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1 **Ecological-fishery forecasting of squid stock dynamics under climate**
2 **variability and change: Review, Challenges, and Recommendations**

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38

39 **Abstract**

40

41 Globally, cephalopods support large industrial-scale fisheries and small-scale to partly
42 largescale local artisanal fisheries. They are of increasing economic importance as
43 evidenced by the rapid rise in their global landings from 1950 to 2014. Cephalopods are
44 sensitive to environmental variability and climate change and many if not all species
45 show wide fluctuations in abundance. This is most evident in ommastrephid nerito-
46 oceanic squid since their life cycle is associated with boundary currents that are
47 changing with climate change. The inter-annual variability in catch presents challenges

48 for fishers and managers due to the ‘boom-or-bust’ nature of the fishery. A key barrier
49 to rational management of squid fisheries is the low level of development of fishery
50 forecasting. Despite substantial progress made in relating squid population dynamics to
51 environmental variability and change, several challenges remain to develop forecast
52 products to support squid fisheries management. Ideally, squid fisheries management
53 needs a forecasting system that includes all time-scales of forecasting, and especially
54 short - and medium-terms forecasts. The present overview first provides current
55 knowledge of the effects of climate change and variability on squid population
56 dynamics, challenges and opportunities to advance ecological-fishery forecast products,
57 and finally a roadmap is proposed for future development of forecasts products to
58 support squid sustainable fisheries management. As for the adoption of specific
59 forecasting methods to the squid fishery management process, what is important is the
60 relationship between needs, feasibility, and the ultimate success of a forecast will be
61 determined by whether it is used by end-users.

62

63 Keywords: Cephalopods, squids, climate change, stock size, ecological-fishery
64 forecasting.

65

66 **Introduction**

67

68 Cephalopods support both large industrial scale fisheries and numerous artisanal fisheries,
69 mostly small-scale but some partly large-scale. They are of increasing economic importance
70 as evidenced by the rapid rise in their global landings over recent decades (Arkhipkin et al.,
71 2015b, Doubleday et al., 2016, and Sauer et al., 2019). World cephalopod catch increased
72 almost 10-fold over the last six decades from around 0.50 million tons annually in 1950 to a
73 peak of 4.85 million tonnes in 2014 (FAO, 2020). In particular, squid catch increased
74 worldwide. This has highlighted the fact that squid abundance is highly variable (Rodhouse,
75 2005; Arkhipkin et al., 2015b; Doubleday et al. 2016), which leads to unpredictable inter-
76 annual and long-term fluctuations in catch and market prices, and significant volatility in the
77 world market for squids, particularly for the well-documented *Illex argentinus* squid market
78 (Harte et al. 2018). The unpredictable nature of squid catch volumes recently highlighted by a
79 dramatic fall in world cephalopod catch in 2016, by over 1.1 million tons, mainly due to an
80 85% drop in the catch of *Illex argentinus* but also reflecting reduced landings of *Dosidicus*
81 *gigas* and *Todarodes pacificus* (FAO, 2020). Large fluctuations in squid abundance and the
82 current lack of robust ecological and fishery forecasting also have large economic
83 consequences.

84

85 Cephalopods play an important role in ecosystems and are a key component of food webs,
86 providing a vital link from smaller invertebrates and fish to marine megafauna, birds, and
87 humans (Boyle and Rodhouse 2005, de la Chesnais et al., 2019). Cephalopods possess a
88 number of unique biological and ecological characteristics that set them apart from many
89 other commercially exploited marine species. As a result of their short lifespan and
90 semelparous reproduction, they have fast growth rates, with high consumption rates and
91 conversion efficiencies. Cephalopods in general and squid in particular have a high
92 fecundities, with Loliginid squids usually producing fewer eggs than ommastrephids. These
93 characteristics have adapted squid to become ecological opportunists that can rapidly exploit
94 favorable environmental conditions, resulting in recruitment and abundance levels with high
95 inter-annual variability (Rodhouse et al., 2014). This is probably why there is usually no clear

96 relationship between spawning stock abundance and subsequent recruitment (Pierce and
97 Guerra, 1994; Basson et al., 1996; Uozumi, 1998). The combination of these characteristics
98 makes it difficult to discriminate between the effects of climate variability on squid
99 populations and those of fishing mortality. In addition, the role of density dependent
100 intraspecific competition in regulating population size is poorly known, although it may be
101 noted that cannibalism is common in squids (Ibáñez and Keyl, 2010).

102

103 Cephalopods are very sensitive to environmental variability and climate change and many if
104 not all species show wide fluctuations in abundance. This is most evident in ommastrephid
105 nerito-oceanic squid. The inter-annual variability in catch presents challenges for fishers and
106 managers due to the ‘boom-or-bust’ nature of the fishery. This has attracted attention to the
107 likely role of climate variability in driving recruitment processes in squid stocks (e.g. Bakun
108 and Csirke, 1998, Pierce et al. 2008, Rodhouse et al., 2014, Arkhipkin et al., 2015b).

109

110 All ommastrephid squid extrude their eggs within voluminous, gelatinous egg masses that
111 protect the embryos from predation by pelagic zooplankton (Puneeta et al., 2017). The
112 pelagic egg masses are found in spawning grounds that are usually located in low latitudes to
113 allow the eggs and paralarvae to develop and grow faster in warmer waters. Paralarvae and
114 early juveniles are passively transported by strong, large-scale currents (e.g., boundary
115 currents) to more productive feeding grounds on continental shelf and upper slope areas.
116 Following maturation in their feeding grounds, adult squid migrate back to their spawning
117 grounds. After spawning, they soon die which brings massive amounts of protein to
118 oligotrophic areas of the open ocean (Boyle and Rodhouse, 2005).

119

120 The relationships between ommastrephid squid stocks and large-scale oceanographic
121 processes have been emphasized by various authors (Froerman, (1981, 1985, 1986; Waluda
122 et al., 1999, 2001, 2004, 2009; Rodhouse, 2005; Rodhouse et al., 2014; Arkhipkin et al.,
123 2015b). We know that large exploited stocks of ommastrephids are mostly associated with
124 the high velocity western boundary current systems and eastern boundary currents of the
125 Atlantic and Pacific Oceans (O’Dor and Coelho, 1993, Rodhouse, 2005, Arkhipkin et al.,
126 2015b).

127

128 There has been a great deal of research to understand the relationship between environmental
129 processes and population dynamics of ommastrephid squids. For example, Froerman, (1981,
130 1985, 1986), based on long-term biological and oceanographic data, was able to formulate an
131 initial hypothesis on the role of the Gulf Stream in the dynamic of distribution of the
132 Northern shortfin squid in northwestern Atlantic. Rowell and Trites (1985), Dawe and Beck
133 (1985) and O’Dor and Coelho, (1993) further developed this hypothesis. Then Bakun and
134 Csirke (1998) developed a conceptual model of how variability in the oceanic environment
135 may drive interannual variability, especially in stocks of the ommastrephid species that
136 depend on the major western boundary current systems. They hypothesized that recruitment
137 variability may be driven by wind effects, fluctuations in prey abundance, variation in
138 predation pressure, potential “match-mismatch” effects, and disease epidemics.

139

140 In fact, there is a strong consensus among cephalopods scientists (Rodhouse et al., 2014;
141 Arkhipkin et al., 2015b, O’Brien et al., 2018) that, in order to be effective in managing
142 cephalopod fisheries, a good scientific understanding of the relationship between the
143 environment and population dynamics is essential.

144

145 Given the historical variability of squid populations, and expected future environmental
146 variability and climate change, there is a clear technical challenge to manage squid fisheries,
147 and as new data and information become available, it is evident that we need to update the
148 existing assessment methods and management measures (Arkhipkin et al., 2020). Because of
149 the complexities involved and the important role of cephalopods in the marine ecosystem as
150 both predator and prey, ecosystem-based fisheries management, integrating environmental
151 and ecosystem considerations is desirable for cephalopod fisheries (Rodhouse et al., 2014).
152 An ecosystem approach to management requires a good scientific understanding of the
153 underlying causes of the links between the environment and squid population dynamics (de la
154 Chesnais et al., 2019).

155
156 Such information could guide the development of predictive models and forecast products to
157 support real-time fishery management and it could lay the foundations for predicting the
158 possible effects of longer-term climate change on squid stocks. Several attempts have been
159 made to develop stock assessment or forecasting models that incorporate environmental and
160 ecosystem processes that drive variability in recruitment, distribution and migration patterns
161 (e.g. Froerman, 1985; Moustahfid et al., 2009, Waluda et al., 1999, 2001a, Sobrino et al.,
162 2020, Arkhipkin et al., 2020). Here it is useful to distinguish forecasts based on empirical
163 statistical relationships, between environment and abundance, and ecosystem-based
164 assessments, which incorporate the mechanisms, by which environmental drivers influence
165 population dynamics - and indeed to note the possibility of hybrid approaches combining
166 empirical statistical and mechanistic mathematical representations of population dynamics.

167
168 Forecasts can be classified according to their time horizons, e.g. short – medium and long-
169 distant term forecasts (Alder et al. 2020). Such horizons will typically differ according to the
170 nature of the process being forecasted (e.g. hydro-meteorological, oceanographic or
171 ecological) and the needs of the forecasts. In fisheries, the time horizon of a forecast needs to
172 mesh the time horizon used in fishery management. A particular issue for squid fishing is
173 that the feasible time horizon of forecasts is likely to be more limited than that for longer-
174 lived iteroparous teleost fish (Nigmatullin, 2004a) in which “short term” forecasts refer to
175 one year, and “medium-term” and “long-term” forecasts refer to several and many years,
176 respectively. For squid “short term” refer to few days to a month and “medium term” to few
177 months and “long-term” to “distant-term” from one year to several years and to decades
178 (Nigmatullin, 2004a).

179
180 Different types of forecasting deal with different periods of the squid life span. Short-term
181 forecasting may be aimed at predicting location of optimal fishing grounds, the size of dense
182 concentrations, and the possible amount of Catch per Unit Effort (CPUE). Medium-term
183 forecasting can be used to predict the state of the stock and the fishing situation 0.5-1 year
184 ahead based on the situation during recruitment. Long- and distant-term forecasting deals
185 with several successive generations, the quantitative relationships between which are usually
186 unclear. Ideally, squid fisheries need a forecasting system that includes all time-scales of
187 forecasting, and especially short - and medium-terms.

188 The present overview first provides current knowledge of the effects of climate change and
189 variability on squid population dynamics, challenges and opportunities to advance ecological-
190 fishery forecast products, and finally a roadmap is proposed for future development of forecasts
191 products to support the sustainable squid fisheries management.

192

193 **Brief overview of observed changes of boundary currents in response to climate change**

194

195 Figure 1. Show the Western Boundary Currents (WBC) and Eastern Boundary Currents
196 (EBC) around the world and their supported squid populations. The WBC are formed in
197 response to large-scale wind forcing on a rotating Earth, are poleward and narrow, swift and
198 organized. In contrast, the shallow and broad equatorward EBC are generally extremely
199 eddy-rich and known for their upwelling regions along the coast. The WBC are the hotspots
200 around the world in terms of the amount of heat being transported poleward by them (Hobday
201 and Pecl, 2014, Shears and Bowen, 2017), and they have also become the major sinks of air-
202 sea CO₂ flux (Takahasi et al., 2009).

203 Using several coupled parameters (e.g. sea surface temperature, ocean surface heat fluxes,
204 ocean surface winds) including reanalysis products and satellite-blended observations of the
205 five major WBC, Yang et al. (2016) connected the changes in atmospheric circulation to
206 poleward movement and intensification of the WBC.

207 Recently, Gangopadhyay et al., (2016) have found that the temporal variability along the Gulf
208 Stream (GS) changes from decadal periods on the western segment of the GS (west of 60°W)
209 to inter-annual (4-5 years) periods to the east of 60°W. Based on 40-years of observational
210 charts of the GS Warm Core Rings (WCR), Gangopadhyay et al., (2019, 2020) found that
211 there has been a significant regime shift in terms of the number of WCR formed in the Gulf
212 Stream between 75°W and 55°W. The average has increased by 15 WCR per year – from 18
213 per year during 1980-1999 to an average of 33 per year in the 2000s, largely affecting the
214 continental shelf and slope waters. The causality of this regime shift have been hypothesized
215 to a number of possible factors such as changes of large scale winds, changes in internal
216 Rossby Radius of the GS itself, more baroclinic/barotropic instability resulting from a change
217 of stratification (Gangopadhyay et al., 2019).

218 In contrast to the GS, the Kuroshio is well known for its bimodality in behavior. The
219 underlying topography of these two western boundary currents are very different, so is their
220 realization while following the coast and after separating at mid-latitude. This is clearly
221 demonstrated by the comparison panels in Figure 1 from Hu et al., (2015). Seager and
222 Simpson (2016) argued that it is the difference of set up of the Kuroshio and the complicated
223 topography over which the Kuroshio flows that makes the Kuroshio behave differently than
224 does the Gulf Stream in response to similar warming trends in both basins.

225 While most of World Ocean has a rising trend in SST, the response in the chlorophyll *a* is
226 found to be mixed (O'Brien et al., 2017). The Patagonian Shelf LME (PLME) region
227 (dominated by the Malvinas Current) has shown a 0.08°C SST increase during the period
228 1982-2006 with alarmingly increasing chlorophyll *a* concentration of 78.33%. There has been
229 no reports of long-term increasing transport of the Malvinas current or long-term changes in
230 the along-slope winds to support the conventional wisdom of increased upwelling leading to
231 this increase (Marrari et al., 2017). An alternate hypothesis would be changes in physiology
232 and composition of the phytoplankton community in a warming context (Behrenfeld et al.,
233 2016).

234 In contrast, the South Brazil LME (SBLME) region experienced much stronger warming of
235 about 0.53°C during the same period (1982-2006), and the chlorophyll concentration was
236 regionally dispersed with no significant trend. Such anomalous behavior of this WBC region
237 require further studies to identify important other drivers of climate change.

238 There is also increasing evidence now that the Agulhas Current is undergoing changes which
239 could have profound effects on local climate and marine and coastal ecosystems off South
240 Africa (Augustyn et al., 2017). SST in the Agulhas Current system (including on the East
241 Coast shelf) have increased significantly, most noticeably in the retroflexion area (Rouault et
242 al., 2012). This has in turn caused an increase in the transport of warm, high-salinity water
243 into the Atlantic Ocean (Loveday et al., 2014).

244 The East Australian Current region is one of the major global hotspots for climate change
245 (Hobday and Pecl, 2014), which experienced increasing water temperatures at a rate of
246 several (3-4) times that of the global average (Ridgeway, 2007; Hill et al., 2008). Nearshore
247 waters in this region are projected to warm by $>1^{\circ}\text{C}$ between 1990 and 2060 (Oliver et al.,
248 2015). Large increases of sea level rise and salinity are also predicted (Hobday and Lough,
249 2011).

250 The productivity of the Humboldt Current System (HCS) and the Oxygen Minimum Zone
251 (OMZ) in South Pacific is strongly effected by El Niño and La Niña events. During an El
252 Niño event, the thermocline and upper region of the OMZ deepen to greater than 600 m. This
253 causes a loss of nitrogen and decrease in export of carbon. El Niño also causes poleward
254 currents to increase in velocity. During non-El Niño years, productivity is very high due to
255 the high nutrient contents, nitrogen recycling through processes such as denitrification,
256 increased carbon export, and re-mineralization. On a longer timescale, Belkin (2009) have
257 shown how the linear SST trend in the HCS showed an increase of 0.41°C from 1957 to
258 2006; while the trend is negative (-0.10°C) between 1982-2006. So, for last 25 years, the
259 HCS region is actually cooling! (See Figure 2, Belkin (2009)).

260 Table 1 lists WBC and EBC, squid species associated with these boundary currents, climatic
261 factors and the oceanographic settings of these currents along with biophysical parameters of
262 interest. While significant knowledge about the impact of variability and change of boundary
263 currents on squid species exist (Dawe et al., 2007; Kidokoro et al., 2010; Sakurai et al.,
264 2013), and highlighted in the next sections, the impacts of long-term and projected climatic
265 changes of the boundary currents on these species are unknown and form current areas of
266 research.

267

268 **Environmental variability and climate change impacts on cephalopods**

269 *Sensitivity of cephalopods to environmental variability and climate change*

270 It is generally recognised that cephalopods, especially oceanic squid, are sensitive to
271 environmental variability, as a consequence of their “live fast, die young” life history (e.g.
272 Summers, 1985; O’Dor, 1992; Hanlon & Messenger, 1996; Jackson & O’Dor, 2001; Pierce et
273 al., 2008; Rodhouse et al., 2014). Their fast growth and rapid maturation, fuelled by a high
274 metabolic rate and high food consumption, contribute to individual sensitivity to
275 environmental changes (e.g. changes in seawater temperature and food availability). In many
276 cephalopod species, their short lives and the seasonality of the lifecycles ((e.g. a defined
277 spawning season) result in non-overlapping annual generations and, consequently, no
278 “buffer” of older animals to maintain populations in years of poor recruitment. They are,
279 thus, in some respects typical *r*-selected species and have been described as pioneer species
280 which can move in and replace overfished teleosts (Caddy & Rodhouse, 1998; Balguerias et

281 al., 2000; Jackson & O’Dor, 2001; Hunsicker et al., 2010) and which generally appear to be
282 increasing in abundance globally (Caddy & Rodhouse, 1998; Doubleday et al., 2016). It
283 should be noted that many cephalopods of shelf waters have relatively low fecundity, show
284 complex behaviour and apparently high intelligence (Mather and Dickel, 2017), and some
285 species display what could be characterised as parental care (i.e. egg-guarding) (Robison et
286 al., 2014). These are all characteristics more typical of *k*-selected species.

287 In practice the concept of non-overlapping generations is misleading. These “annual” squid
288 species do not put all their eggs in one basket. They can display variable phenology and
289 lifespan and, in particular, spawn and hatch over an extended time-period, such that several
290 “microcohorts” may be identified within an annual “cohort”. This seems to reflect a
291 combination of phenotypic plasticity and the fact that animals hatching at different times of
292 year experience different environmental conditions, such that they follow different
293 trajectories and growth and maturation. The outcomes may be counterintuitive: for example,
294 animals hatching during conditions that favour faster growth may mature at a smaller size
295 than those which grew more slowly (e.g. Boyle et al., 1995). Understanding these responses
296 is crucial to forecasting squid abundance and fishery catches.

297 *How are squid affected by environmental variability and climate change; what is the*
298 *evidence?*

299 Effects of environmental variability and climate change on the status of cephalopod
300 populations are expected to follow from effects on individual behaviour, physiology and
301 health, and their consequences for growth, maturation, fecundity and survival (see Table 2 for
302 examples), as mediated by the life history characteristics and phenotypic plasticity of the
303 species in the context of the topographic and oceanographic characteristics of their
304 environment and the structure and function of the ecosystem in which they are embedded.
305 For example, high metabolic rates likely confer high sensitivity to changes in temperature and
306 dissolved oxygen concentration and hugely variable growth rates can result in phenological
307 mismatches between ontogenetic changes in energetic requirements and prey catching
308 abilities of the squid on the one hand and seasonal prey availability on the other.

309 In order to understand year-to-year variation or predict the effects of climate change, there is
310 a need, first, to understand the squid-environment relationships which apply during their
311 annual life cycle. O’Dor and Webber (1991) observed that squid can adjust their reproductive
312 strategies depending on climatic conditions, noting that cooler waters typically result in larger
313 body sizes, later reproduction and higher fecundity in squid. He also quotes Summers (1985)
314 who described cephalopods as “fickle”, presumably a comment on the high variability seen in
315 squid abundance and /or life history characteristics.

316 It is evident that squid abundance, as well as distribution, fluctuates widely from year to year,
317 furthermore that there is wide variation in life cycle phenology and in individual growth
318 rates, both within and between years. The most obvious evidence of the ubiquity of
319 environmental effects on cephalopods comes from the wide year to year fluctuations in
320 catches (and in abundance) of fished species, often but not always apparently independent of
321 fishing pressure. Shifts in distribution may also be revealed from fishery catches. Where
322 cephalopod catches are recorded during fishery surveys (usually trawling surveys), year-to-
323 year variation in distribution and abundance is also apparent, along with shifts in life-cycle
324 phenology, e.g. the timing of migration (Sims et al., 2001).

325 Statistical support for environmental effects on abundance comes in the form of simple
326 correlations, and statistical models of varying sophistication, including linear regression,
327 through generalised additive models and time-series models (e.g. Fogarty, 1989; Pierce &
328 Boyle, 2003; Zuur & Pierce, 2004; Doubleday et al., 2016). Aside from issues of statistical
329 model formulation (e.g. non-normally distributed data, large numbers of zero values, non-
330 linear relationships and the existence of temporal and spatial autocorrelation) and sampling
331 methodology (e.g. limited knowledge of gear selectivity, changes in survey boats and gears
332 over the years, changes in the way fishery data are recorded), such evidence is mainly
333 empirical. Even if based on a sound hypothesis, correlation does not prove causation.

334 Studies under controlled conditions, normally in captivity, have demonstrated a range of
335 environmental effects on cephalopod growth, maturation and survival (not always in squid
336 since octopus and cuttlefish tend to be easier to maintain in captivity) and, importantly,
337 helped to elucidate the mechanisms. For example, multiple studies have confirmed the effects
338 of seawater temperature on growth, maturation, fecundity and adult body size as well as
339 embryonic developmental abnormalities and mortality at various life history stages (e.g.
340 Forsythe, 1993; Sakurai et al., 1996). For squid, studies have documented the adverse effects
341 of carbon dioxide concentration on blood oxygen transport (Pörtner & Reipschläger, 1996), a
342 50% reduction in lifespan associated with high seawater temperatures (Takahara et al., 2016),
343 and adverse effects of low salinity on embryonic development and survival (Furukawa and
344 Sakurai, 2008). Increases in ocean acidification affect statolith microstructure of paralarvae,
345 which consequent adverse effects on their behaviour (Kaplan et al., 2013) and ocean noise
346 such (e.g. arising from seismic surveys) can lead to mortality (M. André et al 2011). In
347 addition, several studies of climate change impacts on cephalopods were based on
348 mathematical models (e.g., J. André et al., 2010), incorporating empirical data and published
349 climate change projections.

350

351 Important inferences about environmental relationships also arise from the detailed
352 description of life-cycle biology and migrations, for example studies on *Illex argentinus* and
353 *Doryteuthis gahi* in the southwest Atlantic and *Loligo reynaudii* in South Africa (Sauer et al.,
354 1997). Indeed, the successful application of “depletion models” for stock assessment of *Illex*
355 *argentinus* in the Falkland Islands followed from an understanding of the migrations and
356 stock structure of this species in the southwest Atlantic. Based on this knowledge it is also
357 makes clear that sustainable fishing of *Illex argentinus* cannot be achieved by effective
358 management of Falkland Islands and Argentinean fisheries alone and a major factor in
359 collapse of catches in 2016 is likely to have been high and unregulated catches in the High
360 Seas.

361 Additional evidence of environmental effects arises from talking to fishers. For example,
362 trawl fishers in Scotland state that squid avoid turbid water, behaviour which will thus affect
363 catches without necessarily impacting on abundance (Hastie et al., 2009).

364 Oceanographic parameters are to different degrees influenced by both natural and
365 anthropogenic processes. Even under directional climate change, the expected nature and
366 direction of change of many of these parameters will continue to vary in space and time (for
367 example under the el Niño-la Niña cycle), with patterns contingent on changes in air
368 circulation, rainfall patterns, ocean currents and human activities. For example, Wei et al.
369 (2018) found that the ENSO events played crucial effects on the incubating and feeding

370 conditions of the winter cohort of Japanese squid during the spawning season and ultimately
371 affected its abundance.

372 Increased atmospheric CO₂ concentrations will feed through into lower ocean pH and
373 reduced surface oxygen concentrations, an effect exacerbated by warming (Rosa & Siebel,
374 2008), and weakening of the Gulf Stream is expected to result in Northwest Europe becoming
375 colder. While salinity may generally decline slightly due to influx of glacial meltwater into
376 the oceans, in coastal areas salinity is driven by river outflow and will in turn depend on
377 rainfall patterns – thus more irregular and more extreme fluctuation in salinity could be an
378 outcome.

379

380 **Progress on relating squid population dynamics to environmental variability**

381

382 As previously mentioned, during the past thirty years, there have been many publications
383 about relationships between various environmental processes and variables (but mainly
384 involving sea surface temperature because it is the most available environmental variable)
385 and the population dynamics of ommastrephid squid (Bakun and Csirke, 1998; Brodziak and
386 Hendrickson, 1999; Dawe et al. 2007; Waluda et al., 1999, 2001a, b; Sakurai et al., 2000).
387 These studies have shown that the effects of environmental factors on squid population
388 dynamics vary depending on ontogenetic phase. Furthermore, the studies have also shown
389 that in order to make any progress in understanding climate effects on these squid stocks, the
390 complex intraspecific structure of squid populations must to be investigated, as well as the
391 role of different intraspecific groups in the fishery and their specific population dynamics
392 (Carvalho and Nigmatullin, 1998).

393

394 *Environmental effects on the spawning grounds*

395

396 Pelagic egg masses of ommastrephid squid are protected from pelagic zooplankton, hence
397 their survival depends on environmental conditions. Squid actively choose the most
398 appropriate locations to extrude their egg masses (Puneeta et al. 2017). Although the
399 temperature tolerance for normal embryonic development is quite wide (e.g., between 4 and
400 20°C for *Illex* squid (Hendrickson and Holmes, 2004)), the optimum temperature range is
401 usually narrower (~ 3°C). Therefore, embryonic survival rates depend on ambient water
402 temperatures which vary depending on transport of the pelagic egg masses by currents,
403 whereas recruitment levels depend on the optimal conditions (i.e. temperature that drive
404 growth rate), on spatial extent of the spawning grounds and spawning stock size, and on the
405 food supplies available to young squid, and on whether there is much predation. For example,
406 the spawner-recruitment relationship for *Todarodes pacificus* changes with environmental
407 conditions; in particular, decadal or inter-decadal changes are assumed to influence the stock
408 status (Kidokoro et al., 2014). A shift in the location of the spawning grounds may affect the
409 survival rate of paralarvae which will translate to a change in recruitment abundance. An
410 analysis of variability in the size and location of *Todarodes pacificus* spawning areas during
411 27 spawning seasons (September–April 1978–2006) in the Sea of Japan and East China Sea
412 showed that changes in importance of the local spawning grounds around Kyushu Island and
413 decreased size of the main spawning ground in the East China Sea during the winter
414 spawning period were associated with a decrease in catches of this squid by both the Japanese
415 and Korean fleets. The decrease in size of the spawning grounds may act as an obstacle for
416 adult squid to reach the most southern grounds, or adversely affect abundance of paralarvae
417 that might not be able to survive the early stages of the feeding migrations (Rosa et al., 2011).

418 Another study also showed that that when the winter-spawning areas in the East China Sea
419 shrank, recruitment decreased during a cool oceanographic regime. During a warm regime,
420 the autumn and winter-spawning areas increased in size and overlapped in the Sea of Japan
421 and East China Sea, resulting in increased recruitment (Sakurai et al., 2000).

422

423 Correlations between sea surface temperatures of the spawning grounds during spawning and
424 recruitment abundance during the subsequent fishing season were studied for *Illex*
425 *argentinus*. Waluda et al. (1999) found that cool sea surface temperatures were associated
426 with higher catches, but at warm temperatures, the relationship with catches was not as
427 strong. The authors hypothesized that the relationship may either be a result of the direct
428 impact of temperature on embryonic and paralarval survival at the spawning grounds or it
429 could be a proxy for oceanographic conditions that favor other oceanographic mechanisms
430 such as the retention of planktonic egg masses and paralarvae within the spawning grounds.
431 Water mass dynamics in the spawning grounds may also important, as in the case of egg
432 mass transport to unfavorable areas (e.g., farther offshore in the case of slope-spawning
433 squid). In summary, additional studies are needed to test the hypotheses suggested for the
434 mechanisms by which sea surface temperature affects the various life history stages on the
435 spawning grounds.

436

437

438 *Environmental effects on paralarvae*

439

440 Temperature has a crucial impact on paralarval survival, growth rate, and timing of
441 reproduction (Rodhouse et al., 2014). Paralarval and small juvenile phases are the most
442 vulnerable phases in the ontogeny of squid. Apart from predation, both ontogenetic phases
443 are also affected by water temperatures. Based on the results of laboratory studies, Forsythe
444 (1993) hypothesized that a 1°C increase in ambient water temperature in juveniles could
445 strongly affect squid growth rates at later ontogenetic phases and could almost double the size
446 of adult squid. Arkhipkin et al. (2000) analyzing statolith of Mediterranean populations of
447 *Illex coindetii* found that juvenile growth rates during summer were faster than winter growth
448 rates.

449 The paralarvae and small juveniles of *Illex argentinus* may develop in quasi-stationary warm
450 eddies and meanders of the Brazil Current before these oceanographic features conjoin with
451 cold water from the Falkland Current at the Confluence Zone over the Continental Slope of
452 Argentina at about 42-45°S. These northern eddies and meanders (coming from north of the
453 Confluence zone) move westward to the Patagonian Shelf bringing juveniles to their feeding
454 grounds (Fu, 2009; Mason et al., 2017). Sometimes warm eddies move across of the
455 Confluence Zone and then move farther in a south-east direction to the open waters of the
456 South Atlantic and may even reach the Polar Front near South Georgia. Obviously, the
457 recruitment of *Illex argentinus* that appeared to be in those eddies will be lost and will not
458 become part of the population on the shelf (Parfeniuk et al., 1992).

459

460

461 *Environmental effects on migrations to and within the feeding grounds*

462

463 Juveniles and subadults actively move to and within their feeding grounds. For example, *Illex*
464 *argentinus* greater than 20 cm mantle length have relatively low natural mortality (Arkhipkin
465 and Roa, 2005). Their presence and abundance in specific areas of their feeding grounds
466 mainly depends on availability of the optimum environment. Immature subadults of *Illex*
467 *argentinus* migrate and inhabit shelf water mass on the Patagonian Shelf with relatively high

468 sea surface temperatures ($>10^{\circ}\text{C}$). In cold years (like 2002) sea surface temperatures are
 469 lower ($8\text{-}9^{\circ}\text{C}$) than those preferred by the squid in the southern part of the Patagonian Shelf
 470 around the Falkland Islands. In these cold years, immature squid of the winter spawning
 471 cohort may not migrate further south to cold parts of the Patagonian Shelf, staying mainly to
 472 the north of 45°S . Obviously, at these times catches of *Illex argentinus* around the Falkland
 473 Islands are very low (Rodhouse et al., 2013).

474

475 *Illex illecebrosus* abundance was found to be positively related to a favorable oceanographic
 476 regime associated with a negative North Atlantic Oscillation (NAO) index (weak winter
 477 northwesterly winds), high water temperatures off Newfoundland and a southward shift in the
 478 position of the Gulf Stream and the boundary between the shelf waters and the offshore slope
 479 waters. In addition, increased meandering of the Gulf Stream appears to promote increased
 480 abundance, probably through enhanced shoreward transport of squid (Dawe et al., 2007).

481

482 Ambient water temperature can also act as a proxy determining indirectly the extent of squid
 483 migrations within the species ranges. It has been demonstrated that water temperatures
 484 encountered between 3rd and 6th months of ontogenesis in the Pacific jumbo squid, *Dosidicus*
 485 *gigas*, had the strongest negative effect on age (Arkhipkin et al. 2015a). Together with
 486 weaker but significant negative effect coming from temperatures encountered during early
 487 life (1st-3rd months) and later ontogenesis (7th and 8th months), these water temperature
 488 parameters (with other environmental factors such as food availability) were important
 489 determinants of whether an individual had a 1 year life cycle (matures early and attains small
 490 sizes), or 1.5-2 year life cycle (delayed maturation and large size). Larger squid usually
 491 migrate much longer distances and may appear in unusually high latitude areas like southern
 492 parts of Chile in the southern Pacific and southern Alaska in the northern Pacific (Arkhipkin
 493 et al., 2015a). Migrations of such large (50-70 cm ML) and voracious predators to high
 494 latitudes have a profound negative impact on some long-lived fish that inhabit this area
 495 (Fields et al., 2014).

496

497

498 *Environmental effects on migrations to the spawning grounds*

499

500 Adult and mature squid take advantage of certain environmental conditions when migrating
 501 from the feeding grounds to the spawning grounds. In *Illex argentinus* the outflows of less
 502 dense Patagonian Shelf Waters over the slope may act as proxies for determining the
 503 pathways of migrations from the shelf to the slope. During maturation, *Illex argentinus*
 504 buoyancy doesn't change much, but the females are slightly more buoyant with depth.
 505 Subsequent movement of mature individuals to denser Sub-Antarctic Superficial waters
 506 located at deeper depths (600-700 m) enable them to approach near-neutral buoyancy and
 507 therefore facilitate the lengthy northward pre-spawning migrations (Arkhipkin et al., 2015b).
 508 Sudden environmental changes can lead to the appearance of migrating, pre-spawning squid
 509 in the areas where they have not previously been observed. For example, in the austral
 510 autumn of 2015, warmer than usual shelf waters spread to a typical areas on the Patagonian
 511 Shelf that are usually occupied by colder waters of Subantarctic origin. This situation caused
 512 changes in migration routes of the pre-spawning winter group of *Illex argentinus* which led
 513 them to unexpectedly appear in the nursery and feeding grounds of the Patagonian longfin
 514 squid, *Doryteuthis gahi*. This resulted in dispersal of commercial aggregations of *Doryteuthis*
 515 *gahi* and caused an early closure of the summer-autumn fishing season. Stomach analysis of
 516 *Illex argentinus* collected in the nursery grounds showed that they mainly preyed on
 517 *Doryteuthis gahi* adults from the summer cohort, but also fed on small individuals that

518 normally recruit to the fishery during the following winter. Consequently, recruitment to the
519 winter fishery was very low and the fishery had to be closed a month early. All of these
520 impacts were initially triggered by atypical water temperatures which produced a domino
521 effect that led to changes in the distribution and migration routes of ommastrephid squid
522 (Arkhipkin et al., 2016).

523

524 In summary, environmental variables influence the distribution, abundance, passive transport
525 and active migration routes of ommastrephid squid, and the impact of an environmental
526 factors may vary between ontogenetic phases. For example, ambient water temperatures may
527 affect growth and survival rates of embryos within pelagic egg masses and in planktonic
528 paralarvae and small juveniles. On the contrary, large subadult and adult squid actively
529 choose their habitats based on optimum environmental conditions, and their distribution and
530 migration routes are influenced by water temperature. A mechanistic model development of
531 squid-environment relationships should be able to provide a better basis for forecasting
532 compared to statistical models of environment-abundance relationships in time-series that are
533 a poor basis for forecasting and such empirical relationships are often impermanent: they
534 work until they don't (Solow, 2002).

535

536

537 **Which environmental variables suitable for squid ecological-fishery forecasting?**

538

539 Habitat variables or niche factors relevant for squid include sea water parameters such as
540 temperature (e.g. Forsythe & Hanlon, 1989; Grist & Des Clers, 1998; Villanueva, 2000;
541 André et al., 2010) salinity (e.g. Furukawa & Sakurai, 2008, Wei et al., 2018), carbon dioxide
542 concentration (and acidity) (e.g. Rosa & Siebel, 2008), Chlorophyll *a* concentration (Wei et
543 al. 2018) and nutrient concentrations (likely mainly due to their effects on productivity),
544 dissolved oxygen concentration, turbidity (Roberts & Sauer, 1994), the strength and direction
545 of ocean currents (e.g. Coelho, 1985), Shelf-Slope Front (SSF) (e.g. Dawe et al., 2007),
546 phases of the North Atlantic Oscillation (NAO) (e.g. Sims et al., 2001, Pierce & Boyle, 2003)
547 and El Niño and La Niña events (e.g. Bjorkstedt et al., 2011, Hoving et al., 2013) (Table 3
548 summarize a selection of environmental variables that may “control” squid population
549 dynamics).

550 The present paper considers the marine environment in relation to the annual squid life cycle.
551 O'Dor (1998) noted that, globally, most squid (especially Ommastrephid nerito-oceanic
552 squid) fisheries are associated with powerful boundary currents as previously mentioned, and
553 squid phenology is adapted to take advantage of annual production events such as blooms.
554 Under this view the interactions between squid and the marine environment can be viewed as
555 operating in four dimensions (the three dimensions of space and the one dimension of time)
556 and at a range of spatial and temporal scales as the animals pass through egg, paralarval,
557 juvenile and adult stages, and interacting with life history and behaviour. A key difference
558 between loliginids and ommastrephids is that the former attaches their eggs to the substrate
559 while eggs of the latter float free. Behaviours such as vertical migration can determine
560 whether squid are retained in an area or carried away with the currents. Certainly, it should
561 not be assumed that cephalopods are passive users of current systems. In Northwest Spain,
562 cephalopod paralarvae seem to be able to use current systems in order to avoid (most species)
563 or undertake (Octopus) movements between inshore and offshore areas (Roura et al., 2016).
564 Recent observations in the Mediterranean Sea evidenced correlations between *Illex coindetii*

565 life cycle and several environmental parameters (Jereb et al., 2017), even though the
566 mechanisms underlying these correlations are unclear. Recruitment seems to be affected by
567 environmental conditions (Jereb et al., 2001, Ceriola et al., 2007, Lefkaditou et al., 2008,
568 Cuccu et al., 2009) because of egg masses properties and main basic requirements of
569 hatchlings.

570 Currents provide transport for squid as well as delivering nutrients to support productivity
571 (e.g. in upwelling systems). Thus, it has been speculated that veined squid *Loligo forbesii*
572 may be transported around to the east coast of Scotland by the North Atlantic current
573 (Waluda & Pierce, 1998), although the likely positive effects of this current on water
574 temperature and food supply are of course also relevant. Mesoscale oceanographic features
575 such as fronts can provide important feeding areas and helping to determine the temperature.
576 Upwelling of cold waters rich in nutrients was considered to influence positively the
577 abundance of *Illex coindetii* in the Gulf of Cadiz (Silva et al., 2011), but it is not necessarily
578 related to areas preferred for spawning (Lefkaditou et al., 2008).

579 Additional direct anthropic pressures include fishing mortality (target and bycatch, the latter
580 including cephalopod eggs laid on fixed nets and traps (Arkley et al., 1996; Dunn, 1999) and
581 damage to sea bed habitats (aside from damage to eggs already laid, such damage may affect
582 opportunities for egg attachment in those species which require a suitable substrate.

583

584 **Challenges and opportunities for forecasting squid stock size**

585

586 Forecasting squid stock size requires knowledge of the species biology and life history,
587 population dynamics, environmental drivers of stock size and fishery characteristics, and how
588 forecast results will feed into the stock assessment and satisfy the needs of fishery managers.
589 Background stock-specific information pertinent to forecast modeling of squid species
590 reviewed in this paper is summarized in Table 4.

591 There are several challenges for developing stock size forecast models for squid stocks. For
592 example, stock assessments of squid are often data-poor, primarily because their short, often
593 sub-annual lifespans require intensive data collection (e.g., abundance, size composition and
594 maturity data) to generate accurate stock size estimates over short timescales (e.g., weekly)
595 and large spatial scales. Ommastrephid squid stocks are especially difficult to assess and
596 manage because their broad geographic ranges which often occur between the maritime
597 jurisdictional boundaries of two or more countries and/or in international waters and may or
598 may not be managed by a Regional Fisheries Management Organization (RFMO). For
599 example, the *Illex illecebrosus* stock migrates between U.S and Canadian waters, as well as
600 international waters managed by the Northwest Atlantic Fisheries Organization (NAFO). The
601 northern stock component is managed by Canada and NAFO and the southern stock
602 component is managed by the U.S.

603

604 Research survey data for stock size estimation are often lacking for squid stocks or stock size
605 is estimated from multispecies survey data for which the survey timing and/or gear types may
606 not be ideal for catching squid (e.g., the survey may occur when the species is migrating on
607 or off the continental shelf and/or the survey is not synoptic across the geographic range of
608 the stock, and in some cases there is no ideal timing because recruitment extends over an
609 extended period). As a result, standardized fishery catch-per-unit-effort (CPUE) indices are
610 often utilized to estimate stock size. The validity of the assumption that CPUE data are

611 proportional to stock size must be examined prior to the use of such data. Pre-recruits (i.e.,
612 small squid that have not recruited to the fishery) are often difficult to quantify either because
613 they are found outside the survey sampling area and/or they are not fully available to the
614 survey or fishing gear. Due to (sometimes) year-round recruitment and the highly migratory
615 nature of squid stocks, the model assumption of a “closed population”, relative to the
616 temporal and spatial scales of the stock being assessed, is generally not met and therefore
617 estimates of immigration into and emigration from the fishing grounds are required. An
618 additional challenge is the estimation of cohort-specific natural mortality rates for these
619 semelparous species. Natural mortality increases with age for mature individuals
620 (Hendrickson and Hart, 2006) and cannibalism and high predation rates must also be taken
621 into account.

622

623 As a result of the high variability of within-year cohort abundance and year-round
624 recruitment, which is highly influenced by environmental factors, an adaptive method of
625 assessing squid stock size is necessary to capitalize on the maximum yield of a squid resource
626 without impacting its sustainability (Arkhipkin et al., 2020). Adaptive assessment methods
627 allow fishery managers to adjust squid fishing effort or catch quotas prior to and/or during
628 each fishing season (effort controls are preferred over catch quotas to reduce the potential for
629 recruitment overfishing of squid stocks) in order to reduce the potential for foregone yield
630 during high abundance years and recruitment overfishing during low abundance years. One
631 type of adaptive method for assessing a squid stock involves expensive, high intensity, real-
632 time sampling of catch, effort and size-at-maturity data, by fleet. This method also requires a
633 pre-fishery stock size estimate derived from research survey data and in-season stock size
634 estimates, generally based on fleet-specific estimates of CPUE computed over short time
635 steps (e.g., weekly). For most squid stocks however, the resources necessary to collect and
636 analyze such datasets are not available. Instead, pre-fishery stock size forecast models that
637 incorporate environmental predictors of stock size, may be a useful alternative method. A
638 pre-requisite for the development of a squid forecast model is the establishment of predictive
639 relationships between stock size and its environmental drivers. This may be achievable using
640 empirical statistical relationships or a mechanistic mathematical model based on a genuine
641 understanding of the underlying mechanisms.

642

643 Mechanistic models tend to be more complex, requiring more knowledge and often contain
644 more variables. These models may be more informative for understanding population
645 dynamics, though more complex models do not necessarily provide more precise predictions
646 (Payne et al., 2017). Rather, with respect to forecast performance, mechanism-free models
647 that rely on emergent statistical properties of the data are recommended for conducting short-
648 term projections (Schindler and Hilborn, 2015). Even if empirical models that link
649 environmental and catch data provide very useful information, their explanatory capacity is
650 limited (Hobday and Hartog, 2014). On the other hand, mechanistic models might not make
651 accurate predictions initially, but they are expected to continue improving (Urban et al.,
652 2016). As global environmental conditions continue to change in an unprecedented fashion
653 as previously mentioned, mechanistic models may provide us with more detailed and
654 accurate insights into the impacts of climate change on marine species and ecosystems than
655 statistical models constrained by past observations. Annual forecasting from historical data
656 can be particularly problematic for species like squid which are characterized by “boom-bust”
657 abundance trends. The numerous relationships between recruitment and environmental
658 variables that have broken down when updated with new data (Myers, 1998) are evidence of
659 this need for new approaches to forecasting. It is possible that as climate change forces

660 ecosystems to enter unprecedented territory, the effectiveness of existing metrics may
 661 change. The validity of the relationships used in forecasting models and the mechanisms
 662 represented or missed in the stock assessment procedures that are continuously operating
 663 need to be examined. Testing the relevance and influence of various processes on squid
 664 recruitment is a necessity. Comparisons among species and oceanographic conditions are also
 665 necessary for constructing robust prediction and forecast models (Nigmatullin 2004a).

666

667 *Examples of squid ecological-fishery forecasting*

668 In the late 1990s, approaches were developed to predicting *Illex argentinus* fishing state on
 669 using satellite data on SST values in the areas of winter-spawning stock (about 70-85% of
 670 total annual catch) spawning and formation of its recruitment of winter-spawning population
 671 as a predictor (Laptikhovsky et al., 2001; Nigmatullin et al., 2004b). They made it possible to
 672 assess the possible situation in the fishery with an advance time of about 5-8 months. It was
 673 found that if the lower the SST values observed in the area of recruitment formation (open
 674 waters between 35-36°S) in July-November of a given year, there would be better the fishing
 675 situation in the fishing ground of High Sea on 45-47°S outside the EEZ of Argentina in
 676 February-June next year. These predictive relationships between SST values in the
 677 recruitment formation area abundance of commercial stock during the fishing season were
 678 quite "workable" for following periods - 1983-1994 ($r=0.6-0.7$) and 1994-2003 ($r=0.7-0.8$)
 679 (Laptikhovsky et al., 2001; Nigmatullin et al., 2004b). But, since 2004 the natural process of
 680 long-term dynamics of the abundance of winter-spawning stock in connection with the future
 681 growth of the fishing pressure no longer hold (Nigmatullin, 2017, 2019), and these links were
 682 not effective for forecasting ($r=0.28-0.48$).

683 Long-term forecasts are based on analysis of relationships between long-term data sets on
 684 catches and environmental factors, including especially subsurface water circulations.
 685 Froerman (1981, 1985, 1986), a pioneer in the development of long-term forecasts, used the
 686 relationship between the Gulf Stream dynamics and squid recruitment abundance in relation
 687 to the shortfin squid *Illex illecebrosus* in the Northwestern Atlantic.

688 In the Japanese stock assessment of *Todarodes pacificus*, the Allowable Biological Catch
 689 (ABC), which is usually set as Total Allowable Catch (TAC), is calculated based on F_{med} (the
 690 fishing mortality rate that will allow the spawning stock biomass to replace itself with new
 691 recruits 50 percent of the time, given the observed recruitment history) (Caddy and Mahon,
 692 1995) and the forecasted abundance of the seasonal stocks, which are both estimated from
 693 their respective Spawner-Recruit (S-R) relationships (Kidokoro, 2009).

694 The S-R relationship of *Todarodes pacificus* is assumed to change with changes in
 695 environmental conditions; in particular, decadal or inter-decadal changes in sea surface
 696 temperature (SST; Kidokoro, 2009). The parameters used in the S-R relationship were
 697 estimated from data collected since 1990 following an apparent regime shift. The S-R
 698 parameters are revised accordingly when the SST regime changes. Consequently, in order to
 699 forecast recruitment and estimate Biological Reference Points (BRPs), it is important to
 700 understand if the current SST regime is favorable or not.

701 For the Japanese flying squid (*Todarodes pacificus*), the spawning grounds (Goto, 2002),
 702 migration routes (Nakata, 1993; Kidokoro et al., 2010), and body size (Takayanagi, 1993)
 703 were all changed coincide with regime shift. In particular, a shift in the spawning grounds is

704 considered as the most important factor to affect the survival rate of paralarvae accounting for
705 the changing stock size. To detect regime shifts and forecast recruits and stock size,
706 oceanographic indices (Pacific Decadal Oscillation (PDO), SST) and the changes in
707 ecological traits are used in the *Todarodes pacificus* stock assessment method (Kidokoro,
708 2009). This approach may also be useful and feasible for the stock assessment and
709 management of other ommastrephid squids affected by regime shifts.

710 In the current Japanese stock assessment, it is reported that regime shifts have not occurred
711 yet, while the current regime for *Todarodes pacificus* is viewed as “favorable” (Kaga et al.,
712 2018; Kubota et al., 2018). In recent years (2015-2017) however, the stock size and catch of
713 *Todarodes pacificus* declined abruptly around the Japanese waters. And to verify which
714 variables are useful to understand regime shift have occurred or not a new data have analyzed
715 (Table 5).

716 Contradictory to the current stock assessment reports, some biological, fisheries and
717 oceanographic variables suggest regime shifts have occurred in recent years and current
718 environmental condition may be unfavorable for *Todarodes pacificus*. Despite this, clear
719 shifts in spawning grounds have not been detected yet (Kaga et al., 2018; Kubota et al.,
720 2018). It made scientists and stakeholders hesitant to declare regime shifts have occurred in
721 recent years and to change management decisions. These experiences to detect regime shifts
722 in the Japanese *Todarodes pacificus* stock assessment procedure may be a good example to
723 improve forecasting methods for squids and especially Ommastrephids squid species.

724 **Current status and recommendations for developing future squid ecological-fishery** 725 **forecasting**

726 As previously mentioned, there are many publications that describe how environmental
727 conditions relate to variability in stock size and recruitment of ommastrephid squids. In
728 recent studies, the lifespan of ommastrephid squids is suggested to be rather flexible
729 (Takahara et al. 2016), which may influence how squid stocks are managed. Squid
730 management plans need to incorporate lifecycle parameters concerning environmental
731 conditions (e.g. suitable water temperature ranges for various life history stages). Based on
732 these parameters, mechanistic models could be developed and used to examine the key
733 oceanographic variables that influence stock size and recruitment variability.

734 On the other hand, some commonalities in the recruitment processes exist at least for
735 ommastrephid squids (Figure 2). Examination of the commonalities between species and
736 regions, by comparing the results of various types of forecast models, would be useful in this
737 regard. These mechanistically derived commonalities can then be tested with models and
738 calibrated against observed trends to improve model predictions. Global cooperation between
739 cephalopod scientists who assess ommastrephid and loliginid squid stocks is essential to
740 optimize this approach.

741 The relationship between environmental variables and stock size had been identified for most
742 of the squid species considered in this study (Figure 1), and because of gaps in the forecast
743 model input data forecasting was only conducted on a few stocks, (i.e., those that are data-
744 rich and well-studied). In order to increase the number of squid stocks for which forecasting
745 is conducted in the future a roadmap is proposed to improve squid forecasts products (Figure
746 3). As for the adoption of specific forecasting methods to the operational fishery management

747 process, what is important in forecasting is the relationship between needs, feasibility and
748 clarify to what extent the present prediction level is (Payne et al., 2017, Jacox et al., 2020).
749 The ultimate success of a forecast is determined by whether it is used by end-users.

750

751 **Conclusions and Recommendations**

752 The above review and analysis of the current knowledge of the effects of climate change on
753 squid species shed the light on the urgent need for further research and development of tools
754 to support squid fisheries management. Ecological-fishery forecasting squid has emerged as a
755 potential tool that could help decision-makers and managers and stakeholders plan for the
756 future, make informed decisions regarding alternative management choices and take
757 appropriate actions to sustainably manage squid resources. Despite substantial progress made
758 in developing ecological-fishery forecasting, a diversity of challenges remains to develop and
759 operationalize forecasts products to inform squid sustainable fisheries management. Although
760 each of the response variables and associated forecast products described above has their own
761 strengths and weaknesses, there are also clear trends and commonalities between them. The
762 following highlight the main directions identified to advance the squid species ecological-
763 fishery forecasting:

764

765 1. Ideally, squid fisheries need a forecasting system that includes all time-scales
766 of forecasting, and especially short - and medium-terms. The effective management
767 of squid fishing with their highly variable stock dynamics is possible only with a
768 working set of predictive models providing forecasts at multiple time-scales.

769

770 2. More research is needed to move these forecasts products toward more realistic
771 mechanistic representations of distribution such as explicitly incorporating movement
772 and life-cycle with the limitations imposed by habitat. Also exploiting the situations
773 where predictive skill is needed and available and linking them to fishery
774 management systems may lead to valuable new ecological fishery forecast products.

775

776 3. Implementation of the Roadmap (Figure 3) through development of demonstration
777 projects that are feasible and end-users driven could help to develop guidelines to
778 adopt and operationalize the ecological-fishery forecasting approaches to inform
779 sustainable squid fisheries management.

780

781 4. More efforts are needed to adopt and communicate the forecasts products to
782 stakeholders in term of the limitations and assumptions, its associated levels of
783 uncertainty to minimize misuse.

784

785 5. Finally continuous active engagement and collaboration with end-users and
786 stakeholders (fishing industry, fishery and market managers etc.) in designing
787 forecasts that can effectively support their specific decision-making requirements is
788 critical.

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Figures

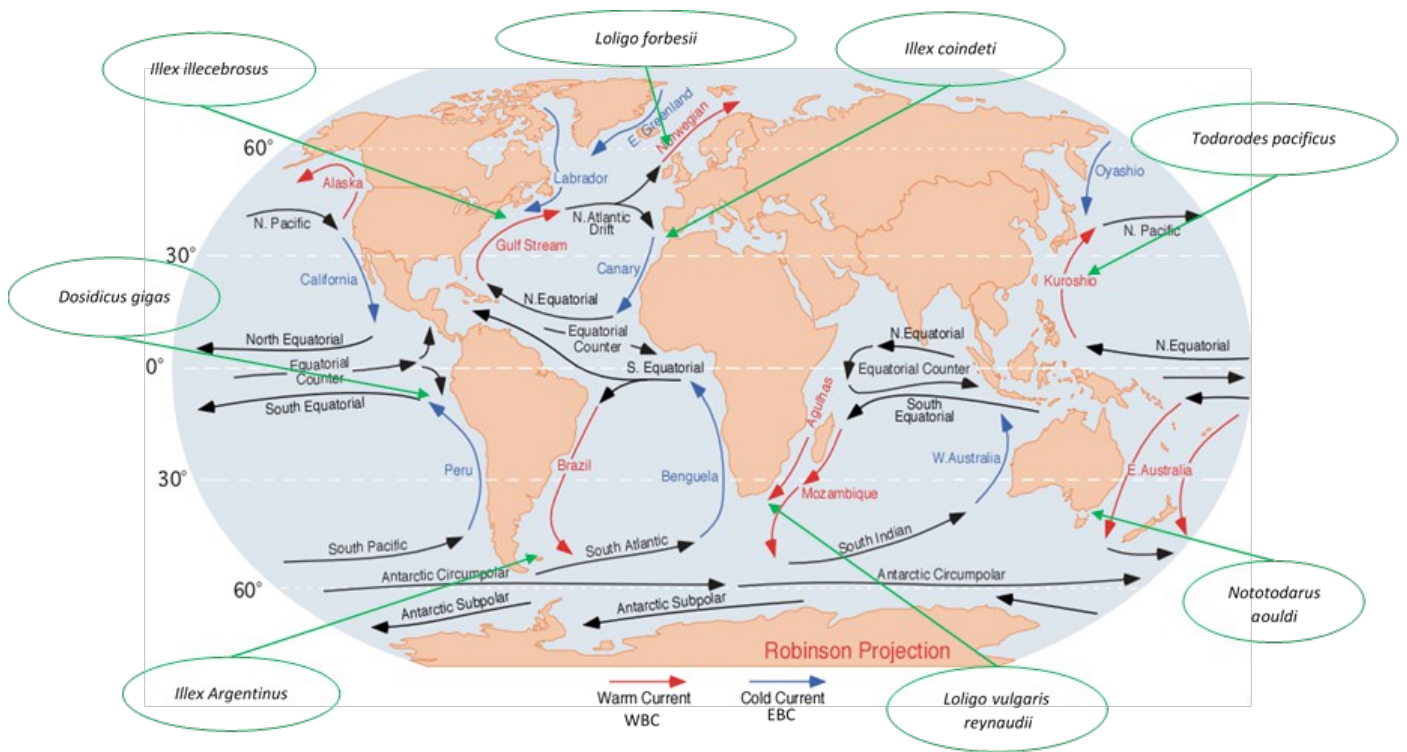


Figure 1. The Western Boundary Currents (WBCs) and Eastern Boundary Currents (EBCs) around the world and their supported squid populations. The base map and major currents of the world map Credit: Pidwirny (2006).

Figure 2. Schematic diagram of the inter-regional and inter-species relationships among the stock dynamics and forecasting models of ommastrephid squids.

Figure 3. Roadmap to progress ecological-fishery forecast models to support squid fisheries management decisions.

1 **Tables**

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3 Table 1. Boundary currents, squid species and climatic connections.

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Current System	Species	Oceanic region	Boundary current	Other important physical features	Oceanic index	Climatic index and/or atmospheric influence	Limiting / control: physical and/or biogeochemical variables
WBCs	<i>Illex illecebrosus</i>	Western North Atlantic	Gulf Stream System	Shelf-Slope Front (SSF), Warm Core Rings (WCR)	Gulf Stream North Wall (GSNW) Index, Atlantic Meredional Overturning Circulation	North Atlantic Oscillation (NAO), Icelandic Low	Bottom temperature, salinity
	<i>Todarodes pacificus</i>	Western North Pacific	Tsushima and Kuroshio currents	South China Sea, Sea of Japan	KSE (Kuroshio Extension) Bimodality	ENSO (El Nino Southern Oscillation), PDO (Pacific Decadal Oscillation), Indonesian Throughflow	Bottom temperature;
	<i>Illex argentinus</i>	Western South Atlantic	Brazil-and Falklands current		SAMOC (South Atlantic Meredional Overturning Circulation)	Wind-stress curl	Chlorophyll
	<i>Nototodarus gouldi</i>	Western South Pacific	East Australian current				
EBCs	<i>Illex coindetii</i>	Eastern North Atlantic	North Atlantic	Eddies,		NAO, Winds	

		Atlantic, Mediterranean	Current near Iberian Peninsula, Canary and Benguela currents	currents, upwelling			
	<i>Dosidicus gigas</i>	Eastern Pacific	Humboldt Current, CCS (California Current System)	Northern California to Southern Chile	Upwelling	ENSO	Oxygen Minimum Zone (Ocean Acidification (OA))
Open/ Mixed System	<i>Loligo forbesii</i>	Atlantic Ocean (Seas around Europe)	Open/Island Chains	Celtic Sea, Red Sea, GS/NAC (North Atlantic Current)	AMOC, Subpolar Gyre Index	NAO, Arctic Oscillation	Salinity
	<i>Loligo reynaudii</i>	South Indian/South Atlantic (South African Waters)	Agulhas Current (WBC) + Benguela Current (EBC)	Wind driven upwelling	Indian Ocean Overturning Circulation	Wind-stress Curl	OA

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Table 2. Examples of environmental effects on cephalopods, based on field observations, captive studies and mathematical models

Effects	Driver	Species, Location,	Reference
Increased growth rate (1 °C increase resulting in a 2% increase in growth rate (Body weight/day) and a three-fold difference in weight at 90 days post-hatching.	Temperature	<i>Loligo forbesii</i> , in captivity	Forsythe & Hanlon (1989)
Higher proportion of hatching area with favourable SST leads to higher abundance	Temperature	<i>Illex argentinus</i> , Falkland Islands	Waluda et al. (2001a)
Earlier migration at higher SST	Temperature	<i>Loligo forbesii</i> , English Channel	Sims et al. (2001)
Modified population trajectories showing complex nonlinear dynamics, mediated by effects of incubation time, survivorship and phenology	Temperature	<i>Octopus pallidus</i> , model-based	J. Andre et al. (2010)
Extended distribution by several hundred kilometres pole-wards, associated with the southwards extension of the warm East Australian Current along south-eastern Australia	Temperature	<i>Octopus tetricus</i> , Australia	Ramos et al. (In Press)
Incubation period decreased from 320 days at 10 °C to 60 days at 26 °C. Normal embryo development occurred between 14 and 22.2 °C and embryo survival drops sharply outside this range	Temperature	<i>Todarodes pacificus</i> , laboratory	Sakurai et al. (1996)
The lifespan may be halved under conditions of higher than normal temperatures. Higher temperatures also seemed to favour faster growth rates with earlier maturation – but also reduced survival.	Temperature	<i>Todarodes pacificus</i> , laboratory	Takahara et al. (2017)
Low salinity produces abnormal embryonic development and reduced survival	Salinity	<i>Todarodes sagittatus</i> , in captivity	Furukawa & Sakurai (2008)
Ocean acidification will substantially depress metabolic rates and activity levels, an effect exacerbated by high. Temperature. Reduced aerobic and locomotory scope in warm, high-CO ₂ surface waters will impair predator–prey interactions with cascading consequences for growth, reproduction, and survival.	[CO ₂]	<i>Dosidicus gigas</i>	Rosa & Siebel (2008)
High turbidity forces spawners to lay eggs in deeper waters, reducing squid	Turbidity	<i>Loligo reynaudii</i> ,	Roberts & Sauer

availability to jig fishing		South Africa	(1994)
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8 Table 3. Examples of environmental variables that have been shown to affect squid population dynamics, including Sea Surface Temperature
 9 (SST), Bottom Seawater Temperature (BST), Southern Oscillation Index (SOI), North Atlantic Oscillation index (NAO), index of the position of
 10 the Shelf-Slope Front (SSF), Trans Polar Index (TPI), and Multivariate ENSO Index (MEI).

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Species	Predictor variable	Response variable	Time scale	Spatial scale	Life history	Reference
<i>Loligo forbesii</i>	BST	LPUE	Monthly, Annual	British Isles	Adult	Pierce et al., 1998;
	SST previous winter	LPUE, Landings	Monthly, Annual	British Isles	Adult	Robin and Denis, 1999; Pierce & Boyle, 2003
	NAO	LPUE, CPUE	Monthly, Annual	Northern North Sea	Adult	Pierce & Boyle, 2003; Pierce et al. 2005; Zuur & Pierce, 2004
<i>Loligo reynaudii</i>	SST	Biomass, catch	Annual	South Africa	Adult	Roberts, 2005; Sauer et al. 2013
	Oxygen BST SST	Abundance	Monthly	South Africa	Adult Eggs	Roberts & Sauer, 1994;
	SOI	Catch	Annual	South Africa	Adult	Roberts & Sauer, 1994
<i>Illex illecebrosus</i>	BST, NAO, SSF	Catch	Annual	NW Atlantic	Adults	Dawe et al. 2000, 2007
<i>Illex</i>	SST, SOI, TPI	CPUE	Annual	Falkland	Adults	Waluda et al., 1999;

<i>argentinus</i>				Islands		2004; Laptikhovsky et al., 2001
	Thermal gradients	Vessel number, CPUE	Weekly	Falkland Islands	Adults	Waluda et al., 2001a
<i>Todarodes pacificus</i>	SST	Recruitment	Annual	S Sea of Japan	Adults	Isoda et al., 2005
	SST	Catch	Annual	S Sea of Japan	Juveniles	Kidokoro et al., 2014
	Temperature at spawning grounds	Catches Migration patterns	Annual Interdecadal	Japan	Paralarvae Adults	Sakurai et al., 2000; Rosa et al., 2011
<i>Dosidicus gigas</i>	Niño 1+2	CPUE	Annual	Peru	Adults	Waluda et al., 2006; Rosa et al., 2013
	SST, Niño 1+2	Catch, Fishing grounds	Monthly, Interdecadal	Peru	Adults	Paulino et al 2016
	Niño 3.4	Habitat suitability index	Monthly, Annual	Peru		Yu et al., 2016
	SOI, TPI	CPUE	Annual	Peru	Adults	Waluda et al., 2004
	SST, Chl, Wind, MEI	Catch	Monthly, Annual, Interannual	Gulf of California	Adults	Robinson et al., 2013, 2016
	Primary productivity	Catch	Monthly	Western Baja	Adults	Medellín-Ortiz et al. (2016)

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Table 4. Stock-specific information pertinent to forecast modeling stock size of squid species reviewed in this paper. Y= Yes, N=No

Species	Unknown portion of stock located beyond fishing grounds?	Fishery locations	Fishery region (period)	Are fished cohorts identified from age data?	Age range of mated females (A ₅₀)	Fishing gear types
<i>Illex illecebrosus</i> ^a	Y		USA, shelf/slope (June-Sept/Oct)	Only the winter cohort	115-215 days (144 days)	Bottom trawl
	Y	East Coast USA	CA, Scotian Shelf and slope (June-Sept/Oct)	N	Mated females are rare	no fishery since 1999
	Y	Canada and international waters	CA, inshore Newfoundland (July-Nov)	Y	Mated females are rare	Hand-reel jig
	Y		International, beyond Canada Exclusive Economic Zone (EEZ)	N	Mated females are rare	Midwater and bottom trawl
<i>Illex argentinus</i>	Y	Falklands, Argentina,	International waters (Dec-May/June)	Y		Automated jigging machines
	Y	Brazil and international waters	Falklands shelf (Feb-May/June)			

	Y		Within Argentine EEZ (Feb to June-Sept)		
		l waters			
<i>Todarodes</i>	Y	Japan and	Sea of Japan (winter)		Jig, trawl,
<i>pacificus</i>	Y	Korea	Sea of Japan and Pacific Ocean (fall)	Y	set net and purse seine

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Species	Pre-fishery stock size estimates	In-season stock size estimates	Age/size composition	Maturity data	Known environmental drivers of stock size?	Known spawning location and timing?	Is the stock assessed and managed?	Existing biological reference points?
<i>Illex illecebrosus</i>	USA spring Bottom Trawl (BT) survey	CPUE	Catch and survey length data	Only for winter cohort	Only during fall for cohort on US shelf	Only for spring and summer spawners	Y, irregularly by USA	Y
	Canada spring BT survey	None	Catch length data	Catch data	N	N	N, not managed by CA	N
	Canada spring BT survey	CPUE	None	None	N	N	Y, annually by NAFO	Y, biomass only
<i>Illex argentinus</i>	None	None	None	None			N	
	Falklands BT survey	CPUE	Catch and survey length data	Catch and survey data	Y	Y	Y, annually	Y, biomass only
	None	None	None	None			N	
<i>Todarodes pacificus</i>	Fall cohort: research jig survey.	CPUE	Catch and survey length data	Catch and survey data	Y	Y	Y, annually	Y
	Winter cohort: jig fishery CPUE	CPUE	Catch and survey length	Catch and survey data	Y	Y	Y, annually	Y
	Jig and parlarvae	CPUE	Catch and survey length	Catch and survey data	Y	Y	Y, annually	Y

surveys

data

30 Table 4 (cont.)

Species	Unknown portion of stock located beyond fishing grounds?	Fishery locations	Fishery region (period)	Are fished cohorts identified from age data?	Age range of mated females (A_{50})	Fishing gear types
<i>Nototodarus gouldi</i>		Australia, State and Commonwealth	South East Australian shelf (Autumn in Bass Strait and Western Victoria and summer in Southern Tasmania) and year round over much of southern Australia			Jig Trawl
<i>Dosidicus gigas</i>	Y	Mexico, Chile, Peru and international waters		Y		
<i>Loligo</i>		United	Inshore	N		Bottom trawl

<i>forbesii</i>	Kingdom	(fall), offshore (summer)		
<i>Loligo reynaudii</i>	South Africa		Y	Hand Jig

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Hendrickson (2004) and H

Table 4
(cont.)
Sources of
Available
Data

Species	Pre-fishery stock size estimates	In-season stock size estimates	Age/size composition	Maturity data	Known environmental drivers of stock size?	Known spawning location and timing?	Is the stock assessed and managed?	Existing biological reference points?
<i>Nototodarus gouldi</i>	None	CPUE		None				N
<i>Dosidicus</i>		CPUE			Y	Y		Y, biomass

<i>gigas</i>						only
<i>Loligo forbesii</i>	CPUE	Landings and survey length data	Y	Y		N
<i>Loligo reynaudii</i>	CPUE	Catch and survey length data	Y	Y		

31 Table 5. Regime shift detection methods in the Japanese *Todarodes pacificus* stock assessment
 32 and results using recent data
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Variables	Reference	1970s-1980s	1990s-2000s	Recent years (2015-2017)	regime shift
(1) Physical conditions					
Pacific Decadal Oscillation (PDO)	Sakurai et al. (2000) Yatsu et al.(2013)	Positive anomaly	Basically, negative anomaly	Positive anomaly	Positive
SST in the East China Sea in Winter	Rosa et al. (2011) Sakurai et al. (2000)	Negative anomaly	Positive anomaly	Negative anomaly in 2015	-
(2) Ecological traits					
Stock structure	Kidokoro(2009) Nakata(1993) Takayanagi(1993)	Mainly autumn cohort	Autumn and winter cohorts		Under monitoring
Spawning ground	Sakurai et al(2000) Goto (2002) Kidokoro et al. (2010; Rosa et al. (2011) Sakurai et al(2000)	Southwest Japan Sea	Expand to East china Sea		Under monitoring
Migration pattern	Kidokoro et al. (2010) Nakata(1993)	In the Sea of japan and local migration along pacific side	Wide, counter clock wise around the Japanese Islands.		Under monitoring
(3) Trends in stock size of other species					
Pacific sardine (<i>Sardinops melanostictus</i>)	Kidokoro(2009) Yatsu et al (2013)	Increased to high level	Decreased to low level	Increasing	Positive

Japanese anchovy (<i>Engraulis japonicas</i>)	Yatsu et al. (2013)	Decreased to low level	Increase d to high level	Decreasing	Positive
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