

1 **Future challenges in cephalopod research***

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34 *From *Role of Cephalopods in the Marine Environment, a Symposium in Honor of Dr.*
35 *Malcolm R. Clarke, FRS* held at the World Congress of Malacology, 21-28 July 2013 in
36 Ponta Delgada, Azores, Portugal

37 **Abstract**

38 Cephalopods (Mollusca: Cephalopoda) play an important role as keystone invertebrates
39 in various marine ecosystems as well as being a valuable fisheries resource. At the
40 World Malacological Congress, held 21-28 July 2013 in Ponta Delgada, Azores,
41 Portugal, a number of cephalopod experts convened to honour the contribution of the
42 late Malcolm R. Clarke, FRS (1930-2013) to cephalopod research. Endorsed by the
43 Cephalopod International Advisory Council (CIAC), the meeting discussed some of the
44 major challenges that cephalopod research will face in the future. These challenges were
45 identified as follows: 1. To find new ways to ascertain the trophic role and food web
46 links of cephalopods using hard tissues, stable isotopes and novel concepts in theoretical
47 ecology; 2. To explore new approaches to the study of cephalopod morphology; 3. To
48 further develop cephalopod aquaculture research; 4. To find new ways to ascertain
49 cephalopod adaptation and response to environmental change; 5. To strengthen
50 cephalopod genetics research; and 6. To develop new approaches for cephalopod
51 fisheries and conservation. The present contribution presents brief reviews on these
52 topics, followed by a discussion of the general challenges that cephalopod research is
53 bound to face in the near future. By contributing to initiatives both within CIAC and
54 independent of CIAC, the principle aim of the article is to stimulate future cephalopod
55 research.

56

57

58 **Introduction**

59 There is a long tradition of researchers striving to predict what might happen in the
60 future. Until recently, most research related to biodiversity and conservation has been
61 performed in an unsystematic manner (Sutherland & Woodroof, 2009, Sutherland et al.,
62 2013). However, an assessment of future research opportunities, knowledge gaps and
63 new areas of science constitutes the first step in identifying and communicating
64 hypotheses and insights for the future (Rands et al., 2010, Sutherland et al., 2010).
65 Prognoses for marine ecosystems are becoming increasingly important, because of the
66 threats that have been emerging in recent decades and which require urgent scientific
67 attention. These threats include global climate change, ocean warming, sea level rise,
68 biodiversity loss, overfishing, ocean acidification and expanding hypoxia (Pauly, 1998,
69 Pauly et al., 1998, Pauly et al., 2003, Orr et al., 2005, Rockstrom et al., 2009, Turner et
70 al., 2009). Addressing these challenges asks for greater synergy between research,
71 management and policy, and it will be important to inform researchers and funding
72 agencies as to where their efforts might best be focused.

73 Cephalopods (Mollusca: Cephalopoda) are widely recognized as playing a
74 pivotal role in many marine ecosystems, both as predators and prey (Clarke, 1996,
75 Piatkowski et al., 2001, Boyle & Rodhouse, 2005). Furthermore, cephalopod fisheries
76 have been increasing steadily in recent decades and it is likely that more species will be
77 commercially exploited in the future (FAO, 2005). As marine biologists whose research
78 is focused on cephalopods, our aims include a better understanding of cephalopod
79 biology and ecology and the role of these organisms in marine ecosystems, identifying
80 patterns and mechanisms, quantifying changes at different scales, recognizing problems
81 and testing potential solutions (e.g. related to conservation, fisheries management and
82 aquaculture). Except for nautiluses, cephalopods have a short life span, rapid growth,
83 and semelparous maturation patterns (Boyle & Rodhouse, 2005). These life cycle traits
84 may have positive or negative effects on cephalopod species in relation to
85 environmental change, as cephalopods can be both sensitive (in terms of rapid response)
86 and resilient (in terms of recovery) to phenomena such as overfishing or climate
87 variability and change (Pecl & Jackson, 2008, Rosa & Seibel, 2008, André et al., 2010,
88 Pierce et al., 2010, Hoving et al., 2013, Rodhouse, 2013). However, exactly how these,
89 and other, phenomena affect cephalopods is not yet fully understood. Therefore, a broad
90 discussion of these issues can be valuable in providing guidance for future directions of
91 cephalopod research.

92 The 2013 World Malacological Congress, held 21-28 July in Ponta Delgada,
93 Azores, Portugal, brought together a number of cephalopod experts to participate in a
94 symposium focusing on the role of cephalopods in the world's oceans. The symposium
95 was held in honour of the late Malcolm R. Clarke, FRS (1930-2013), and was endorsed
96 by the Cephalopod International Advisory Council (CIAC). Malcolm Clarke himself
97 had initiated the CIAC in 1981, and the council was officially founded two years later
98 as an international forum to encourage research on cephalopods, promote international
99 collaboration in cephalopod science, and to provide an official body to answer the
100 increasing number of questions about cephalopods, particularly those related to
101 cephalopod fisheries (Hochberg & Hatfield, 2002). In the present article, cephalopod
102 experts, including present and former members of CIAC, working in specific fields and
103 at different organisational scales, ranging from a species perspective to the ecosystem
104 level, discuss some of the challenges that cephalopod research will face in the future.
105 The individual sections provide brief reviews of topics in cephalopod research that
106 deserve further attention.

107

108 **1. New ways to ascertain the trophic role and food web links of cephalopods**

109 *Studying cephalopods in the world's oceans using top predators as biological samplers:*
110 *where are we heading? (José C. Xavier)*

111 Knowledge on cephalopods, particularly those from oceanic waters that are not
112 commercially caught, largely originates from analyses of stomach contents collected
113 from their natural predators, such as toothed whales, seals, seabirds, sharks and teleost
114 fish (Clarke, 1996). This is, because current methods for direct sampling, especially of
115 oceanic squid, are still inefficient (Clarke, 1977, Xavier et al., 2007, Hoving et al., in
116 press). Therefore, an essential tool in the study of cephalopod remains found in predator
117 stomachs is the identification and measurement of their chitinized upper and lower
118 beaks (Clarke, 1986, Cherel et al., 2004, Xavier & Cherel, 2009, Xavier et al., 2011),
119 and, to a lesser extent, the morphological and molecular analysis of soft tissues in case
120 these should still be available (Pierce & Boyle, 1991, Barrett et al., 2007, Karnovsky et
121 al., 2012).

122 However, the analysis of hard tissues can be biased. For instance, a recent study
123 showed that the ratio of upper to lower beaks in diet samples from top predators varied
124 significantly during one year as well as between years. This bias was larger in some
125 cephalopod species than in others, resulting in the underestimation of the relative

126 importance of some species in data derived from this approach (Xavier et al., 2011).
127 This can result in an under- or over-estimation of relative cephalopod abundance and
128 suggests that it is essential to count both (i.e. lower and upper) beaks in stomach content
129 analyses. Furthermore, in instances where there is a consistent bias (>30%), all beaks
130 should be identified, and the higher quantity of beak type should be considered to
131 reconstruct the cephalopod component of the diet by mass (Santos et al., 2001, Xavier et
132 al., 2011).

133 In samples collected from predators that tend to retain material, it is of
134 importance to separate old and fresh material during the initial sorting process in order
135 to obtain a qualitative assessment of the degree of erosion of the material as well
136 (Piatkowski & Pütz, 1994, Cherel et al., 2000, Xavier et al., 2005). These components
137 can then be analysed separately, as required, and the results compared. In general, more
138 effort should be put into describing upper beak morphology to aid identification
139 (Clarke, 1962, Imber, 1978, Pérez-Gándaras, 1983, Wolff, 1984, Kubodera &
140 Furuhashi, 1987, Lu & Ickeringill, 2002, Xavier & Cherel, 2009), to measuring upper
141 beaks in diets, and to developing regressions or allometric equations for estimating
142 cephalopod mass based on both lower and upper beak measurements. Indeed, for
143 numerous species no allometric equations are yet available, which is why scientists have
144 to rely on equations from closely related species. In addition, various allometric
145 equations were produced based on a limited number and size range of cephalopod
146 specimens. Therefore, more material must be collected, particularly from cephalopod
147 natural predators or by research as well as commercial fishing vessels.

148 Malcolm Clarke emphasized the importance of additional ship time devoted to
149 cephalopod research, as well as the need for the development of better capture methods
150 (Xavier et al., 2007, Hoving et al., in press). Many cephalopods are fast-swimming
151 organisms and therefore only the small or less-mobile specimens are usually captured
152 (Clarke, 1977). This dilemma still holds true, despite a long history of sampling. In
153 order to maximize the success rate of capturing bigger specimens, larger nets and
154 modified net gear (e.g. underwater lights) have been developed to attract cephalopods
155 into the nets (Clarke & Pascoe, 1997, Clarke & Pascoe, 1998, Clarke, 2006). However,
156 new techniques are required to enhance the catch ratio of poorly-known cephalopod
157 species in the world's oceans in order to complement the work already being carried out
158 on the feeding and foraging ecology of cephalopod predators.

159

160 *Stable isotopes, hard tissues and the trophic ecology of cephalopods (Yves Cherel)*
161 Stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) have recently emerged as new efficient intrinsic
162 markers of the trophic ecology of cephalopods (Jackson et al., 2007), and pioneer
163 investigations (Takai et al., 2000, Cherel & Hobson, 2005) have lead to a steady
164 increase in the use of the method over the last ten years (Navarro et al., 2013). In this
165 section, attention will be paid to the most recent findings, methodological issues and
166 perspectives on the use of these tools on hard tissues of cephalopods.

167 In contrast to soft tissues (e.g. mantle), hard tissues (i.e. beaks, gladii, statoliths,
168 and eye lenses) are metabolically inactive structures that grow continuously by
169 accretion of new molecules with no turnover after synthesis. Consequently, these
170 structures retain molecules laid down throughout the lives of cephalopods, and their
171 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values thus integrate the feeding ecology of individuals over their
172 lifetime. Indeed, various parts of hard tissues have different isotopic signatures. For
173 example, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the tip of the wings and anterior tip of the gladius (i.e.
174 the most recently synthesized parts of lower beaks and gladii, respectively) integrate the
175 feeding ecology prior to capture (Cherel & Hobson, 2005, Hobson & Cherel, 2006,
176 Cherel et al., 2009a). Gladii have the advantage over beaks that their growth increments
177 are larger, better defined and easier to sample along the longitudinal proostracum axis
178 (Cherel et al., 2009a). Furthermore, in the most recent part of the gladius, assuming
179 increments are daily, a day-by-day picture can also be established which can directly be
180 related to body size (as gladii length is approximately the same as the dorsal mantle
181 length; Graham Pierce, unpublished data).

182 Stable isotopes from hard structures have two practical advantages and one
183 methodological disadvantage. Firstly, measuring the isotopic signature of serially
184 sampled beaks and gladii presents the unique opportunity to reconstruct the foraging
185 history of individuals. For example, $\delta^{15}\text{N}$ profiles of beaks from *Architeuthis dux*
186 suggest an ontogenetic shift early in life (Guerra et al., 2010), and sequential isotopic
187 values along gladii of *Dosidicus gigas* highlight contrasted individual foraging
188 strategies (Ruiz-Cooley et al., 2010, Lorrain et al., 2011). In the same way, the only
189 published investigation on concentric eye lens layers reveals variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
190 values at fine temporal scales, indicating substantial variability in squid feeding patterns
191 (Hunsicker et al., 2010a). Secondly, the combination of the stable isotope techniques
192 with the use of predators as biological samplers, and cephalopod identification using

193 external features of accumulated beaks in predators' stomachs (Clarke, 1986, Xavier &
194 Cherel, 2009) allows information to be gathered on poorly known species. This method
195 has already revealed new trophic relationships and migration patterns together with the
196 trophic structure of deep-sea cephalopod assemblages (Cherel & Hobson, 2005, Cherel
197 et al., 2009b).

198 However, a main problem with using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of hard structures is
199 that biological interpretation is confused by differences in biochemical composition
200 between hard and soft tissues. Beaks and gladii contain not only protein but also chitin
201 (Hunt & Nixon, 1981, Rubin et al., 2010), a modified polysaccharide that contains
202 impoverished ^{15}N nitrogen (Schimmelmann, 2011). The presence of chitin explains why
203 hard tissues have consistently much lower $\delta^{15}\text{N}$ values than soft tissues (Cherel et al.,
204 2009a). Moreover, the ratio of chitin to protein varies within beaks, with the
205 undarkened, darkening and darkened parts of beaks containing decreasing amounts of
206 chitin (Rubin et al., 2010). Chitin content is thus likely to be different between
207 individual beaks (e.g. small, undarkened versus large, darkened beaks), and the gladius
208 is richer in chitin than darkened beaks (Hunt & Nixon, 1981). This particular issue is
209 analogous to that arising from the different fractionation apparent in lipids compared to
210 other components of soft tissues. Three different approaches enable the 'chitin effect' to
211 be dealt with, namely the use of isotopic correction factors between hard and soft tissues
212 (Hobson & Cherel, 2006, Cherel et al., 2009a), the removal of chitin and measuring
213 stable isotopes on amino acids. Determining the stable isotope ratios of chemically
214 extracted proteins from hard tissues has not yet been performed, but a more promising
215 way is to measure $\delta^{15}\text{N}$ values of amino acids resulting from protein hydrolysis.
216 Selecting appropriate source and trophic amino acids (e.g. phenylalanine and glutamic
217 acid, respectively) allows quantification of both $\delta^{15}\text{N}$ baseline levels and the trophic
218 position of consumers relative to the baseline [i.e. the $\delta^{15}\text{N}$ signature of source amino
219 acids (e.g. phenylalanine) does not increase along the food chain, while that of trophic
220 amino acids (e.g. glutamic acid) does - hence the $\delta^{15}\text{N}$ difference between trophic and
221 source amino acids is a direct estimation of the trophic position of an organism]. This
222 approach was recently used on cephalopod hard tissues, including cuttlefish cuttlebone
223 (Ohkouchi et al., 2013) and squid gladii (Ruiz-Cooley et al., 2013) and has the potential
224 to depict previously unknown trophic relationships, habitat use and migration patterns
225 of cephalopods in marine ecosystems.

226

227 *Population dynamics of cephalopods under a trophic relations (as well as age and*
228 *growth) context: possible future research (Marek R. Lipinski)*

229 The present-day population dynamics of cephalopods are still largely at the descriptive,
230 natural-history stage. The best summaries of current knowledge were given by Boyle
231 and Boletzky (1996), Boyle and Rodhouse (2005) and Rodhouse et al. (in press).

232 The known data on cephalopod population dynamics that has been widely and
233 comprehensively quantified may serve a practical purpose in the management of
234 fishable stocks of selected species of octopods, cuttlefish and squid (Rodhouse et al., in
235 press). This part, however, largely ignores the general theoretical framework of
236 population dynamics in ecology (described by Turchin (2003)), based on predator-prey
237 interactions. However, there are efforts aimed at incorporating predator-prey
238 relationships in sustainable resource management (Bowman et al., 2000, Overholtz et
239 al., 2000, Overholtz et al., 2008, Tyrrell et al., 2008, Tyrrell et al., 2011). Hence,
240 predation should be considered in setting Maximum Sustainable Yield (MSY) for a
241 fishery, including those fisheries exploiting squid (such as *Doryteuthis pealeii* and *Illex*
242 *illecebrosus*). When this is done, MSY is usually considerably smaller. Model inputs are
243 usually based on stomach contents analysis, and actual consumption is calculated
244 (subject to some assumptions). The underlying reasoning is that a lack of this resource
245 in the diet of predators will be to the detriment of these predators.

246 However, this may not correspond to reality. This approach usually assumes
247 either a specialist character of these predators, or at best, a hyperbolic response of a
248 generalist predator, according to a model where $dN/dt = rN(1-N/k) - gN/d + N$ [with N:
249 population density; r: per capita rate of population change; k: carrying capacity
250 (logistic); d: half-saturation constant (hyperbolic); g: total killing rate by generalist
251 predators; h: half saturation constant (sigmoid)] (Turchin, 2003). However, cephalopods
252 are opportunistic generalists both as a predators and in turn are preyed upon by
253 generalist predators themselves (preyed upon by fishes, birds, mammals and
254 cephalopods), giving a sigmoid response to predation according to the model $dN/dt =$
255 $rN(1-N/k) - gN^2/h^2 + N^2$. These two scenarios are illustrated in Figure 1, where solid lines
256 represent per capita growth rates of the prey population in the absence of predators,
257 whilst dashed curves represent per capita death rate of prey as a result of predation.
258 Numbers correspond to the specific cases (out of many possible). In the hyperbolic
259 scenario (Fig. 1A), case 1 refers to the total extinction of prey as a result of predation.

260 Case 2 is the situation where only very high density of prey secures the end equilibrium
261 (and hence the survival of prey). Case 3 ends with survival of the prey population
262 regardless what happens, therefore predators have a minimum impact upon their prey.
263 In the sigmoid scenario (Fig. 1B), case 1 refers to an equilibrium where prey densities
264 are low (survival is probable); case 2 represents three equilibria and therefore the final
265 result depends upon the initial conditions, but all of them are likely to be stable
266 (survival of prey is probable in most situations); and in case 3 equilibrium is reached at
267 high prey densities, therefore survival is even better than in case 1.

268 Given the above, future work should apply theoretical ecology models to real
269 cephalopod populations, and only then should feed into well-intentioned resource
270 management. This is not happening as of yet, simply because it is a complicated task.
271 Cephalopods will require the development of a 'multi-opportunistic links model'
272 compatible with other findings of theoretical ecology. This model may be useful for
273 fisheries management only if the required parameters can be obtained or assessed in
274 practice.

275 A second case study considered here is on cephalopod age, ageing, longevity
276 and growth from a population dynamics perspective. This field also has a background in
277 theoretical ecology (Turchin, 2003), with its emphasis on changing ages, different
278 average longevity (and ultimately, growth parameters) with change between subsequent
279 generations, and on the influence these changes may have on oscillating numbers of
280 individuals in a population. Here, in contrast to the field of predator-prey relationships,
281 theoretical ecology feeds into practical applications (Quinn & Deriso, 1999), although
282 the focus is somewhat different. Cephalopods, however, have not yet been the subjects
283 of thorough studies in this discipline. This is, because it is felt that some fundamental
284 problems in understanding population structuring have not yet been resolved. There is a
285 relative abundance of age data, but a paucity of studies using these data to model
286 population structure based either on generations (for theoretical purposes) or to
287 construct suitable keys (e.g. age-length) for stock assessment and management analyses.

288 Therefore, there is a need for new research and more data. Firstly, there is a
289 requirement for physiological studies on the interpretation of age marks (mostly
290 biomineralization studies) to construct true instead of biased validation procedures.
291 Secondly, no one has so far adequately addressed Daniel Pauly's paradoxon regarding
292 the metabolic limitation of squid growth (Pauly, 1998): according to him, large squid
293 cannot grow quickly due to their energetic requirements, which goes against the age

294 readings of squid statoliths (supported by aquarium observations), which in turn support
295 the inference that large squid do grow quickly. However, a good start to reconciling
296 these contradictory data was made by O’Dor and Hoar (2000). Thirdly, studies of
297 cephalopod growth are required, that will combine a theoretical ecology approach
298 (suffering at the moment from an assumption of non-overlapping generation cycles)
299 (Turchin, 2003), a wealth of matrix models (Quinn & Deriso, 1999), and a solid
300 physiological basis (which is lacking at the moment). It is to be hoped that the state of
301 the art, presently fragmented into these three areas (Arkhipkin & Roa-Ureta, 2005,
302 André et al., 2009, Keyl et al., 2011, Semmens et al., 2011, Zavala et al., 2012), will
303 improve in the future.

304

305 **2. New approaches to the study of cephalopod morphology (Elizabeth K. Shea,** 306 **Alexander Ziegler)**

307 Comparative morphology is an essential, yet increasingly rare specialty in organismic
308 biology. The slow pace of work for detailed analysis and the current lack of a
309 centralized repository for morphological data contribute to the widely-cited 'taxonomic
310 impediment' that contemporary biodiversity research is facing (Crisci, 2006, de
311 Carvalho et al., 2007). Due to the lack of open access to structural data, molecular
312 methods (e.g. barcoding) are rapidly supplanting morphology in systematics and
313 taxonomy research, resulting in a one-sided discussion about invertebrate relationships
314 and evolution. Rejuvenating morphological research through the development of online
315 repositories for morphological data will provide new avenues of inquiry that would
316 contribute substantively to systematic and taxonomy research. In addition, morphology
317 would become a more accessible contributor to large interdisciplinary research
318 initiatives such as the Census of Marine Life (Decker & O’Dor, 2003) or major online
319 compilations of organismic data such as the Encyclopedia of Life (Wilson, 2003). In
320 this section, we highlight several new and developing digital techniques that have the
321 potential to expedite morphological work, and which could encourage a shift in focus
322 from data acquisition to data analysis, consequently resulting in a more rapid and
323 regular research output in cephalopod morphological research.

324 Cephalopod beak identification is notoriously difficult, but an in-depth
325 understanding of beak morphology is critical to stomach content analyses, as well as a
326 for an understanding of predator-prey dynamics (Clarke, 1986, Xavier & Cherel, 2009).
327 Three-dimensional (3D) anaglyph images constitute an alternative to complex line

328 drawings or photographs (Xavier & Cherel 2009). Richard E. Young is in the process of
329 building a collection of such images, archiving them on the Tree of Life Web Project
330 website (http://www.tolweb.org/notes/?note_id=4541). The upper and lower beaks of
331 over 140 species from all major clades have so far been analyzed (Young, 2009). In
332 addition, new hybrid approaches such as rotational SEM could be used to image
333 miniscule morphological features such as statoliths, sucker dentition or cartilaginous
334 strips and tubercles at very high resolutions and in 3D (Cheung et al., 2013).

335 In addition, robotic microscopy systems developed for applications in pathology
336 permit rapid digitization of histological sections on a large scale and at high resolutions
337 (Al-Janabi et al., 2012). Such systems could be used to digitize and catalogue
338 histological data on cephalopod neuroanatomy, such as, for example, the John Z. Young
339 slide collection deposited at the National Museum of Natural History (Washington, DC,
340 USA). The resulting tomographic image stacks can be aligned using semi-automatic and
341 automatic algorithms (Eliceiri et al., 2012), and can subsequently be made accessible as
342 full 3D datasets in online repositories. These image stacks would then become a
343 baseline of information that permits directly connecting past research (Young, 1971) to
344 present compilations (Nixon & Young, 2003), as well as future studies.

345 Furthermore, non-invasive scanning techniques such as magnetic resonance
346 imaging (MRI), computed tomography (CT), or micro-computed tomography (μ CT)
347 now allow analyzing whole specimens from the millimetre to the metre scale (Walter et
348 al., 2010). Following dataset acquisition, specialized (but often open source) software
349 can be used to virtually dissect the scanned specimen in real-time and in 3D (Ziegler &
350 Menze, 2013). While MRI is particularly suitable for soft tissue imaging (Ziegler et al.,
351 2011a), the X-ray-based techniques CT and μ CT constitute the methods of choice for
352 hard part imaging (Ziegler et al., 2010). However, specimen state (*in vivo* or *ex vivo*),
353 scanning medium (e.g. air, ethanol, formalin, water), scanning time (minutes to hours),
354 dataset resolution (nm to μ m), as well as scanning cost per specimen (up to many
355 hundreds of US-\$) may vary considerably and primarily depend on the system used.

356 Due to the dominance of soft tissues, cephalopods constitute suitable candidates
357 for MRI scanning (Ziegler et al., 2011a). For example, 3D MRI datasets can be used to
358 visualize internal organs in their natural context (Fig. 2A, B). In contrast, mineralized
359 tissues present in cephalopods (e.g. eye lenses, beaks, statoliths, shells) can be rapidly
360 visualized using CT or μ CT (Fig. 2C-E). However, whole specimen staining using
361 electron-dense elements such as iodine or tungsten (Metscher, 2009, Kerbl et al., 2013)

362 also allows analyzing soft tissues of smaller cephalopod specimens using μ CT (Fig. 2 F,
363 G).

364 Current online projects such as The Digital Fish Library (Berquist et al., 2012)
365 or The Digital Morphology website (<http://digimorph.org/>) provide a good starting point
366 for the web-based hosting of morphological data and constitute potential infrastructures
367 for future efforts in cephalopod research. In addition, dissemination of complex
368 biological structures is still carried out primarily in the form of 2D publications (Ziegler
369 et al., 2011b), although interactive 3D models based, for example, on the ubiquitous
370 portable document format (PDF) have been integrated into electronic publications
371 already for several years (Ruthensteiner & Heß, 2008, Kumar et al., 2010). Nonetheless,
372 continued development of such approaches is required in order to adapt them, for
373 example, to mobile devices. Furthermore, 3D printing is poised to become an important
374 tool in the communication of complex biological structures, whether in research or in
375 teaching (Kelley et al., 2007, Ziegler & Menze, 2013).

376 In general, digital morphological techniques permit shifting the workload from
377 data acquisition to data analysis, which will open new avenues of research both across
378 and within cephalopod species. Previously collected, well-identified, and data-rich
379 museum specimens could form the backbone of a large-scale, non-invasive scanning
380 program (Ziegler, 2012). Apart from developing a collection of 3D datasets that can be
381 accessed in the form of a digital museum collection, the novel, high-throughput
382 scanning techniques described above provide new opportunities for a variety of
383 cephalopod specimens. For example, scanning of bulk-collected, commercially-trawled
384 cephalopods could be employed to answer long-standing questions of character
385 variation within species (Vecchione et al., 2005). Reared cephalopods such as *Sepia*
386 *officinalis* could be used for *in vivo* experiments, where images taken before and after a
387 stimulus would be required. Furthermore, specimens too valuable for dissection (e.g.
388 holotypes) can now be scanned with virtually no impact on the specimen and be made
389 fully accessible online in 3D.

390 Cephalopods constitute a small-enough class of molluscs that an effort to
391 digitally scan one representative from each genus or species would constitute a realistic
392 goal, and one that should be pursued in parallel to molecular barcoding (Strugnell &
393 Lindgren, 2007). A concise, user-friendly, widely-disseminated, morphological
394 infrastructure that parallels ongoing efforts to barcode all cephalopod species would

395 render cephalopods not just a group with multiple model organisms, but also a model
396 clade for systematic and taxonomy research.

397

398 **3. Challenges in cephalopod culture (Roger Villanueva, Erica A. G. Vidal)**

399 Experimental approaches have been an important tool for understanding fundamental
400 principles of cephalopod life cycles, physiology and behaviour, thus providing the basis
401 for pilot commercial culture of some species. A recent publication summarizes modern
402 culture techniques used for the most common cephalopod species (Iglesias et al., 2014).
403 Another publication focuses on four species which are highlighted as cephalopod
404 culture models for which there are comprehensive data available, primarily because they
405 are frequently used by researchers around the world, namely *Sepia officinalis*,
406 *Sepioteuthis lessoniana*, *Octopus maya* and *O. vulgaris* (Vidal et al., 2014). These four
407 species show versatile characteristics for culture, such as fast growth and high food
408 conversion rates. In addition, these species mate and spawn in captivity, laying eggs
409 that, with the exception of *O. vulgaris*, produce large hatchlings. These biological
410 features make them suitable candidates as experimental laboratory animals with a
411 potential for aquaculture. However, nearly all zootechnical aspects related to the culture
412 of these species still require improvement and need to be adapted for closely related
413 species from different geographic regions.

414 At present, most of our knowledge on cephalopod culture techniques relies on
415 shallow water species. This is due to the relatively easy access to this group of
416 cephalopods, most of them with commercial interest, and to the ease of reproducing the
417 characteristics of coastal waters in the laboratory. In contrast, techniques for the
418 maintenance of oceanic or deep sea cephalopods remain virtually unexplored. In
419 particular, little experimental work has been directed towards deep sea octopods (Wood
420 et al., 1998, Hunt, 1999), oceanic squids (O'Dor et al., 1977, Bower & Sakurai, 1996,
421 Hunt, 1999, Bush, 2012, Hoving & Robison, 2012, Villanueva et al., 2012), or polar
422 species (Daly & Peck, 2000). However, as research efforts in the open ocean, the deep
423 sea, and polar regions are bound to increase around the world in the near future,
424 methods for the study of captured cephalopods from these regions will be needed to
425 obtain new information on their life cycles and ecology.

426 High-priority research targets in cephalopod culture are the development of
427 sustainable artificial foods and the control of reproduction (Villanueva et al., 2014).
428 Littoral cephalopods are carnivorous and require food rich in protein to maintain their

429 vigorous metabolism, as well as high quality lipids rich in essential fatty acids,
430 phospholipids and cholesterol to sustain their fast growth. Recent efforts to obtain
431 artificial foods have shown promising results (Rosas et al., 2008, Rosas et al., 2013,
432 Martínez et al., 2014). However, a major challenge will be to develop a sustainable
433 artificial diet independent from fisheries products, completely formulated from plant
434 sources, and in addition supporting good survival and growth, as is now a reality for
435 some marine carnivorous fishes (Watson et al., 2013). The study of feeding dynamics of
436 delicate planktonic paralarvae of cephalopods should also become a priority, because it
437 would enable the commercial culture of octopod species such as *O. vulgaris*, which
438 produce small eggs (Iglesias et al., 2007, Villanueva & Norman, 2008). For example, an
439 adapted, enriched *Artemia* protocol would be desirable to feed planktonic octopods or
440 squids - recent work is currently shedding light on this aspect (Guinot et al., 2013).

441 A further area of development required to facilitate cephalopod culture is the
442 control of reproduction and an understanding of the effects of maternal condition on egg
443 quality and offspring competence. Currently, egg masses are collected from the field,
444 are obtained by spontaneous spawning in aquaria, or stem from *in vitro* fertilization. As
445 cephalopods are semelparous and often have a natural spawning period restricted to a
446 few months in the year, researchers currently need to adapt their laboratory studies,
447 timing and experimental protocols to the natural sexual maturation period of the target
448 species. The development of methods to accelerate or retard sexual maturation and
449 spawning in aquaria will open new experimental possibilities and will be particularly
450 useful to the planning and development of commercial culture. The influence of light
451 intensity and photoperiod on sexual maturation has been studied in a few cases
452 (Richard, 1971, Zúñiga et al., 1995) and, if extended, could open new opportunities for
453 the control of reproduction. Furthermore, in cephalopod culture, the development of
454 ethical guidelines that aim to reduce pain, suffering and stress are strongly encouraged
455 and should be based on the 3Rs principle, i.e. *replacement*, *refinement* and *reduction*
456 (Mather & Anderson, 2007, Moltschanivskyj et al., 2007, Andrews et al., 2013, Fiorito
457 et al., 2014).

458 Finally, genetic intervention has already been applied to other metazoans in
459 culture in order to enhance production of cultured animals and to tackle challenges in
460 culture (Hulata, 2001). Such an approach can be expected to have the potential for
461 taking cephalopod culture to the next level. Important new research topics in this respect
462 would be genomic sequencing or studies looking for genes that code for particular traits

463 or that govern protein expression. For example, it would be interesting to identify the
464 genes responsible for desirable broodstock features, control of sexual maturation,
465 growth, immunology, and pathology.

466

467 **4. New ways to research cephalopod adaptations and responses to environmental** 468 **change**

469 *Cephalopods and climate change (Paul G. K. Rodhouse)*

470 The effects of global climate change will include warming of the atmosphere and the
471 oceans, intensification of ocean currents, more frequent and intense extreme weather
472 events, retreat of sea ice in the polar regions, reduction in the depth of the oxygen
473 minimum layer and reduced seawater pH (Raven et al., 2005). These physical changes
474 will drive changes in marine ecosystems, which are predicted to reduce biodiversity,
475 although they will not necessarily reduce overall primary and secondary production.
476 However, these effects will not be uniform. Currently, warming of the atmosphere is
477 most intense in Alaska, Siberia, and the Antarctic Peninsula. In addition, warming of the
478 ocean surface and upper layers in the vicinity of the Antarctic Peninsula has been
479 reported by Meredith and King (2005).

480 Because cephalopods are poikilotherms, they could be expected to
481 physiologically respond to ocean warming. Warming will increase growth rate (subject
482 to food availability and sufficient water oxygen), shorten life span, and increase
483 turnover, which in turn might drive changes in life history parameters (Pecl & Jackson,
484 2008). This will only happen if the species do not shift their distribution in response to
485 warming in order to remain within their present thermal environment. However, there is
486 evidence that some species expand their distribution when facing a warmer environment
487 (Zeidberg & Robison, 2007, Golikov et al., 2013).

488 Furthermore, many cephalopods, especially the oegopsid squids, produce
489 planktonic paralarvae, which, by definition, are transported by ocean currents and have
490 been shown in some species to be dependent on mesoscale structuring in the ocean to
491 complete their planktonic phase (Bakun & Csirke, 1998, Dawe et al., 2000). Such
492 species are likely to be affected by changes in oceanic circulation, the effects of which
493 may be positive or negative. For example, small changes in large-scale circulation are
494 unlikely to affect Antarctic squid, but changes in mesoscale oceanography may have a
495 significant impact (Rodhouse, 2013).

496 Extreme local events such as storms or basin-scale events such as the El Niño
497 Southern Oscillation or North Atlantic Oscillation, which are predicted to be intensified
498 by global climate change, will influence changes in populations (Hoving et al., 2013).
499 Basin-scale events are known to drive variability in the recruitment and abundance of
500 species, including *Illex argentinus* (Waluda et al., 1999), *I. illecebrosus* (Dawe et al.,
501 2000), and *Dosidicus gigas* (Waluda et al., 2006). Intensification of such events might
502 be deleterious and/or advantageous to these species, but there are currently no models
503 which can predict likely outcomes.

504 In the polar regions, changes in sea ice may cause changes in the distribution of
505 some species, but there are no species known to be dependent on sea ice as, for instance,
506 is the Antarctic krill *Euphausia superba* (Murphy et al., 2007, Constable et al., in press,
507 Xavier & Peck, in press). In these high latitudes, changes in ocean ecology driven by
508 retreating sea ice may have a greater effect on cephalopod populations than the direct
509 effect of ice retreat.

510 At least two cephalopod species, *D. gigas* and *Vampyroteuthis infernalis*, are
511 associated with the oxygen minimum layer, where they descend to during daylight
512 (Robison et al., 2003, Rosa & Seibel, 2008, Hoving & Robison, 2012). These two
513 species are physiologically adapted to survive the low oxygen tension of the oxygen
514 minimum layer, and probably enjoy the selective advantage of avoiding active water-
515 breathing predators in this zone. Depending on how widespread this habit is among
516 pelagic cephalopods, changes in the oxygen minimum layer associated with global
517 climate change will have effects on other species (Bograd et al., 2008, Stramma et al.,
518 2008, Keeling et al., 2010, Gilly et al., 2013).

519 Furthermore, all cephalopods possess calcareous statoliths, while some possess
520 larger mineralized structures such as an external shell (e.g. nautilus) or an internal
521 shell (e.g. cuttlefish). Although there is some evidence that cuttlefish are pre-adapted to
522 ocean acidification (Gutowska et al., 2008), there is still a need for more data on the
523 effects of reduced ocean pH on cephalopods.

524 Cephalopods evolved from an ancestral mollusc in the Cambrian. They have
525 survived major extinction events at the end of the Palaeozoic and at the end of the
526 Mesozoic, and have thrived in spite of competition from fishes (Packard, 1972,
527 Rodhouse, 2013). Although some cephalopod groups such as ammonites and belemnites
528 became extinct in geological time, the coleoids have survived and radiated. Their life
529 history traits have adapted them for ecological opportunism and provide them with the

530 potential to quickly evolve in response to new selection pressures (Murphy et al., 1994,
531 Murphy & Rodhouse, 1999, Hoving et al., 2013). There is therefore reason to believe
532 that these characteristics will enable cephalopods to evolve under global climate change,
533 enabling them to avoid becoming extinct, and ultimately giving rise to new forms
534 adapted to a new 'greenhouse world'.

535

536 *Physiological adaptations of cephalopods to environmental change (Rui Rosa)*

537 Coastal marine ecosystems are warming at a higher rate than most other
538 ecosystems (MacKenzie & Schiedek, 2007). Because many coastal organisms already
539 live close to their thermal tolerance limits (Helmuth et al., 2006), ocean warming is
540 expected to negatively impact their performance and survival. Cephalopods are some of
541 the most adaptable marine organisms, capable of adjusting their biology (and life
542 cycles) according to the prevailing environmental conditions (Boyle & Rodhouse, 2005,
543 Hoving et al., 2013). Yet, although their short life spans and great life history plasticity
544 allow them to respond rapidly to new climate regimes, ocean warming may cause
545 serious biological impairments to the more vulnerable early ontogenetic stages, namely
546 shorter embryonic periods and an increased likelihood of premature hatching (Rosa et
547 al., 2012b, Rosa et al., 2014). Future changes in ocean chemistry are also expected to
548 pose particular problems. Cephalopods possess statoliths that may be reduced and
549 abnormally shaped (with increased porosity) under hypercapnia (Kaplan et al., 2013). It
550 is also noteworthy, that along with the rise of $p\text{CO}_2$ in the embryo (combined with a
551 drop in pH and $p\text{O}_2$), the current record of oxygen tension below critical $p\text{O}_2$ values
552 reveals that the harsh (i.e. hypoxic and hypercapnic) conditions inside cephalopod egg
553 capsules are expected to be magnified in the future (Rosa et al., 2013a). Such
554 environmental conditions may promote untimely hatching and smaller post-hatching
555 body sizes (Table 1), thus challenging survival and fitness.

556 In the last few decades, marine hypoxia has become a major ecological concern
557 (Diaz & Rosenberg, 2008). Surprisingly, some squids that were thought to be driven
558 from hypoxic areas due to anatomical and physiological constraints (e.g. *Dosidicus*
559 *gigas*) instead seem to benefit from expanding hypoxia (Rosa et al., 2013b).
560 Nonetheless, the synergistic impact of these climate-related factors (i.e. hypoxia, global
561 warming, and ocean acidification) is expected to compress the habitable night-time
562 depth range of these vertically migrating squid species due to unfavorable high
563 temperature and decreasing pH at the ocean surface (Rosa & Seibel, 2008).

564 At macroecological scales, a species distribution model (SDM) linked to the
565 field of conservation physiology may help to explore future changes in the global
566 patterns of cephalopod diversity. However, the reliability of SDM-based predictions
567 needs to be improved, because models often lack a physiological underpinning and rely
568 on assumptions that may be unrealistic under global climate change. For instance,
569 additional information on the limits of thermal tolerance [e.g. maximum critical
570 temperature (CT_{Max}), lethal temperature at which 50% of the sample population dies
571 (LT₅₀)] will improve our ability to predict the effects of climate change on the present
572 distribution patterns of cephalopods (Rosa et al., 2008a, Rosa et al., 2008b, Rosa et al.,
573 2012a).

574

575 **5. Future cephalopod research in genetics (Jan M. Strugnell)**

576 The volume of research that contains cephalopod genetic sequences has increased
577 markedly over the last 20 years, in particular thanks to the decreasing costs of molecular
578 sequencing. Prices are now sufficiently low for sequencing to become an attractive
579 research tool for scientists representing a range of disciplines, including fisheries
580 science, systematics, or neuroscience and developmental biology. The next exciting
581 wave of genetic research on cephalopods is approaching as the first cephalopod
582 genomes are being sequenced. Genome sequencing of at least ten cephalopod species is
583 currently underway, representing a broad range of taxonomic groups, including *Octopus*
584 *vulgaris*, *O. bimaculoides*, *Hapalochlaena maculosa*, *Sepia officinalis*, *Doryteuthis*
585 *pealeii*, *Euprymna scolopes*, *Idiosepius paradoxus*, *I. notoides*, *Architeuthis dux*, and
586 *Nautilus pompilius* (Albertin et al., 2012). Obtaining high-quality whole genome
587 sequences of cephalopods will stimulate new inquiries by providing a wide range of
588 research opportunities in which a reference genome is required, as well as in the
589 interpretation of the genomes themselves.

590 However, the sequencing of cephalopod genomes is not without its challenges,
591 and early work has shown cephalopod genomes to be large and to contain many
592 repeated regions, making sequence assembly difficult (Albertin et al., 2012). In
593 addition, at least one whole genome duplication event has been suggested to have
594 occurred during the evolution of the Cephalopoda (Hallinan & Lindberg, 2011), which
595 may further complicate assembly. Nonetheless, important lessons in sequencing whole
596 molluscan genomes have been learned through sequencing of the few whole molluscan
597 genomes that exist to date (i.e. *Lottia*, *Aplysia*, and *Biomphalaria*). But, although best-

598 practice methods of sequencing and assembly are being implemented (Albertin et al.,
599 2012), the task will not be trivial.

600 In addition, annotation of cephalopod genomes will likely prove to be a
601 significant challenge as well. Part of the annotation process for a novel genome
602 typically involves *de novo* gene prediction, a task that is known to be difficult and error-
603 prone (Albertin et al., 2012, Yandell & Ence, 2012). Large taxonomic distances exist
604 between cephalopods and taxa with well-annotated animal genomes, which will
605 increase the difficulties of annotation. Therefore, the sequencing of corresponding
606 transcriptome data will be essential to supplement any *de novo* predictions, because it
607 definitively identifies regions of the genome that are transcribed, and thus can help to
608 identify boundaries between genes through differences in transcript abundance.

609 Despite these initial difficulties, the sequencing of the first cephalopod genome
610 holds great promise for improving our understanding of the evolution and function of
611 this fascinating group of marine organisms. Completely sequenced genomes will
612 provide researchers with the ability to thoroughly study the function of different genes
613 and also to investigate evolutionary relationships, not only within cephalopods, but also
614 more broadly within molluscs and lophotrochozoans. In addition, whole genomic data
615 of cephalopods will open up fields of research that have to date largely been unavailable
616 or subject to only a handful of studies. Such research areas include epigenetic
617 modification, RNA editing and microRNAs (Albertin et al., 2012).

618 The development of a cephalopod model organism (possibly *Idiosepius* due to
619 its small size) will allow focused studies of the development of the cephalopod body
620 plan. This will facilitate investigation and understanding of many morphological
621 features characteristic of cephalopods that are commonly suggested to be 'vertebrate-
622 like', such as complex eyes, well-developed brains and highly differentiated vascular
623 and neuroendocrine systems. As such, research of the evolution and development of
624 these features, facilitated by whole-genome data, may not only provide further insight
625 into cephalopod evolution, but also into the evolution of man (depending on whether the
626 similarity of vertebrate structures is superficial or based on genuine homology).

627

628 **6. Challenges in cephalopod fisheries and conservation**

629 *The future trends in cephalopod fisheries (Graham J. Pierce)*

630 Historically, cephalopod fisheries have been less important in the northeast Atlantic
631 compared to much of the rest of the world (Caddy & Rodhouse, 1998, Hunsicker et al.,

632 2010b), despite a strong tradition of cephalopod consumption in southern Europe.
633 However, a combination of declines in other fishery resources has led to an increase in
634 directed cephalopod fishing as well as increased attention from fishers, national
635 governments, and fisheries organizations such as the International Council for the
636 Exploitation of the Sea. In Europe, therefore, the short-term trend is likely to be an
637 increased effort in cephalopod fishing, extending exploitation to currently under- or
638 unexploited species, coupled with novel implementation of formal stock assessment and
639 regulated fishing policies. However, it is fairly unlikely that existing stocks can absorb a
640 substantial increase in fishing pressure (Royer et al., 2002) and past experience shows
641 that the unpredictable nature of cephalopod abundance tends to discourage commercial
642 fishery interests (Young et al., 2006).

643 These remarks can be generalised to world cephalopod fisheries in the sense that
644 landings have been increasing (at least until around 2005), new species have assumed
645 high importance (notably *Dosidicus gigas* in the eastern Pacific) and evidence is already
646 being seen of overexploitation in some areas (Pierce and Portela, 2014). A key issue will
647 be understanding the rise (and fall) of important cephalopod fisheries, especially those
648 of ommastrephid squids such as *Todarodes pacificus*, *Illex argentinus* and *D.*
649 *gigas*. While we suspect that environmental sensitivity is one key to understanding
650 population trajectories, effects of overexploitation may at least partially explain some of
651 the spectacular crashes like that of the *T. sagittatus* fishery off Norway in the mid-
652 1980s. As suggested above, global climate change may have a range of impacts on
653 cephalopod populations and may result in a shift in the relative importance of fisheries
654 and environment in controlling population dynamics.

655 Cephalopod culture, especially for *Octopus* spp. (Iglesias et al., 2014), may help
656 to fill the growing demand for cephalopods in Europe and its export markets. Relevant
657 recent developments in cephalopod culture include *in vitro* fertilization (Villanueva et
658 al., 2011). Nonetheless, artisanal fisheries will remain important, and are increasingly in
659 need of assessment and management that is appropriate to the small scale of the
660 fisheries and the particular biological features of the resource species. However, perhaps
661 the biggest question mark concerns whether exploitation of deep sea cephalopod
662 resources is capable of expansion. Malcolm Clarke, among other cephalopod scientists,
663 suggested that there are vast resources of oceanic squids in the world. His assessment
664 was based on the estimated amount of food needed to sustain the world's sperm whale
665 population (Clarke, 1996, Santos et al., 2001). This potential resource presents an

666 enticing opportunity for fisheries, but others have cast doubt on the large abundance of
667 such species. In addition, a practical challenge relates to palatability, although fishery
668 companies are currently developing processing methods for ammonium-rich squid
669 tissues to permit their marketing as food products.

670 Fisheries management and governance in Europe is currently undergoing a
671 revolution, with the implementation of an integrated ecosystem assessment and
672 management approach as part of the reform of the Common Fisheries Policy, while at
673 the same time looking ahead to a future integrated marine management, in which
674 fisheries are simply one of many relevant sectors. The move towards an ecosystem
675 approach to fisheries is of course not unique to Europe. However, the steep increase in
676 data requirements (compared to single species assessments) presents a real obstacle,
677 especially in a period of economic recession; thus, alternative approaches based on
678 indicators and expert judgement are also likely to be needed. In this context, the Marine
679 Strategy Framework Directive (MSFD) of the European Union is relevant, as it focuses
680 on the development of indicators of ocean health. At least in the United Kingdom, there
681 are plans to develop cephalopod indicators for the MSFD. As a final note, cephalopod
682 waste from fishery processing, and cephalopod species of lesser interest for human
683 consumption, may be increasingly used in animal feedstuffs, fertilizers (Fetter et al.,
684 2013), or other industrial products such as pharmaceuticals.

685

686 *Cephalopod conservation (A. Louise Allcock)*

687 Assessing the conservation status of a wide range of cephalopod taxa reveals just how
688 little is known about many species. Studies carried out for the International Union for
689 the Conservation of Nature (IUCN) Red List, focusing on different higher cephalopod
690 taxa (e.g. Sepiida, Oegopsida, Cirrata), have found that between about 50 and 75% of
691 species in these higher taxa are 'Data Deficient' (Kemp et al., 2012). Many species are
692 known from just a few specimens, so that little is known about their biology and
693 ecology. In some cases, we can conclude that species meet the IUCN category of 'Least
694 Concern' simply because their very wide geographic distribution and high fecundity
695 with planktonic dispersal means that they are unlikely to be impacted across their entire
696 distribution range, despite the possible existence of local threats, so the lack of data is
697 actually under-reported.

698 In particular, data are lacking for cirrate octopods. These cephalopods are
699 potentially long-lived, are slow to reach maturity and have low fecundity (Collins &

700 Villanueva, 2006). *Opisthoteuthis*, the most shallow cirrate genus, is characterized by a
701 close association to the benthos, and is therefore the genus most affected by commercial
702 deep sea trawling. *O. chathamensis* was considered 'Nationally Critical' on the New
703 Zealand Red List (Freeman et al. 2010) and Collins and Villanueva (2006) suggested
704 that populations of other species may already have declined as a result of deep sea
705 trawling. However, a lack of specific population data and information on fisheries
706 impacts will likely prevent many potentially vulnerable species being listed in a
707 category other than 'Data Deficient'. Therefore, one of the future challenges for
708 cephalopod biologists is to improve the quality and consistency of population estimates
709 for all cephalopod species, particularly those subjected to direct or indirect
710 anthropogenic impacts, including fishing.

711 Taxonomic issues may also prevent the actual vulnerability of a species from
712 being reflected in its conservation assessment. Recent dramatic declines in the size of
713 the *Sepia apama* population in the upper Spencer Gulf (South Australia) have been well
714 documented (Hall, 2008, Hall, 2010), but attempts to have this population listed as
715 'Critically Endangered' under Australia's Environment Protection and Biodiversity
716 Conservation Act 1999 failed (Anonymous, 2011), apparently because the population
717 had not been formally described as a distinct species, despite little evidence of it inter-
718 breeding with other populations (Anonymous, 2011). However, a temporary localised
719 ban on fishing was enacted in 2013. *S. apama* was assessed as 'Near Threatened' on the
720 IUCN Red List (Barratt & Allcock, 2012), but this assessment considered the whole
721 range of the species, as is normal practice. The IUCN assessment notes that "If the
722 population in the upper Spencer Gulf is shown to be a separate species then the Spencer
723 Gulf species would be assessed as Endangered."

724 Conservation efforts for *Nautilus* are similarly hindered. The slow growth and
725 low fecundity of nautiluses (Dunstan et al., 2011) make them vulnerable to fishing
726 pressure and several overfished populations have crashed (Dunstan et al., 2010). The
727 very wide distribution range reported for *N. pompilius* suggests that threats are likely to
728 be local, until one considers recent genetic data. For example, molecular phylogenetic
729 work (Bonacum et al., 2011, Sinclair et al., 2011, Williams et al., 2012) indicates that *N.*
730 *pompilius* comprises several distinct phylogenetic species. This suggests that the impact
731 of fisheries is far more likely to lead to species extinctions than previously thought.
732 However, descriptions of individual species within the *N. pompilius* species complex
733 and accurate information on the range of these species are required if conservation

734 listings are to reflect the perceived vulnerability to anthropogenic impacts. Therefore,
735 ensuring that all cephalopod species are accurately described, and that species
736 complexes and cryptic species are distinguished, constitutes an essential future
737 challenge for cephalopod conservation.

738

739 **Discussion**

740 Cephalopods will continue to attract scientific interest, particularly in the fields of
741 physiology, genetics, ecology and fisheries. Furthermore, the traditional scientific
742 disciplines of taxonomy and morphology are currently being rejuvenated by the
743 application of new technologies. Studies on cephalopods will continue to range from the
744 organismic level (e.g. physiology, behaviour), to the species level (e.g. taxonomy,
745 systematics, population dynamics, distribution, abundance), and finally to the ecosystem
746 level (e.g. fisheries, biodiversity, conservation). In addition, new cephalopod research is
747 emerging on issues such as global climate change and ocean acidification or habitat and
748 food-web modelling.

749 Cephalopods constitute an important trophic link between the lower levels of
750 food webs and top predators (Young et al., 2013). About 800 species of extant
751 cephalopods have been described, but we only have sufficient data to understand the life
752 history (e.g. distribution, habitat, feeding ecology, reproductive biology) for
753 approximately 60 species (Jereb & Roper, 2005, Jereb & Roper, 2010, Jereb et al.,
754 2014). Therefore, taxonomists and geneticists must increasingly work together to ensure
755 that specimen data uploaded to databases are based on correctly identified specimens.
756 The combination of molecular genetics, DNA barcoding, and digital morphological
757 techniques offers new ways to resolve numerous outstanding issues in cephalopod
758 taxonomy and evolution. In this context, an increase in molecular work is of particular
759 importance, because the lack of transcriptomic and genomic information, for example,
760 has limited advances in neurobiology research, where cephalopods act as model
761 organisms (Zhang et al., 2012).

762 Cephalopods have several interesting traits, which make them suitable model
763 organisms for broad evolutionary research. For instance, they have one of the largest
764 size range of any metazoan class and could therefore become model species for
765 studying metazoan growth and metabolism. Furthermore, cephalopods show a
766 remarkable diversity of life history traits and a better understanding of evolutionary
767 relationships among cephalopods would help to determine the plasticity of these traits

768 or could reveal simple switches between individual strategies. In addition, because of
769 the presence of mineralized structures or the planktonic early life stages, most
770 cephalopod species may be highly sensitive to global climate change and/or ocean
771 acidification, because of the presence of mineralized structures or the planktonic early
772 life stages. Hence, cephalopods should be increasingly used as model organisms to
773 predict the effects of global warming on ocean life (Hanlon et al., 1989, Rodhouse,
774 2013).

775 In addition, a quantitative PCR approach should finally allow reliable
776 identification of cephalopod species as prey. Also, because top predators are still a
777 major source of information on cephalopods, novel techniques in trophic research such
778 as the analysis of stable isotopes, DNA, or fatty acids as well as 3D imaging will
779 complement the data obtained by conventional means (Jarman et al., 2004, Barrett et al.,
780 2007, Karnovsky et al., 2012). These latter techniques have suffered due to a decline in
781 taxonomists actually able to perform this type of work (Pearson et al., 2011).
782 Furthermore, the use of ecological tracers, especially fine-scale analyses of tracer
783 molecules within informative structures such as statoliths, beaks or shells will offer new
784 insights into stock structuring and individual life history (Cherel & Hobson, 2005,
785 Cherel et al., 2009a, Ramos & Gonzalez-Solis, 2012). In addition, recent improvements
786 in specimen tagging now allow studying movements of cuttlefish and squid (Gilly et al.,
787 2006, Semmens et al., 2007, Wearmouth et al., 2013). If tag weight could be further
788 reduced and some attachment issues resolved, this approach might be extendible to
789 smaller cephalopod species or earlier developmental stages.

790 Future research should certainly also focus on the ecology of cephalopod
791 species, particularly for those species with immediate commercial fishery interest. As a
792 result of the increasing international capacity to explore deeper environments, deep sea
793 cephalopods will attract the attention of fisheries and research. For example, the
794 increasing amount of deep sea imagery calls for creative solutions to compiling and
795 using such data. Advanced and more complete morphological data will improve our
796 ability to identify specimens based on photographic records alone. For the well-known
797 commercial cephalopod species, long-term monitoring and the establishment of marine
798 protected areas will be the primary focus of discussion in cephalopod conservation.
799 Furthermore, the usage of the continental shelf slope, deep sea, and oceanic areas by
800 numerous pelagic predators and cephalopods is a further area that will receive attention
801 from conservationists (Harris et al., 2007, Game et al., 2009, Tancell et al., 2012). In

802 order to catch fast-swimming cephalopods, efforts should be channeled into the use of
803 more efficient nets that allow catching sub-adult or adult stages of the larger species.
804 Incorporating such research foci into major multidisciplinary projects could become
805 essential for success in obtaining funding.

806 At present, the effects of global climate change, linked with acidification,
807 warming, and expanding hypoxia, perhaps represent the biggest threat to certain species
808 of cephalopods, but also constitute a challenge to researchers, policymakers, and society
809 at large. From a scientific point of view, one of the greatest challenges in this discipline
810 will be to discriminate between the effects of global climate change and fisheries on
811 cephalopod populations. In this regard, experimentation has always been an important
812 approach to resolving open questions in cephalopod research. From a technological
813 perspective, cephalopod culture should be further developed to meet challenges such as
814 the development of sustainable artificial foods or the control of reproduction and genetic
815 manipulation. In addition, the successful maintenance of deep sea and oceanic
816 cephalopods in captivity would be a major step forward to understanding their life
817 cycles and would contribute to assessing the potential impact of fisheries targeted at
818 other species in their habitats. Such research efforts would also constitute an important
819 contribution to cephalopod conservation efforts (Hoving et al., in press).

820 Finally, collaboration, in particular between scientific disciplines, is essential for
821 tackling some of the big scientific challenges the world is currently facing. Early career
822 scientists, such as the CIAC Young Researchers group, should make ample use of
823 novel, digital approaches to networking, communication, and collaboration. Social
824 media, along with digital repositories as well as new data and research sharing
825 protocols, will continue to facilitate international and interdisciplinary research on
826 cephalopods and related scientific areas. Furthermore, education and outreach initiatives
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829

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840

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1344 **Figures**

1345 Figure 1. Different per capita growth rates of prey, according to the presence or absence
1346 of predators. (A) Hyperbolic response. (B) Sigmoid response. See the main text for
1347 explanation. Modified from Turchin (2003), with copyright permission from Princeton
1348 University Press.

1349

1350 Figure 2. Analysis of cephalopod specimens using non-invasive imaging techniques.
1351 The two- and three-dimensional visualizations shown here are based on a MRI dataset
1352 of a whole museum wet specimen of *Bathypolypus arcticus* (A, B), a μ CT dataset of the
1353 dry shell of *Spirula spirula* (C-E), and a μ CT dataset of a tungsten-stained wet specimen
1354 of *Idiosepius pygmaeus* (F, G) (dataset courtesy of Brian D. Metscher).

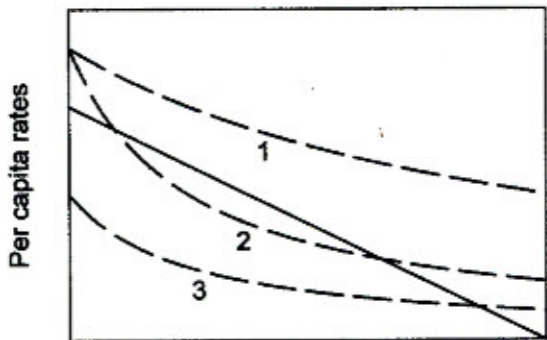
1355

1357 Table 1. Responses of different cephalopod life stages to ocean acidification.

Species	Life stage	Ecological parameters	Effect	Reference
<i>Sepia officinalis</i>	Embryo	$p\text{CO}_2$ 400–1650 ppmv; pH 8.0–7.5; 18 and 22°C	Lower survival rate; metabolic depression; premature hatching; lower hypoxic threshold	(Rosa et al., 2013a)
<i>Sepia officinalis</i>	Juvenile	$p\text{CO}_2$ 705–6068 ppmv; pH 8.0–7.1; 16–17°C	4% daily increase in body mass; mass of calcified cuttlebone increased 5- to 7-fold	(Gutowska et al., 2008, Gutowska et al., 2010)
<i>Loligo vulgaris</i>	Embryo	$p\text{CO}_2$ 424–1680 ppmv; pH 8.0–7.5; 13, 15, 17, and 19°C	Lower survival rate; shorter mantle length; premature hatching; greater incidence of abnormalities; metabolic depression; lower thermal limit; increased heat shock response	(Rosa et al., 2014)

<i>Doryteuthis pealeii</i>	Paralarva	$p\text{CO}_2$ 390–2200 ppmv; pH 8.0-7.3; 20°C	Increased time of hatching; shorter mantle length; statoliths with reduced surface area; abnormally shaped statoliths with increased porosity and altered crystal structure	(Kaplan et al., 2013)
<i>Dosidicus gigas</i>	Juvenile	$p\text{CO}_2$ 380-1000 ppmv; pH 8.0-7.5; 10°C	Metabolic depression; reduced aerobic scope; reduced level of activity	(Rosa & Seibel, 2008)

(a) Hyperbolic response



(b) Sigmoid response

