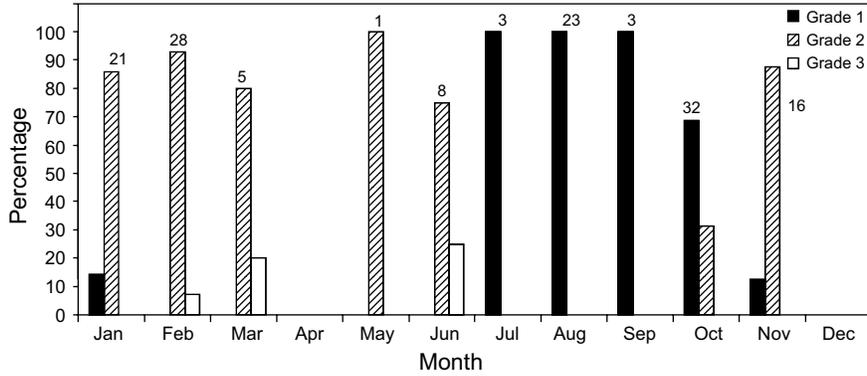
Fig. 2. Temporal characteristics in the growing edge of centrum sagittal sections, from *R. brachyura*, using a grading system defined by Yudin and Cailliet (1990). Columns indicate percent frequency of each grade, with associated numbers denoting monthly totals examined.
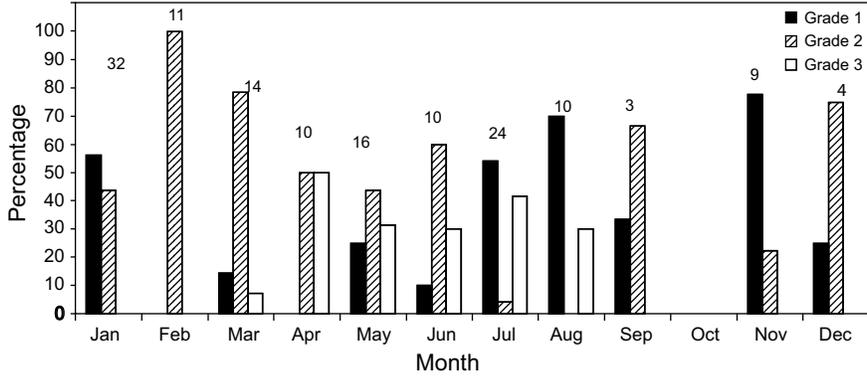
Fig .3. Temporal characteristics in the growing edge of centrum sagittal sections, from *R. clavata*, using a grading system defined by Yudin and Cailliet (1990). Columns indicate percent frequency of each grade, with associated numbers denoting monthly totals examined.
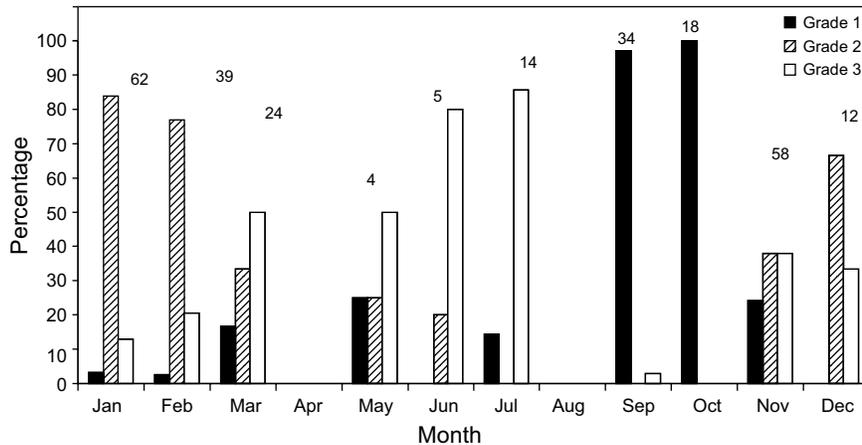
Fig. 4. Temporal characteristics in the growing edge of centrum sagittal sections, from *R. montagui*, using a grading system defined by Yudin and Cailliet (1990). Columns indicate percent frequency of each grade, with associated numbers denoting monthly totals examined.
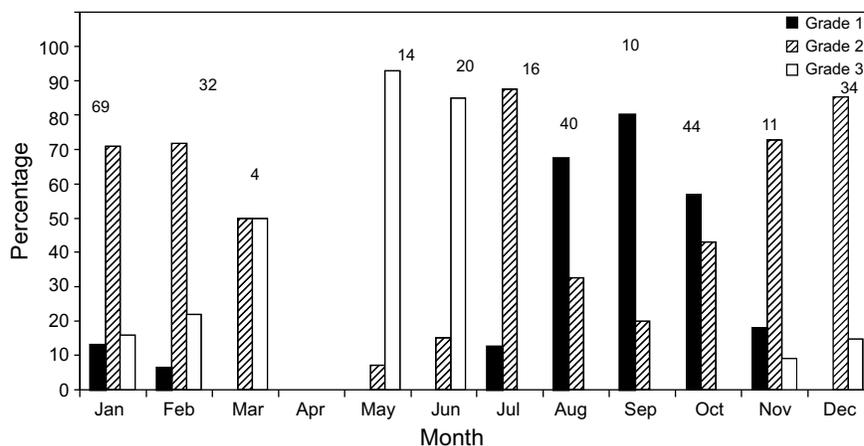
Fig. 5.   Temporal characteristics in the growing edge of centrum sagittal sections, from
          R. naevus, using a grading system defined by Yudin and Cailliet (1990). Columns
          indicate percent frequency of each grade, with associated numbers denoting monthly
          totals examined.

TABLE 4.   Chang's (1982) coefficient of variation (*V*) and mean reader precision (*D*) for sagittal section band counts
           made by three readers for *R. brachyura, R. clavata, R. montagui,* and *R. naevus*. *n* = sample size.

Species	Structure		Reader 1		Reader 2		Reader 3	
		n	*V*	*D*	*V*	*D*	*V*	*D*
R.brachyura	Male	30	0.079	0.045	0.087	0.050	0.072	0.042
	Female	30	0.096	0.055	0.096	0.055	0.072	0.042
R. clavata	Male	30	0.055	0.032	0.112	0.065	0.154	0.089
	Female	30	0.059	0.034	0.087	0.050	0.081	0.047
R.montagui	Male	30	0.117	0.068	0.099	0.057	0.068	0.039
	Female	30	0.088	0.051	0.094	0.054	0.073	0.042
R.naevus	Male	30	0.083	0.048	0.143	0.083	0.145	0.083
	Female	30	0.116	0.067	0.118	0.068	0.103	0.060

TABLE 5.   Analysis of covariance, testing for difference in
           length at age between the sexes of *Raja brachyura,
           R. clavata, R. montagui* and *R. naevus.* Ages based on
           sagittal section band counts. *n* = sample size.

	n	*F* ratio	*P* value
R. brachyura	127	7.704	0.006
R. clavata	93	1.072	0.302
R. montagui	194	2.057	0.152
R. naevus	209	2.537	0.112

of Fahy (1991), which are the most recent and geographi-
cally relevant estimates relative to this study (Table 1).
Overestimations of L_∞ relative to maximum observed
sizes was evident in this study for both the blonde and

thornback rays and is largely due to the dearth of samples
in the larger size-classes. In fact Fahy's (1989, 1991) L_∞
estimates for both species were in closer agreement to
the maximum observed sizes derived in this particular
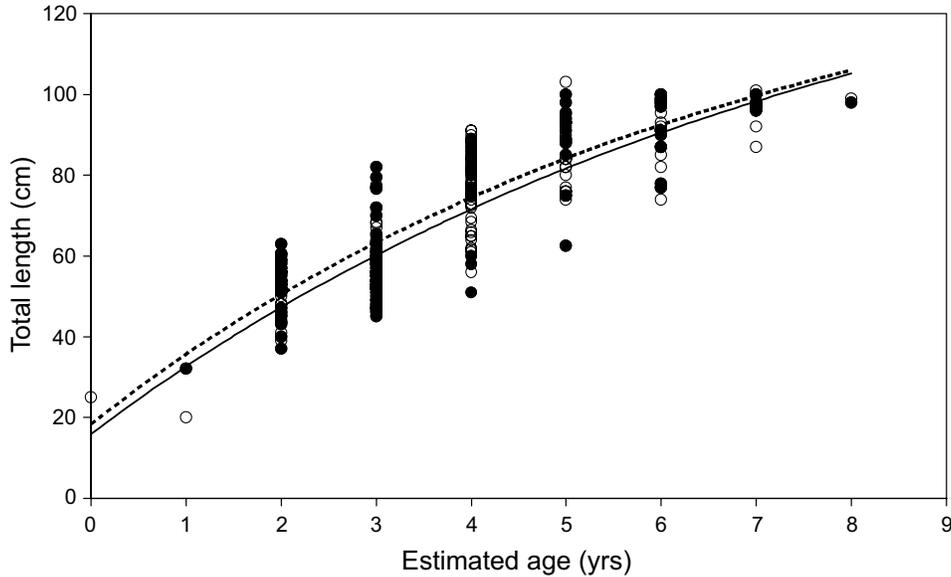
Fig. 6. Observed length-at-age data for *Raja brachyura,* by sex, with predicted von Bertalanffy growth curves fitted using Fishparm (Prager *et al.*, 1987). Ages based on sagittal section band counts.
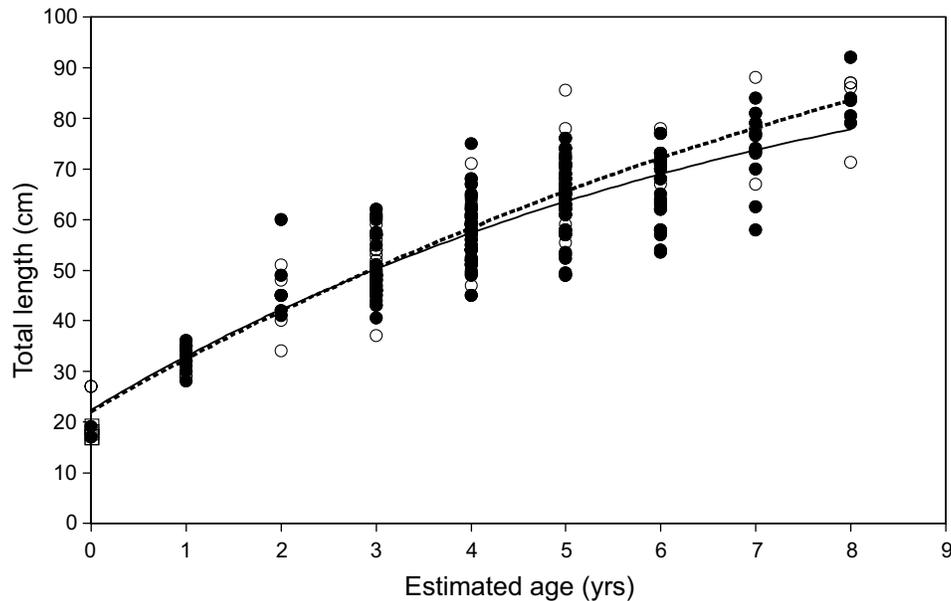
Fig. 7. Observed length-at-age data for *Raja clavata,* by sex, with predicted von Bertalanffy growth curves fitted using Fishparm (Prager *et al.*, 1987). Ages based on sagittal section band counts.

study, possibly suggesting more realistic growth for both species. However an examination of Fahy's (1991) data reveals an overestimation of length at age in the smaller size-classes and widely varying t_0 estimates. This may be due to the fact that Fahy (1989, 1991) used whole centra for age estimation purposes and further highlights the fact that poor resolution of growth increments near the nucleus of whole centra is a recognised problem in Irish Sea ray species (Taylor and Holden, 1964; Brander and Palmer, 1985).
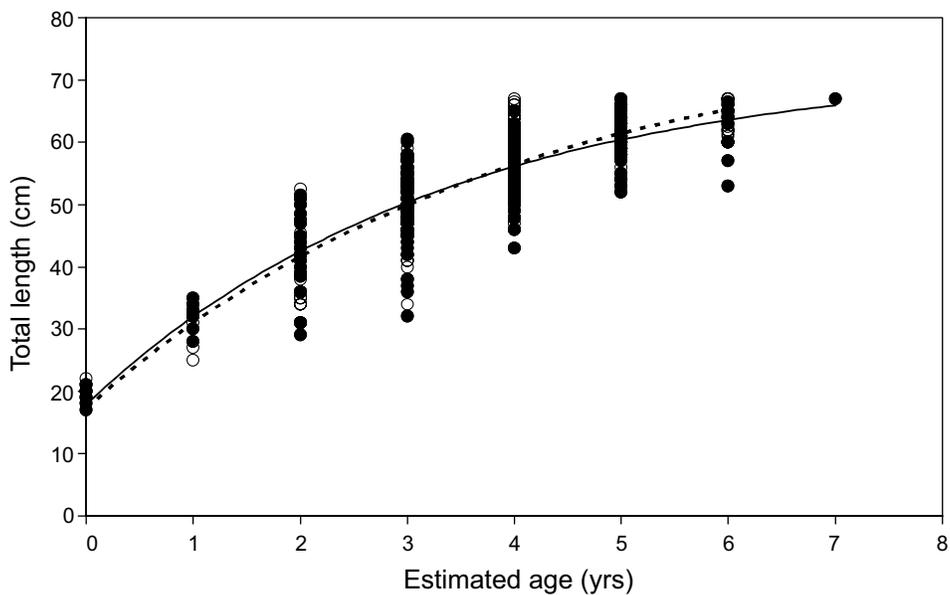
Fig. 8.   Observed length-at-age data for *Raja montagui,* by sex, with predicted von Bertalanffy growth curves fitted using Fishparm (Prager *et al.*, 1987). Ages based on sagittal section band counts.
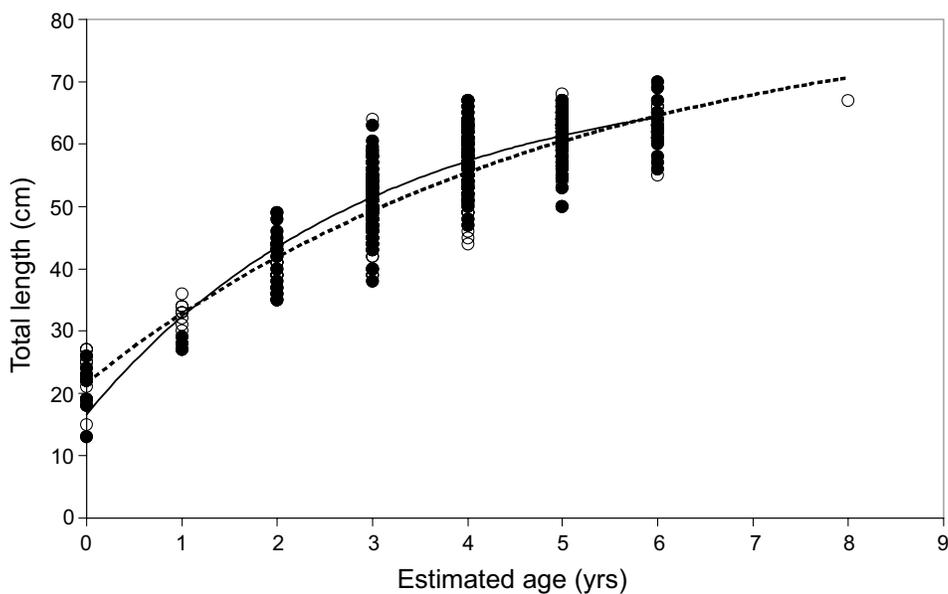
Fig. 9.   Observed length-at-age data for *Raja naevus,* by sex, with predicted von Bertalanffy growth curves fitted using Fishparm (Prager *et al.*, 1987). Ages based on sagittal section band counts

Growth estimates for the spotted and cuckoo rays appeared more robust in this study, owing to comprehensive sample sizes, and L_∞ and maximum observed sizes are also in close agreement in each species.

The results for the spotted and cuckoo rays were also in very close agreement with those of Fahy (1989). It is interesting to note that although there was close agreement between the growth estimates between both Fahy's (1989,

TABLE 6.   von Bertalanffy growth parameters of L_∞ = theoretical maximum length (total length (cm)), K = Brody growth coefficient, t_0 = theoretical age at which length is zero, based on sagittal section band counts, with standard error of each parameter given in parentheses and maximum observed sizes (max. obs. size) (total length (cm)) based on field observations for *Raja brachyura, R. clavata, R. montagui, R. naevus. n* = sample size.

Species	Sex	n	Max. obs. size (cm)	L_∞	K	t_0	r^2
R. brachyura	M	127	109	145.800 (31.820)	0.145 (0.065)	-0.926 (0.602)	0.76
	F	141	108	154.700 (29.820)	0.129 (0.045)	-0.840 (0.406)	0.79
R. clavata	M	165	90	106.500 (14.380)	0.135 (0.040)	-1.740 (0.470)	0.75
	F	93	104	139.500 (32.530)	0.093 (0.037)	-1.841 (0.049)	0.82
R. montagui	M	274	75	72.400 (2.812)	0.304 (0.035)	-0.924 (0.155)	0.77
	F	194	77	78.430 (4.750)	0.256 (0.043)	-0.968 (0.242)	0.75
R. naevus	M	351	71	74.570 (2.177)	0.294 (0.025)	-0.997 (0.125)	0.8
	F	209	70	83.920 (6.152)	0.197 (0.033)	-0.151 (0.206)	0.83
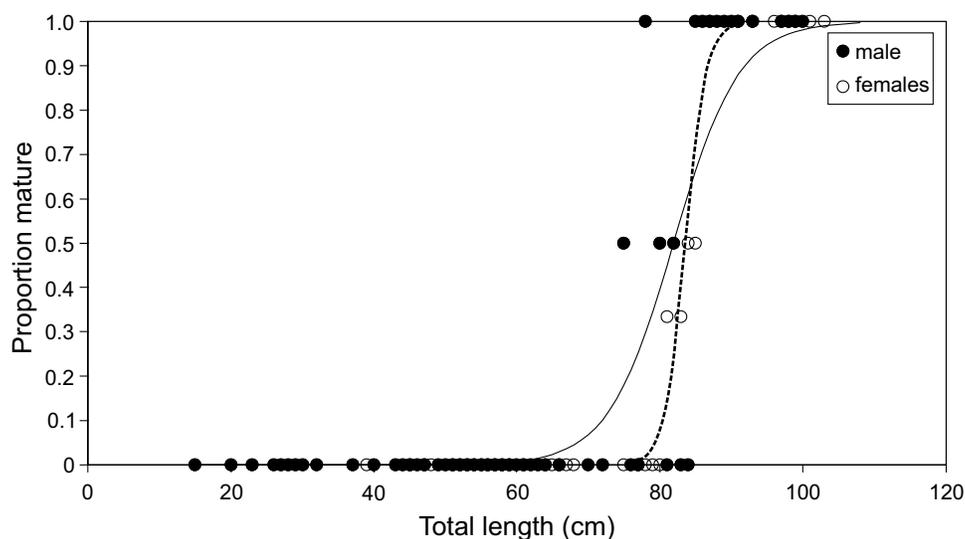
Fig. 10.   Ogive of size (total length (cm)) at maturity for *R. brachyura,* by sex.

1991) and this study increases in the growth rates of these two species are suggested compared to previous studies (Holden, 1972; Ryland and Ajayi, 1984).

Despite the almost certain variability in maturity estimates between studies owing to differing maturity assessment methods, the results for the thornback ray in this and other studies (Williams *et al*., 1965; Nottage and Perkins, 1983; Ryland and Ajayi, 1984) suggest that both size- and age-at-maturity has decreased over the long term (Steven, 1936). One of the more recent studies of commercial ray species in the eastern Irish Sea (Ryland and Ajayi, 1984) reported both lower size- and age-at-maturity estimates for the thornback ray than this study,
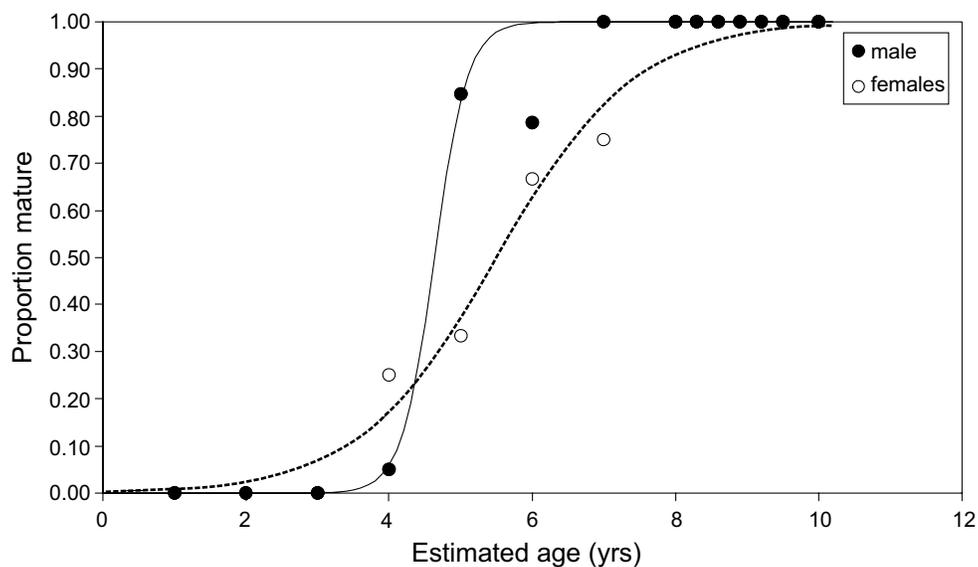
Fig. 11. Ogive of age (yrs) at maturity for *R. brachyura,* by sex. Ages based on sagittal section band counts.
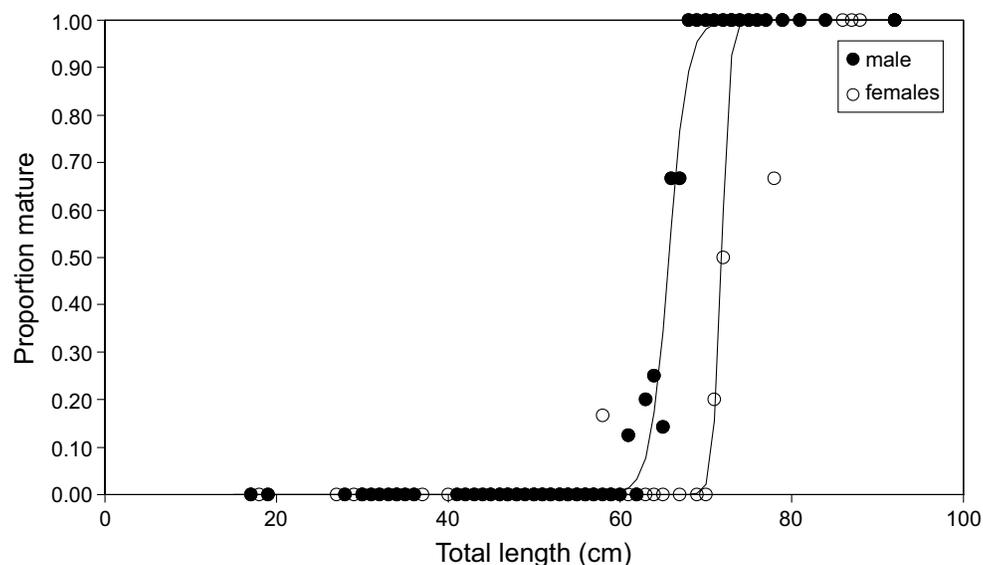
Fig. 12. Ogive of size (total length (cm)) at maturity for *R. clavata,* by sex.

which is to be expected to some extent as first maturity was quoted, whereas 50% maturity was estimated in this study. However when maturity estimates for the spotted ray are compared between both studies, the same trend is not evident, with both lower age and smaller size-at-maturity evident in this study. This would suggest that in addition to increases in the growth rate, reductions in both the size- and age-at-maturity have occurred for the spotted ray recently. Although no previous maturity estimates are available for the cuckoo ray in the Irish Sea it is probable

that similar changes in growth and maturity have also occurred for this species.

The affects of long-term exploitation on life history traits through changes in stock structures and relative abundances have also been suggested for a number of other ray fisheries (Anon, 1999b; Agnew *et al.*, 2000; Kulka and Miri, MS 2003). For the Irish Sea it is apparent that historical levels of fishing mortality were too high to sustain the slow growing ($K = 0.060$) and late
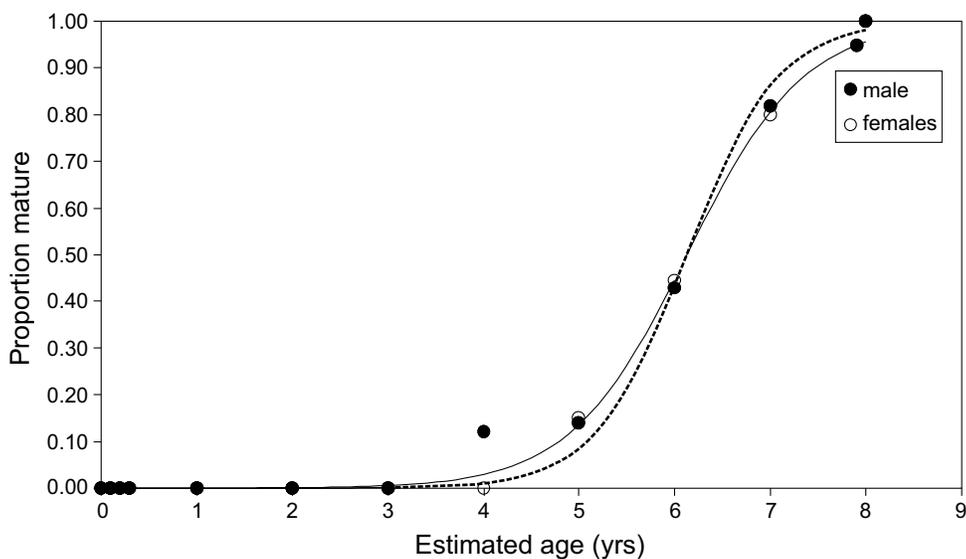
Fig. 13.   Ogive of age-at-maturity (yrs) for *R. clavata,* by sex. Ages based on sagittal band counts.
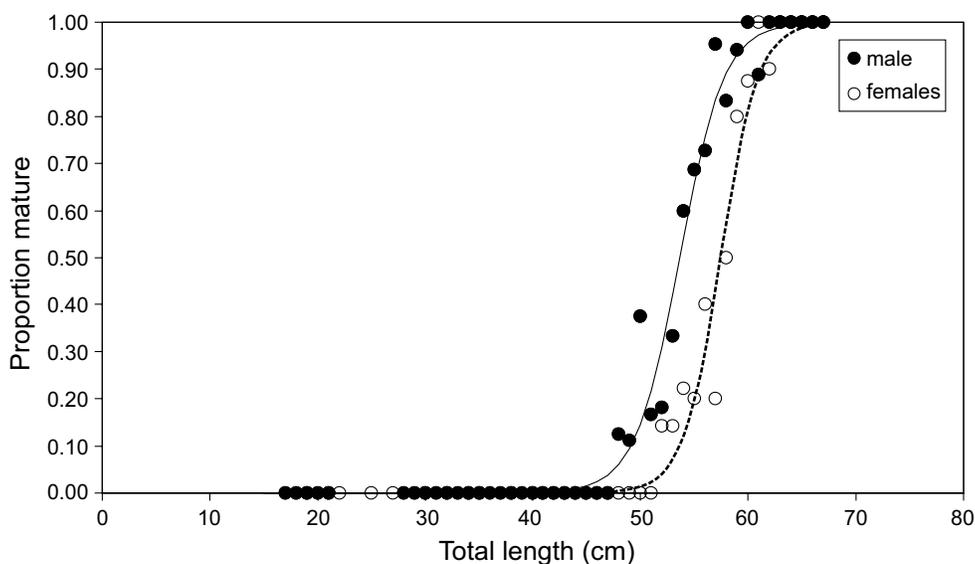
Fig. 14.   Ogive of size (total length (cm)) at maturity for *R. montagui,* by sex.

maturing (11 yrs) common skate (*R. batis*), which was commercially extirpated in the 1970s (Brander, 1981). In addition, although aggregated landings and catch statistics suggested relative stability in the Irish Sea ray fishery, examination of species-specific trawl survey data over a 60-year period indicated that the slower growing and later maturing thornback ray dropped in abundance (Dulvy *et al*., 2000). In addition to changes in population density the size structure of the stock has also changed for the thornback ray, with few specimens reported above 90 cm total length over recent decades (Holden, 1977;

Fahy, 1989; Gallagher, 2000), whereas specimens above 100 cm were commonplace in the earlier part of the last century (Steven, 1936). These changes effected possible reductions in age- and size-at-maturity of this species (Steven, 1936; Williams *et al*., 1965; Nottage and Perkins, 1983; Ryland and Ajayi, 1984; Gallagher, 2000) but were not sufficient to prevent a reduction in abundance (Fahy, 1989; Dulvy *et al*., 2000; Gallagher, 2000).

Increases in abundance have recently been noted for the cuckoo ray in the western Irish Sea from commercial
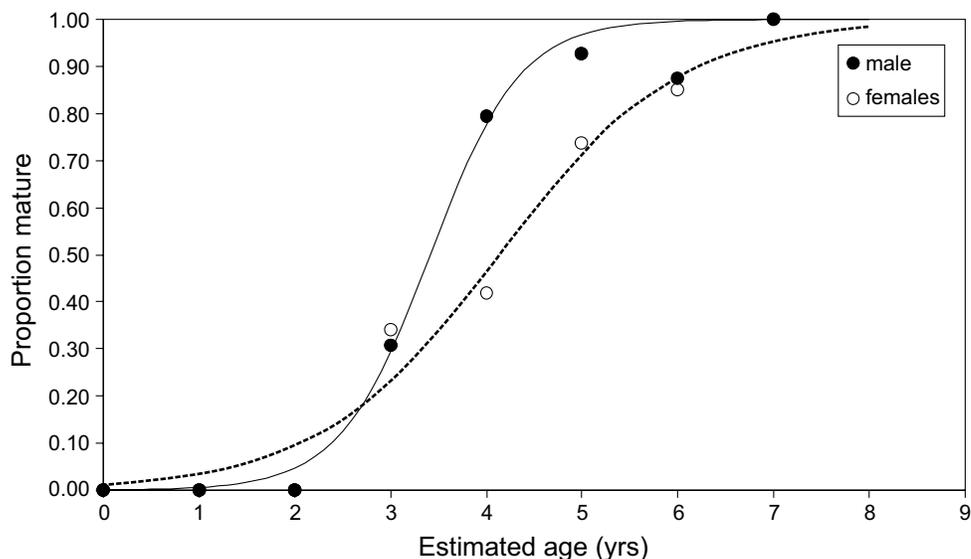
Fig. 15. Ogive of age (yrs) at maturity for *R. montagui,* by sex.
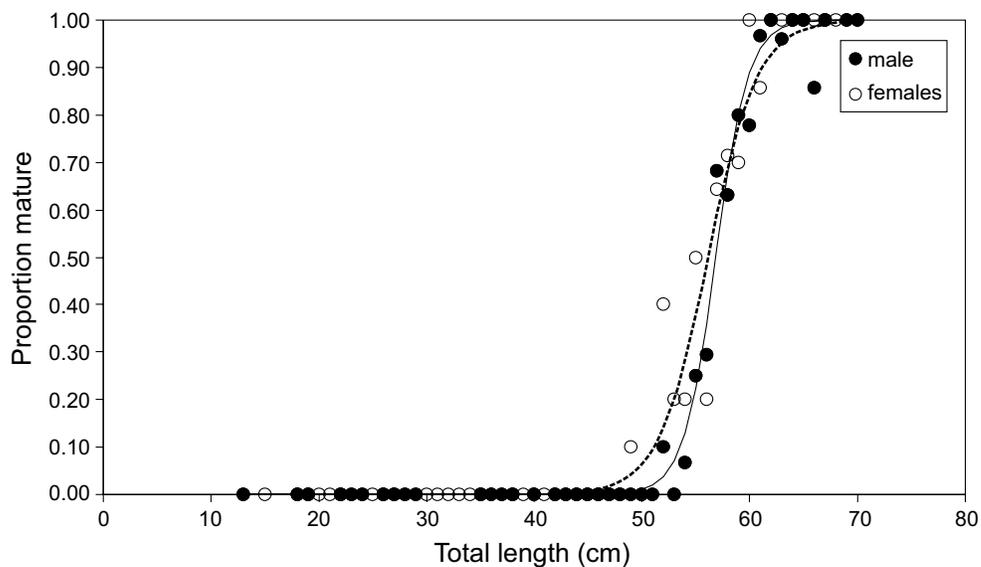
Fig. 16. Ogive of size (total length (cm)) at maturity for *R. naevus,* by sex.

landings (Fahy, 1989, Gallagher, 2000) and for both the cuckoo and spotted rays in the eastern Irish Sea from long-term trawl survey data (Dulvy *et al*., 2000). Dulvy *et al.* (2000) suggested that these increases in abundances are a result of additional food availability due to the decline in abundance of the larger sized species. However it is equally likely that the compensatory changes in life history traits (growth and maturity) of these less *k*-selected species have resulted in the increases in abundance. A similar phenomenon was also noted in the North Sea (Walker and Hislop, 1998), and was also attributed to the

changes in life history traits of the rapid growing early maturing starry ray, *R. radiata*.

Other factors also influence the sustainability of a species. Protection of the reproductive potential of a stock is important, particularly in elasmobranchs, given the close stock/recruitment relationship (Holden, 1974; Anderson, 1990). The blonde ray, the largest and most commercially important species, has sustained almost a century of directed effort (Steven, 1936; Gallagher, 2000). However despite the fact that this species is slower
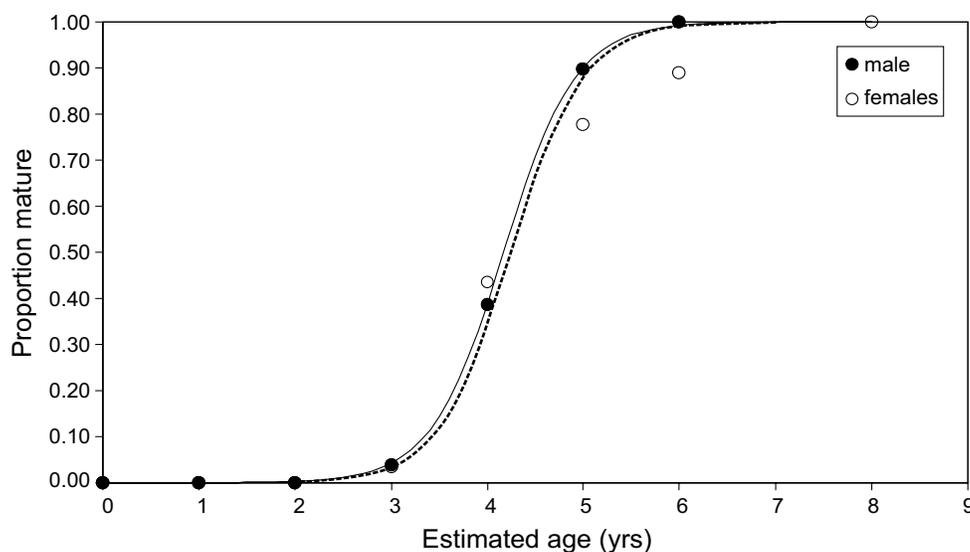
Fig. 17.   Ogive of age (yrs) at maturity for *R. naevus,* by sex.

TABLE 7.   Total length (TL (cm)) and age (yrs) at 50% maturity for Irish Sea ray species, by sex, based on the logistic model (Fishparm Prager *et al.*, 1987). Figures in parentheses denote standard error values for maturity estimate. Ages based on sagittal section band counts. *n* = sample size.

Species	Sex	*n*	TL at 50% maturity	r^2	Age at 50% maturity	r^2
R. brachyura	M	123	81.92 (1.063)	0.77	4.63 (0.155)	0.96
	F	61	83.56 (0.154)	0.99	5.504 (1.155)	0.97
R. clavata	M	165	65.7 (0.218)	0.96	6.13 (0.076)	0.99
	F	90	71.809 (0.107)	0.97	6.13 (0.039)	1
R. montagui	M	274	53.65 (0.185)	0.98	3.41 (0.095)	0.98
	F	175	57.44 (0.189)	0.98	4.135 (0.172)	0.95
R. naevus	M	353	56.87 (0.132)	0.99	4.17 (0.006)	1
	F	191	56.16 (0.266)	0.97	4.25 (0.076)	0.99
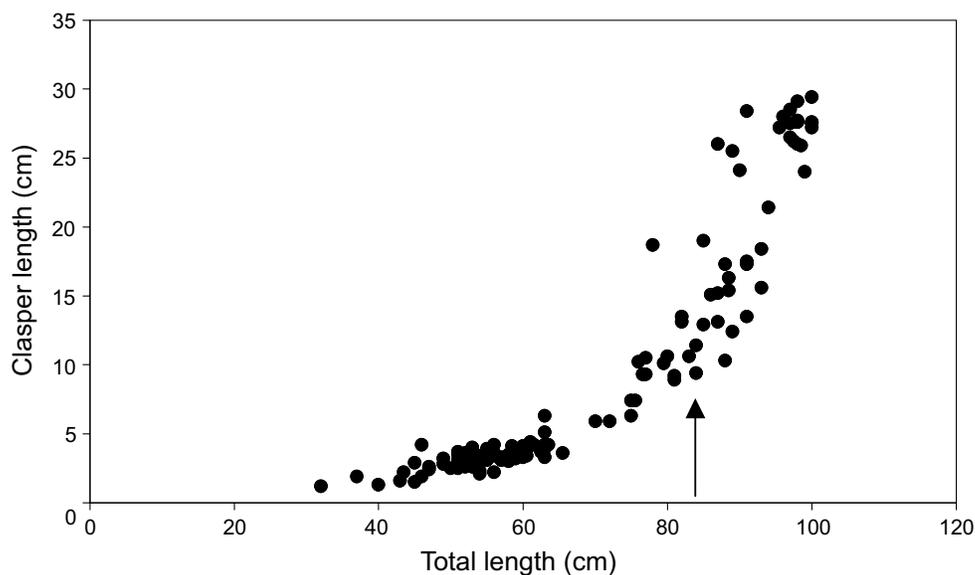
Fig. 18. Relationship between clasper length (cm) and total length (cm) for *R. brachyura*. Arrow on X-axis denotes 50% maturity.
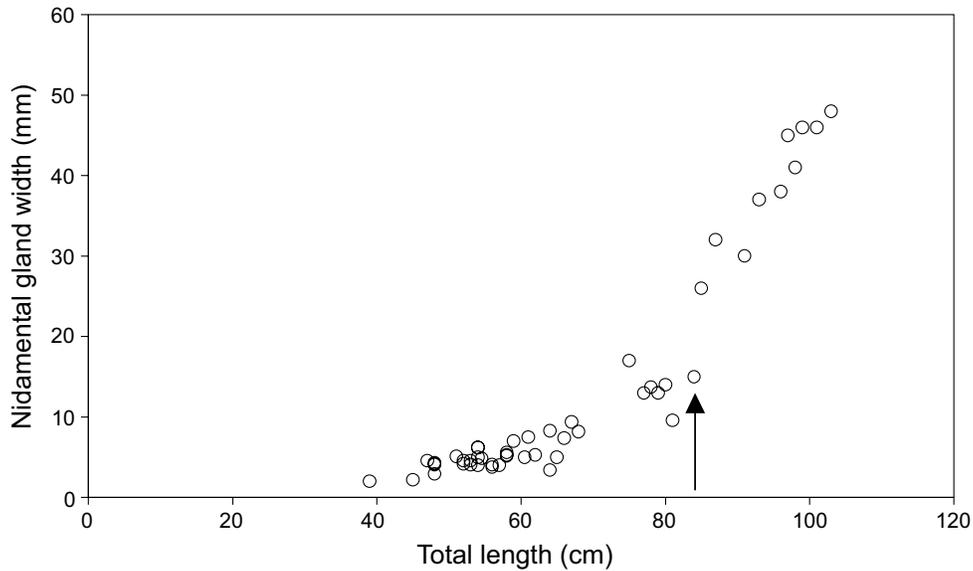
Fig. 19. Relationship between nidamental gland width (mm) and total length (cm) for *R. brachyura*.
Arrow on X-axis denotes 50% maturity.
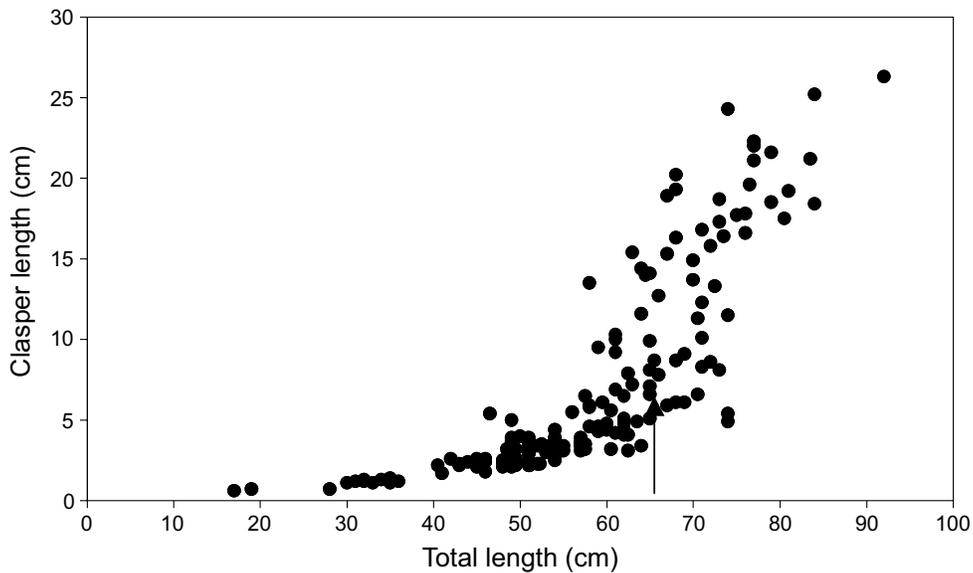
Fig. 20. Relationship between clasper length (cm) and total length (cm) for *R. clavata*. Arrow on X-axis
denotes 50% maturity.

growing, matures at a later age and larger size than the smaller sized spotted and cuckoo rays, numbers have not diminished substantially (Gallagher, 2000). It has been suggested that a higher proportion of females of this species remain in inshore nursery grounds and therefore are not vulnerable to the directed fishery (Gallagher, 2000).

The Irish Sea is a heavily exploited environment that has yielded consistent aggregated catches of rays for almost a century (Steven, 1936; Pawson and Vince, 1999; Gallagher, 2000); however, it is clear that under these conditions only the species with the appropriate life history traits and the capacity to respond to changes
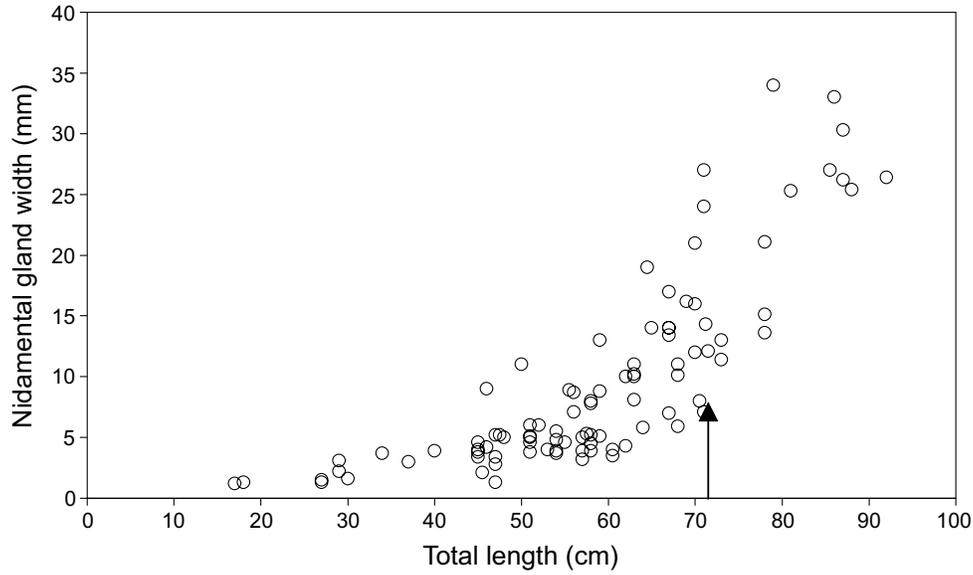
Fig. 21. Relationship between nidamental gland width (mm) and total length (cm) for *R. clavata*. Arrow on X-axis denotes 50% maturity.
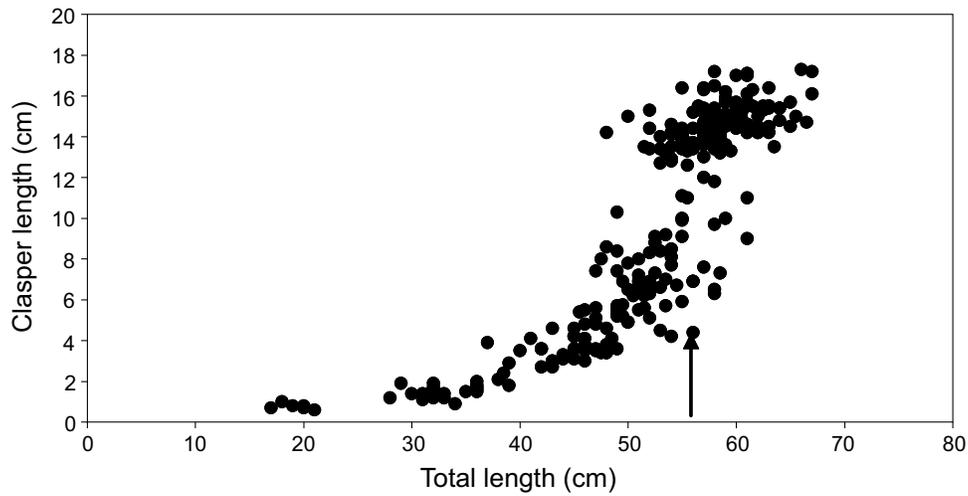
Fig. 22. Relationship between clasper length (cm) and total length (cm) for *R. montagui*. Arrow on X-axis denotes 50% maturity.

in fishing pressures will flourish. Further work is warranted in this area especially on the collection of more detailed time series fisheries independent trawl survey data to fully verify if these suggested changes have occurred. In addition comparisons of growth and maturity characteristics of heavily fished and relatively un-fished sub-populations of each species is also required to verify if differing pressures are exerting proportionate changes in life history traits. It is also important that the same growth and maturity techniques are used for each study to minimize the confounding variations resulting from different techniques.
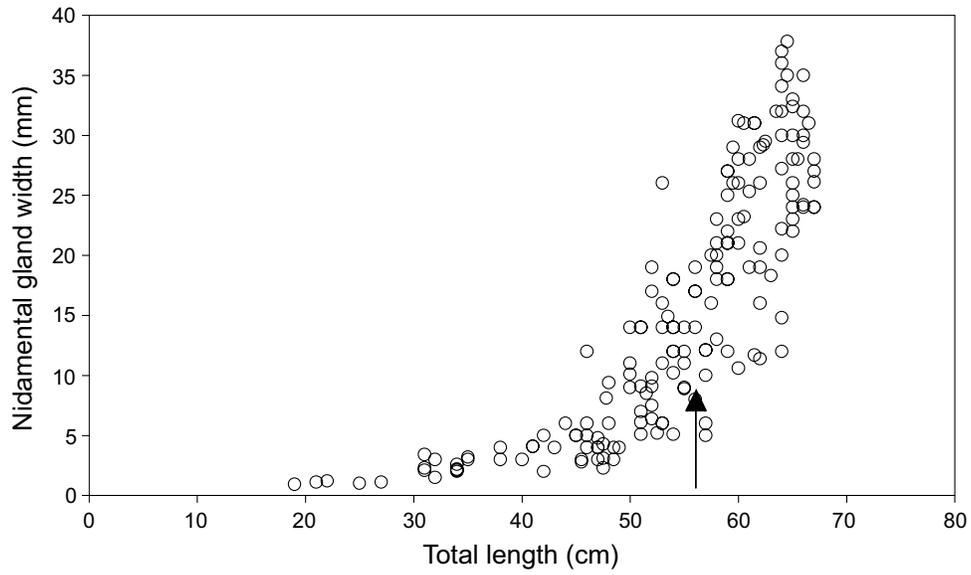
Fig. 23. Relationship between nidamental gland width (mm) and total length (cm) for *R. montagui*.
Arrow on X-axis denotes 50% maturity.
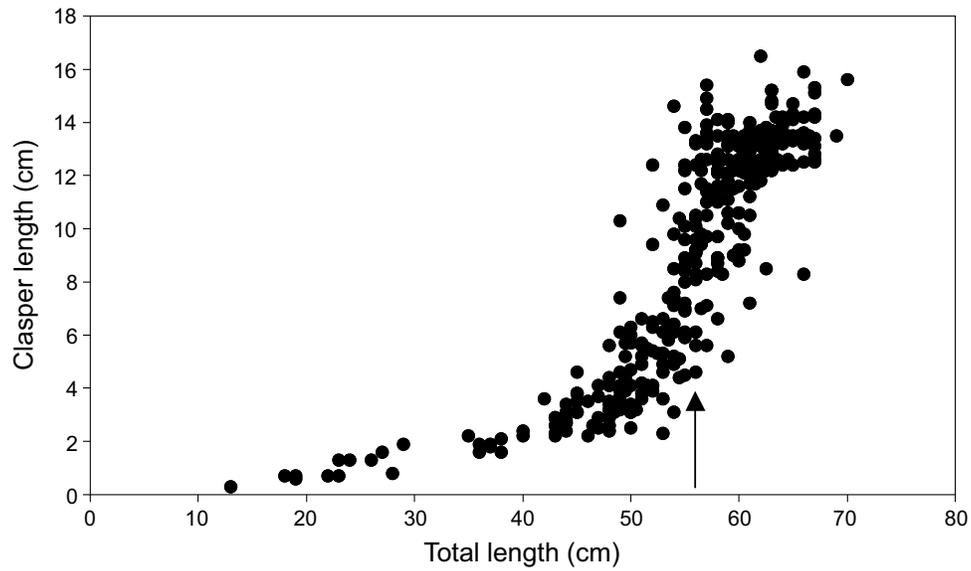
Fig. 24. Relationship between clasper length (cm) and total length (cm) for *Leucoraja naevus*. Arrow
on X-axis denotes 50% maturity.
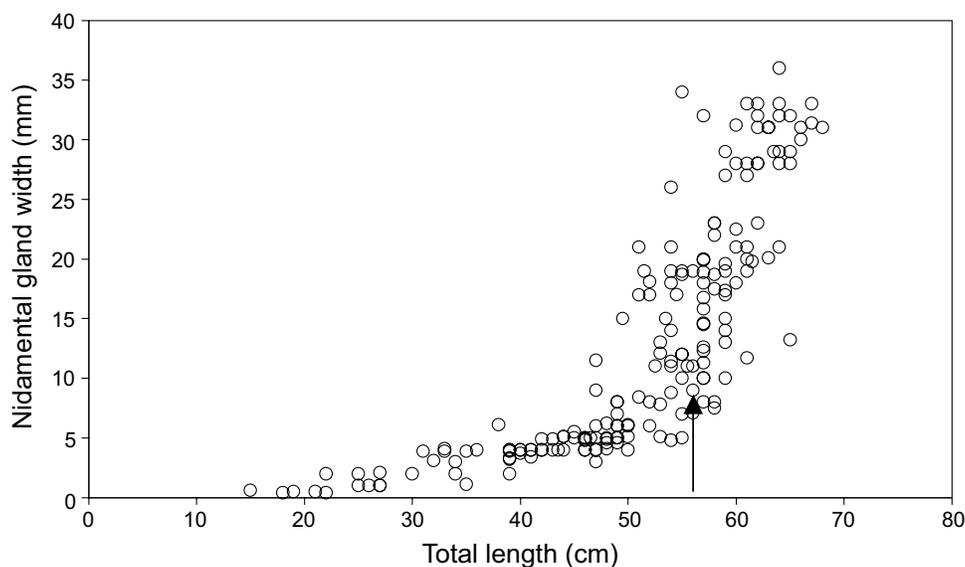
Fig. 25. Relationship between nidamental gland width (mm) and total length (cm) for *L. naevus*.
Arrow on X-axis denotes 50% maturity.

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