The benthic and pelagic phases of *Muraenolepis marmorata* (Muraenolepididae) off the Kerguelen Plateau (Indian sector of the Southern Ocean)

by

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Life cycle

Abstract. – *Muraenolepis marmorata* life cycle is poorly investigated. This benthic species occurs mainly on the shelf slope and deep-sea as juvenile and adult stages but its early life is strictly pelagic off the Kerguelen Plateau. The upper layers (0-500 m) of the pelagic waters off the shelf are used by fingerlings both day and night during summertime. Dense aggregations (swarms) are sometimes observed by echo sounder (gas swim bladder detection) then have been confirmed by midwater trawl sampling. Fingerlings reach the size of about 55 mm before disappearing (ontogenic migration to the bottom) from the pelagic catches in autumn. *M. marmorata* and the myctophid *Krefftichthys anderssoni* are the only species to be present during the day in the upper layers of the water column off the Kerguelen Plateau. *M. marmorata* becomes a prey for top predators such as king penguins (*Aptenodytes patagonicus*) in their known depth diving range of their foraging area. Strong interannual variations in density of fingerlings are noted. The biomass of *M. marmorata*, evaluated in the bathymetric range 100-1000 m, was about 300 tonnes, which places the species at the 17^{th} rank of the 19 demersal species occurring on the shelf and slope of the Kerguelen Islands.

Résumé. – Phases benthique et pélagique de *Muraenolepis marmorata* (Muraenolepididae) au large du Plateau de Kerguelen (secteur indien de l'océan Austral).

Le cycle biologique de *Muraenolepis marmorata* est méconnu. Cette espèce démersale se rencontre sur les pentes et les grandes profondeurs au large du Plateau de Kerguelen aux stades juvénile et adulte mais est exclusivement pélagique au stade larvaire. Les niveaux supérieurs (0-500 m) des eaux pélagiques au large du Plateau sont le domaine des alevins tant de jour comme de nuit pendant la période estivale. Des agrégations importantes (de type essaim) sont parfois observées à l'échosondeur (résultant de la détection des vessies natatoires gazeuses) et ont été confirmées par échantillonnage au chalut pélagique. Les alevins atteignent la taille de 55 mm environ avant de disparaître (par migration ontogénique vers le fond) des captures pélagiques à l'automne. À ce stade, *M. marmorata* est la seule espèce, avec le Myctophidae *Krefftichthys anderssoni,* à être présente de jour dans les strates supérieures de la colonne d'eau au large des îles Kerguelen. *M. marmorata* peut devenir alors une proie pour les prédateurs supérieurs tels que les manchots royaux (*Aptenodytes patagonicus*) dans leur intervalle de plongée habituel sur leurs zones d'alimentation reconnues. De fortes variations interannuelles d'abondance des alevins sont observées. La biomasse de *M. marmorata*, estimée dans l'intervalle bathymétrique 100-1000 m, est d'environ 300 tonnes, ce qui place l'espèce au 17^{e} rang des 19 espèces démersales rencontrées sur le plateau et la pente des îles Kerguelen.

Günther (1880) first described *Muraenolepis marmorata* (Muraenolepididae, Gadiformes) from the Kerguelen Islands (Indian sector of the Southern Ocean). The species exhibits mainly a subantarctic geographical distribution (Chiu and Markle, 1990). The body form of the genus with second dorsal, caudal and anal fins confluent is at the origin of the vernacular names: "eel cod" or "marbled moray cod". Chin barbell presence and elongate rays of the pelvic and first dorsal fins characterise the family. *M. marmorata* is a demersal species with benthic feeding habits and moderate size; a size of 42 cm TL (700 g in weight) has been recorded (Duhamel *et al*., 2005). *M. marmorata* is not an abundant species among the ichthyofauna of the Kerguelen Plateau but is regularly caught as by-catch in the bottom trawl surveys conducted on the Kerguelen shelf and slope (Duhamel, 1993; Duhamel *et al.,* 2005; Duhamel and Hautecoeur, 2009). The species is also a regular by-catch in the longline fishery occurring from slope to the deep-sea (PECHEKER database source). Recent surveys in the epi- and mesopelagic layers off the Kerguelen Plateau area have revealed (Duhamel, 1998; Duhamel *et al*., 2000) the presence of the pelagic phase (fingerlings) of this eel cod. Little information is available about the species and any new knowledge helps to place the species within the marine ecosystem of the Kerguelen Plateau. Here, both the benthic distribution of the species and the occurrence of fingerlings in the water column in relation to the depth profile were investigated.

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MATERIAL AND METHODS

Bottom trawling/ longlining

Time series of demersal biomass benthic trawl surveys (in the bathymetric range 100-1000 m), independent from the fishery, have been conducted in the Kerguelen EEZ during spring time (September) since 2006 (POKER 1, 2006; POKER 2, 2010; POKER 3, 2013 and forecast POKER 4, 2017) with the same chartered trawler *Austral* focusing on a dedicated random and stratified sampling strategy. These surveys provide information on the distribution range, both geographical and bathymetrical, and density/abundance of the retained species by the trawl selectivity. A total of about 200 standardized 30 min randomly selected stations (using a 33 m bottom trawl) were occupied, covering the whole Plateau and banks (100-1000 m) in the northern part of the Kerguelen Plateau (Fig. 1A). All the catch of each station (Duhamel *et al.*, 2005) was sorted, counted and weighed onboard by species (19 fish species) (see Duhamel and Hautecoeur, 2009), including *M. marmorata,* and data were lodged in the PECHEKER database (11G Oracle® hosted at the Muséum national d'Histoire naturelle – MNHN – serv-

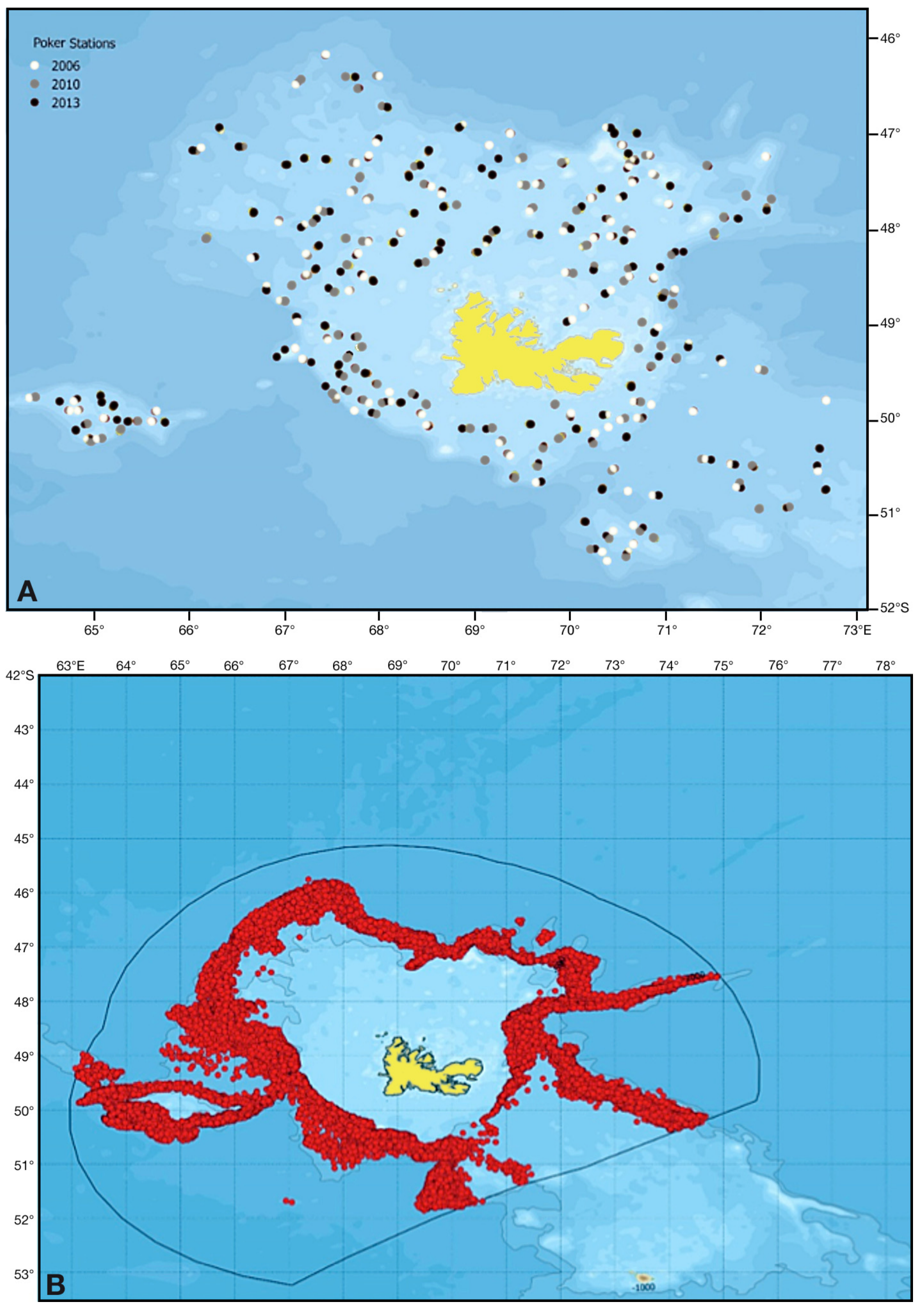

Figure 1. – Geographical coverage. **A**: Bottom trawl stations conducted during the "POKER" 1 (2006 in white), POKER 2 (2010 in grey), and POKER 3 (2013 in black) surveys off the Kerguelen Islands; **B**: Bottom commercial longlines conducted from 2006 to 2016 off the Kerguelen Islands (source: PECHEKER database). Continuous line shows the boundary of the 200 Nautical Mille French Exclusive Economic Zone.

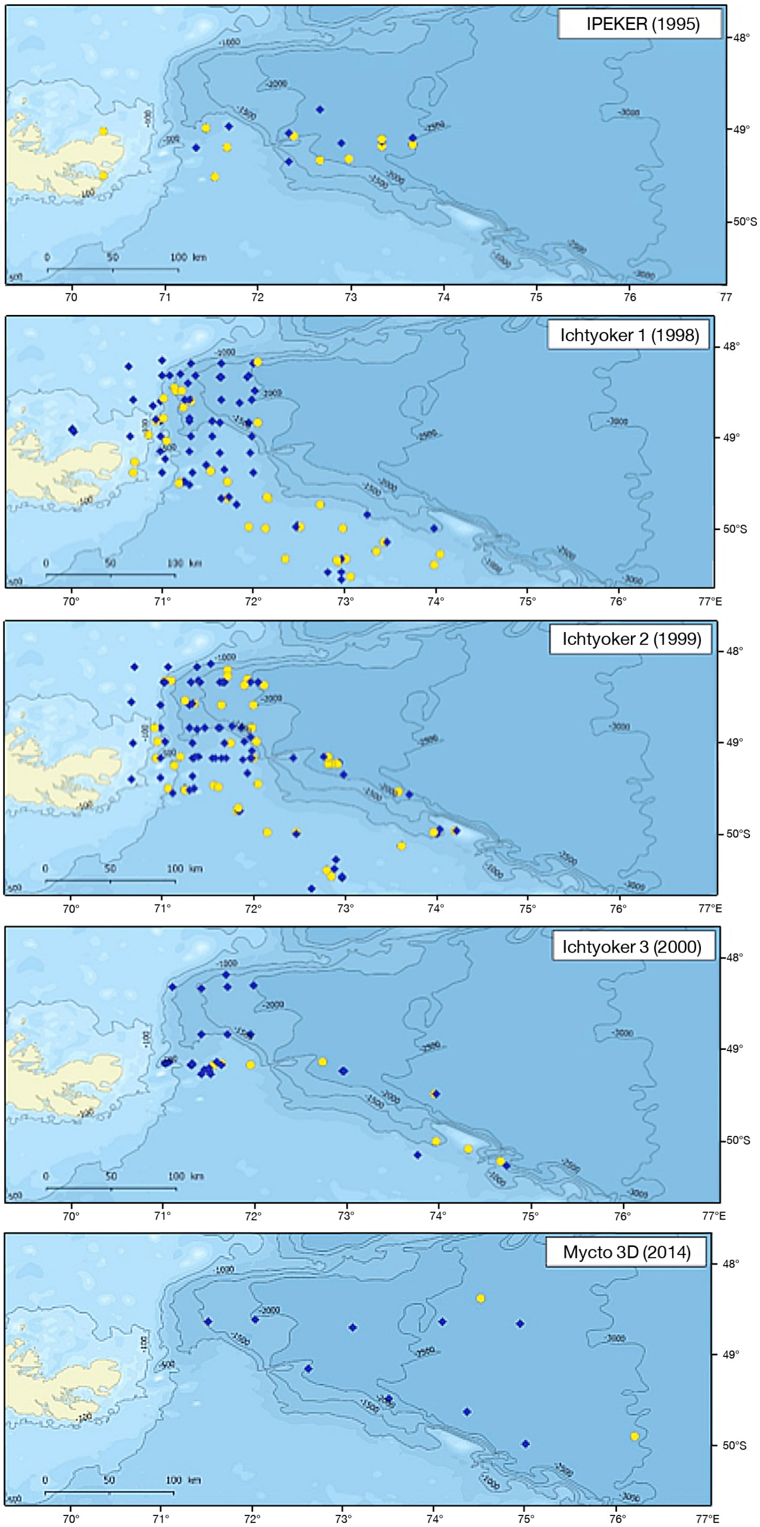

Figure 2. – Geographical pelagic survey coverage off the Kerguelen Islands during the "IPEKER" (1995), "ICHTYOKER 1, 2 & 3" (1998-2000) and "MYCTO 3 D" (2014) cruises. Each station includes four depths hauls (sub-surface, 50, 150, 300 m). Yellow circles are day stations, deep blue diamond-shaped are night stations.

ers) (Martin and Pruvost, 2007). To have comparative results, only the POKER 1 and 2 surveys, using the same mesh size in the codend (40 mm), were considered.

A bootstrap algorithm was used to estimate the *M. marmorata* biomass (in tonnes) and abundance (in thousands of specimens) for each survey cruise.

Additional longline fishery by-catch information collected by fishery observers (conducting to a full coverage of the deep-sea fishing grounds up to 2000 m) under the CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) standards is registered in PECHEKER (as for the POKER cruises). These randomly based 25% line observations by species on each haul complete the set of data for *M. marmorata* in the deeper range 500-2000 m. The selected set of data (Fig. 1B) concerns the more recent seasons (2006-2016).

Pelagic trawling

Pelagic surveys offshore the Kerguelen Islands have been regularly conducted since 1995 to investigate the pelagic fish community (Duhamel, 1998; Duhamel *et al.*, 2000). These surveys were devoted to study the foraging range of marine top predators (king penguin *Aptenodytes patagonicus* Miller, 1778 and fur seals *Arctocephalus gazella* (Peters, 1875)) (Bost *et al.*, 2002, 2011; Lea *et al.*, 2006) breeding at the eastern coast in relation to the proximity of the Polar front (PF) area, a major hydrological frontal system (Park and Vivier, 2011) driving the productivity of the offshore waters. Some inner shelf pelagic stations were added for depth range comparisons.

Two midwater gears (the International Young Gadoid Pelagic Trawl – IYGPT – and the "Mesopelagos" net) were used to investigate the epi- and mesopelagic layers at different time of the day and year from 1995 to 2014. The first cruise (March 1995), conducted with the small 25 m long scientific vessel *La Curieuse*, was named "IPEKER". The epi- and the upper mesopelagic ranges 0-300/500 m were investigated from both standardized day and night trawl stations (61 hauls) using IYGPT with a 10 mm mesh size in the codend. Trawls were towed horizontally 30 min at four levels of depths (sub-surface, 50 m, 150 m, 300 m and up controlled by SCANMAR® system). Another monthly protocol (but with gaps due to the sea conditions in the roaring forties, a rescue and careening obligations) in the same geo-

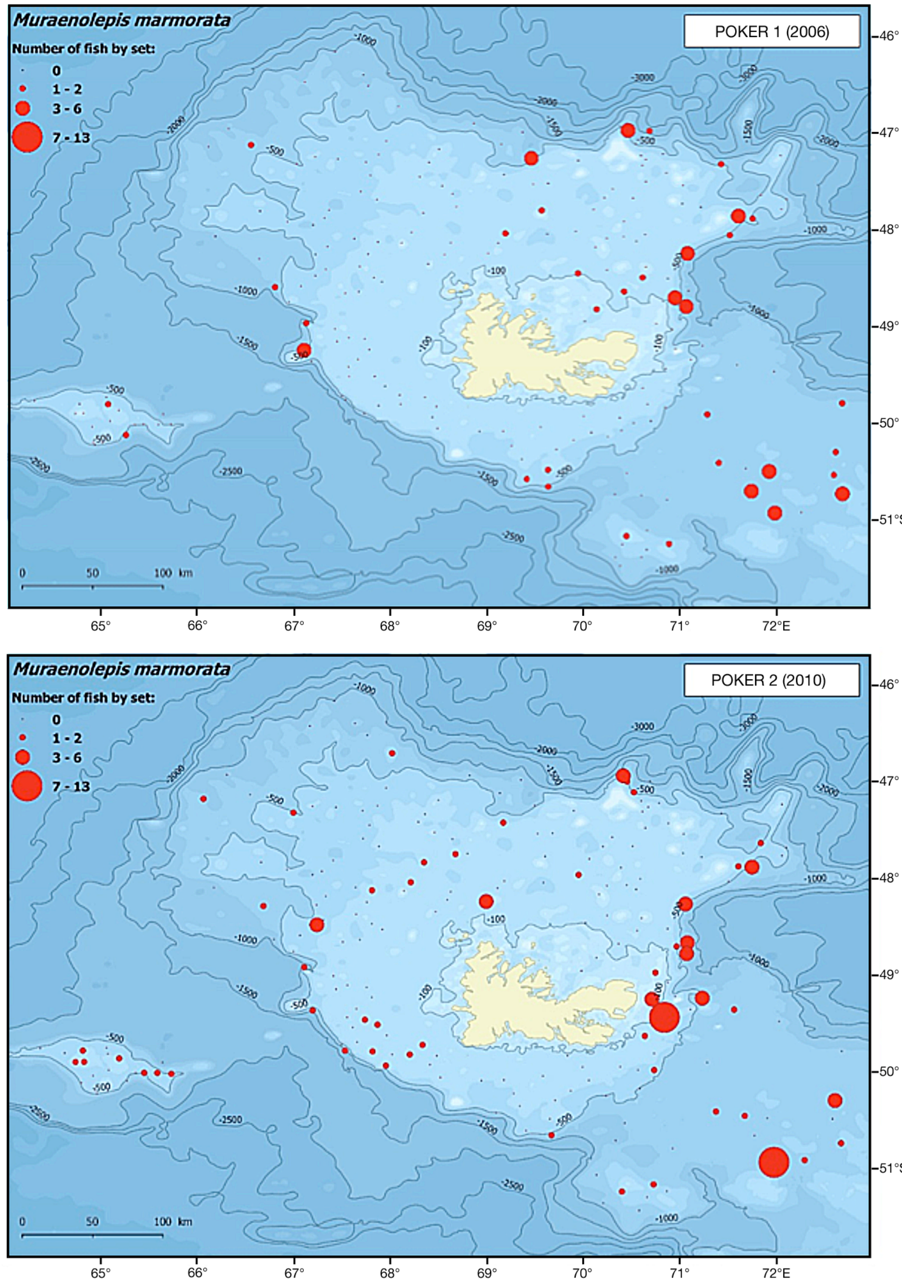

Figure 3. – Densities (n/set) of *Muraenolepis marmorata* during the POKER surveys: POKER 1 2006 (top); POKER 2 2010 (bottom).

graphical area, with the same gear and vessel, was conducted from February 1998 to November 2000: cruises "ICHTYOKER" 1, 2 & 3 (accounting for up to 832 hauls). Finally the cruise "MYCTO 3D" with the RV *Marion-Dufresne* (January-February 2014) reinvestigated the deep-sea part of the same area but using another gear ("Mesopelagos" net specially designed trawl – see Behagle *et al*., 2017 –, using a codend of 4 mm: 37 hauls, mainly night stations). The coverage of the stations is shown by cruise (IPEKER, MYCTO 3D) or annual series (ICHTYOKER) in figure 2.

The day and night stations were considered separately (dawn and dusk stations excluded). Three categories of pelagic habitats were selected for pooling the stations:

– the shelf zone (to the limit of the shelf break, about 200 m depth),

– the slope (to the lower limit of the mesopelagic layer: 400-1000 m) (including epi- and the mesopelagic waters) and

– the deep-sea, up to 1000 m depth (to a maximum bottom depth of 2600 m) (including epi-, meso- and a large part of the bathypelagic waters).

Table I. – Available datasets from pelagic hauls conducted off the Kerguelen Islands during summer 1995-2014 (January to March).

				Inner shelf		Slope		Deep-sea	
				< 200 m		400-1000 m		> 1000 m	
Cruise	Vessel	Dates	Used gear	Day	Night	Day	Night	Day	Night
IPEKER	*La Curieuse*	Mar. 1995	IYGPT	2	–	12	8	17	22
ICHTYOKER 1	*La Curieuse*	1998	IYGPT	3	12	53	40	18	21
ICHTYOKER 2	*La Curieuse*	1999	IYGPT	3	6	18	26	25	27
ICHTYOKER 3	*La Curieuse*	2000	IYGPT	–	–	2	34	2	8
MYCTO 3 D	*Marion-Dufresne*	Jan.-Feb. 2014	Mesopelagos	–	–	–	–	4	33

The used set of data has a common period to all cruises, summertime (Tab. I), but the "ICHTYOKER" cruises also allow comparisons with other seasons.

All the catch of each haul from these pelagic surveys was sorted by species using available Southern Ocean fish keys (Hulley, 1981; Gon and Heemstra, 1990; Duhamel *et al.*, 2005) then counted and weighed. Size of fish was individually registered using standard (SL) or total length (TL) when possible. The data (gear characteristics, station position, date and hour, depth, hour and species analysis, including *M. marmorata* occurrence and specimens size), were stored in an Access® database (named BASEXP hosted at MNHN).

Table II. – Mean abundance (in number) and biomass (in tonnes) of *Muraenolepis marmorata* in the range 100-1000 m off the Kerguelen Islands estimated by bootstrap statistical method from the hauls results of POKER 1 (2006) and 2 (2010) bottom cruises surveys. SE: Standard error, CL: confidence interval; oneside95: lower one-sided 95% confidence interval.

	Year	Mean	SE	Lower CL	Upper CL	One-side95
Abundance (n X 1000)						
POKER 1	2006	1622	363	967	2382	1057
POKER 2	2010	1956	533	1099	3142	1196
Biomass (tonnes)						
POKER 1	2006	246	46	159	340	172
POKER 2	2010	342	89	196	539	213

RESULTS

Bottom trawl surveys and commercial longlining

The geographical distribution of densities resulting from the POKER bottom trawl surveys shows a relative low density of *M. marmorata* over the main shelf and the southwestern Skif bank (Fig. 3). Few stations reveal the presence of the eel cod, mainly observed on the slope and the deep-sea with the major part of the catches occurring in the eastern to southeastern part of the area. Interannual cruises do not show major difference in the global geographical occurrence but densities variations seem important.

Mean abundance and biomass (and associated statistics based on bootstrap sample), were low (Tab. II) for *M. marmorata* with a maximum mean biomass (342 tonnes) observed in 2010 in the range 100-1000 m.

Pooled Length Frequency distributions (LFD) extend from 10 to 40 cm with the bulk of the specimens ranging between 25-35 cm TL (Fig. 4).

By-catch records from the longline fishery extend the distribution outside the bathymetric range of the POKER cruises (Fig. 5) with a gradual decrease of occurrence with increasing depths. The maximum depth record reaches about 1400 m. LFD associated to the observations show that the majority of fish were 20-50 cm TL in size (Fig. 4). Length-weight relationships can be produced: $W = 0.0119\ e^{0.0929TL}$ ($n = 143$ from 20 to 52 cm TL, $R^2 = 0.9256$).

The examination of gonads stages (males and females) of by-catch specimens reveals mature females from 29 cm TL and spawning and post-spawning specimens occurring during May-June. However fecundity has not been evaluated due to few specimens available.

Pelagic surveys

When stations are pooled, *M. marmorata* seems quasi-absent from the shelf stations (Tab. III) where nearly only larval stages of shelf species [*Gobionotothen acuta* (Günther, 1880), *Lepidonotothen squamifrons* (Günther, 1880), *L. mizops* (Günther, 1880), *Harpagifer kerguelensis* Nybelin, 1947, *Channichthys rhinoceratus* Richardson, 1844] are present.

By contrast, *M. marmorata* is present as fingerling (fully pigmented young stage), both on the slope (Tab. IV) and deep-sea stations (Tab. V), throughout day and night during summertime. *M. marmorata* (and larval stage of the demersal Nototheniidae *Lepidonotothen squamifrons*) can raise the density level of the species from the true pelagic fish community (*i.e.* myctophids and some other mesopelagic species such as *Notolepis coatsi* Dollo, 1908, *Stomias* spp. Cuvier, 1816, *Bathylagus tenuis* Kobyliansky, 1986) during this season.

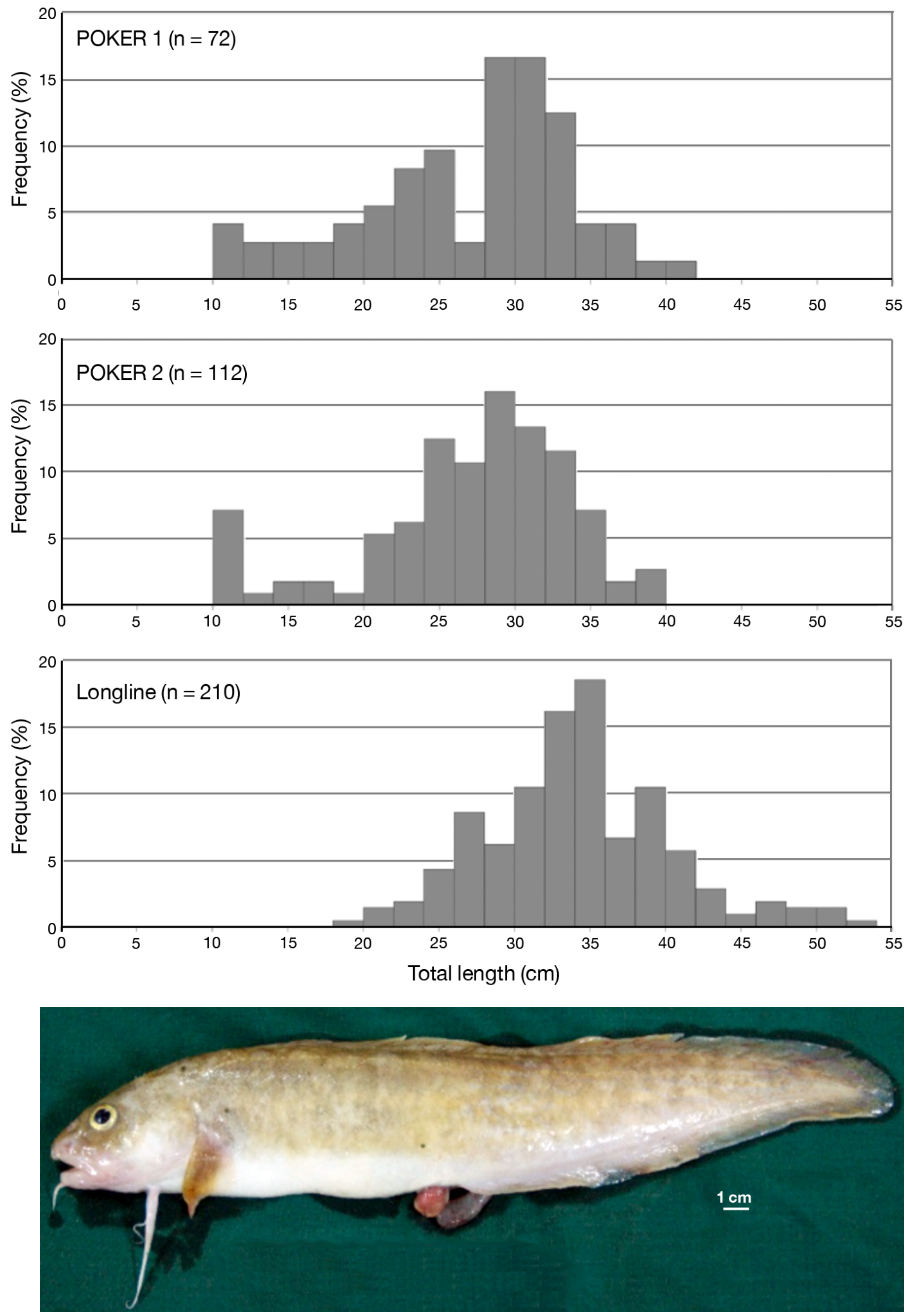

Figure 4. – Length Frequency Distributions (LFD) of *Muraenolepis marmorata* from POKER 1 (2006), POKER 2 (2010) Kerguelen Islands fish bottom biomass surveys and by-catch in the bottom longline fishery (2006-2016) off the Kerguelen Islands. Photo: *Muraenolepis marmorata* (photo ©POKER 2).

Annual densities were compared using Kruskal-Wallis test. For slope stations at daytime, the test reveals that the distributions of annual densities are non-homogeneous (chi-squared = 8.711, df = 3, p-value = 0.033). The year pair-wise comparison using the Bonferroni method exhibits a different density distribution between ICHTYOKER 1 (1998) and ICHTYOKER 2 (1999) (p-value adjusted = 0.036). For slope station at nighttime, annual densities are also non-homogeneous (chi-squared = 37.8794, df = 3, p-value = 2.998e-08) and the year pair-wise comparison shows different distribution between ICHTYOKER 3 (2000) and IPEKER (1995) (p-value adjusted = 8.917623e-04) and also ICHTYOKER 1 (1998) (p-value adjusted = 4.717730e-06), and similarly between ICHTYOKER 2 (1999) and IPEKER (1995) (p-value adjusted = 2.621796e-03) and ICHTYOKER 1 (1998) (p-value adjusted = 1.024937e-04). The deep-sea stations also show a non-homogeneous density distribution at daytime (chi-squared = 19.6577, df = 4, p-value = 0.0006) and nighttime (chi-squared = 33.4549, df = 4, p-value = 9.638e-07). Regarding deep-sea station at daytime, the year pair-

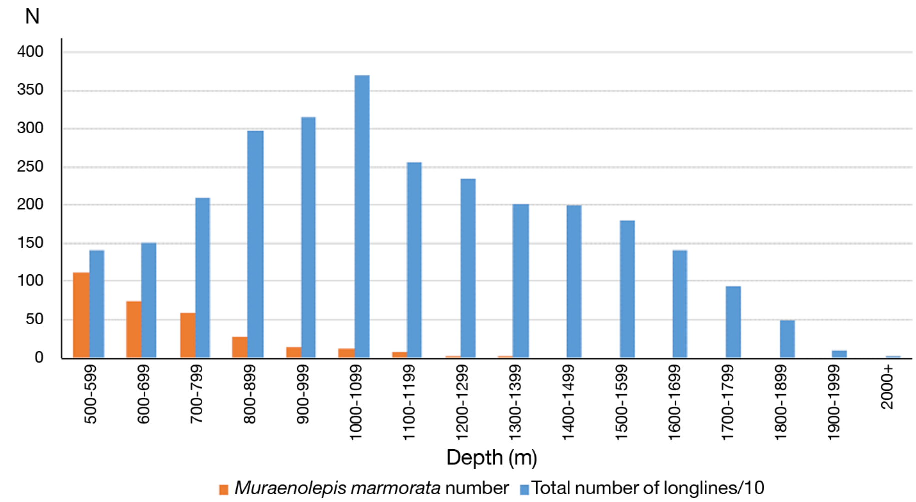

Figure 5. – Depth range occurrence of *Muraenolepis marmorata* by-catch in the total bottom longlines deployed in the fishery (2006-2016) off the Kerguelen Islands (500-2000 m).

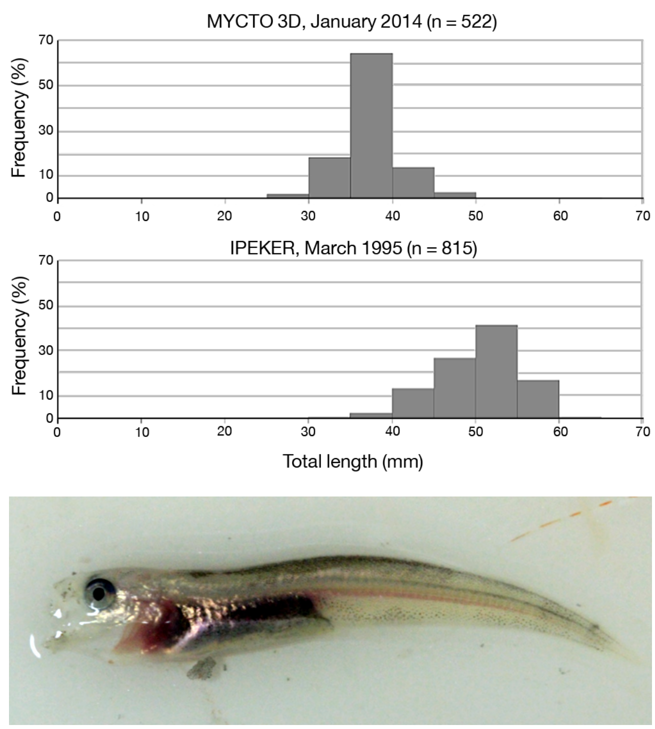

Figure 6. – Length Frequency Distributions (LFD) of *Muraenolepis marmorata* fingerlings during early (January 2014, MYCTO 3 D) or late summer (March 1995, IPEKER) pelagic surveys. Photo: *Muraenolepis marmorata*, fingerling TL 35 mm (photo ©MYCTO 3D).

wise comparison shows different distribution between ICHTYOKER 2 (1999) and IPEKER (1995) (p-value adjusted = 0.0009) and also ICHTYOKER 1 (1998) (p-value adjusted = 0.049).

The year pair-wise comparison shows even more different distributions for deep stations at nighttime: between IPEKER (1995) and ICHTYOKER 1 (1998) (p-value adjusted = 1.954437e-01) and ICHTYOKER 3 (2000) (p-value adjusted = 3.068454e-02) and also between ICHTYOKER 2 (1999) and ICHTYOKER 1 (1998) (p-value adjusted = 3.551007e-01) and MYCTO 3D (2014) (p-value adjusted = 2.703473e-05), and IPEKER (1995) (p-value adjusted = 4.024205e-05) and finally between MYCTO 3D (2014) and ICHTYOKER 3 (2000) (p-value adjusted = 4.445896e-02), and ICHTYOKER 1 (1998) (p-value adjusted = 2.868581e-01).

Day-night abundances, all years taken together and year-by-year, were compared using Mann-Whitney test. No significant differences between day and night distributions for slope station were observed (W = 5028, p-value = 0.161). But, for deep station, the highest values were observed at night (W = 2429, p-value = 3.285e-05), specifically for IPEKER (1995) and MYCTO 3D (2014).

An exceptional mono-specific dense concentration (6128 specimens recorded) has even been detected (from gas-filled swimbladder) by acoustics (38 Khz) and partially sampled at station 14 (70 m fishing depth over 2050 m bottom depth at night). The occurrence of *M. marmorata* in the pelagic layers outside the summer season (from ICHTYOKER cruises) is anecdotal (Tabs III, IV) and concerns isolated specimens.

The distribution of specimens was scattered when summer abundance was high (1995, 1998, 2014). Up to 45% of the total number of stations allow to catch fingerlings, both over slope and deep-sea depths (up to 2500 m) (Tab. VI). Catches mainly concern few specimens (less than 10 by station) but some stations can aggregate large number of specimens, both day and night.

The pelagic occurrence of *M. marmorata* concerns only a limited size range of fish (up to 27 mm TL, mainly ranging from 3 to 5 cm). No larval stages have been found but fingerling stages, as revealed by coloration and size of specimens (all cruises), are recorded. Early summertime samples (January 2014) give a near normal distribution of similar

Table III. – Day/night shelf occurrence of species in the pelagic surveys off the Kerguelen Islands (1995-2014). Summer seasons (IPEKER, ICHTYOKER surveys) on the left, other ICHTYOKER seasons on the right. NB: rare species not included in the table.

Cruise	IPEKER		ICHTYOKER				ICHTYOKER							
Date	1995	1995	1998	1998	1999	1999	1999	1999	1998	1998	2000	2000	1998	1998
Number of 30' hauls	2	–	3	12	3	6	–	12	–	14	–	2	5	–
Season	Summer						Autumn		Winter				Spring	
Time of the day	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Lanternfish (Myctophidae)														
Electrona antarctica	0	–	0	0	1	24	–	0	–	1	–	0	7	–
Electrona carlsbergi	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Electrona subaspera	0	–	0	4	0	0	–	0	–	1	–	0	0	–
Gymnoscopelus bolini	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Gymnoscopelus braueri	0	–	0	0	0	3	–	1	–	0	–	0	0	–
Gymnoscopelus fraseri	0	–	0	0	1	1	–	0	–	0	–	0	2	–
Gymnoscopelus nicholsi	0	–	0	18	1	10	–	1	–	0	–	0	13	–
Gymnoscopelus piabilis	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Krefftichthys anderssoni	0	–	2	1	2	0	–	13	–	0	–	0	4	–
Metelectrona ventralis	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Protomyctophum andriashevi	0	–	0	0	0	0	–	0	–	0	–	0	2	–
Protomyctophum bolini	0	–	0	2	0	23	–	1	–	0	–	2	10	–
Protomyctophum choriodon	0	–	0	14	0	2	–	0	–	0	–	0	1	–
Protomyctophum gemmatum	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Protomyctophum luciferum	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Protomyctophum normani	0	–	0	0	0	0	–	1	–	0	–	0	0	–
Protomyctophum tenisoni	0	–	0	16	1	1	–	34	–	0	–	1	0	–
Other meso-bathypelagic fish species														
Arctozenus risso	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Astronesthes psychrolutes	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Bathylagichthys australis	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Bathylagus tenuis	0	–	0	1	0	0	–	0	–	0	–	0	0	–
Benthalbella elongata	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Diplophos rebainsi	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Echiodon cryomargarites	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Icichthys australis	0	–	0	0	0	0	–	1	–	0	–	0	0	–
Idiacanthus atlanticus	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Melanonus gracilis	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Melanostigma gelatinosum	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Nansenia antarctica	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Notolepis coatsi	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Paradiplospinus gracilis	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Paraliparis thalassobathyalis	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Pseudoscopelus australis	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Stomias boa boa	0	–	0	0	0	0	–	3	–	3	–	0	0	–
Stomias gracilis	0	–	0	0	0	0	–	0	–	0	–	0	0	–
Shelf–coastal fish species (larval stages) by-catch														
Champsocephalus gunnari	0	–	0	2	0	3	–	0	–	6	–	0	0	–
Channichthys rhinoceratus	6	–	20	77	0	31	–	21	–	9	–	0	0	–
Dissostichus eleginoides	0	–	0	2	0	3	–	0	–	0	–	0	0	–
Gobionotothen acuta	109	–	1	255	0	23	–	0	–	30	–	0	0	–
Harpagifer kerguelensis	46	–	57	192	0	39	–	25	–	2	–	0	0	–
Muraenolepis marmorata	0	–	1	4	0	0	–	0	–	0	–	0	0	–

Table III. – Continued.

Cruise	IPEKER		ICHTYOKER				ICHTYOKER							
Date	1995	1995	1998	1998	1999	1999	1999	1999	1998	1998	2000	2000	1998	1998
Number of 30' hauls	2	–	3	12	3	6	–	12	–	14	–	2	5	–
Season	Summer						Autumn		Winter				Spring	
Time of the day	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Lepidonotothen mizops	0	–	10	50	0	27	–	8	–	161	–	0	0	–
Lepidonotothen squamifrons	0	–	0	17	0	1	–	18	–	3	–	1	0	–
Notothenia rossii	0	–	0	4	1	0	–	0	–	0	–	0	0	–
Paranotothenia magellanica	0	–	0	7	0	3	–	0	–	1	–	0	0	–
Zanclorhynchus spinifer	0	–	0	1	0	0	–	0	–	2	–	0	0	–

sized (27 to 48 mm) fish (cohort) with a modal length of 35-40 mm. Later in the season, but for another year (March 1995), a modal length 50-55 mm (for fish ranging from 31 to 57 mm) suggests size group moving toward larger size with spreading of the lengths (as observed in the length frequency distribution) in relation to the various growths of specimens (Fig. 6). The maximum observed size (all seasons) in the pelagic realm was 57 mm. The few specimens observed outside the summer period (Tabs III-V) exhibit similar size to summer samples.

DISCUSSION

M. marmorata is not an abundant demersal species, in the surveyed bathymetric range (100-1000 m), among the 19 fish species occurring on the Kerguelen Islands marine shelf and slope. The total species biomass ranges from 246 (POKER 1) to 342 tonnes (POKER 2) (considering a total of 232,126 and 241,136 tonnes, respectively, for all 19 demersal fish species) ranking at the 17th place. However, the occurrence of the species in the longline by-catch indicates that the estimation of the biomass is partial and should be higher than observed. Such result is similar with those obtained around South Georgia (the major comparable area of the Atlantic sector of the Southern Ocean), where *Muraenolepis microps* Lönnberg, 1905 occurs (Gregory *et al*., 2016), and ranking 10th of the 13 significant species. *Muraenolepis* sp. seems again to be not a key species in the demersal fish community in the vicinity of the Prince Edward Islands (Pakhomov *et al.,* 2006), westward to the Kerguelen Plateau.

The Kerguelen Islands inner shelf does not seem to be the bathymetric optimum range for the species because the slope concentrates the majority of the species occurrence, especially in the eastern/southeastern sector of the area, a recognized high productivity area close to the Polar Frontal Zone (Mongin, 2011). Additional data obtained from the commercial longline by-catch helped finding the maximal depth range extension (1400 m) that the species reaches, and also its maximum size (52 cm TL) and weight (probably close to 1 kg from the 920 g observed for a 48 cm TL specimen). It is up to the known size range (Duhamel, 2005). However, the maximum depth range given by Chiu and Markle (1990) for the species (1600 m) seems not to be valid for the Kerguelen Plateau area.

Spawning specimens were observed during winter suggesting a probable hatching time at spring. Efremenko (1983) described early stages of a *M. microps* species occurring in South Georgia with spawning during winter, pelagic eggs 1.5-1.6 mm in size caught in August at depth 500-1000 m, yolk sac larvae (5.8-6.5 mm) in September/October (spring), preflexion larvae (8.5-9.8 mm) in October-November in the epipelagic layers (0-100 m) and postflexion larvae (16.5-28.5 mm) in January/March. In a more coastal environment, Belchier and Lawson (2013) confirm that the relative abundance of Muraenolepididae (*i.e. M. microps*) larvae is restricted from September to January. The first early life stages (before fingerlings) for *M. marmorata* have not been sampled at Kerguelen but probably also occur in the deep sea as for *M. microps*. Fingerlings seem well sampled in summer from the water column between sub-surface down to 550 m and from the slope to deep-sea eastward from the Kerguelen shelf. As the sampling shows moving of size groups (cohorts) during summer towards the largest pelagic lengths, the autumn samples indicate the pelagic phase coming to an end. Despite the low level of demersal juvenile and adult abundance, the densities of fingerlings are noticeable off the Kerguelen Plateau in some years and even become a principal component of the species composition, besides the dominant lanternfish species during summertime. During the day, it is even the only species (excluding the larval stage of the Nototheniidae *Lepidonotothen squamifrons*) occurring in the upper water column with the Myctophidae *Kreffichthys anderssoni* (Lönnberg, 1905). It should be noted that such regular and significant presence of *M. marmorata* was not observed outside the Kerguelen shelf area where the family occurs. Summer and autumn presence of fingerlings (38-51 mm TL) are noted in the Scotia Sea from the upper layers (3-212 m) (Collins *et al*., 2012) but are unusual. Dense concentrations (swarms) can be sometimes encountered

Table IV. – Day/night slope occurrence of species in the pelagic surveys off the Kerguelen Islands (1995-2014). Summer seasons (IPEKER, ICHTYOKER surveys) on the left, other ICHTYOKER seasons on the right. NB: rare species not included in the table.

Cruise	IPEKER		ICHTYOKER						ICHTYOKER															
Date	1995	1995	1998	1998	1999	1999	2000	2000	1998	1998	1999	1999	2000	2000	1998	1998	2000	2000	1998	1998	1999	1999	2000	2000
Number of 30' hauls	12	8	53	40	18	26	2	34	–	18	29	68	1	–	–	38	–	27	18	31	–	11	–	8
Season	Summer								Autumn						Winter				Spring					
Time of the day	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Lanternfish (Myctophidae)																								
Electrona antarctica	5	564	889	3060	767	1884	0	1151	–	1141	449	3240	9	–	–	917	–	432	57	1357	–	975	–	121
Electrona carlsbergi	1	124	364	94	105	145	1	1930	–	75	357	303	0	–	–	3	–	3	0	37	–	17	–	1
Electrona subaspera	0	57	32	90	15	85	0	48	–	7	7	32	0	–	–	3	–	34	3	23	–	3	–	3
Gymnoscopelus bolini	0	15	16	64	16	12	0	59	–	6	9	4	2	–	–	2	–	13	0	14	–	1	–	2
Gymnoscopelus braueri	0	149	25	1466	90	418	2	799	–	23	58	460	6	–	–	113	–	125	0	34	–	179	–	11
Gymnoscopelus fraseri	1	466	278	1625	39	309	0	517	–	295	175	759	16	–	–	390	–	284	13	304	–	39	–	22
Gymnoscopelus nicholsi	10	49	126	258	18	397	0	400	–	70	139	564	3	–	–	103	–	154	21	339	–	192	–	74
Gymnoscopelus piabilis	0	26	12	224	10	54	1	185	–	17	13	57	0	–	–	0	–	2	0	5	–	2	–	0
Krefftichthys anderssoni	108	211	2215	9922	3054	2083	6	1106	–	83	2309	2950	24	–	–	71	–	574	6	247	–	106	–	222
Metelectrona ventralis	0	0	0	1	1	4	0	0	–	3	2	13	0	–	–	1	–	0	0	0	–	0	–	0
Protomyctophum andriashevi	200	46	452	166	164	123	8	124	–	65	211	242	15	–	–	49	–	109	56	119	–	41	–	11
Protomyctophum bolini	84	761	741	1318	332	661	6	2095	–	261	837	1222	35	–	–	23	–	101	68	304	–	292	–	40
Protomyctophum choriodon	7	6	15	63	9	27	0	17	–	8	1	5	0	–	–	0	–	1	1	11	–	0	–	0
Protomyctophum gemmatum	1	0	0	8	0	0	0	2	–	0	3	0	0	–	–	0	–	0	0	1	–	1	–	0
Protomyctophum luciferum	0	0	2	4	0	0	0	0	–	171	9	17	0	–	–	21	–	0	0	25	–	0	–	0
Protomyctophum normani	0	0	0	0	0	0	0	0	–	0	0	1	0	–	–	0	–	2	0	0	–	0	–	0
Protomyctophum tenisoni	0	630	385	1631	86	931	0	129	–	967	1543	3433	18	–	–	1644	–	1951	73	79	–	103	–	12
Other meso-bathypelagic fish species																								
Arctozenus risso	0	2	9	2	0	0	0	0	–	0	0	0	0	–	–	0	–	0	0	0	–	0	–	0
Astronesthes psychrolutes	0	0	0	1	0	0	0	0	–	0	0	1	0	–	–	1	–	1	0	0	–	0	–	0
Bathylagichthys australis	0	0	0	6	0	1	0	1	–	0	0	0	0	–	–	0	–	0	0	0	–	0	–	0
Bathylagus tenuis	0	0	1	13	0	28	0	185	–	0	0	20	0	–	–	0	–	0	0	2	–	0	–	0
Benthalbella elongata	0	0	0	0	0	0	0	0	–	0	0	0	1	–	–	1	–	0	0	0	–	0	–	0
Diplophos rebainsi	0	0	0	0	0	2	0	0	–	0	0	0	0	–	–	0	–	0	0	0	–	0	–	0
Echiodon cryomargarites	0	0	0	0	0	0	0	0	–	0	0	1	0	–	–	1	–	0	0	1	–	0	–	0
Icichthys australis	0	1	1	32	3	6	0	25	–	0	2	13	0	–	–	1	–	1	0	26	–	5	–	3
Idiacanthus atlanticus	0	0	0	5	0	0	0	0	–	0	0	0	0	–	–	0	–	0	0	0	–	0	–	0
Melanonus gracilis	0	0	0	0	0	0	0	0	–	0	0	1	0	–	–	0	–	0	0	0	–	0	–	0
Melanostigma gelatinosum	0	1	1	2	1	2	0	29	–	0	0	1	0	–	–	2	–	3	0	0	–	7	–	0
Nansenia antarctica	0	0	0	2	0	0	0	7	–	0	0	1	0	–	–	0	–	0	0	0	–	1	–	0
Notolepis coatsi	2	14	107	150	39	12	0	32	–	33	32	163	1	–	–	7	–	11	1	1	–	4	–	0
Paradiplospinus gracilis	0	6	16	33	11	12	0	344	–	35	17	82	3	–	–	13	–	27	6	11	–	32	–	2
Paraliparis thalassobathyalis	0	0	0	0	0	0	0	1	–	0	0	0	0	–	–	0	–	3	0	0	–	0	–	0
Pseudoscopelus australis	0	0	0	0	0	0	0	0	–	0	0	2	0	–	–	0	–	0	0	0	–	0	–	0
Stomias boa boa	0	9	10	80	12	11	0	34	–	7	16	76	1	–	–	31	–	29	0	2	–	3	–	1
Stomias gracilis	0	0	0	0	0	0	0	155	–	0	0	5	0	–	–	0	–	13	0	0	–	0	–	2

Table IV. – Continued/

Cruise	IPEKER		ICHTYOKER						ICHTYOKER															
Date	1995	1995	1998	1998	1999	1999	2000	2000	1998	1998	1999	1999	2000	2000	1998	1998	2000	2000	1998	1998	1999	1999	2000	2000
Number of 30' hauls	12	8	53	40	18	26	2	34	–	18	29	68	1	–	–	38	–	27	18	31	–	11	–	8
Season	Summer								Autumn						Winter				Spring					
Time of the day	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Shelf-coastal fish species (larval stages) by-catch																								
Champsocephalus gunnari	1	0	1	0	1	1	0	0	–	0	0	0	0	–	–	0	–	0	0	0	–	0	–	0
Channichthys rhinoceratus	0	0	1	0	3	2	0	0	–	0	3	0	0	–	–	0	–	0	0	0	–	1	–	0
Dissostichus eleginoides	1	0	1	1	0	1	0	1	–	0	0	0	0	–	–	0	–	0	0	0	–	0	–	0
Gobionotothen acuta	0	0	0	0	1	0	0	0	–	0	0	0	0	–	–	0	–	0	0	0	–	0	–	0
Harpagifer kerguelensis	0	0	0	0	0	0	0	0	–	0	0	0	0	–	–	0	–	0	0	0	–	0	–	0
Muraenolepis marmorata	126	382	173	319	3	1	0	0	–	0	0	3	0	–	–	0	–	1	0	0	–	0	–	0
Lepidonotothen mizops	0	0	0	0	0	0	0	0	–	0	0	0	0	–	–	3	–	0	0	0	–	0	–	0
Lepidonotothen squamifrons	130	0	385	267	94	855	0	0	–	3	263	148	0	–	–	8	–	2	1	1	–	0	–	0
Notothenia rossii	1	1	3	1	0	0	0	0	–	0	0	0	0	–	–	0	–	0	2	0	–	0	–	0
Paranotothenia magellanica	1	0	0	0	2	1	0	0	–	0	0	0	0	–	–	0	–	0	0	0	–	0	–	0
Zanclorhynchus spinifer	0	0	0	2	0	0	0	0	–	0	0	0	0	–	–	0	–	0	0	0	–	0	–	0

Table V. – Day/night deep-sea occurrence of species in the pelagic surveys off the Kerguelen Islands (1995-2014). Summer season (IPEKER, ICHTYOKER, MYCTO 3D surveys) on the left, other ICHTYOKER seasons on the right. NB: rare species not included in the table. *one haul.

Cruise	IPEKER		ICHTYOKER						MYCTO 3D		ICHTYOKER									
Date	1995	1995	1998	1998	1999	1999	2000	2000	2014	2014	1999	1999	2000	2000	1998	1998	1998	1998	1999	1999
Number of 30' hauls	17	22	18	21	25	27	2	8	4	33	17	73	3	38	–	42	3	9	–	16
Season	Summer										Autumn				Winter		Spring			
Time of the day	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Lanternfish (Myctophidae)																				
Electrona antarctica	16	2772	408	2960	670	3250	64	271	73	539	196	6031	1	1647	–	1595	0	91	–	638
Electrona carlsbergi	13	28	727	76	51	81	1	29	0	4	41	721	0	9	–	0	0	0	–	147
Electrona subaspera	0	69	23	46	26	104	4	24	0	1	20	126	0	68	–	22	0	3	–	20
Gymnoscopelus bolini	1	71	16	26	27	42	2	12	0	5	2	43	0	23	–	0	0	1	–	3
Gymnoscopelus braueri	0	2349	6	418	76	909	67	392	3	505	37	2573	1	1206	–	617	0	93	–	440
Gymnoscopelus fraseri	2	342	19	1319	30	617	19	99	0	0	41	750	1	427	–	447	0	28	–	35
Gymnoscopelus nicholsi	1	111	46	96	39	450	3	169	0	4	17	541	2	102	–	137	0	4	–	64
Gymnoscopelus piabilis	0	47	0	23	21	109	10	94	0	0	1	81	0	5	–	3	0	0	–	111
Krefftichthys anderssoni	346	1342	246	1790	1396	12117	81	291	187	1618	892	3298	1	554	–	16	0	9	–	347
Metelectrona ventralis	0	2	0	1	0	5	0	1	0	0	0	31	0	1	–	1	0	0	–	0
Protomyctophum andriashevi	2	69	188	50	27	44	6	8	0	2	26	385	197	209	–	94	0	0	–	20
Protomyctophum bolini	81	1076	887	967	621	1191	16	518	0	113	771	2970	259	383	–	16	0	1	–	267
Protomyctophum choriodon	2	4	1	10	8	84	1	0	0	1	0	2	0	1	–	1	0	0	–	0
Protomyctophum gemmatum	0	0	0	0	1	3	0	0	0	0	1	2	0	0	–	0	0	0	–	2
Protomyctophum luciferum	0	0	2	0	0	3	0	0	0	0	1	12	2	2	–	14	0	5	–	0

Table V. – Continued.

Cruise	IPEKER		ICHTYOKER						MYCTO 3D		ICHTYOKER									
Date	1995	1995	1998	1998	1999	1999	2000	2000	2014	2014	1999	1999	2000	2000	1998	1998	1998	1998	1999	1999
Number of 30' hauls	17	22	18	21	25	27	2	8	4	33	17	73	3	38	–	42	3	9	–	16
Season	Summer										Autumn				Winter		Spring			
Time of the day	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Protomyctophum normani	0	0	0	0	0	0	0	0	0	0	0	37	1	15	–	0	0	0	–	0
Protomyctophum tenisoni	13	969	48	1574	300	1591	0	10	2	118	224	9051	1	1337	–	2127	3	38	–	135
Other meso-bathypelagic fish species																				
Arctozenus risso	0	0	0	2	0	1	0	0	0	0	0	1	0	0	–	0	0	0	–	0
Astronesthes psychrolutes	0	0	0	0	0	0	0	0	0	0	0	3	0	1	–	1	0	0	–	0
Bathylagichthys australis	0	0	0	15	0	7	0	3	0	1	0	2	0	0	–	0	0	0	–	0
Bathylagus tenuis	0	227	0	2	15	76	3	19	0	127	0	175	0	70	–	11	0	0	–	199
Benthalbella elongata	0	4	0	1	0	18	0	0	0	0	0	15	0	6	–	3	0	0	–	1
Diplophos rebainsi	0	0	0	1	1	3	0	0	0	0	0	14	0	5	–	1	0	0	–	0
Echiodon cryomargarites	1	0	1	0	1	0	0	0	0	1	0	0	0	1	–	0	0	0	–	1
Icichthys australis	0	1	0	8	2	15	0	2	0	0	0	31	0	3	–	7	0	0	–	4
Idiacanthus atlanticus	0	0	0	5	0	0	0	1	0	1	0	0	0	3	–	0	0	0	–	0
Melanonus gracilis	0	0	0	0	0	0	0	0	0	23	0	13	0	8	–	0	0	0	–	1
Melanostigma gelatinosum	0	0	0	0	0	0	0	0	0	4	0	6	0	4	–	1	0	0	–	1
Nansenia antarctica	0	0	2	3	1	7	0	0	0	0	0	5	0	0	–	1	0	0	–	2
Notolepis coatsi	5	34	20	19	18	15	0	1	3	35	2	106	1	26	–	11	0	0	–	19
Paradiplospinus gracilis	0	29	2	6	9	12	0	6	0	4	3	54	1	39	–	37	0	2	–	22
Paraliparis thalassobathyalis	0	1	0	0	0	0	0	0	0	0	0	7	0	1	–	0	0	0	–	7
Pseudoscopelus australis	0	8	0	0	0	2	0	0	0	0	0	15	0	5	–	0	0	0	–	1
Stomias boa boa	0	109	17	57	22	120	0	3	2	69	14	617	1	162	–	214	0	4	–	45
Stomias gracilis	0	0	0	0	4	6	0	6	0	0	0	13	0	143	–	0	0	0	–	3
Shelf–coastal fish species (larval stages) by-catch																				
Champsocephalus gunnari	0	0	0	0	0	0	0	0	0	1	0	0	0	0	–	0	0	0	–	0
Channichthys rhinoceratus	0	0	0	0	1	0	0	0	0	0	0	1	0	0	–	0	0	0	–	0
Dissostichus eleginoides	0	0	0	0	0	1	0	0	0	0	0	0	0	0	–	0	0	0	–	1
Gobionotothen acuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	–	0
Harpagifer kerguelensis	0	0	0	0	10	0	0	0	0	0	0	1	0	0	–	0	0	0	–	0
Muraenolepis marmorata	56	574	25	167	1	14	0	3	0	6455 (*6128)	0	2	0	0	–	0	0	0	–	0
Lepidonotothen mizops	0	0	0	1	1	0	0	0	0	0	0	0	0	0	–	1	0	0	–	0
Lepidonotothen squamifrons	565	56	2	1	64	28	0	0	0	0	36	104	0	0	–	1	0	0	–	0
Notothenia rossii	0	1	0	2	0	0	0	0	0	15	0	0	0	0	–	0	0	0	–	0
Paranotothenia magellanica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	6	0	0	–	0
Zanclorhynchus spinifer	5	1	0	0	1	1	0	0	0	0	7	1	0	0	–	0	0	0	–	0

Table VI. – Frequency of occurrence (% of stations with positive catch) of *Muraenolepis marmorata* fingerlings during the summer sampling seasons 1995 (IPEKER), 1998 (ICHTYOKER) and 2014 (MYCTO 3D) and observed highest values in one catch (with associated noted trawling depths).

Summer	Day		Night		Day		Night		
Cruise	IPEKER	ICHTYOKER	IPEKER	ICHTYOKER	IPEKER	ICHTYOKER	IPEKER	ICHTYOKER	MYCTO 3D
Year	1995	1998	1995	1998	1995	1998	1995	1998	2014
Area	Slope				Deep-sea				
Station (n)	12	53	8	40	17	18	22	21	33
M. marmorata: – frequency of occurrence (%)	41.2	47.2	62.5	50	58.8	44.4	86.4	52.4	75.8
– total number of *M. marmorata*	126	173	382	319	56	25	574	167	6455
– maximal number fingerlings at one station	122	99	366	228	14	9	414	82	6128
Trawling depth (m) for the maximal number	150	144	300	72	250	260	100	48	70

(MYCTO 3 D), pointing out the aggregative characteristics of *M. marmorata* during this part of its life cycle. Top predators such as king penguins *Aptenodytes patagonicus,* foraging in the upper layers of the water column at day, can take the opportunity to swift to another potential energetic prey besides their common lanternfish prey, such as *K. anderssoni,* of similar size range (Bost *et al.,* 2002).

The pelagic communities off the Kerguelen Islands allow to distinguish shelf area, dominated by only the ichthyoplanktonic stages of demersal local species (Nototheniods: *Gobionotothen acuta, Harpagifer kerguelensis, Channichthys rhinoceratus, Lepidonotothen mizops*), from others (slope, deep-sea). The slope community is dominated with lanternfish [*Kreffichthys anderssoni, Electrona antarctica* (Günther, 1878)*, Protomyctophum bolini* (Fraser-Brunner, 1949), *Protomyctophum tenisoni* (Norman, 1930)*, Gymnoscopelus fraseri* (Fraser-Brunner, 1931), *G. braueri* (Lönnberg, 1905), *G. nicholsi* (Gilbert, 1911) and *P. andriashevi* Becker, 1963, respectively], some other mesopelagic species [*Paradiplospinus gracilis* (Brauer, 1906), *Notolepis coatsi, Stomias boa* (Risso, 1810) / *S. gracilis* Garman, 1899*, Bathylagus tenuis*] and pelagic stages of *L. squamifrons* (early stages) and *M. marmorata* (fingerlings). The deep-sea community retains the first three dominant lanternfish but the others move in their dominant position *G. braueri, P. tenisoni, G. fraseri, Electrona carlsbergi* (Tåning, 1932), and *G. nicholsi*. The other pelagic dominant species are *B. tenuis* and *Stomias* spp. From the bathypelagic realm, *N. coatsi* and again the early-life stages of shelf/slope species such as *L. squamifrons* and *M. marmorata*. However, *M. marmorata* is only a summer occupant of the pelagic layers unlike the permanent living meso/bathypelagic species. Day-night differences in densities of *M. marmorata* underline probable diel migration pattern similar to those of mesopelagic species (Duhamel *et al*., 2014).

The pelagic occurrence of *M. marmorata* fingerlings off the Kerguelen shelf could be linked to the local oceanography. Northward strong deep-sea currents (Park *et al*., 2008; Park and Vivier, 2011) on the eastern flank of the Kerguelen Islands, before retroflecting south-easternward, provide passive transport of summer fingerlings before settling from deep-sea spawning grounds (probably occurring in the south-east from local densities of adults) to the slope. Local densities are probably enhanced by the presence of the productive area initiated by the Antarctic polar front crossing the investigated area (Park and Vivier, 2011; Dragon *et al*., 2011). Summer secondary production (micro-zooplankton, mainly copepods from stomach contents analysis of fingerlings) seems to offer growing condition for fingerlings some years (1995, 1998, 2014 for the studied years) before their settlement on the slopes both of the shelf and surrounding banks. However, other great annual variation in fingerlings densities (1999, 2000) suggests irregular annual spawning or some post-larval mortality. Dispersion over deep-sea depths by fingerlings during summertime off the Kerguelen Islands gives the opportunity to the local population to colonize surrounding suitable new habitats such as seamounts or banks off the Kerguelen Plateau.

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