

Population biology and ageing of the deep water sharks *Galeus melastomus*, *Centroselachus crepidater* and *Apristurus aphyodes* from the Rockall Trough, north-east Atlantic

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This study presents new information on the population biology, growth and maturation schedules of Galeus melastomus, Centroselachus crepidater and Apristurus aphyodes sampled from the Rockall Trough, a region where deep sea fishing activity has been prevalent for the past 40 years and where shark by-catch is considerable. Both G. melastomus and C. crepidater showed significant sexual size dimorphism with females attaining a greater length and mass. The size (L_{50}) at first maturity was estimated to be 55.6 cm total length (TL) for males and 59.7 cm TL for females in G. melastomus, 57.2 cm TL for males and 75.4 cm TL for females in C. crepidater and 49.0 cm TL for males and 56.9 cm TL for females in A. aphyodes. This represents the first TL_{50} analysis for Apristurus aphyodes globally. Sharks were aged using a technique which employed cobalt (II) nitrate to stain growth bands in vertebra centra. Band pairs were successfully viewed in G. melastomus and pair counts ranged from 0 to 5 in males and 2 to 7 in females. A higher asymptotic length was deduced from the von Bertalanffy growth equation for females than males (females: $L_{\infty} = 69.3$ cm; males: $L_{\infty} = 60.8$ cm) in G. melastomus. Staining was unsuccessful in C. crepidater and A. aphyodes and age could not be determined using this technique.

Keywords: Rockall Trough, ageing, TL_{50} , von Bertalanffy

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INTRODUCTION

It is widely acknowledged that many species of elasmobranchs are undergoing serious declines in abundance and are threatened with extinction (Musick *et al.*, 2000; Stevens *et al.*, 2000; Myers & Worm, 2005). Although the most publicized threat comes from targeted shark fin fisheries, mixed fisheries where sharks are caught as incidental catch also pose a considerable threat (Musick *et al.*, 2000). Dealing with this substantial level of shark by-catch in non-target fisheries may be the greatest challenge in managing global shark resources (Barker & Schluessel, 2005). Overfishing and declining shelf sea fish stocks are driving the need to seek new fishing grounds and deep sea fish stocks have been targeted to help meet the demand for fish (Large *et al.*, 2003). With this comes the inevitable risk to deep water shark species. Defined as those species which are predominantly distributed, restricted to, or spend the majority of their life-cycle at depths below 200 m (following Kyne & Simpfendorfer, 2010), many deep water sharks have slow growth rates, relatively large size and age at maturity and low fecundity making them

particularly vulnerable to population depletion. The impacts of fishing activity in the deep sea are relatively poorly understood despite having good baseline data for many deep sea fishery ecosystems owing to their relatively young age and modern fisheries monitoring (Koslow *et al.*, 2000; Bailey *et al.*, 2009). An understanding of the biology and population size/structure of both the target and by-catch species is essential in order to effectively manage deep sea fisheries and to understand the impacts of fishing on the structure and function of deep sea ecosystems.

Deep water fisheries are well established in the Rockall Trough region which lies to the west of Ireland and the United Kingdom (Gordon, 2003). In 2003, a total allowable catch (TAC) system was introduced in an attempt to manage fisheries in the region more sustainably (Heymans *et al.*, 2011). CPUE estimates continued to decline for squaloid sharks including *Centroselachus coelolepsis*, *Centrophorus squamosus*, *Dalatias licha* and *Deania calcea* (Basson *et al.*, 2002; Heesen, 2003; Jones *et al.*, 2005). Consequently, TACs for sharks were consistently reduced, until 2010 when the TAC for deep water sharks was reduced to zero, with no by-catch allowance. Landings of commercially targeted species of deep water sharks in this region have declined by 90% over the past decade which partly reflects TAC reduction, but also the decline of the stocks (ICES, 2010).

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In this study, the population biology of three deep-sea shark species found in the Rockall Trough region of the north-east Atlantic were examined. These species were selected as being most abundant at different depth strata on the continental slope: the black mouthed catshark *Galeus melastomus* Rafinesque, 1810, the longnose velvet dogfish *Centroselachus crepidater* (Bocage & Capello, 1864), and the white ghost catshark, *Apristurus aphyodes* Nakaya & Stehmann, 1998. Owing to their deep water habitat, all of these species have been less well studied relative to many coastal elasmobranch species, especially *A. aphyodes*. In particular, very little is known about the age structure and growth patterns for the three shark species, both key parameters to understand the population biology of a species. The ageing of deep-sea sharks presents a unique problem because: (1) they have been shown to have much less calcification of the vertebrae than shallow and coastal species (Cailliet, 1990) rendering many shark ageing techniques (e.g. Cailliet *et al.*, 1983; Cannizzaro *et al.*, 1995; Wintner, 2000) unsuitable; and (2) the vertebra of deep-sea sharks exhibit a deep cone structure which limits the penetration of stains and cleaning agents (Correia & Figueiredo, 1997). Gennari & Scacco (2007) presented a new technique to age the velvet belly dogfish, *Etmopterus spinax*, using acid to etch the softer translucent band (Correia & Figueiredo, 1997) as well as utilizing a stain (cobalt(II) nitrate) to gain further definition and visibility. This may provide a more effective technique for ageing deep-water shark species. It is important to note that within this study shark 'ages' remain unvalidated owing to current validation methods being unsuitable for deep sea species; thus all 'ages' are here on presented as 'band counts'.

Therefore, the aims of this study were twofold: (1) to provide fundamental information on the population biology (size structure, length/mass relationships and maturity ogives) of *G. melastomus*, *C. crepidater* and *A. aphyodes*; and (2) to apply the band enhancement ageing method described by Gennari & Scacco (2007) to try to determine the age structure and to derive growth curves for each study species.

MATERIALS AND METHODS

Sample collection

This study was based upon samples collected during an annual Marine Scotland—Science deep water trawl survey (Cruise 1209S) of the Rockall Trough area during September 2009 (Neat *et al.*, 2010; Campbell *et al.*, 2011). Samples were collected by bottom trawling from onboard the FRV 'Scotia' in a depth range of 500–1800 m on the continental slope between 54°N and 59°N (Figure 1). Trawl duration of approximately sixty minutes was maintained throughout the survey (not including time for descent and ascent of the trawl gear). The bottom trawl (BT184) was rigged with 16 in rock-hopper ground gear (Jackson Trawls Ltd, Peterhead, UK), 1700 kg doors of area 5.82 m² (Morgere, St Malo, France), 100 m sweeps and floats rated to 2500 m. Warp to bottom-depth ratio ranged between approximately 2.5:1 and 2:1 decreasing gradually with depth. The cod-end was fitted with an internal liner with 20 mm mesh size which ensured retention of fish as small as a few centimetres in length.

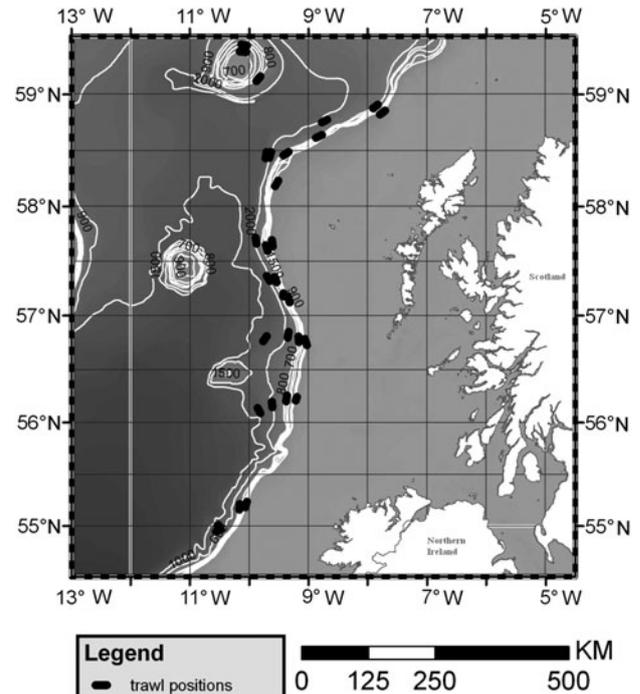


Fig. 1. Trawl sites in and around the Rockall Trough, north-east Atlantic, for the Marine Scotland—Science deep water trawl survey, September 2009 (Cruise 1209S).

A total of 30 trawls were conducted lasting an average of 58 ± 12 minutes, ranging in depth from 523 to 1796 m. Length, mass, sex and maturity status were recorded for all sharks caught. Total length (TL, measured to the nearest centimetre) was taken as the anterior tip of the snout to the posterior tip of the caudal fin, with the caudal fin depressed along the anterior–posterior axis. Total mass (*W*) was measured to the nearest gram. Sex was determined by the presence (male) or absence of claspers. Maturity status was established by macroscopic examination of the gonad using the scale presented in Stehmann (2002): individuals at stage three or more (i.e. capable of successful sexual reproduction), for either sex, were considered mature.

For logistical reasons it was not possible to retain all sharks for ageing so a length-stratified sub-sample was kept for each species to represent the whole size range of individuals caught. For *Galeus melastomus*, a total of 106 (68 females, 38 males) individuals were caught and 64 (40 females, 24 males) were retained for ageing. For *Centroselachus crepidater*, a total of 173 (100 females, 73 males) individuals were caught with 89 (51 females, 38 males) retained for ageing. For *Apristurus aphyodes*, a total of 33 (23 females, 10 males) individuals were caught, all of which were retained for ageing. Heads of specimens were removed by a single dorsal-ventral cut just anterior of the dorsal fin origin and frozen for later removal of vertebrae in the laboratory. Where target species were caught sampled sharks made up an average of 4.7% of the total trawl mass (range: 0.3–16.3%). Twenty per cent of hauls captured none of the target species.

Vertebrae extraction and preparation

A series of incisions were made to defrosted heads to remove a section of vertebrae, typically 2–3 cm in length and consisting

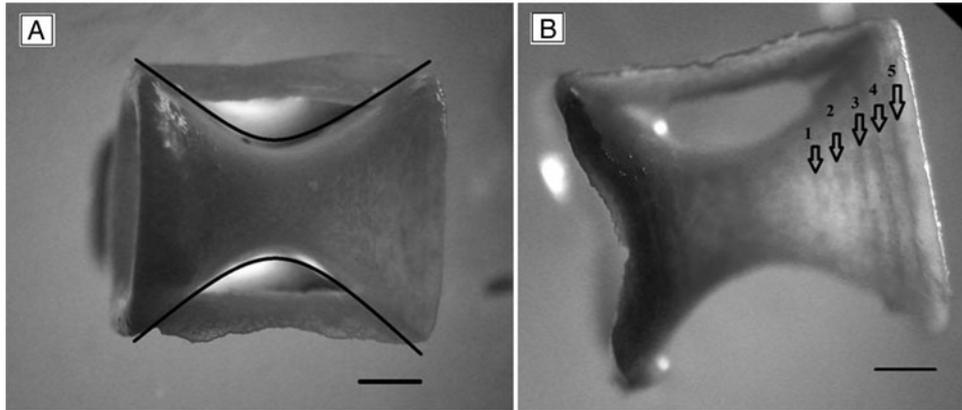


Fig. 2. (A) Sections of calcified wall surrounding vertebra centra which require manual removal. Calcification above and below black lines require removal; (B) example of band definition in vertebra of *Galeus melastomus* (male, TL= 57 cm) where $N_B = 5$. Vertebra is viewed using a stereomicroscope under transmitted light. Scale bars = 1 mm.

of 3–4 individual vertebra. Excess muscle tissue and the vertebral arches were removed manually. Vertebral sections of small specimens (i.e. *G. melastomus* and *A. aphyodes*) were stored in 95% ethanol within small vials until cleaning whilst the larger vertebral sections from *C. crepidater* were stored frozen at -20°C .

Cleaning of the vertebral column section largely followed the method outlined in Gennari & Scacco (2007) until the vertebrae separated from each other and no remaining tissue was visible. Each cleaning cycle consisted of immersion in a sodium hypochlorite solution (10–15% active chlorine) for 15 minutes followed by a 15 minute rinse in distilled water. The number of repetitions of the cleaning cycle varied depending on residual tissue volume and vertebrae size but a typical vertebral column section of *G. melastomus* or *A. aphyodes* required 4–5 repetitions. The larger vertebral sections of *C. crepidater* were found to be more resistant to cleaning and required longer immersion times (typically 6 h cf. 15 min for the smaller vertebrae). After cleaning, sections of the calcified wall surrounding the centra were removed to ensure that the growth bands in the centra would be clearly visible after staining (Figure 2A). Clean vertebrae were stored in 70% ethanol solution until staining.

Staining and reading of vertebrae

Staining of the vertebrae followed the method proposed by Gennari & Scacco (2007) with the following modifications: (1) vertebrae were immersed in the cobalt (II) nitrate solution for 1 to 5 min depending on the cone depth and observed degree of calcification; (2) the solution was agitated to allow penetration of the stain into the cavities formed by the deep coned nature of deep sea elasmobranch vertebra; and (3) after initial staining, vertebrae were rinsed thoroughly in distilled water to halt further staining as excessive staining prevented growth bands from being visible. Vertebrae were then immersed in an acid bath (1M hydrochloric acid and 70% ethanol in a 1:20 v:v) for approximately 30 s to etch the growth bands followed by a thorough rinsing in distilled water. After air-drying, vertebrae were viewed using a stereomicroscope under transmitted light and a digital image was taken using a Nikon Coolpix 4500 camera which was then used for reading of growth bands. Band pairs (Figure 2B),

defined as a dark layer followed by a lighter layer (Cailliet *et al.*, 2006), were read independently by two readers. Each reader counted the number of band pairs (N_B) for each vertebra once without knowledge of the length of the specimen from which the vertebra was taken or the other reader's count.

Statistical analyses

Statistical analyses were conducted using SPSSTM v.14 and MinitabTM 15. A sex-ratio was calculated for each species (female:male) and the Chi-squared test (Zar, 1996) used to test for differences between this ratio and an expected ratio of 1:1. The non-parametric Mann–Whitney *U*-test was used to examine differences in length and mass distribution by sex owing to the non-normal distribution of the data. The length–mass relationships for each sex in each species were calculated using the following equation:

$$\ln W = \ln a + b \ln L \quad (\text{King, 2007})$$

where W is the mass (g), L is the TL (cm), and a and b are constants. The b values for each sex were tested for isometric growth against a value of $b = 3$ (where 3 = isometric growth) using a *t*-test. Total length at 50% maturity (TL_{50}) was calculated for each sex within each species using the logistic equation

$$Y = \frac{1}{1 + e^{-r(L-L_{50})}}$$

where Y is the percentage of mature individuals in each size class L (cm) and r is a constant (King, 2007). The index of average percentage error (IAPE) was estimated for reader's growth band counts following Beamish & Fournier (1981). The IAPE is defined as:

$$\text{IAPE} = \frac{100}{N} \sum_{j=1}^N \left(\frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - X_j|}{X_j} \right)$$

where N is the number of fish aged, R is the number of times fish are aged, X_{ij} is the i th age determination for the j th fish, and X_j is the average estimated age of the j th fish. The non-

parametric Wilcoxon test (Conover, 1971) was used to test the null hypothesis that there were no differences between reader counts. In addition, the average coefficient of variation (CV) between counts was calculated using:

$$CV_j = 100\% \times \frac{\sqrt{\sum_{i=1}^R \frac{(X_{ij} - X_j)^2}{R-1}}}{n}$$

where CV_j is the age precision estimate for the j th fish (Campana, 2001). Assuming that one band pair is formed each year, the von Bertalanffy growth model was used to estimate L_∞ :

$$L_t = L_\infty [1 - \exp^{-k(-t_o)}]$$

where L_t = length at 'age' (i.e. number of band pairs) t ; L_∞ = asymptotic length; k = the rate at which L_∞ is reached ('years'⁻¹) and t_o = 'age' ('years') of the fish at theoretical zero length (King, 2007).

RESULTS

Galeus melastomus

Galeus melastomus specimens were collected between 533 and 1049 m depth. More females than males (Chi square test, $\chi^2 = 8.49$, $P < 0.05$) were caught (1 ♀:0.56 ♂) with females ranging in total length from 32 to 69 cm and males ranging from 34 to

64 cm (Figure 3). Body mass ranged from 100 to 1370 g in females and 128 to 777 g in males. *Galeus melastomus* showed significant sexual size dimorphism with females attaining a greater mass and length than males (Mann-Whitney U -tests; total length, $U = 723$, $N_1 = 68$, $N_2 = 38$, $P < 0.05$; mass, $U = 637$, $N_1 = 68$, $N_2 = 38$, $P < 0.05$). Relationships between L_n length and L_n mass for males and females are presented in Figure 4. Both male and female *G. melastomus* exhibited isometric growth (t -test, ♂, $t = -0.55$, $df = 66$, $P = 0.58$; ♀, $t = 0.21$, $df = 36$, $P = 0.83$). All maturity stages were present in the *G. melastomus* catch with a maturity rate of 65% for females and 55% for males respectively. Figure 5 presents the maturity ogives for female and male *G. melastomus* with TL_{50} values calculated as 59.7 cm for females and 55.6 cm for males respectively. Both reader's agreed on band pair counts in *G. melastomus* vertebrae for a subsample of 32 individuals (50% of the total sample size). There was disagreement of band counts for the remaining 32 samples with the largest disagreement being two band pairs (3.13% of the disagreements). However, most disagreements were by only one band pair. The IAPE between readers was estimated as 2.75% with the average CV between reader's counts being 14.1%. There were no significant differences present between the two reader's total counts (Wilcoxon signed-ranks test, $T = -3.24$, $N = 64$, $P < 0.05$). Band pair counts ranged from 0 to a maximum of 7. Using the band pair counts as an estimate of age to fit a von Bertalanffy growth function to the size at 'age' data, males attained a lower asymptotic length than females with L_∞ values of 60.8 cm and 69.3 cm for males and females, respectively. Values for k and t_o are not presented as the

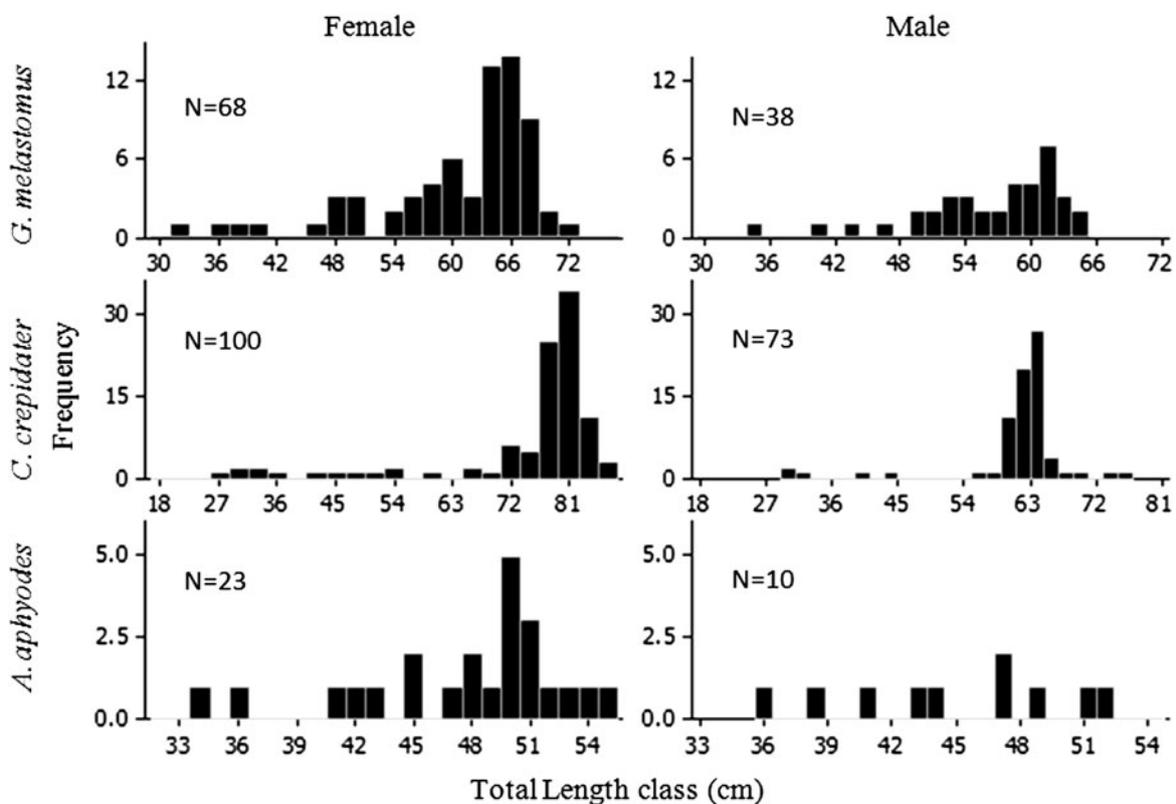


Fig. 3. Length–frequency distribution of female (left) and male (right) *Galeus melastomus*, *Centroselachus crepidater* and *Apristurus aphyodes* from the Rockall Trough, 2009.

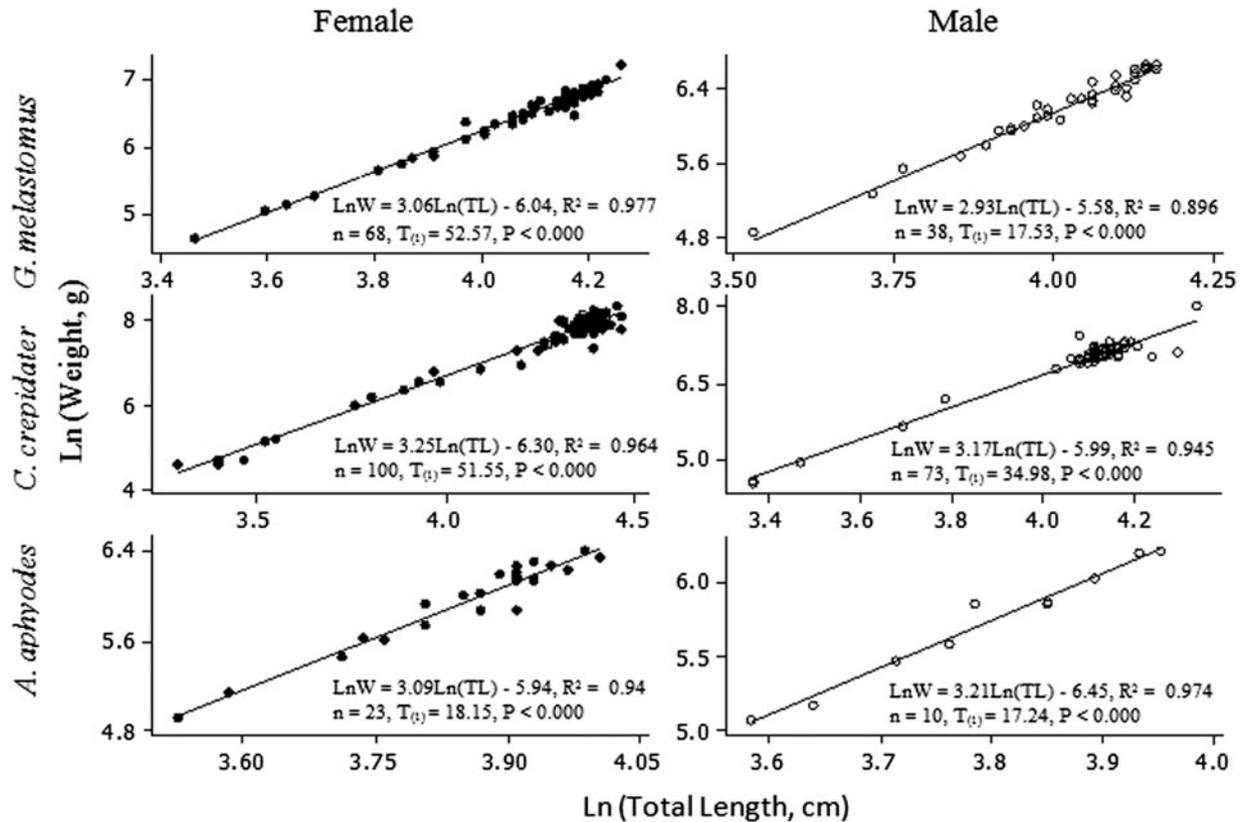


Fig. 4. Natural logarithm length/weight relationships of *Galeus melastomus*, *Centroselachus crepidater* and *Apristurus aphyodes* from the Rockall Trough, 2009, with females (left) and males (right).

lack of smaller individuals in the data set render these values meaningless.

Centroselachus crepidater

Centroselachus crepidater specimens were collected between 837 and 1512 m depth although very few individuals were caught around their mid-depth range (1050–1085 m). Significantly more females than males (Chi square test, $\chi^2 = 4.21$, $P < 0.05$) were caught (1♀:0.73♂). *Centroselachus crepidater* showed sexual dimorphism in length and mass with females being significantly longer and heavier than males (Mann–Whitney U -tests; total length, $U = 11432$, $N_1 = 100$, $N_2 = 73$, $P < 0.05$; mass, $U = 11,328$, $N_1 = 100$, $N_2 = 73$, $P < 0.05$). Few small individuals of either sex were caught (Figure 3). Females ranged in total length from 27 to 87 cm and males ranged in total length from 29 to 76 cm. Body mass ranged from 99 to 4726 g in females and 94 to 3024 g in males. The relationships between \ln length and \ln mass for male and female *C. crepidater* are shown in Figure 4. Both male and female *C. crepidater* exhibited isometric growth (t -test, ♂, $t = 1.96$, $df = 98$, $P = 0.35$; ♀, $t = 0.94$, $df = 70$, $P = 0.35$). Nearly all maturity stages were found to be represented in this species over the duration of this survey with the exception of female stage five (embryo differentiation stage), of which no examples were found. Amongst females, 66.3% individuals were found to be mature and amongst males 71.2% individuals were found to be mature. Figure 5 presents the maturity ogives for *C. crepidater* males and females with TL_{50} values calculated as 75.4 cm for

females and 57.2 cm for males respectively. Preliminary investigations showed that the preparation and staining method did not reliably distinguish between the growth bands in this species. A sub-sample of thirty individuals was selected at random and after being prepared and stained only 13.3% of samples ($N = 4$) showed any discernible growth bands and the maximum number of bands counted was two. Since this number of band counts was not comparable to similar sized fish in other ageing studies for this species (e.g. Irvine *et al.*, 2006), no age determinations were conducted for *C. crepidater* in this study.

Apristurus aphyodes

Apristurus aphyodes individuals were collected from a depth range of 1519–1569 m with significantly more females caught than males (Chi square test, $\chi^2 = 5.12$, $P < 0.05$) (1♀:0.43♂). Female *A. aphyodes* ranged in total length from 34 to 55 cm, whilst males ranged in total length from 36 to 52 cm. Un-eviscerated mass ranged from 136 to 609 g in females and 161 to 506 g in males. There was no difference in length and mass frequency between males and females for *A. aphyodes* (Mann–Whitney U -tests; total length, $U = 428$, $N_1 = 23$, $N_2 = 10$, $P = 0.15$; mass, $U = 435$, $N_1 = 23$, $N_2 = 10$, $P = 0.08$) (Figure 3). The relationships between \ln length and \ln mass for male and female *A. aphyodes* are shown in Figure 4. Both male and female *A. aphyodes* exhibited isometric growth (t -test, ♂, $t = -0.26$, $df = 21$, $P = 0.80$; ♀, $t = -0.57$, $df = 8$, $P = 0.58$). Few mature individuals of either sex were caught with only 13.0% of female and 20.0%

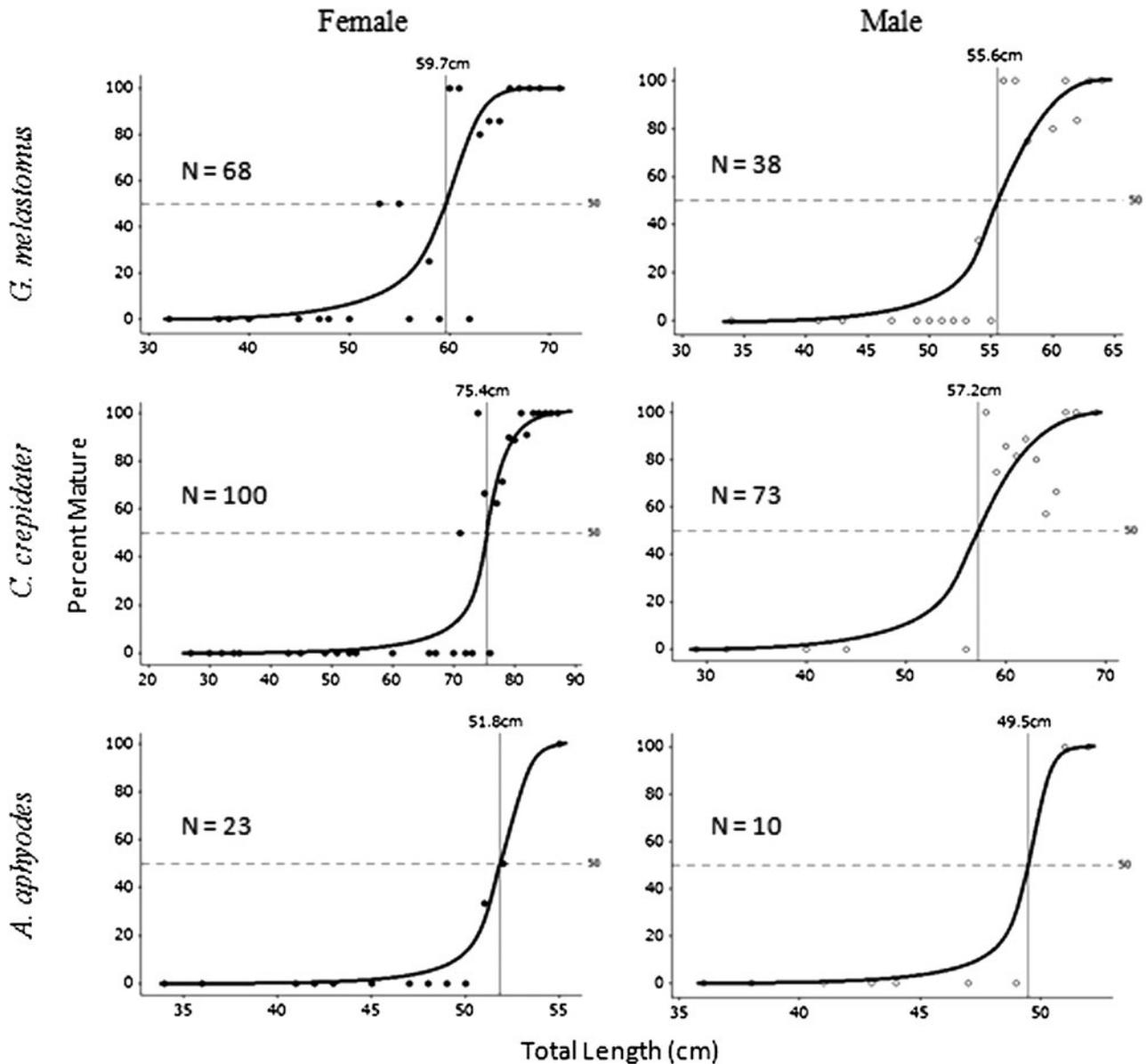


Fig. 5. Maturity ogives for *Galeus melastomus* (♀, top left, $N = 68$, $L_{50} = 59.7$ cm; ♂, top right, $N = 38$, $L_{50} = 55.6$ cm), *Centroselachus crepidater* (♀, middle left, $N = 100$, $L_{50} = 75.4$ cm; ♂, middle right, $N = 73$, $L_{50} = 57.2$ cm) and *Apristurus aphyodes* (♀, bottom left, $N = 23$, $L_{50} = 56.9$ cm; ♂, bottom right, $N = 10$, $L_{50} = 49.0$ cm) from the Rockall Trough, 2009.

of the males found to be mature. Figure 5 indicates that the estimated lengths for 50% maturity (TL_{50}) were 56.9 cm and 49.0 cm for female and male *A. aphyodes* respectively. Like *Centroselachus crepidater*, the method used for developing vertebral growth bands in this study was unsuccessful and no growth bands were visible in any *A. aphyodes* individuals.

DISCUSSION

This study has provided new information on the population biology of three deep sea shark species, *Galeus melastomus*, *Centroselachus crepidater* and *Apristurus aphyodes* in the Rockall Trough region. The results of this study are presented together with the available published data for the three species in Table 1.

In the present study which surveyed during one calendar month only, smaller individuals of all three target species were in low abundance in the catches, as has been reported for other studies on deep-sea sharks in the Rockall Trough region (Girard & Du Buit, 1999; Clarke *et al.*, 2001; Clarke *et al.*, 2002) which also surveyed for short calendar durations. However, it is unlikely that this is an artefact of the fishing gear used in our study as crustaceans and teleost fish with maximum total lengths of less than 30 mm were retained in the same trawls. It is possible that ontogenetic or seasonal movements between habitats, as seen for other deep-water shark species, may explain the absence of smaller individuals in the Rockall Trough region. For example *Deania calcea*, another deep-water squaloid shark, is highly migratory (Clark & King, 1989) with smaller individuals of *D. calcea* found off the coast of Portugal but absent in the Rockall Trough region where larger size-classes dominate (Clarke

Table 1. Summary of ecology and population biology of the deep-sea sharks *Galeus melastomus*, *Centroscelachus crepidater* and *Apristurus aphyodes*. M and F, male and female; TL, total length; TL₅₀ is the length at 50% maturity; $W = aL^b$; TL₅₀ is the length at 50% maturity.

Species	Sex	Max. recorded TL (cm)	Max. TL (cm)	TL ₅₀ (cm)	TL ₅₀ (cm)	This study TL (cm)	a (size range, cm)	a This study (size range, cm)	b (size range, cm)	b This study (size range, cm)	Known depth distribution (m)	Reproductive mode	Fecundity (young yr ⁻¹)	Diet	Max. age (yr)	Max. age (yr) This study
<i>Galeus melastomus</i>	M	75 ^{1,2}	64	49.37 ⁸	55.6	55.6	0.0025 ^{1,7*} (9.5–60.0)	0.0038 (34–64)	3.02 ^{1,7*} (9.5–60.0)	2.93 (34–64)	55–1873 ^{1,4}	Oviparous ⁷	97–193 ²	Crustaceans & Bony fish ³	8 ⁵ * [◇]	7 [◇]
	F	90 ^{1,2}	69	69.69 ⁸	59.7	59.7	0.0017 ^{3*} (11.1–66.1)	0.0024 (32–69)	3.15 ^{3*} (11.6–66.1)	3.06 (34–64)						5 [◇]
<i>Centroscelachus crepidater</i>	M	92 ^{1,9}	76	51.89 ⁴	57.2	57.2	0.0015 ^{1,6*} (24.2–48.0)	0.0025 (29–76)	3.19 ^{1,6*} (24.2–48.0)	3.17 (29–76)	230–1500 ⁷	Ovoviparous ¹⁵	3–9 ⁹	Bony fish & squid/ cuttlefish ⁶	34 ^{1,3}	No data
	F	103 ^{1,9}	87	68.13 ⁴	75.4	75.4	0.0024 ^{1,1*} (27–87)	0.0018 (27–87)	3.25 ^{1,1*} (27–87)	3.25 (27–87)						54 ^{1,3}
<i>Apristurus aphyodes</i>	M	54 ^{1,8*}	52	No data	49.0	49.0	No data	0.0016 (36–52)	No data	3.21 (36–52)	1014–1800 ¹⁵	Oviparous ¹⁰	No data	Crustaceans, squid & bony fish ¹⁸	No data	No data
	F		55		56.9	56.9		0.0026 (34–55)		3.09 (34–55)						No data

¹, Borges *et al.*, 2003; ², Capapé *et al.*, 2008; ³, Carrasón *et al.*, 1992; ⁴, Clarke *et al.*, 2001; ⁵, Correia & Figueiredo 1997; ⁶, Cortés 2006; ⁷, Cox & Francis 1997; ⁸, Costa *et al.*, 2005; ⁹, Daley *et al.*, 2002; ¹⁰, Dulvy & Reynolds 1997; ¹¹, Blackwell 2010; ¹², IGFA 2001; ¹³, Irvine *et al.*, 2006; ¹⁴, Jones *et al.*, 2003; ¹⁵, Last & Stevens 2009; ¹⁶, Mendes *et al.*, 2004; ¹⁷, Merella *et al.*, 1997; ¹⁸, Nakaya & Stehmann 1998. *, sex unspecified. ◇, no size range. ◇, un-validated.

et al., 2002). It is possible that a similar migration pattern could exist for the morphologically similar *C. crepidater*. Small individuals of *G. melastomus* were also infrequently caught in our sampling. The available data on their diet indicate that juvenile *G. melastomus* feed mainly upon small invertebrates such as crustaceans switching to teleost fish with increasing size (Olaso *et al.*, 2005; Fanelli *et al.*, 2009). It would be expected, in contrast to this study, that smaller individuals preying upon benthic crustaceans would be more prone to capture by bottom trawling than their larger conspecifics which feed upon pelagic teleosts such as blue whiting, *Micromesistius poutassou*, horse mackerel, *Trachurus trachurus* and Atlantic saury, *Scorpaenopsis scorpaenoides* (Olaso *et al.*, 2005); unless they occupy shallower water early in ontogeny moving into deeper water as they increase in size. This is supported by data in Rinelli *et al.* (2005) who found an increase in mean TL with increasing depth for this species. Such an ontogenetic dietary shift has been reported for the spurdog *Squalus acanthias* (Jones & Geen, 1977; Ketchen, 1986). Clearly further studies on the trophic ecology and movement patterns of deep sea sharks are needed.

Significantly higher numbers of females were caught for all target species. Our finding of a sex-ratio in favour of females for *G. melastomus* is in contrast with that reported by Rey *et al.* (2005) for *G. melastomus* in the Alboran Sea where males significantly outnumbered females. However, a sex-ratio in *C. crepidater* in favour of females was also reported by Clarke *et al.* (2001) for the Rockall Trough in the same sampling region. In addition, Clarke *et al.* (2001) also reported a sexually dimorphic length–frequency distribution for *C. crepidater* with females reaching a significantly larger size than males (Table 1). Interestingly, we caught few *C. crepidater* females containing pups and none collected at the embryo differentiation stage (Stage F5; Stehmann, 2002) during this survey. Neat *et al.* (2008) report that all *C. crepidater* caught in trawls conducted in the Anton Dohrn seamount region, located to the north of the Rockall Trough, during 2006 and 2007, were exclusively female and in the latter stages of pregnancy suggesting that this seamount may be a pupping and potential nursery area for *C. crepidater*.

Although data on the length–mass relationships for the three shark species under study are limited, the values for *a* and *b* obtained in the present study were found to be comparable to those reported in previous studies (Table 1). In particular for *G. melastomus* where *a* and *b* values from multiple studies (Merella *et al.*, 1997; Borges *et al.*, 2003; Mendes *et al.*, 2004) were available, the results from this study lie close to the regression line obtained when plotting log *a* vs log *b* (Froese, 2006) providing confidence in our results.

The TL₅₀ estimates reported for *G. melastomus* and *C. crepidater* are comparable to values reported in earlier studies (Table 1) and in agreement for a lower TL₅₀ for males than females. Costa *et al.* (2005) estimated TL₅₀ values of 49.4 cm for males (*N* = 31) and 69.7 cm for females (*N* = 35) for *G. melastomus*. Costa *et al.* (2005) used clasper length to calculate TL₅₀ for male *G. melastomus* in contrast with the internal examination used in this study. Estimates of TL₅₀ for *C. crepidater* reported by Clarke *et al.* (2001) were 51.9 cm for males and 68.1 cm for females, respectively. The TL₅₀ values estimated by Clarke *et al.* (2001) benefitted from larger sample sizes and multiple sampling methods compared to the present study. The estimates of TL₅₀ for *A. aphyodes* presented

here are the first conducted for this species. Nakaya & Stehmann (1998) have suggested that *A. aphyodes* of both sexes are fully mature between 47 and 50 cm TL and the estimates of TL_{50} for both sexes presented in this study are within/close to these suggested maturity ogives. However, our data would suggest that the upper boundary suggested by Nakaya & Stehmann (1998) is too low for females and is likely to be an artefact of the small sample size from which it was derived.

This study applied the ageing technique of Gennari & Scacco (2007) to three species of deep-water shark, *G. melastomus*, *C. crepidater* and *A. aphyodes*, that differ in their mean depth profiles (see Table 1). The method developed by Gennari & Scacco (2007) was shown to be successful when applied to *Etmopterus spinax* owing to the low disagreement in band counts between readers ($14.1\% \pm 1$ band). The results of this study indicate limited success with staining of growth bands only possible in *G. melastomus*. However, the high level of agreement in band counts between readers for *G. melastomus* indicates that the band pair data reported for this species in the present study can be treated with confidence. In addition, an IAPE of less than 5% is considered good in fish ageing studies and a CV greater than 10% is not uncommon in ageing sharks via vertebral analysis (Campana, 2001). The low level of disagreement between readers is most likely to be attributable to the use of high definition digital images as recommended by Gennari & Scacco (2007). In the present study, disagreement in band counts was mostly by ± 1 band, as has been reported previously by Correia & Figueredo (1997), with disagreements being more common in larger individuals. This is most likely to be attributable to: (1) the reduced distance between distal bands in older individuals (as a result of slowed rate of growth) making them harder to distinguish (Cortés, 2000); and (2) vertebral margin re-folding with increasing age found in many deep-sea species that exhibit deep coned vertebrae (Gennari & Scacco, 2007). The maximum number of band pairs observed in the present study (seven) is similar to Correia & Figueredo (1997) who observed a maximum of eight. The L_{∞} values estimated in the present study for *G. melastomus* using the number of band pairs as a proxy for age correspond to the maximum observed size for the species (Rey *et al.*, 2005; Rinelli *et al.*, 2005). However, given the low numbers of smaller (younger) sharks in the present study, we have chosen not to present the k or t_0 values derived from the von Bertalanffy growth curves as they are likely to be erroneous.

Clear resolution of the band pairs in the ventral centra of *Centroselachus crepidater* and *Apristurus aphyodes* using the staining technique of Gennari & Scacco (2007) was not successful. It is possible that the homeothermic cold water masses of the deeper habitat in which these species live reduces the effects of seasonality and this, coupled with sporadic food availability, reduces deposition of growth materials in periodic intervals. However, *C. crepidater* have been successfully aged using dorsal fin spines where maximum growth band count was 54 years (Irvine *et al.*, 2006) assuming annual deposition. This suggests that either vertebrae centra are unsuitable for aging in deeper species as the lack of calcification makes growth bands indistinguishable from the rest of the centra or that the chemical composition of vertebral centra of deeper species makes the use of cobalt (II) nitrate as a stain unsuitable for distinguishing growth bands. Gennari & Scacco (2007) used *Etmopterus spinax* sampled from a depth range of

300–900 m in the Tyrrhenian Sea to develop their staining technique. Whilst *E. spinax* can be classed as a deep-water species (Kyne & Simpfendorfer, 2010), these sample depths cover only the upper depth range of *C. crepidater* and may affect the direct transferability of this method to deeper dwelling species. Thus, conventional use of dorsal fin spines is thus likely to remain the established method for ageing *C. crepidater* and further study is required to find a suitable method for ageing *A. aphyodes*.

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REFERENCES

- Bailey D.M., Collins M.A., Gordon J.D.M., Zuur A.F. and Priede I.G. (2009) Long-term changes in deep-water fish populations in the north-east Atlantic: a deeper reaching effect of fisheries? *Proceedings of the Royal Society of London. Series B: Biological Sciences* 276, 1965–1969.
- Barker M.J. and Schluessel V. (2005) Managing global shark fisheries: suggestions for prioritizing management strategies. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15, 325–347.
- Basson M., Gordon J.D.M., Large P., Lorange P., Pope J. and Rackham B. (2002) *The effects of fishing on deepwater fish species to the West of Britain*. Joint Nature Conservation Committee Report No. 324. Peterborough: JNCC, 150 pp.
- Beamish R.J. and Fournier D.A. (1981) A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* 38, 982–983.
- Blackwell R.G. (2010) *Distribution and abundance of deepwater sharks in New Zealand waters, 2000–01 to 2005–06*. New Zealand Aquatic Environment and Biodiversity Report No. 57. Wellington: Ministry of Fisheries.
- Borges T.C., Olim S. and Erzini K. (2003) Weight–length relationship for fish species discarded in commercial fisheries of the Algarve (southern Portugal). *Journal of Applied Ichthyology* 19, 394–396.
- Cailliet G.M., Martin L.K., Kusher D., Wolf P. and Welden B.A. (1983) Techniques for enhancing vertebral bands in age estimation of California elasmobranchs. In Prince E.D. and Pulos L.M. (eds) *Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks*. US Department of Commerce, NOAA Tech. Rep. NMFS 8, pp. 157–165.

- Cailliet G.M.** (1990) Elasmobranch age determination and verification: an updated review. In Pratt H.L., Gruber S.H. and T. Taniuchi (eds) *Elasmobranchs as living resources: advances in the biology, ecology, systematic, and status of the fisheries*. US Department of Commerce, NOAA Technical Report 90, pp. 157–165.
- Cailliet G.M., Smith W.D., Mollet H.F. and Goldman K.J.** (2006) Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. *Environmental Biology of Fishes* 77, 211–228.
- Campana S.E.** (2001) Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* 59, 197–242.
- Campbell N., Neat F., Burns F. and Kunzlik P.** (2011) Species richness, taxonomic diversity, and taxonomic distinctness of the deep-water demersal fish community on the Northeast Atlantic continental slope (ICES Subdivision VIa). *ICES Journal of Marine Science* 68, 365–376.
- Cannizzaro L., Rizzo P., Levi D. and Gancitano S.** (1995) Age determination and growth of *Squalus blainvillei* (Risso, 1826). *Fisheries Research* 23, 113–125.
- Capapé C., Reynaud C., Vergne Y and Quignard J.P.** (2008) Biological observations on the smallspotted catshark *Scyliorhinus canicula* (Chondrichthyes: Scyliorhinidae) off the Languedocian coast (southern France, northern Mediterranean). *Journal of Aquatic Science* 3, 282–289.
- Carrasón M., Stefanescu C. and Cartes J.E.** (1992) Diets and bathymetric distributions of two bathyal sharks of the Catalan deep sea (western Mediterranean). *Marine Ecology Progress Series* 82, 21–30.
- Clark M.R. and King K.J.** (1989) *Deepwater fish resources off the North Island, New Zealand: results of a trawl survey, May 1985–June 1986*. Fisheries Technical Report No. 11. Wellington: Fisheries Research Centre.
- Clarke M.W., Connolly P.I. and Bracken J.J.** (2001) *Biology of exploited deep-water sharks west of Ireland and Scotland*. North Atlantic Fisheries Organisation Scientific Council Report. 01/108. Serial No. N4496, 18 pp.
- Clarke M.W., Connolly P.I. and Bracken J.J.** (2002) Catch, discarding, age estimation, growth and maturity of the squalid shark *Deania calcea* West and North of Ireland. *Fisheries Research* 56, 139–153.
- Conover W.J.** (1971) *Practical nonparametric statistics*. New York: John Wiley & Sons, 474 pp.
- Correia J.P. and Figueiredo I.** (1997) A modified decalcification technique for enhancing growth bands in deep-coned vertebrae of elasmobranchs. *Environmental Biology of Fishes* 50, 225–230.
- Cortés E.** (2000) Life history patterns and correlations in sharks. *Reviews in Fisheries Science* 8, 299–344.
- Costa M.E., Erzini K. and Borges T.C.** (2005) Reproductive biology of the blackmouth catshark, *Galeus melastomus*, off the south coast of Portugal. *Journal of the Marine Biological Association of the United Kingdom* 85, 1173–1183.
- Cox G.J. and Francis M.** (1997) *Sharks and rays of New Zealand (Volume 24)*. Christchurch: Canterbury University Press, 64 pp.
- Daley R.K., Stevens J.D. and Graham K.** (2002) *Catch analysis and productivity of the deepwater dogfish resource in southern Australia*. CSIRO Marine Research, Fisheries Research and Development Corporation (FRDC), and NSW Fisheries, Australia, FRDC Project No. 1998/108.
- Dulvy N.K. and Reynolds J.D.** (1997) Evolutionary transitions among egg-laying, live-bearing and maternal inputs in sharks and rays. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 264, 1309–1315.
- Fanelli E., Rey J., Torres P. and de Sola L.G.** (2009) Feeding habits of blackmouth catshark, *Galeus melastomus*, and velvet belly lantern shark, *Etmopterus spinax*, in the western Mediterranean. *Journal of Applied Ichthyology* 25, 83–93.
- Froese R.** (2006) Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology* 22, 241–253.
- Gennari E. and Scacco U.** (2007) First age and growth estimates in the deep water shark, *Etmopterus spinax* (Linnaeus, 1758), by deep coned vertebral analysis. *Marine Biology* 152, 1207–1214.
- Girard M. and Du Buit M.H.** (1999) Reproductive biology of two deep-water sharks from the British Isles, *Centroscymnus coelolepis* and *Centrophorus squamosus* (Chondrichthyes: Squalidae). *Journal of the Marine Biological Association of the United Kingdom* 79, 923–931.
- Gordon J.D.M.** (2003) The Rockall Trough, Northeast Atlantic: the cradle of deep-sea biological oceanography that is now being subjected to unsustainable fishing activity. *Journal of Northwest Atlantic Fishery Science* 31, 57–83.
- Heesen H.J.L.** (2003) *Development of Elasmobranch Assessments, DELASS*. Final Report of European Commission DG Fish Study. Contract 99/055.
- Heymans J.J., Howell K.L., Ayers M., Burrows M.T., Gordon J.D.M., Jones E.G. and Neat F.** (2011) Do we have enough information to apply the ecosystem approach to management of deep-sea fisheries? An example from the West of Scotland. *ICES Journal of Marine Science* 68, 265–280.
- International Council for the Exploration of the Sea** (2010) Report of the Working Group on Elasmobranch Fishes (WGEF), 22–29 June 2010, Horta, Portugal. *International Council for the Exploration of the Sea (CM Papers and Reports)* CM 2010/ACOM:19. 558 pp.
- International Game Fish Association** (2001) *Database of IGFA angling records until 2001*. Fort Lauderdale, TX: IGFA.
- Irvine S.B., Stevens J.D. and Laurensen L.J.B.** (2006) Surface bands on deepwater squalid dorsal-fin spines: an alternative method for ageing *Centroscymnus crepidater*. *Canadian Journal of Fisheries and Aquatic Sciences* 63, 617–627.
- Jones B.C. and Geen G.H.** (1977) Food and feeding of spiny dogfish (*Squalus acanthias*) in British Columbia waters. *Journal of the Fisheries Research Board of Canada* 34, 2067–2078.
- Jones E.G., Tselepides A., Bagley P.M., Collins M.A. and Priede I.G.** (2003) Bathymetric distribution of some benthic and benthopelagic species attracted to baited cameras and traps in the deep eastern Mediterranean. *Marine Ecology Progress Series* 251, 75–80.
- Jones E., Beare D., Dobby H., Trinkler N., Burns F., Peach K. and Blasdale T.** (2005) *The potential impact of commercial fishing activity on the ecology of deepwater Chondrichthyans from the west of Scotland*. ICES CM 2005/N:16
- Ketchen K.S.** (1986) *The spiny dogfish (Squalus acanthias) fishery in northeast Pacific and a history of its utilisation*. Canadian Special Publication of Fisheries and Aquatic Sciences 88. Department of Fisheries and Oceans, Ottawa, 78 pp.
- King M.** (2007) *Fisheries biology, assessment and management*. 2nd edition. Oxford: Blackwell Publishing, 382 pp.
- Koslow J.A., Boehlert G.W., Gordon J.D.M., Haedrich R.L., Lorange P. and Parin N.** (2000) Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES Journal of Marine Science* 57, 548–557.
- Kyne P.M. and Simpfendorfer C.A.** (2010) Deepwater chondrichthyans. In *Sharks and their relatives II: biodiversity, adaptive physiology, and conservation*. CRC Marine Biology Series. Boca Raton, FL: CRC Press, pp. 37–113.

- Large P.A., Hammer C., Bergstad O.A., Gordon J.D.M. and Lorange P.** (2003) Deep-water fisheries of the Northeast Atlantic: II assessment and management approaches. *Journal of Northwest Atlantic Fishery Science* 31, 151–163.
- Last P.R. and Stevens J.D.** (2009). *Sharks and rays of Australia*. 2nd edition. Cambridge, MA: Harvard University Press, 644 pp.
- Mendes B., Fonseca P. and Campos A.** (2004) Weight–length relationships for 46 fish species off the Portuguese west coast. *Journal of Applied Ichthyology* 20, 355–361.
- Merella P., Quetglas A., Alemany F. and Carbonell A.** (1997) Length–weight relationship of fishes and cephalopods from the Balearic Islands (western Mediterranean). *Naga ICLARM Q* 20, 66–68.
- Musick J.A., Burgess G., Cailliet G., Camhi M. and Fordham S.** (2000) Management of sharks and their relatives (*Elasmobranchii*). *Fisheries* 25, 9–13.
- Myers R.A. and Worm B.** (2005) Extinction, survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society*, B 360, 13–20.
- Nakaya K. and Stehmann M.** (1998) A new species of deepwater catshark, *Apristurus aphyodes* n. sp., from the eastern North Atlantic (Chondrichthyes: Carcharhiniformes: Scyliorhinidae). *Archive of Fishery and Marine Research* 46, 77–90.
- Neat F., Burns F. and Drewery J.** (2008) *The deepwater ecosystem of the continental slope and seamounts of the Rockall Trough: a report on the ecology and biodiversity based on FRS surveys*. Fisheries Research Services Internal Report No 02/08. Aberdeen: Fisheries Research Services.
- Neat F., Kynoch R., Drewery J. and Burns F.** (2010) *Deepwater trawl survey manual*. Marine Scotland Science Report 03/10. Aberdeen: Marine Scotland—Science.
- Olaso I., Velasco F., Sánchez F., Serrano A., Rodríguez-Cabello C. and Cendero O.** (2005) Trophic relations of lesser-spotted catshark (*Scyliorhinus canicula*) and blackmouth catshark (*Galeus melastomus*) in the Cantabrian Sea. *Journal of Northwest Atlantic Fishery Science* 35, 481–494.
- Rey J., de Sola L.G. and Massutí E.** (2005) Distribution and biology of the blackmouth catshark *Galeus melastomus* in the Alboran Sea (Southwestern Mediterranean). *Journal of Northwest Atlantic Fishery Science* 35, 215–223.
- Rinelli P., Bottari T., Florio G., Romeo T., Giordano D. and Greco S.** (2005) Observations on distribution and biology of *Galeus melastomus* (Chondrichthyes, Scyliorhinidae) in the southern Tyrrhenian Sea (central Mediterranean). *Cybiurn* 29, 41–46.
- Stehmann M.F.W.** (2002) Scales of maturity stages for sharks, rays and skates, and chimaeras. *Archive of Fishery and Marine Research* 50, 30–48.
- Stevens J.D., Bonfil R., Dulvy N.K. and Walker P.A.** (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* 57, 476–494.
- Wintner S.P.** (2000) Preliminary study of vertebral growth rings in the whale shark, *Rhincodon typus*, from the east coast of South Africa. *Environmental Biology of Fishes* 59, 441–451.
- and
- Zar J.H.** (1996) *Biostatistical analysis*. 3rd edition. Upper Saddle River, NJ: Prentice Hall, 662 pp.
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