What does the giant squid *Architeuthis dux* eat?

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Abstract

Architeuthis dux diet has been analysed according to information available from literature and from the analysis of gut contents of five females and two males from Mediterranean and Atlantic Iberian waters (20 specimens in total). This is the first time that *A. dux* diet from Atlantic and Mediterranean waters is described. Body weight of specimens ranged from 22.5 to 200 kg. In order to infer common patterns in giant squid diet according to its geographic distribution range, size and sex, available data on their diet composition structure were joined and examined with multivariate techniques. No significant differences in the trophic level on which *A. dux* prey on were found, considering size, sex and location. Thus, *A. dux* seems to play the same role in the trophic webs throughout the distribution range examined in this paper, which takes up a very wide geographic area. The trophic level estimated from the diet composition is 4.7. Obtained results show that this species preys mainly on pelagic fast swimmers and shoaling fishes and cephalopods as an opportunistic ambushing hunter.

Keywords: *Architeuthis dux*, diet, trophic level, feeding strategy.

Introduction

Very recent mitochondrial genomic analyses showed that there is only one global species of giant squid, *Architeuthis dux* Steenstrup, 1857 (Winkelmann et al., 2013). It is a deep-ocean dwelling invertebrate, usually inhabiting the near continental and island slopes of all the world's oceans, although rare in tropical and polar latitudes (Guerra et al., 2010; Roper & Jereb, 2010). The giant squid has been considered a charismatic invertebrate that can raise awareness for the conservation of marine biodiversity (Guerra et al., 2011). Despite this, very little is known about its biology, behaviour and role in the marine trophic webs. In fact, the first-ever photos of a live giant squid in the wild were published by Kubodera & Mori (2005), and the first ever video record of a giant squid in its natural habitat was recently showed by Discovery Channel (2013).

Available information about the giant squid is fragmentary, based on dead or dying animals that have been washed ashore or been inadvertently captured in commercial trawl nets (Aldrich, 1991; Roeleveld & Lipinski 1991; Okiyama, 1993; Förch, 1998; González et al., 2002; Guerra et al., 2004; Kubodera, 2004). Most of *A. dux* specimens collected through occasional landing or stranding are in poor condition and their guts are often empty, with no morphologically recognisable content (Förch, 1998; Guerra et al., 2006). Available information describing the diet of *A. dux* from different locations reveals that fish and cephalopods are the main components, with the occasional presence of crustaceans (Pérez-Gándaras & Guerra, 1978; Förch, 1998; Lordan et al., 1998; Bolstad & O'Shea, 2004). Other more unusual items have also been reported, including bivalves, ascidians, cestodes (Lordan et al., 1998),

nematodes (Pippy & Aldrich, 1969; Lordan et al., 1998), algae (Kjennerud, 1958; Aldrich, 1991) and even pebbles (Lordan et al., 1998; Ré et al., 1998), although it is likely that some of these types of records in the stomach contents correspond to secondary prey.

The main aim of the present paper is to test whether there are significant differences in the trophic level at which subadults and adults of *A. dux* feed, taking into account size, sex and geography. The secondary objectives are: (i) to describe the diet of the giant squid from the Iberian Peninsula, for the first time and (ii) to define the overall profile of the trophic-level of its prey throughout its geographic range.

Materials and methods

The stomach contents of 13 *A. dux* from New Zealand, Ireland and Namibia were compiled from the literature (Perez-Gándaras & Guerra, 1978; Förch, 1998; Lordan et al., 1998; Bolstad & O'Shea, 2004; Deagle et al., 2005). This material comprises all available diet data to date for this species (Table 1). In addition, information coming from six specimens from the northern Spanish waters (north-eastern Atlantic Ocean) and one from the western Mediterranean Sea was added. Spanish specimens were weighed, measured and sexed, and maturity stages were assigned according to Lipinski maturation scale (1979). All published information until now on *Architeuthis* diet was compiled and analysed together with our results. When mantle length (ML) or body weights (BW) were not available, the following BW–ML equation (Pérez-Gándaras, unpublished data) was used:

$$\ln (\text{BWg}) = -7.938 + 2.628 \ln (\text{MLmm}); r=0.855, n=10$$

The stomach contents of the Spanish specimens were fixed in 4% formalin and then preserved in 70% ethanol until detailed examination. The remains were identified and, when possible, prey sizes were estimated from the dimensions of otoliths, jaws and vertebrae, according to the information available in Watt et al. (1997) and Tuset et al. (2008). Based on these data, we tested whether there was a significant relationship between the size of prey and the tentacular club length of the giant squid. A relationship between club length and prey size was expected taking into account previous results in *Rossia macrosoma* and *Sepia orbignyana* (Bello, 1998; Bello & Piscitelli, 2000).

In order to infer common dietary patterns in *A. dux* diet taking into account its geographic distribution range, size and sex, the diet composition structure of the whole set of animals was examined employing multivariate techniques using the software package PRIMER 6 (Clarke & Gorley, 2006).

A trophic-level value was assigned to each prey item using the information from Sa-a et al. (2013) for fishes and the *Sea around us project* webpage for cephalopods. Examination of diet compositions entered up to mid-1999 ($n > 1,800$) showed that typically, the relative contribution of different food items to the overall diet composition follows a pattern described by the following empirical model:

$$\log_{10}P = 2 - 1.9\log_{10}R - 0.161\log_{10}G$$

where P is the contribution of an item to the total diet (%); R is the rank of the food item (in terms of its relative contribution to the total diet); and G is the number of food items (in the DIET table, we always have $1 < G < 10$). The trophic level of *A. dux* was estimated from the mean trophic level of the prey plus one.

This information was then structured as a trophic-level matrix for each *A. dux* specimen (Table 2), allowing a comparison of the diet of all the specimens considered, regardless of the species composition of individual diet and considering the trophic level at which *A. dux* prey on.

Prior to the above-mentioned analysis, for each *A. dux* specimen the trophic-level matrix was transformed using the function $\log(x + 1)$, where x is the binomial value (0 or 1) assigned to each prey item according to its trophic level. Afterwards, a new data matrix was created using size, weight, sex and location of each *A. dux* individual. Categorical variables in this matrix were binary encoded, and the resultant matrix was then normalised. Resemblance matrices were obtained from each of the above mentioned matrix, undertaking a Bray–Curtis transformation in the case of trophic level data, and Euclidean distance in the case of morphometric and location data. To perform a visual expression of the resemblance matrices a non-metric multi-dimensional scaling was used. In order to test whether there was significant relationship between both resemblance matrices, a RELATE analysis was carried out. The significance was tested using a Spearman rank correlation (ρ).

Results

Of the seven examined specimens, two were found floating at surface, two stranded and three were caught by pair trawlers. All individuals were in good state of preservation and all were dissected by the last author (A. G.). No recent remains were found in the gut contents, but mainly hard structures, unlikely to come from feeding on other net items during the capture. Chitinous sucker rings and beaks of cephalopods, dermal denticles of cartilaginous fish, otoliths, vertebrae, jaws, other bones and eye lens of bony fish were the main remains. A total of 11 types of prey

were identified. Nine of them were fish and two were cephalopods. Table 2 shows the identified prey items from all the stomachs. An unidentified gobiid, an unidentified ray and *Atherina* sp. were considered to represent secondary prey items (Table 2) due to their small size and lifestyle. Estimated prey size ranged from 122 to 340 mm total length. No significant relationship was found between tentacular club length and prey size, either taking into account overall data, or discarding possible secondary prey (data not shown).

Figure 1a illustrates the differences between all *A. dux* specimens ($n=20$) accordingly to their ML, BW, sex and geographic source. Multi-dimensional scaling made from these data shows an expected grouping of data. Figure 1b shows the resemblance of each *A. dux* specimen based on the trophic level of each prey item. This MDS graph does not show any consistent pattern or grouping of samples. No significant relationship (Spearman Rho, ρ : 0.085) was found between the two resemblance matrices. In consequence, the trophic level of the analysed specimens of *A. dux* does not vary consistently according to ML, BW, sex or geographic position, suggesting homogeneity in the trophic level at which *A. dux* preys, regardless of the size (930–2020 mm ML), sex or geographic origin. Therefore, *A. dux* appears to play the same role in the marine trophic webs throughout the wide distribution range examined in this paper.

Trophic levels estimated from diet composition data of *A. dux* is 4.7 (Table 2).

Discussion

The 'Russian doll' effect is a kind of contamination or a secondary ingestion which has been observed in studies on the diet (e.g., Pierce & Boyle, 1991). It is possibly an important source of error, which is difficult to avoid. The remains of gobiids, *Atherina*

sp. and the Rajidae remains found in the guts contents of the Spanish specimens (stomachs 19 and 17; Table 2) were removed from the analysis considering that they are secondary prey due mainly to their small size and benthic life style. In addition, these items appeared in the stomachs together with other remains that could well belong to animals that had previously fed on them. Supporting this fact is the presence of gobiid remains in the stomach 19 (Table 2) together with those of the hake *Merluccius merluccius*, a common predator of gobiid fish (Bozzano et al., 1997). The combined results of the literature (Pitcher, 1993; Roper et al., 2010) and the present study suggest that *A. dux* preys mainly upon pelagic, active swimmers and schooling fish and cephalopod species. However, some studies have also proposed benthic species (e.g., *E. cirrhosa* and *N. norvegicus* in Irish waters or *Phycis blennoides* in our samples) as potential prey for the giant squid (Förch, 1998; Lordan et al., 1998). We lack reliable data to reject the possibility that *A. dux* could feed on the seabed. Nevertheless, in agreement with the present results this seems to be very occasional.

The regular presence of pelagic, actively swimming prey in all the stomach contents analysed, suggests that the giant squid is a much more active predator than previously suggested based on morphological and anatomical characteristics (Roper & Boss, 1982). Recent records (Kubodera & Mori, 2005) and the first-ever footage of the giant squid recently broadcast by Discovery Channel (2013) have also shown that the giant squid is able to actively attack bait. This agrees with a preference of active and energetic preys, as shown in the present paper. On the other hand, the weak relationship found between tentacular club length and prey size supports the hypothesis of the giant squid as an “opportunistic ambushing hunter” in the pelagic realm, as previously suggested by Pérez-Gándaras & Guerra (1978). Animals with

small suckered arms, tentacles and mouth are able to seize and overpower prey much larger than them (Hanlon & Messenger, 1996). This is an indirect evidence of a weak relationship between size of the tentacular club and prey size.

Based on available data on daily feeding rate in other cephalopod species, such as *Illex illecebrosus*, in which the daily feeding rate (% of body weight) for specimens of 30–100 g ranged from 3.5 to 6.7 (O'Dor & Wells, 1987), *A. dux* adults should require relatively large food intakes. Nevertheless, based on the equation by DeMont & O'Dor (1984) for *I. illecebrosus*, feeding rate in a 22 kg BW *A. dux* at 5–12°C would be 231.78–402.41 kcal day⁻¹, while a 200 kg BW specimen would be 1325.51–2297.1 kcal day⁻¹. According to this and assuming a mean energy intake of 1.3 kcal g⁻¹ (based on data available in O'Dor & Wells, 1987), we can approximate that daily food intake of a 22 Kg *A. dux* would be 178–309 g*day⁻¹, and a 200 Kg BW *A. dux* 1019.6–1767 g*day⁻¹, which means a daily feeding rate of 0.5–0.8% of its own weight at 5°C, and 0.8–1.4% at 12°C. The low metabolic rate derived from these results also supports the hypothesis of opportunistic ambusher hunting strategy.

According to the trophic level estimated for *A. dux* (4.7), subadults and adults of this species (see Table 1 for sizes) should be considered as top predators. The fact that *A. dux* plays the same role in the trophic webs throughout the distribution range examined in this paper and its preference to prey upon shoals of fish and cephalopods are powerful clues that the giant squid inhabits productive areas where food resources are abundant, which is reinforced by the results found using stable isotope signatures recorded in beaks (Guerra et al., 2010).

199 **REFERENCES**

- 200 Aldrich, F. A., 1991. Some aspects of the systematics and biology of squid of the genus
201 *Architeuthis* based on a study of specimens from Newfoundland waters. Bulletin of
202 Marine Science, 49: 457-481.
- 203 Bello, G., 1998. Bearing of tentacle club length on food intake and body growth in
204 males and females of *Rossia macrosoma* (Cephalopoda: Sepiolidae). Biología
205 Marina Mediterránea, 5 (1): 90-96.
- 206 Bello, G. and G. Piscitelli, 2000. Effect of sex on tentacular club development and
207 relationships with feeding efficiency and growth in *Sepia orbignyana*. Ophelia
208 53(2): 113-118.
- 209 Bolstad, K. S. and S. O'Shea, 2004. Gut contents of a giant squid *Architeuthis dux*
210 (Cephalopoda: Oegopsida) from New Zealand waters. New Zealand Journal of
211 Zoology, 31: 15-21.
- 212 Bozzano, A., L. Recasens and P. Sartor, 1997. Diet of the European hake *Merluccius*
213 *merluccius* (Pisces: Merlucciidae) in the Western Mediterranean. Scientia Marina,
214 61: 1-8.
- 215 Clarke, K. R. and R. N. Gorley, , 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E,
216 Plymouth.
- 217 Deagle, B.E., S.N. Jarman, D. Pemberton & N. J. Gales, 2005. Genetic screening for prey
218 in the gut contents from a giant squid (*Architeuthis* sp.). Journal of Heredity, 96(4):
219 417-423.
- 220 DeMont, M. E. & R. K. O'Dor, 1984. The effects of activity, temperature and mass on
221 the respiratory metabolism of the squid, *Illex illecebrosus*. Journal of Marine
222 Biological Association of United Kingdom, 64: 535-543.
- 223 Discovery Channel, 2013. Monster squid: the giant is real. <http://dsc.discovery.com/>

224 Förch, E. C., 1998. The marine fauna of New Zealand: Cephalopoda: Oegopsida:
 225 *Architeuthidae* (giant squid). NIWA Biodiversity Memoir, 110: 1-113.

226 González, Á. F., A. Guerra, F. Rocha and J. Gracia, 2002. Recent findings of the giant
 227 squid *Architeuthis* in northern Spanish waters. Journal of the Marine Biological
 228 Association United Kingdom, 82: 859-861.

229 Guerra, A., A. F. González & F. Rocha, 2004. A review of the records of giant squid in
 230 the north-eastern Atlantic and severe injuries in *Architeuthis dux* stranded after
 231 acoustic explorations. ICES CM 2004/CC: 29 pp.

232 Guerra, A., A. F. González, F. Rocha, L. Laria and J. Gracia, 2006. Enigmas de la ciencia:
 233 el calamar gigante. Fundación Caja Rural de Asturias e Instituto de Investigaciones
 234 Marinas (CSIC), Vigo: 316 pp.

235 Guerra, A., A. B. Rodríguez-Navarro, A. F. González, C. S. Romanek, P. Álvarez-Lloret
 236 and G. J. Pierce, 2010. Life-history traits of the giant squid *Architeuthis dux* revealed
 237 from stable isotope signatures recorded in beaks. ICES Journal of Marine Science,
 238 67: 1425-1431.

239 Guerra, A., A. F. González, S. Pascual and E. G. Dawe, 2011. The giant squid
 240 *Architeuthis*: an emblematic invertebrate that can represent concern for the
 241 conservation of marine biodiversity. Biological Conservation, 144: 1989-1997.

242 Hanlon, R. T., and J. B. Messenger, 1996. Cephalopod Behaviour. Cambridge:
 243 Cambridge University Press.

244 Kjennerud, J., 1958. Description of a giant squid, *Architeuthis*, stranded on the west
 245 coast of Norway. Universitetet i Bergen. Årbok 1958, Naturvitenskapelig rekke, 9: 1-
 246 14.

247 Kubodera, T., 2004. Studies on systematic and phylogeny of giant squid, *Architeuthis*,
 248 around Japanese waters. Report of JSPS Grand-in-Aid for Scientific Research,
 249 2001–2003: 1–15.

250 Kubodera, T. & K. Mori, 2005. First-ever observations of a live giant squid in the wild.
 251 Proceedings of the Royal Society, B: Biological Sciences, London, 272(1581): 2583–
 252 2586.

253 Lipinski, M., 1979. Universal maturity scale for the commercially important squids.
 254 The results of maturity clasification of the *Illex illecebrosus* population for the years
 255 1973-77. ICNAF Research Document 79/2/38, Serial 5364, 40 pp.

256 Lordan, C., M. A. Collins and C. Perales-Raya, 1998. Observations on morphology, age
 257 and diet of three *Architeuthis* caught off the west coast of Ireland in 1995. Journal
 258 of the Marine Biological Association of the United Kingdom, 78: 903-917.

259 O'Dor, R. K. & M. J. Wells, 1987. Energy and nutrient flow. In Boyle P. R. (ed.).
 260 Cephalopod Life Cycles, Vol. II. Comparative Reviews. Academic press, London:
 261 109–133.

262 Okiyama M., 1993. Kinds, abundance and distribution of oceanic squids in the Sea of
 263 Japan. In: Okutani, T., O'Dor R. K., & Kubodera, T. (eds), Recent Advances in
 264 Cephalopod Fisheries Biology. Tokai University Press, Tokyo: 403–451.

265 Pérez-Gándaras, G. and A. Guerra, 1978. Nueva cita de *Architeuthis* (Cephalopoda:
 266 Teuthoidea): descripción y alimentación. Investigación Pesquera, 42: 401-414.

267 Pierce, G. J. and P. R. Boyle, 1991. A review of methods for diet analysis in piscivorous
 268 marine mammals. Oceanography and Marine Biology Annual Review, 29: 409-486.

269 Pippy, J. H. C. and F. A. Aldrich, 1969. *Hepatoxylon trichiuri* (Holden, 1802) (Cestoda:
 270 Trypanorhyncha) from the giant squid *Architeuthis dux* Steenstrup, 1857 in
 271 Newfoundland. Canadian Journal of Zoology, 47: 263-264.

272 Pitcher, T. J., 1993. Functions of shoaling behaviour in teleosts. In Pitcher, T. J. & J. K.
 273 Parrish (eds), Behaviour of Teleost Fishes, chap. 12. Chapman & Hall, London: 294–
 274 337.

275 Ré, M. E., P. J. Barón, J. C. Berón, A. E. Gosztonyi, L. Kuba, M. A. Monsalve and N. H.
 276 Sardella, 1998. A giant squid *Architeuthis* sp. (Mollusca: Cephalopoda) stranded on
 277 the Patagonian shore of Argentina. South African Journal of Marine Science, 20:
 278 109-122.

279 Roeleveld, M. A. C and M. R. Lipinski, 1991. The giant squid *Architeuthis* in southern
 280 African waters. Journal of Zoology, London 224: 431–477.

281 Roper, C. F. E. & K. J. Boss, 1982. The giant squid. Scientific American, 246: 82-89.

282 Roper, C. F. E. and P. Jereb, 2010. Family Architeuthidae. In Cephalopod of the World.
 283 An Annotated and Illustrated Catalogue of Species Known to Date. Myopsid and
 284 Oegopsid Squids. FAO Species Catalogue for Fisheries Purposes, no 4, vol. 2. FAO
 285 Rome: 121–123.

286 Roper, F. E., C. Nigmatullin & P. Jereb, 2010. Family Ommastrephidae. In P. Jereb and.
 287 Roper, C. F. E. (eds), Cephalopods of the World. An Annotated and Illustrated
 288 Catalogue of Species Known to Date. Volume 2. Myopsid and Oegopsid Squids. FAO
 289 Species Catalogue for Fishery Purposes. no. 4, vol. 2. Rome, FAO: 269–347.

290 Sa-a, P., M. L. D. Palomares & D. Pauly, 2013. Food items table.
 291 http://www.fishbase.de/manual/English/fishbasethe_food_items_table.htm.

292 Sea around us project. www.seaaroundus.org/topic/species/

293 Tuset, V. M., A. Lombarte and C. A. Assis, 2008. Otolith atlas for the western
 294 Mediterranean, north and central eastern Atlantic. Scientia Marina, 72: 7-198.

295 Watt, J., G. J. Pierce & P. R. Boyle, 1997. Guide to the identification of north sea fish
296 using premaxillae and vertebrae. ICES Cooperative Research Report 220: 231 pp.

297 Winkelmann I., P.F. Campos, J. Strugnell, Y. Cherel, P.J. Smith, T. Kubodera, L. Allcock,
298 M-L. Kampmann, H. Schroeder, A. Guerra, M. Norman, J. Finn, D. Ingraio, M. Clarke
299 and M.T.P. Gilbert, 2013. Mitochondrial genome diversity and population structure
300 of the giant squid *Architeuthis*: genetics sheds new light on one of the most
301 enigmatic marine species. Proceedings of the Royal Society B, 280 (1759): 1471-
302 2954, doi: 10.1098/rspb.2013.0273.

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305 Figure 1. Multidimensional scaling representation of *A. dux* specimens resemblance
306 according to **A** mantle length, body weight, sex and geographic area, and **B** trophic
307 level of the prey items.

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309 Table captions:

310 Table 1. List published data until today of *Architeuthis dux* analysed in diet studies.

311 SN: Specimen number; ML: Mantle Length; W: Weight. (* According to its size, most
312 likely this specimen is not a male, as the original paper indicates, so we considered
313 it as a female in this study).

314 Table 2. List of all prey taxa identified in *Architeuthis* gut contents by SN (Specimen
315 Number) and trophic level (Tr. L.). Asterisk indicates possible secondary prey.

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Table 1. List published data until today of *Architeuthis dux* analysed in diet studies. SN: Specimen number; ML: Mantle Length; W: Weight. (* According to its size, most likely this specimen is not a male, as the original paper indicates, so we considered it as a female in this study).

SN	Author	Location	Sex	Maturity	ML (mm)	W (Kg)
1	Lordan et al. (1998)	Ireland	Male	Mature	1028	26.9
2	Lordan et al. (1998)	Ireland	Male	Mature	975	22.5
3	Lordan et al. (1998)	Ireland	Male	Mature	1084	26.5
4	Bolstad & O'Shea (2004)	New Zealand	Female	Mature	1600	93.9
5	Deagle et al. (2005)	New Zealand	Female*	Mature	1501	190
6	Pérez-Gándaras & Guerra (1978)	South Africa	Female	Inmature	1950	200
7	SN 2 of Förch (1998)	New Zealand	Female	-	1930	155
8	SN 3 of Förch (1998)	New Zealand	Female	-	1770	123
9	SN 5 of Förch (1998)	New Zealand	Female	-	930	23
10	SN 6 of Förch (1998)	New Zealand	Female	-	1560	88
11	SN 7 of Förch (1998)	New Zealand	Female	-	2020	174
12	SN 9 of Förch (1998)	New Zealand	male	-	1260	51
13	SN 16 of Förch (1998)	New Zealand	Female	-	2000	170
14	Present paper	Asturias (N Spain)	Female	Maturing	1270	92
15	Present paper	Asturias (N Spain)	Female	Mature	1500	104
16	Present paper	Asturias (N Spain)	Female	Maturing	1270	90
17	Present paper	Galicia (N Spain)	Female	Mature	1680	132
18	Present paper	Asturias (N Spain)	Male	Mature	1000	42
19	Present paper	Valencia (W Spain)	Male	Mature	1100	47
20	Present paper	Asturias (N Spain)	Female	Maturing	950	61

328 Table 2. List of all prey taxa identified in *Architeuthis* gut contents by SN (Specimen Number) and
329 trophic level (Tr. L.). Asterisk indicates possible secondary prey.

SN	Author	Phylum	Class	Family	Prey taxa identified	Tr.L
1	Lordan et al. (1998)	Chordata	Actinopterygii	Carangidae	<i>Trachurus trachurus</i>	3.6
1	Lordan et al. (1998)	Mollusca	Cephalopoda	Ommastrephidae	<i>Todarodes sagittatus</i>	4.0
1	Lordan et al. (1998)	Mollusca	Bivalvia	Mytilidae	<i>Modiolus paseolinus*</i>	2.0
2	Lordan et al. (1998)	Chordata	Actinopterygii	Sternoptychidae	<i>Maurolicus müelleri</i>	3.0
2	Lordan et al. (1998)	Arthropoda	–	–	Crustacea*	2.6
3	Lordan et al. (1998)	Chordata	Actinopterygii	Gadidae	<i>Micromesistius poutassou</i>	4.0
3	Lordan et al. (1998)	Arthropoda	Malacostraca	Nephropidae	<i>Nephrops norvegicus*</i>	2.9
3	Lordan et al. (1998)	Mollusca	Cephalopoda	Octopodidae	<i>Eledone cirrhosa*</i>	3.7
4	Bolstad & O'Shea (2004)	Mollusca	Cephalopoda	Ommastrephidae	<i>Nototodarus</i>	3.2
4	Bolstad & O'Shea (2004)	Mollusca	Cephalopoda	Architeuthidae	<i>Architeuthis dux</i>	4.7
5	Deagle et al. (2005)	Chordata	Actinopterygii	Gadiforme	<i>Mora moro</i>	3.8
5	Deagle et al. (2005)	Chordata	Actinopterygii	Merlucciidae	<i>Macruronus novaezelandiae</i>	4.5
5	Deagle et al. (2005)	Chordata	Actinopterygii	Cyttidae	<i>Cyttus traverse</i>	4.3
6	Pérez-Gándaras & Guerra (1978)	Mollusca	Cephalopoda	Histioteuthidae	<i>Histioteuthidae</i>	4.2
6	Pérez-Gándaras & Guerra (1978)	Mollusca	Cephalopoda	Ommastrephidae	<i>Ommastrephes bartramii</i>	4.2
6	Pérez-Gándaras & Guerra (1978)	Mollusca	Cephalopoda	Histioteuthidae	<i>Histioteuthis reversa</i>	4.2
7	SN 2 of Förch (1998)	Chordata	Actinopterygii	Macrouridae	<i>Caelorinchus fasciatus</i>	3.7
7	SN 2 of Förch (1998)	Chordata	Actinopterygii	Macrouridae	<i>Caelorinchus oliverianus</i>	3.6
8	SN 3 of Förch (1998)	Chordata	Actinopterygii	Macrouridae	<i>Caelorinchus oliverianus</i>	3.6
8	SN 3 of Förch (1998)	Chordata	Actinopterygii	Macrouridae	<i>Caelorinchus fasciatus</i>	3.7
9	SN 5 of Förch (1998)	Chordata	Actinopterygii	Trachichthyidae	<i>Hoplostethus atlanticus</i>	4.3
9	SN 5 of Förch (1998)	Mollusca	Cephalopoda	Onychoteuthidae	<i>Onykia ingens</i>	3.2
9	SN 5 of Förch (1998)	Chordata	Actinopterygii	Macrouridae	Macrouridae	3.6
9	SN 5 of Förch (1998)	Mollusca	Cephalopoda	Onychoteuthidae	<i>Onykia ingens</i>	3.2
10	SN 6 of Förch (1998)	Mollusca	Cephalopoda	Ommastrephidae	<i>Nototodarus sloanii</i>	4.2
11	SN 7 of Förch (1998)	Mollusca	Cephalopoda	Ommastrephidae	<i>Nototodarus sloanii</i>	4.2
11	SN 7 of Förch (1998)	Chordata	Actinopterygii	Macrouridae	<i>Lepidorhynchus ?denticulatus</i>	4.1
11	SN 7 of Förch (1998)	Chordata	Actinopterygii	Macrouridae	<i>Caelorinchus sp.</i>	3.6
12	SN 9 of Förch (1998)	Chordata	Actinopterygii	Macrouridae	<i>Caelorinchus oliverianus</i>	3.6
12	SN 9 of Förch (1998)	Chordata	Actinopterygii	Macrouridae	<i>Caelorinchus sp.</i>	3.6
12	SN 9 of Förch (1998)	Mollusca	Cephalopoda	–	Unidentified oegopsid	4.2
13	SN 16 of Förch (1998)	Chordata	Actinopterygii	Macrouridae	<i>Kuronezumia leonis</i>	3.6
14	Present paper	Mollusca	Cephalopoda	Ommastrephidae	<i>Todaropsis eblanae</i>	4.2
14	Present paper	Mollusca	Cephalopoda	Cranchiidae	<i>Galiteuthis armata</i>	4.2
14	Present paper	Chordata	Actinopterygii	Gadidae	Gadidae	3.7
15	Present paper	Chordata	Actinopterygii	Scombridae	Scombridae	3.2
16	Present paper	Chordata	Actinopterygii	Phycidae	<i>Phycis blennoides</i>	3.7
17	Present paper	Chordata	Chondrichthyes	Rajidae	Rajidae*	3.6
18	Present paper	Chordata	Actinopterygii	Gadidae	<i>Micromesistius poutassou</i>	4.0
18	Present paper	Chordata	Actinopterygii	Atherinidae	<i>Atherina sp.*</i>	3.7
19	Present paper	Chordata	Actinopterygii	Gobiidae	Gobiidae*	3.2
19	Present paper	Chordata	Actinopterygii	Merlucciidae	<i>Merluccius merluccius</i>	4.4
20	Present paper	Chordata	Actinopterygii	Gadidae	<i>Micromesistius poutassou</i>	4.0
20	Present paper	Chordata	Actinopterygii	Gadidae	<i>Trisopterus sp.</i>	3.6
A. <i>dux</i> trophic level: Tr. L. mean + 1=						4.7

330 A

331

332 B

333

334