

Aspects of lanternfish distribution in the Kerguelen Plateau region

by

P. Alexander HULLEY* (1) & Guy DUHAMEL (2)

ABSTRACT. - Mesopelagic fishes play a major ecological role in the Southern Ocean by partitioning energy throughout the water column during diel vertical migration. In the region, lanternfishes (Myctophidae) represent the most abundant mesopelagic fish family by species, number and biomass. There has been some intensive, localized sampling of myctophids in the Kerguelen Plateau region, but this has been geared mainly to the elucidation of larval fish biology, and to trophic studies of bird and mammal predators, and was focused in the upper 200-300 m depth stratum and mainly to the east of the Plateau. In this paper, a number of published and unpublished datasets are examined in order to clarify “regional boundaries”, and to establish the distributional characteristics and nuances of some representative convergence, subantarctic and antarctic species in the light of their proposed phylogeny. To improve this knowledge base going forward, the high costs of ship-board sampling could well be off-set by the use of modeling techniques.

RÉSUMÉ. - Aspects de la distribution des poissons-lanternes dans la région du Plateau de Kerguelen.

Les poissons mésopélagiques jouent un rôle écologique majeur dans l’océan Austral en répartissant l’énergie à travers la colonne d’eau au cours des migrations nyctémérales. Dans la région, les poissons-lanternes (Myctophidae) représentent la famille de poissons mésopélagiques la plus abondante tant en nombre d’espèces qu’en nombre d’individus et biomasse. S’il y a eu quelques échantillonnages intensifs et localisés de Myctophidae autour du Plateau de Kerguelen, les études étaient essentiellement dévolues à la compréhension de la biologie des phases larvaires et aux études des régimes alimentaires des prédateurs que sont oiseaux et mammifères marins et elles furent limitées aux 200-300 m de la couche de surface, principalement dans le secteur oriental du Plateau. Dans cette contribution de nombreuses données publiées et non-publiées sont examinées pour clarifier les “zonages régionaux” et établir les caractéristiques de distribution, ainsi que leurs nuances, de quelques espèces typiques dites de convergence, subantarctique et antarctique en relation avec leur phylogénie proposée. Pour améliorer cette base de connaissance et la faire avancer, les coûts élevés des échantillonnages nécessitant des navires pourraient être compensés par l’utilisation de techniques de modélisation.

Key words. - Myctophidae - Kerguelen - Distribution - Ecology.

Lanternfishes (family Myctophidae) are the dominant fish family of the mesopelagic and bathypelagic zones of the Southern Ocean in terms of their species richness, biomass and abundance (Hulley, 1981; Linkowski, 1983; Zemsky, 1987; Nevinsky and Efremenko, 1989; Filin *et al.*, 1990; Kock, 1992; Loeb *et al.*, 1993; Donnelly *et al.*, 2004; Donnelly and Torres, 2008). Some 33 species have been recorded from Antarctic region (McGinnis, 1982; Hulley, 1990a; Duhamel *et al.*, 2005), where their total biomass has been estimated between 70-200 x 10⁶ tonnes (Lubimova *et al.*, 1983). The representative mesopelagic species all undertake diel vertical migration to a greater or lesser extent (Torres and Somero, 1988; Lancraft *et al.*, 1989; Piatkowski *et al.*, 1994; Duhamel, 1998; Duhamel *et al.*, 2000), but evidence for the non-migratory behaviour of the deep-dwelling species is lacking. The energy derived during nocturnal feeding by myctophids at shallower depths (Rowedder, 1979; Naumov *et al.*, 1981; Ascenio and Moreno, 1984; Kozlov and

Tarverdieya, 1989; Gerasimova, 1991; Kozlov and Shust, 1991; Podrazhanskaya and Tarverdieva, 1991; Kozlov, 1993a; 1993b; 1995; Pakhomov *et al.*, 1996; Pusch *et al.*, 2004; Schreeve *et al.*, 2009), is subsequently partitioned within the water column by predatory fishes (Bulman *et al.*, 2002), squids (Rodhouse *et al.*, 1992; Phillips *et al.*, 2001; 2003a; 2003b; 2003c; Bradshaw *et al.*, 2003), seabirds (Cherel *et al.*, 1993; 1996; Guinet *et al.*, 1996; Bost *et al.*, 1997) and mammals (Lea *et al.*, 2002; 2006) via the dynamic Antarctic trophic-web structure. Myctophid trophic levels have been estimated to range from 3.8-4.2 (Cherel *et al.*, 2008). Robison (2003) has postulated that in high southern latitudes, predator avoidance may be the principal driver for diel vertical migration, rather than behaviour directed to gaining a metabolic bonus, because the upper structure of the Antarctic water column is nearly isothermal.

In general and for mesopelagic species, the Indian Sector of the Southern Ocean has not been adequately sampled

(1) Department of Marine Biology, Iziko Museums of Cape Town, P.O. Box 61, Cape Town 8000, South Africa.

(2) Département des milieux et peuplements aquatiques, UMR 7208 BOREA, Muséum national d’Histoire naturelle, Case postale 26, 43 rue Cuvier, 75231 Paris CEDEX 05, France. [duhamel@mnhn.fr]

* Corresponding author [pahulley@iziko.org.za]

(Nafpaktitis and Nafpaktitis, 1969; Hulley, 1972; 1990b; Hulley *et al.*, 1989; Iwami and Kubodera, 1990; Duhamel and Hulley, 1993; Duhamel, 1998; Duhamel *et al.*, 2000). There has been an intensive, localized off-slope sampling programme using the International Young Gadoid Pelagic Trawl (IYGPT) east of Kerguelen (Wilson *et al.*, 1993; Bost *et al.*, 2002; Duhamel *et al.*, 2005), but trawling depths were geared mainly to trophic studies of bird and mammal predators (Lescroël *et al.*, 2004; Lea *et al.*, 2008; Cherel *et al.*, 2009), and were consequently restricted to the upper 300 m (Duhamel, 1998; Duhamel *et al.*, 2005). Similarly, several cruises have been undertaken during which standard, oblique Bongo-net hauls to 200 m (or shallower with a shoaling bottom) were made in order to elucidate the distribution, biology and ecology of fish eggs and larvae of both on-shelf and off-shelf species (including myctophids) at Marion-Prince Edward, Crozet and Kerguelen Islands (Koubbi *et al.*, 1991; 2003; 2009; Koubbi, 1992; 1993; Pakhomov *et al.*, 1994; Duhamel *et al.*, 2000). Some modeling of these data has been done (Loots *et al.*, 2007).

The aim of this paper is to re-examine a number of unpublished and published myctophid datasets in order to clarify mesopelagic “boundaries” to the Kerguelen Plateau region, and to elucidate the distributional characteristics and nuances of some representative (but poorly documented) Convergence, Subantarctic and Antarctic species in the light of their proposed phylogeny (Hulley, 1998). Such knowledge can assist in the development of more robust ecoregionalization models of Southern Ocean mesopelagic fish distribution (Koubbi *et al.*, 2010), and may well provide a firmer biological understanding to the availability and utilization of mesopelagic stocks by upper-level predators.

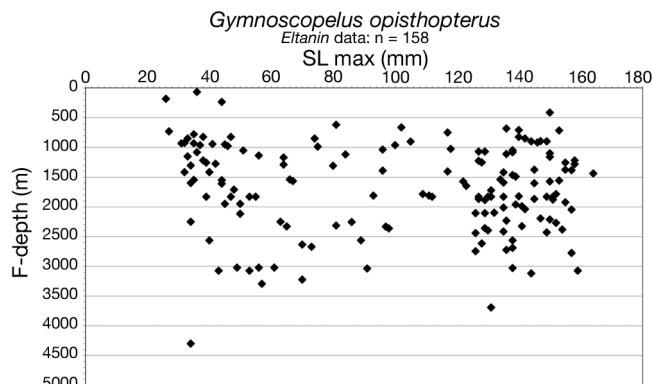


Figure 1. - *Gymnoscopelus opisthopterus*. Variation of standard length (SL) with maximum fishing depth of haul. *Eltanin* data: n = 158 hauls.

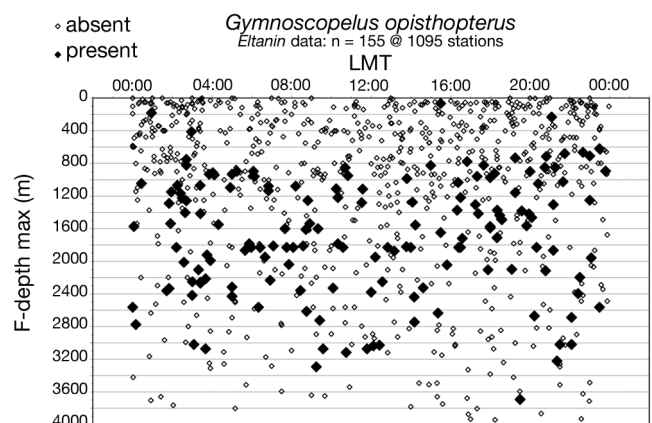


Figure 2. - *Gymnoscopelus opisthopterus*. Diel migration pattern. *Eltanin* data: n = 158 hauls at 1095 stations. LMT = local mean time.

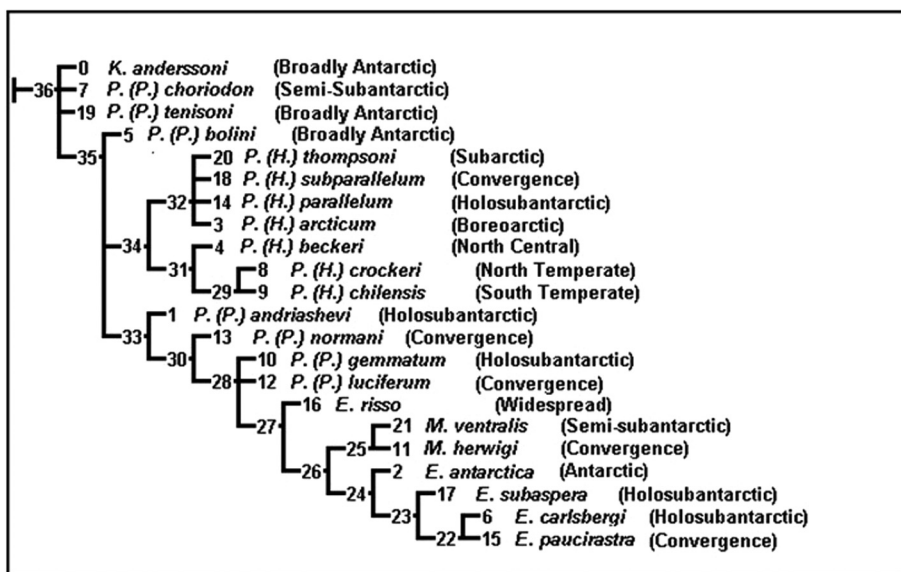


Figure 3. - Cladogram for *Electronini*. After Hulley (1998).

MATERIAL AND METHODS

The following published myctophid datasets, including details of nets, sampling strategies and geographic locations from the South Atlantic and Kerguelen Plateau region, were re-examined for the purposes of this paper: Japanese Antarctic Research Expedition-28 (Iwami and Kubodera, 1990); FFS *Walther Herwig* Cruises 1966, 1968, 1972, 1975 (Hulley, 1981; Post, 1987); NO *Marion Dufresne* Cruise 50 (Hulley *et al.*, 1989); Cruises Skalp and Skif 1897, 1988 (Duhamel and Hulley, 1993); and Ichtyoker Cruises 1-34 (Bost *et al.*, 2002). Data from a collated (and partly unpublished) set for the East Antarctic region, including records from Kerguelen, Crozet and Prydz Bay were also used (Philippe Koubbi and Anne Gourant, personal communication), and is termed the Koubbi-Gourant dataset in this paper; this set includes data from Duhamel *et al.* (2000); Duhamel (1998); Koubbi (1993; 2001); Koubbi *et al.* (1991; 2001; 2003; 2009); Loots *et al.* (2007). Distributional point-data records were also obtained from FishBase (Froese and Pauly, 2011) and the following bio-

The vertical distribution of *Gymnoscopeus opisthopterus* Fraser-Brunner, 1949 with respect to SL (Fig. 1) and diel cycle (Fig. 2) were collated from the species-station data given by McGinnis (1982: Appendix 1), in association with additional *Eltanin* station data supplied by Dr Rick Feeny (LACM; personal communication).

For our own data, all measurements were taken to the nearest 1 mm with digital sliding calipers in accordance with Hubbs and Hubbs (1953) and Nafpaktitis and Nafpaktitis (1969).

PRIMER Version 5.2.2 was used to examine the relationships of the eight stations from JARE-28 (Iwami and Kubodera, 1990: Table 2) using the Bray-Curtis similarity measure on root-root transformed abundance data, and the stations clustered using group-average sorting. SIMPER-analysis of the resulting groups was undertaken. An edited subset of the Koubbi-Gourant dataset, encompassing the region 45°-55°S, 60°-85°E and consisting of presence-

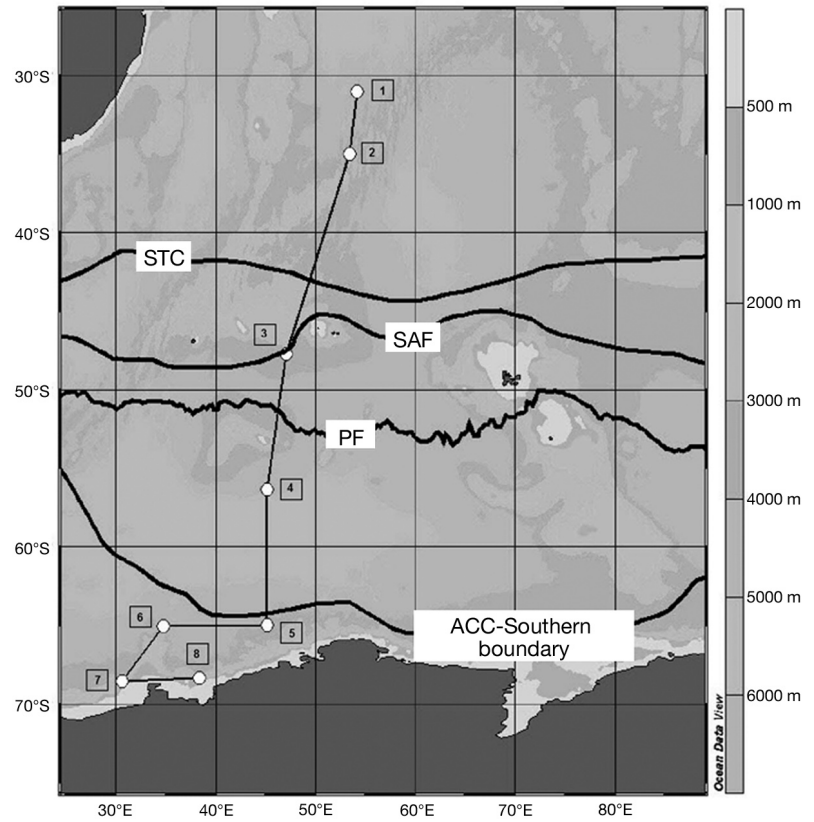


Figure 4. - JARE Cruise 28. Station positions (arbitrary numbering). STC = Subtropical Convergence; SAF = Subantarctic Front; PF = Polar Front; ACC = Antarctic Circumpolar Current (after Orsi, 1995).

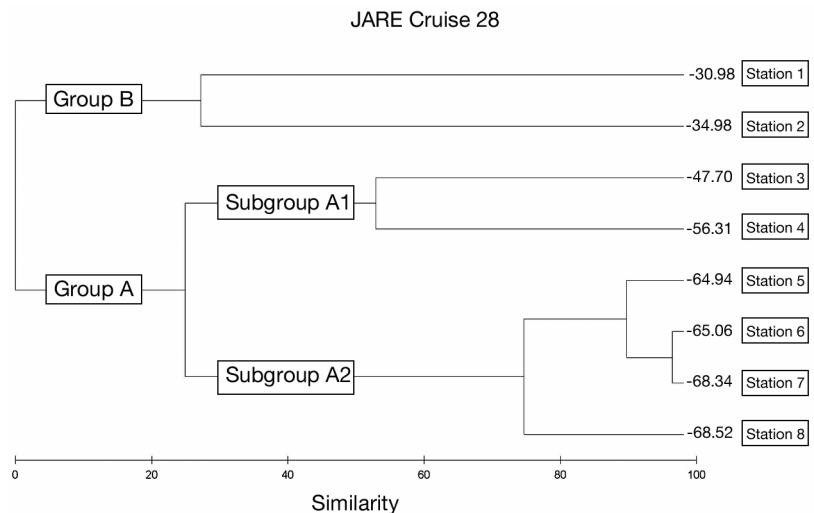


Figure 5. - JARE Cruise 28. Dendrogram of station relationships with respect to latitude in decimal degrees.

absence data records, was also analyzed with PRIMER as above. Species that were poorly represented, namely *Lowei-na interrupta* (Tåning, 1928), *Protomyctophum gemmatum* Hulley, 1981 and *P. parallelum* (Lönnberg, 1905), were excluded from the final analyses. Distributional maps were

Table I. - JARE Cruise 28. SIMPER analysis of species in subgroups A1 and A2 (average dissimilarity 75.09%).

Species	Subgroup A2		Subgroup A1		Contrib %	Cum. %
	Av. Abund	Av. Abund	Av. Diss	Diss / SD		
<i>Protomyctophum bolini</i>	0.00	9.00	15.09	17.24	20.09	20.09
<i>Krefflichthys anderssoni</i>	0.00	7.50	14.54	6.93	19.37	39.47
<i>Gymnoscopelus braueri</i>	0.00	4.50	12.76	13.49	16.99	56.46
<i>Electrona antarctica</i>	14.50	9.50	8.77	1.17	11.68	68.14
<i>Protomyctophum parallelum</i>	0.00	4.00	6.84	0.93	9.11	77.26
<i>Nannobranchium achirus</i>	0.00	2.50	6.08	0.93	8.01	85.36
<i>Protomyctophum tenisoni</i>	0.00	2.50	6.08	0.93	8.01	93.46
<i>Gymnoscopelus opisthopterus</i>	1.25	0.50	4.91	1.05	6.54	100.00
<i>Benthoosema suborbitale</i>	0.00	0.00	0.00	–	0.00	100.00
<i>Bolinichthys indicus</i>	0.00	0.00	0.00	–	0.00	100.00
<i>Ceratoscopelus warmingii</i>	0.00	0.00	0.00	–	0.00	100.00
<i>Gonichthys barnesi</i>	0.00	0.00	0.00	–	0.00	100.00
<i>Hygophum hyomii</i>	0.00	0.00	0.00	–	0.00	100.00
<i>Lampanyctus pusillus</i>	0.00	0.00	0.00	–	0.00	100.00
<i>Lobianchia dofleini</i>	0.00	0.00	0.00	–	0.00	100.00

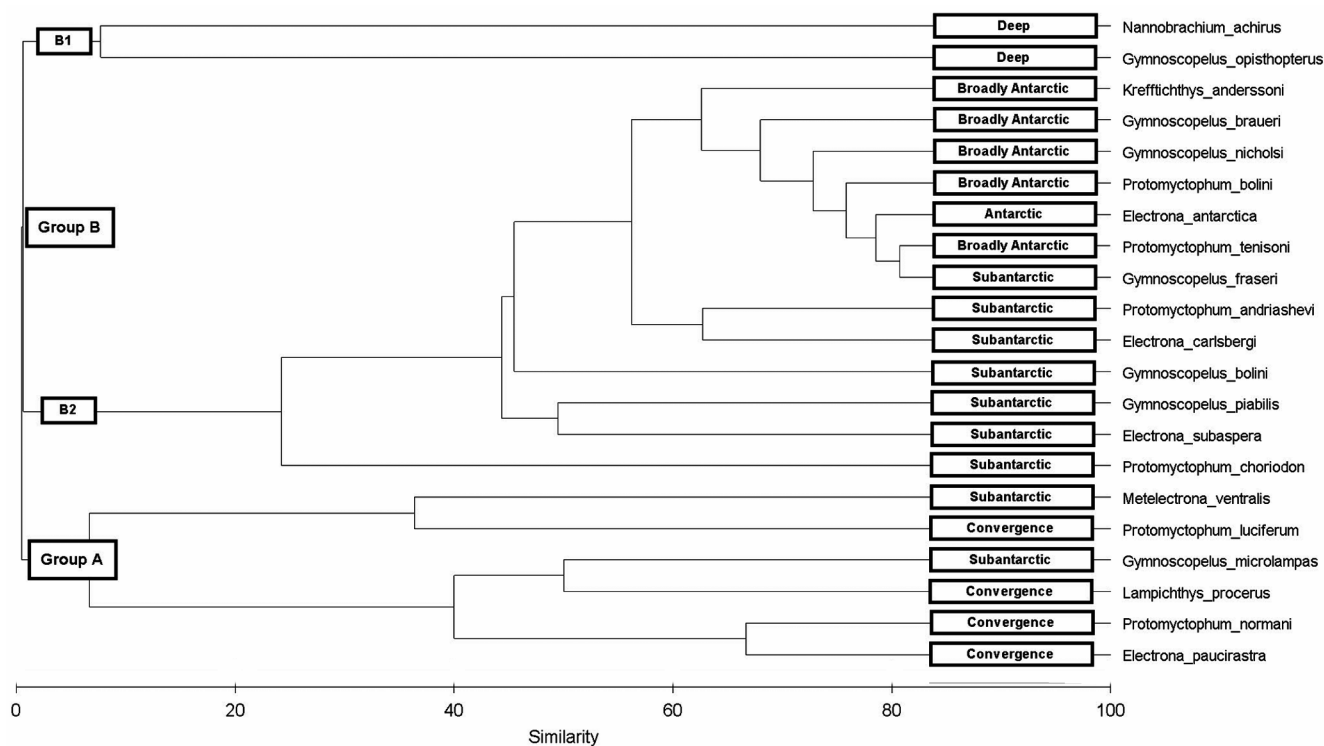


Figure 6. - Koubbi-Gourant Data Subset. Dendrogram of species relationships with respect to distribution pattern types (after Hulley, 1981).

created with Versamap Version 3.01, and Ocean Data View (ODV; Schlitzer, 2005) was used to construct visual correlations of distributional data with oceanographic datasets in ODV format. These datasets included annual hydrographic data from U.S. NODC World Ocean Atlas 2005, and from

the Southern Ocean Atlas (Olbers *et al.*, 1992). Both datasets were downloaded from the Alfred-Wegener Institute website (<http://odv.awi.de/>).

The cladogram of species of the Tribe Electronini (Fig. 3), which includes the Southern Ocean representatives

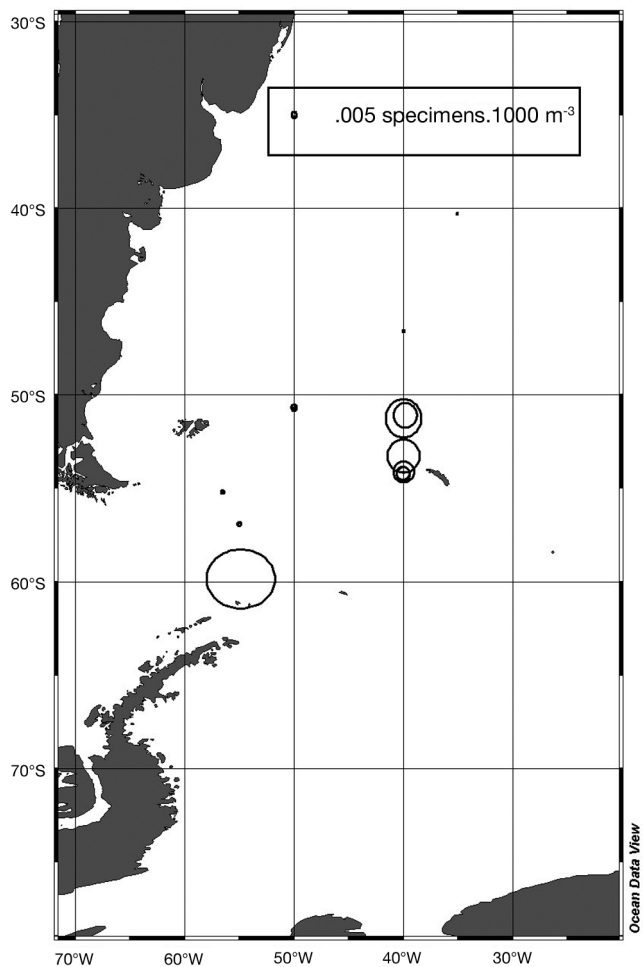


Figure 7. - *Electrona antarctica*. Southwest Atlantic: abundances based on FFS Walther Herwig data.

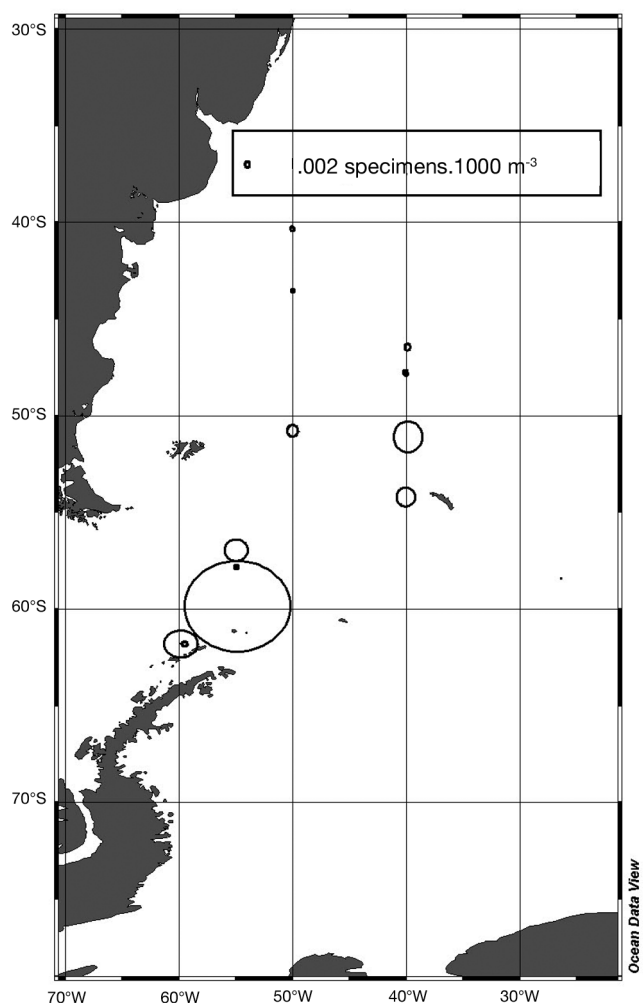


Figure 8. - *Gymnoscopelus opisthopterus*. Southwest Atlantic: abundances based on FFS Walther Herwig data.

of the genera *Krefftichthys*, *Protomyctophum*, *Electrona* and *Metelectrona* is taken from Hulley (1998).

Parameter values for Circumpolar Deep Water (upper) and Circumpolar Deep Water (lower) were taken from the source water type definitions given by Tomczak and Liefriink (2005: Tab. II) for the Southern Ocean region south of Australia.

RESULTS

Localities of the eight JARE-28 stations are given in figure 4, together with the positions of the Subtropical Front (STC), the Antarctic Polar Front (APF) and the southern boundary of the Antarctic Circumpolar Current (ACC) as defined by Orsi *et al.* (1995).

The dendrogram resulting from the cluster analysis of these stations is given in figure 5. Two major groups of stations may be recognized: Group A (comprising stations 3-8) found to the south of the STC; and Group B (comprising

stations 1-2) found to the north of the STC. In general, the station array (1-8) can be arranged by increasing latitude (Fig. 4). Group B stations have no species in common with and are totally dissimilar to Group A stations. Group A may be further divided at the 25% similarity level into Subgroup A1 (stations 3-4), located to the north of the ACC, and Subgroup A2 (stations 5-8), located south of the ACC southern boundary. The SIMPER-analysis of Subgroups A1 and A2 is given in table I. While *Gymnoscopelus braueri* (Lönneberg, 1905), *Krefftichthys anderssoni* (Lönneberg, 1905), *Protomyctophum bolini* (Fraser-Brunner, 1949), *P. parallelum* and *P. tenisoni* (Norman, 1930) are perfect indicator species for Subgroup A1; *G. opisthopterus* and *Electrona antarctica* (Günther, 1878) are the characteristic indicator species of the Subgroup A2 stations. Neither of these is a perfect indicator species.

The species-clustering of the Koubbi-Gourant subset is given in figure 6. Two groups of species may be deline-

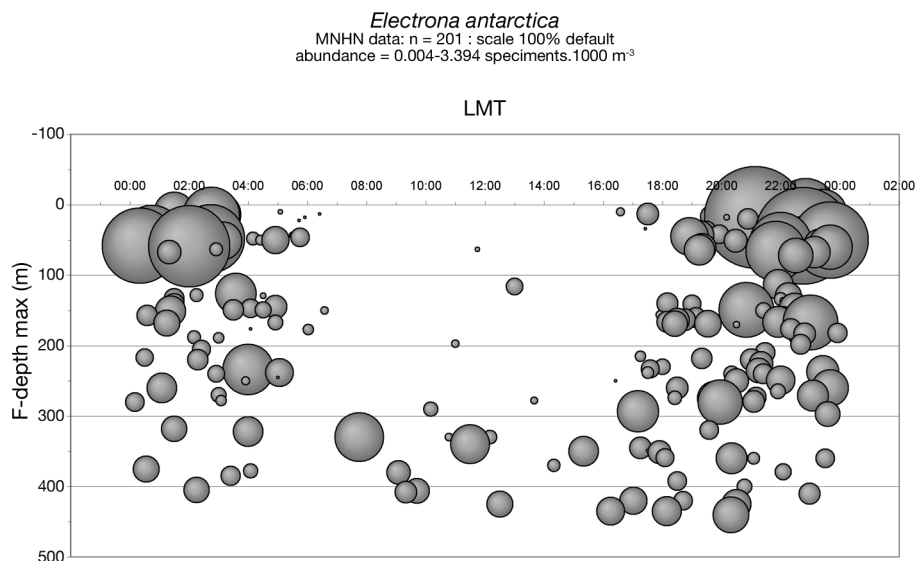


Figure 9. - *Electrona antarctica*. Kerguelen region: diel migration pattern showing scaled relative abundances. IYGPT data: n = 201 hauls.

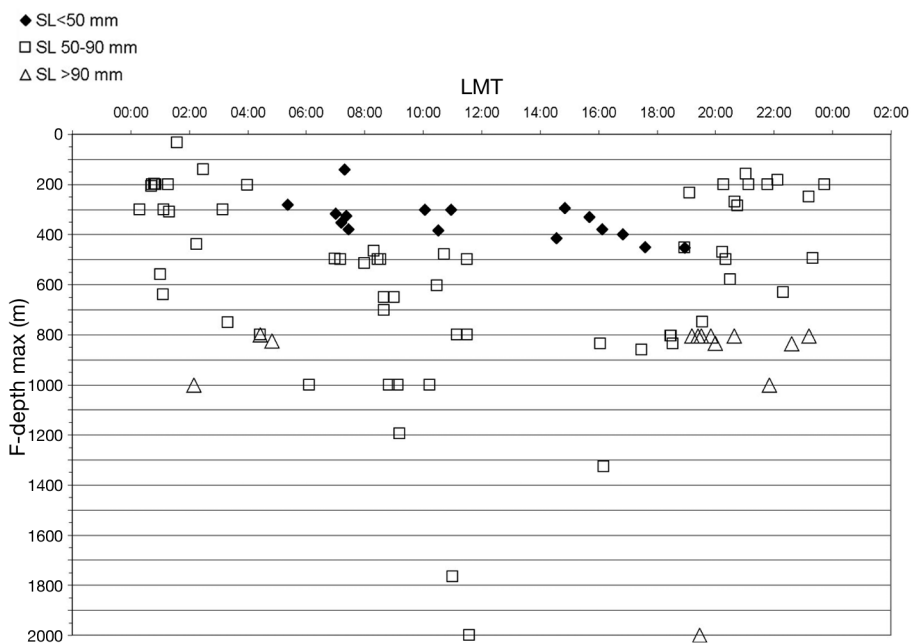


Figure 10. - *Electrona antarctica*. Diel migration pattern showing variation in standard length (SL) with maximum fishing depth of hauls. Hulley, pers. data, South Atlantic sector: n = 2668 specimens.

ated at the 6% similarity level. Group A comprises four Convergence species *Electrona paucirastra* (Bolin, 1962), *Lampichthys procerus* (Brauer, 1904), *Protomyctophum luciferum* Hulley, 1981 and *P. normani* (Tåning, 1932) and two Subantarctic species *Gymnoscopelus microlampas* Hulley, 1981 and *Metelectrona ventralis* (Becker, 1963). Group B can be divided into two subgroups at the 8% similarity level: Subgroup B1, consisting of two bathypelagic species, *Gymnoscopelus opisthopterus* and *Nannobranchium achirus* (Andriashev, 1962), see Hulley (1981); and Subgroup B2, consisting of various mesopelagic Subantarctic, Broadly Antarctic and Antarctic species.

Density distributions (specimens.1000 m⁻³) were calculated for *Electrona antarctica* and *Gymnoscopelus opisthopterus* from WH stations in the Southwest Atlantic (Figs 7-8).

DISCUSSION

Our results indicate that the lanternfish fauna of the Kerguelen Plateau region comprises the typical array of Southern Ocean species (cf. Collins *et al.*, 2009). The array includes both bathypelagic species and mesopelagic species, with the latter encompassing Convergence, Subantarctic,

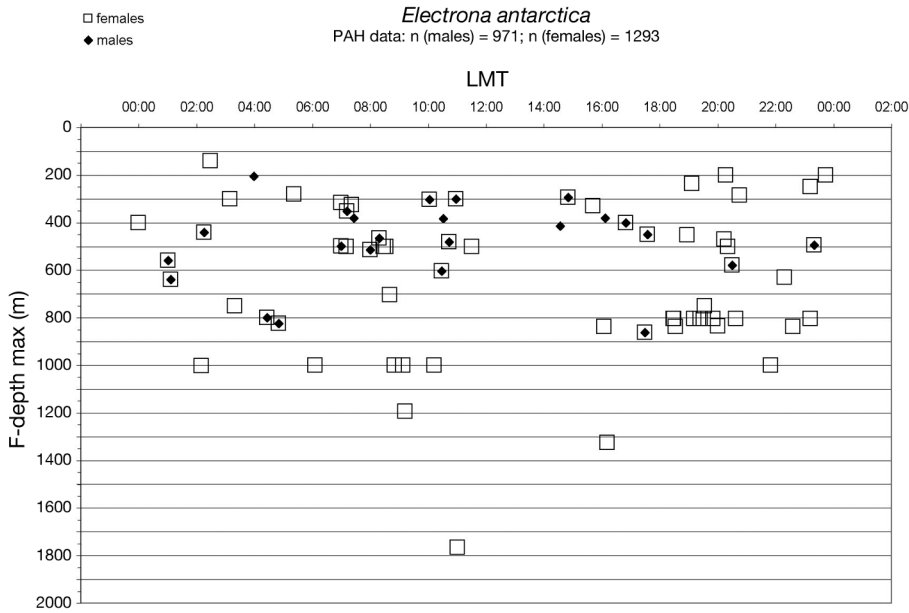


Figure 11. - *Electrona antarctica*. Diel migration pattern in males and females. Hulley, personal data, South Atlantic sector: n (males) = 971 specimens; n (females) = 1293.

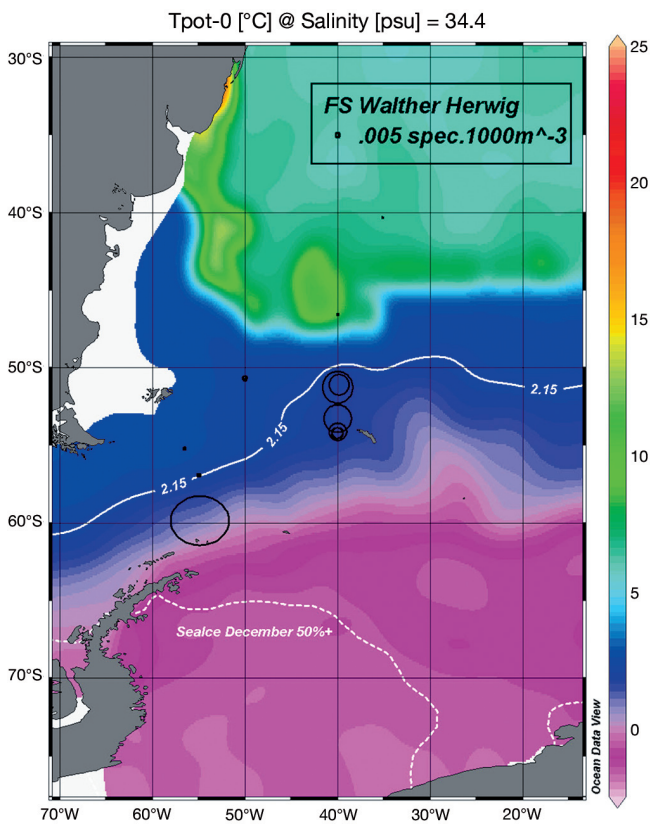


Figure 12. - *Electrona antarctica*. Southwest Atlantic: abundances based on FFS Walther Herwig data. Dotted line = sea ice cover December 50%+; solid line = 2.15°C isotherm (Tpot-0) at salinity 34.4 p.s.u.

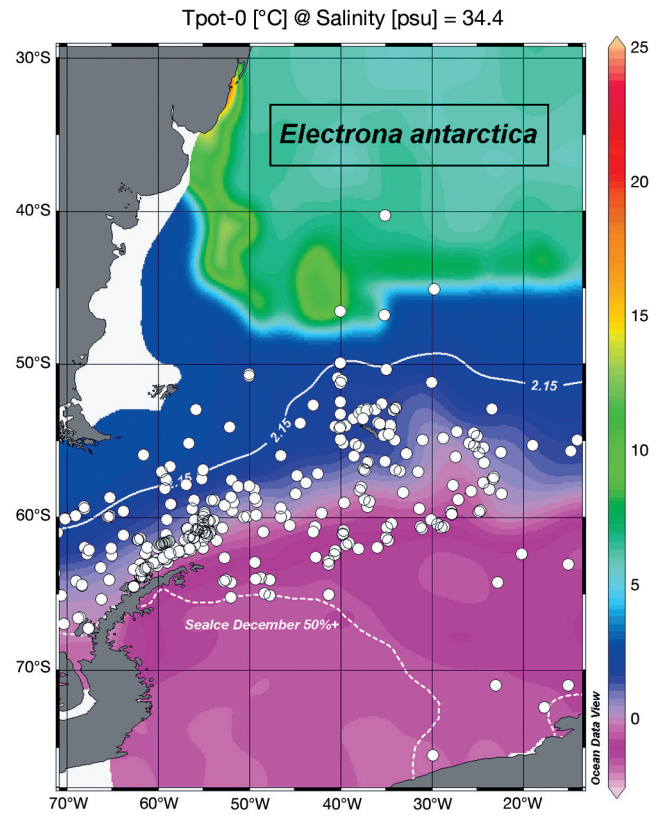


Figure 13. - *Electrona antarctica*. Southwest Atlantic: point data from various sources (see text). Dotted line = sea ice cover December 50%+; solid line = 2.15°C isotherm (Tpot-0) at salinity 34.4 p.s.u.

Broadly Antarctic and Antarctic pattern species. However, species composition may vary seasonally and in accordance with the latitudinal shifts in the positions of the STC and PF.

To the south of the ACC southern boundary, lanternfishes are characterized by two species, *Electrona antarctica* and *Gymnoscopelus opisthopterus* (Tab. I, Fig. 4). Both of these

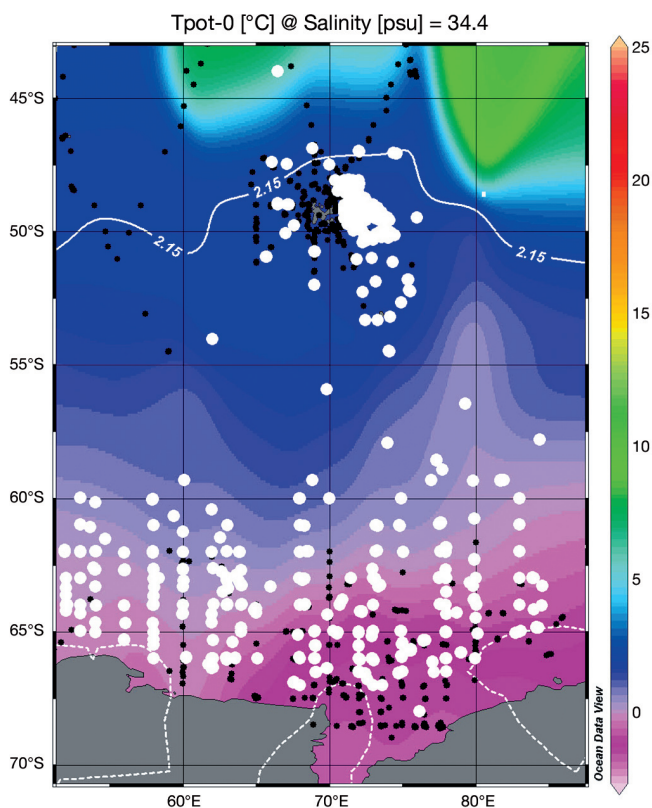


Figure 14. - *Electrona antarctica*. Kerguelen region: point data from various sources (see text). White symbol = present; black symbol = absent; dotted line = sea ice cover December 50%+; solid line = 2.15°C isotherm (Tpot-0) at salinity 34.4 psu.

are Antarctic Pattern species (Hulley, 1981) and both are present in the Kerguelen Plateau region (Fig. 6). The pattern itself has been postulated to have evolved comparatively late in the evolution of Southern Ocean myctophids (Hulley, 1998), at least in terms of the phylogeny of the Electronini (Fig. 3). It has been associated with the Late Pliocene development of a thermo-haline circulation in the eastern North Atlantic, and the consequent production of both North Atlantic Deep Water and derived Circumpolar Deep Water (CDW) in more southern latitudes. According to Tomczak and Liefink (2005: Tab. II), there are two CDW water types, each with its own physical signature. Upper and lower CDW are defined by a potential temperature of 2.15°C and 2.06°C respectively; salinity of 34.4 psu and 34.77 psu respectively; dissolved oxygen $165 \mu\text{mol.kg}^{-1}$ and $195 \mu\text{mol.kg}^{-1}$; phosphate $2.6 \mu\text{mol.kg}^{-1}$ and $1.9 \mu\text{mol.kg}^{-1}$; nitrate $36 \mu\text{mol.kg}^{-1}$ and $29 \mu\text{mol.kg}^{-1}$; and silicate $55 \mu\text{mol.kg}^{-1}$ and $95 \mu\text{mol.kg}^{-1}$. Minimum dissolved oxygen values are typical for both upper and lower CDW, when compared with other Southern Ocean water types.

Off the east coast of Kerguelen, *Electrona antarctica* is one of the most important mesopelagic species in terms of its biomass. It exhibits a typical, mesopelagic, diel pattern

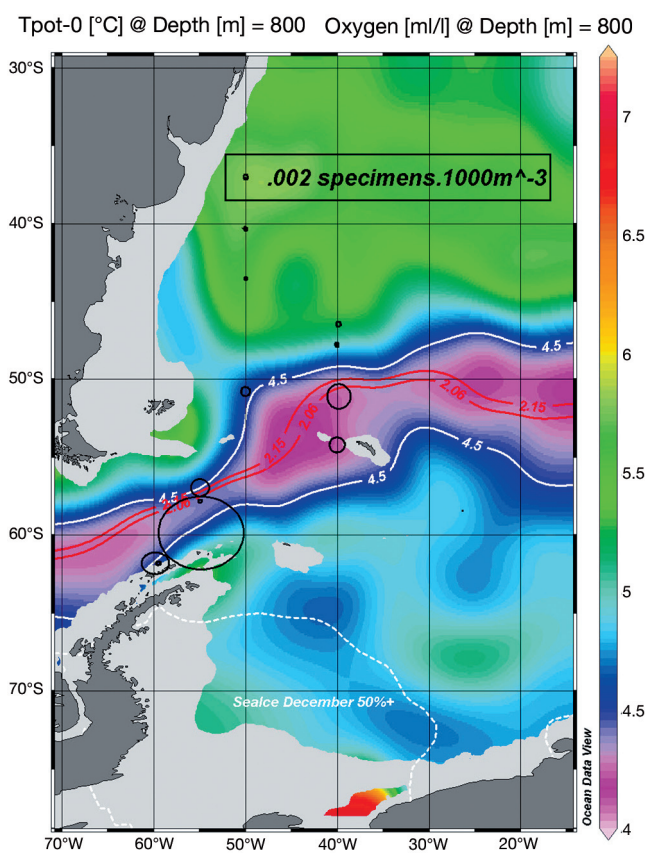


Figure 15. - *Gymnoscopelus opisthopterus*. Southwest Atlantic: abundances based on FFS Walther Herwig data. Solid line (white) = 4.5 ml/l oxygen isopleth at 800 m; solid line (red) = 2.06°C and 2.15°C isotherms (Tpot-0) at 800m; dotted line = sea ice cover December 50%+.

of behaviour (Fig. 9), being present in the upper 50 m of the water column during the night, but descending to 300-400 m (and below) during the day. In terms of abundance, it appears to have a very patchy distribution at all depths during its diel cycle. There is also a size component which may have to be considered in this diel distribution, since analysis of more extensive data from other regions of the Southern Ocean reveal that specimens > 90 mm SL are found deeper than 800 m at night, while small specimens (< 50 mm SL) occupy depth of 300-400 m during the day (Fig. 10). There appears to be no sexual differentiation with regard to diel behaviour in this species (Fig. 11). However, off Kerguelen, females reach sexual maturity in summer from about 74 mm SL (Duhamel *et al.*, 2005), and attain a maximum size of 103 mm standard length (SL); males are smaller, attaining a maximum size of about 82 mm SL.

In comparison, *Gymnoscopelus opisthopterus* reaches a maximum size of 162 mm SL, with females attaining sexual maturity at about 142-143 mm SL (McGinnis, 1974; 1982; Hulley, 1981; 1990a). Larvae and small juveniles have been taken at depths of 60-200 m and in water temperatures

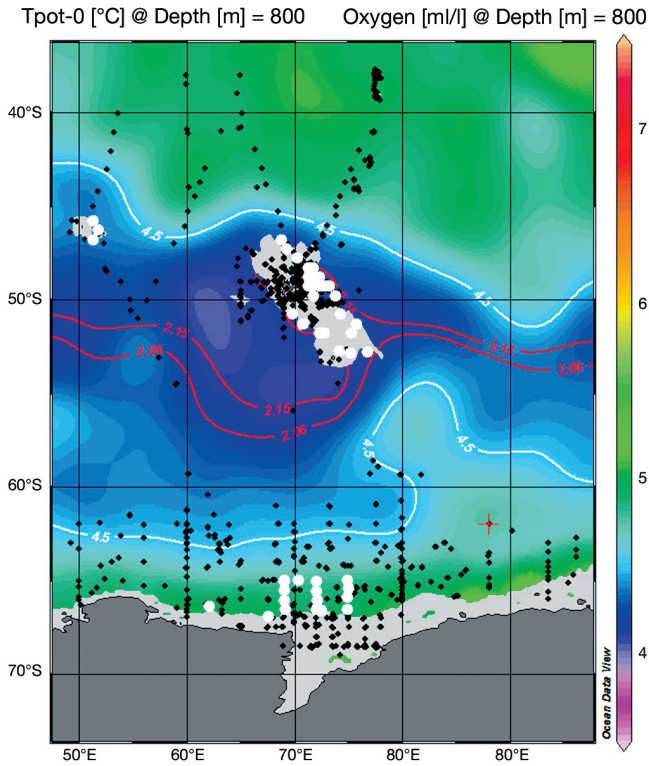


Figure 16. - *Gymnoscopelus opisthopterus*. Kerguelen region: point data from various sources (see text). White symbol = present; black symbol = absent; solid line (white) = 4.5 ml/l oxygen isopleth at 800 m; solid line (red) = 2.06°C and 2.15°C isotherms (Tpot-0) at 800 m.

between -0.18° - 6.23°C (Efremenko, 1977), and some small specimens (*Eltanin* 1206: 5 (35-36 mm SL) have been taken at 66 m (Fig. 1) (McGinnis, 1974; 1982). But offshore of the continental slope, *G. opisthopterus* mainly occurs deeper than 600 m and shows little evidence of diel migration (Fig. 2). More recent catch data indicate a benthopelagic distribution for larger specimens over the East Antarctic slope regions at depths below about 400 m (Koubbi *et al.*, 2010).

Taking into consideration both the phylogeny and the depth analyses given above, we hypothesize that the distribution of *Electrona antarctica* appears to be associated with upper CDW at depths of about 400 m, while the distribution of *Gymnoscopelus opisthopterus* appears to be associated with lower CDW at depths of about 600-800 m. Horizontal distributional plots are now presented to test these hypotheses.

In the western South Atlantic (Fig. 7), *Electrona antarctica* occurs between about 40°S and the northern limit of the 50% coverage of sea ice (December). However, abundance data for the species from the *Walther Herwig* cruises (Fig. 12) indicate a much closer correlation with upper CDW, whose northern limit at 400 m is demarcated by the 2.15°C potential temperature isotherm at 34.4 psu. Point data records to the north of the limit appear then to be due to isolates, rather than associated with the core distribution (Fig. 13). Extrapolation of this correlation to point data from the Kerguelen Plateau region is given in figure 14. Again, while there are isolates to the north, the core distribution at 400 m for *E. antarctica* appears to lie to the south of the 2.15°C poten-

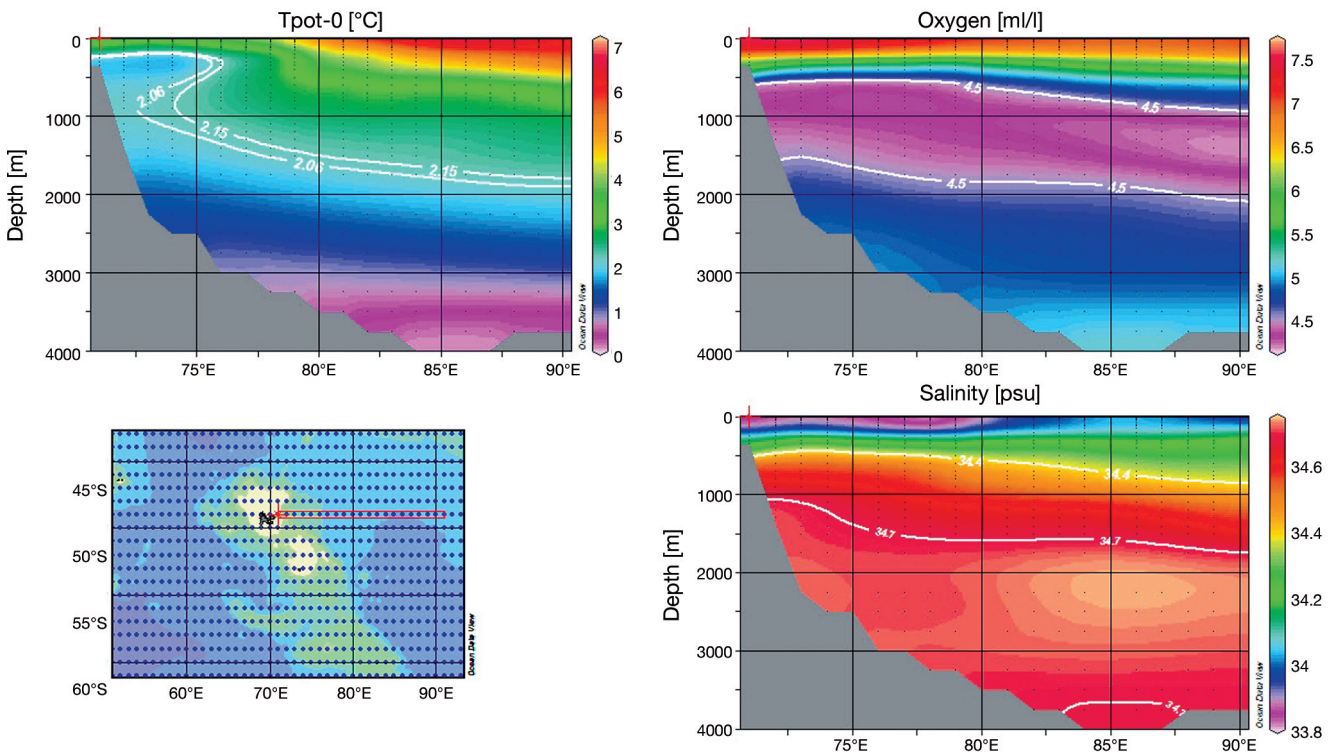


Figure 17. - Potential temperature, salinity and dissolved oxygen sections off the east coast of Kerguelen Island.

tial temperature isotherm at 34.4 psu. This would substantiate an association with the upper CDW mass.

Distributional data for *Gymnoscopelus opisthopterus* in the western South Atlantic is given in figure 8. The species occurs between about 41°S and 62°S. For *Walther Herwig* data alone, abundance data distributions with respect to the 2.06°C and 2.15°C potential temperature isotherms at 800 m, and the oxygen minimum layer (as demarcated by the 4.5 ml.l⁻¹ isopleths at 800 m) are given in figure 15. The core distribution of this species can therefore be correlated with lower CDW, although isolated occurrences of the species north of these limits are evident. Extrapolation of this correlation to point data from the Kerguelen Plateau region is given in figure 16. While the distribution of *G. opisthopterus* conforms to the critical parameters for lower CDW around Kerguelen and Crozet, more obvious is the fact that the species appears to be associated with the eastern slope regions of these islands (below about 600 m) and with continental slope regions off Antarctica (Fig. 16).

Off the east coast of Kerguelen (Fig. 17), there appears to be a shoaling of the isotherms and isohalines, so that core critical values for lower CDW can be encountered at depths of about 400-600 m, where they may circumscribe the benthopelagic distribution of *G. opisthopterus* in this region.

It should be noted that in terms of the depth distributions given above, the presence of *G. opisthopterus* otoliths in the stomachs of avian predators (Ainley *et al.*, 1992; Ferretti *et al.*, 2001) may not be "ecologically equivalent" in all cases. A surface-scavenging behaviour on dead material is indicated for snow, Antarctic, Cape and Kerguelen petrels, while active predation in the region of the shelf break and upper slope may be the case in emperor penguins.

In conclusion, it must be noted that oceanic sampling for mesopelagic fishes in the Kerguelen region is inadequate and is limited mainly to the deployment of Bongo nets in the 0-200 m depth stratum, except above the eastern slope regions of Kerguelen Island, and around Heard Island (Figs 14, 16; see also Williams *et al.*, 2001; Bost *et al.*, 2002; Duhamel *et al.*, 2005). Therefore, any future investigation into the horizontal and vertical distributional patterning in lanternfishes should address this constraint by: (1) undertaking a series of sampling cruises further offshore, and with the deployment of larger nets (e.g., IYGPY with multiple-closing cod-end) over the diel period; and (2) modeling the various lanternfish distributions on the basis of satellite-derived physical/biological oceanographic data. The latter approach, already underway (Koubbi *et al.*, 2010), should allow for a more objective, synoptic and predictive analysis of both existing and future datasets. It will cover a larger geographic area and will be more cost-effective in its execution than traditional techniques.

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