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REVIEW

Ecological-Fishery Forecasting of Squid Stock Dynamics under Climate Variability and Change: Review, Challenges, and Recommendations

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ABSTRACT
Globally, cephalopods support large industrial-scale fisheries and small-scale to partly large-scale local artisanal fisheries. They are of increasing economic importance as evidenced by the rapid rise in their global landings from 1950 to 2014. Cephalopods are sensitive to environmental variability and climate change and many if not all species show wide fluctuations in abundance. This is most evident in ommastrephid nerito-oceanic squid since their life cycle is associated with boundary currents that are changing with climate change. The inter-annual variability in catch presents challenges for fishers and managers due to the 'boom-or-bust' nature of the fishery. A key barrier to rational management of squid fisheries is the low level of development of fishery forecasting. Despite substantial progress made in relating squid population dynamics to environmental variability and change, several challenges remain to develop forecast products to support squid fisheries management. Ideally, squid fisheries management needs a forecasting system that includes all time-scales of forecasting, and especially short - and medium-terms forecasts. The present overview first provides current knowledge of the effects of climate change and variability on squid population dynamics, challenges and opportunities to advance ecological-fishery forecast products, and finally a roadmap is proposed for future development of forecasts products to support squid sustainable fisheries management. As for the adoption of specific forecasting methods to the squid fishery management process, what is important is the relationship between needs, feasibility, and the ultimate success of a forecast will be determined by whether it is used by end-users.

KEYWORDS
Cephalopods; squid fisheries management; climate change; stock size; ecological-fishery forecasting

Introduction

Cephalopods support both large industrial scale fisheries and numerous artisanal fisheries, mostly small-scale but some partly large-scale. They are of increasing economic importance as evidenced by the rapid rise in their global landings over recent decades (Arkhipkin, Rodhouse, et al., 2015, Doubleday et al. 2016, and Sauer et al., 2019). World cephalopod catch increased almost 10-fold over the last six decades from around 0.50 million tons annually in 1950 to a peak of 4.85 million tonnes in 2014 (FAO. 2020). In particular, squid catch increased worldwide. This has highlighted the fact that squid abundance is highly

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variable (Rodhouse 2005; Arkhipkin, Rodhouse, et al., 2015; Doubleday et al. 2016), which leads to unpredictable inter-annual and long-term fluctuations in catch and market prices, and significant volatility in the world market for squids, particularly for the well-documented *Illex argentinus* squid market (Harte et al. 2018). The unpredictable nature of squid catch volumes recently highlighted by a dramatic fall in world cephalopod catch in 2016, by over 1.1 million tons, mainly due to an 85% drop in the catch of *Illex argentinus* but also reflecting reduced landings of *Dosidicus gigas* and *Todarodes pacificus* (FAO. 2020). Large fluctuations in squid abundance and the current lack of robust ecological and fishery forecasting also have large economic consequences.

Cephalopods play an important role in ecosystems and are a key component of food webs, providing a vital link from smaller invertebrates and fish to marine megafauna, birds, and humans (Boyle and Rodhouse 2005, de la Chesnais et al. 2019). Cephalopods possess a number of unique biological and ecological characteristics that set them apart from many other commercially exploited marine species. As a result of their short lifespan and semelparous reproduction, they have fast growth rates, with high consumption rates and conversion efficiencies. Cephalopods in general and squid in particular have a high fecundities, with Loliginid squids usually producing fewer eggs than ommastrephids. These characteristics have adapted squid to become ecological opportunists that can rapidly exploit favorable environmental conditions, resulting in recruitment and abundance levels with high inter-annual variability (Rodhouse et al., 2014). This is probably why there is usually no clear relationship between spawning stock abundance and subsequent recruitment (Pierce and Guerra, 1994; Basson et al. 1996; Uozumi 1998). The combination of these characteristics makes it difficult to discriminate between the effects of climate variability on squid populations and those of fishing mortality. In addition, the role of density dependent intraspecific competition in regulating population size is poorly known, although it may be noted that cannibalism is common in squids (Ibáñez and Keyl 2010).

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

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

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

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

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

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

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

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

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

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

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

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

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

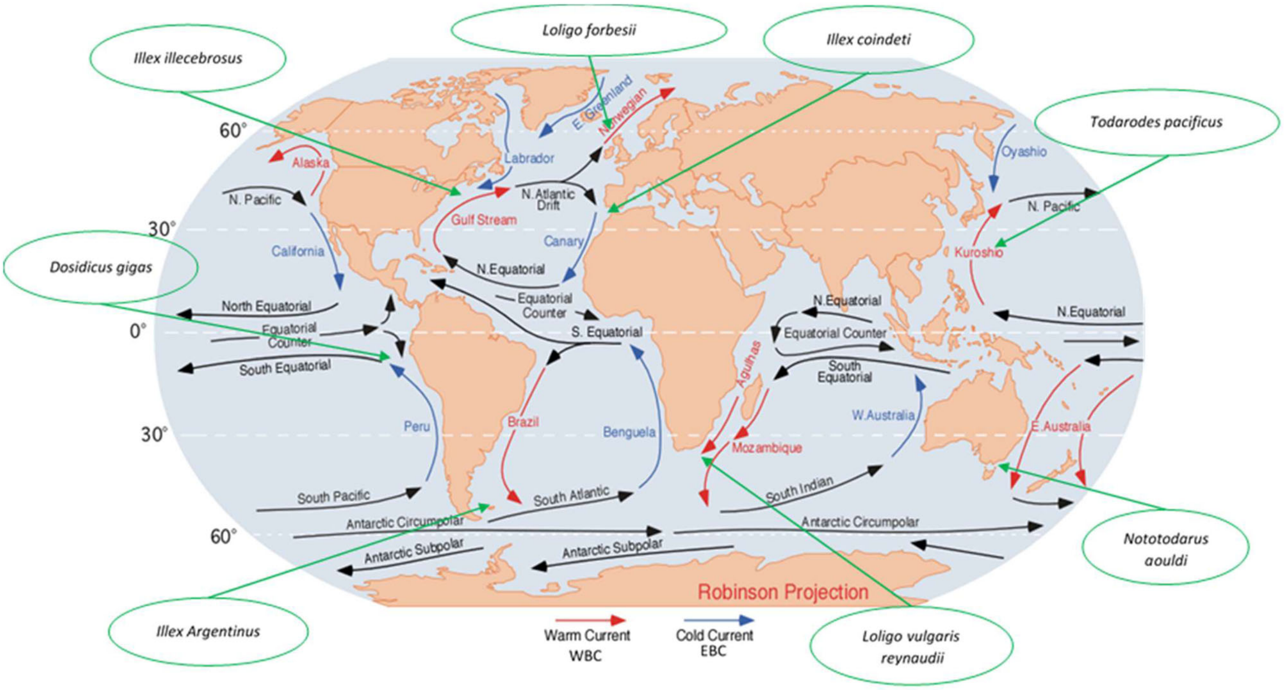

Figure 1. The Western Boundary Currents (WBCs) and Eastern Boundary Currents (EBCs) around the world and their supported squid populations. The base map and major currents of the world map Credit: Pidwirny (2006).

circulation to poleward movement and intensification of the WBC.

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

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

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

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

There is also increasing evidence now that the Agulhas Current is undergoing changes which could have profound effects on local climate and marine and coastal ecosystems off South Africa (Augustyn et al. 2017). SST in the Agulhas Current system

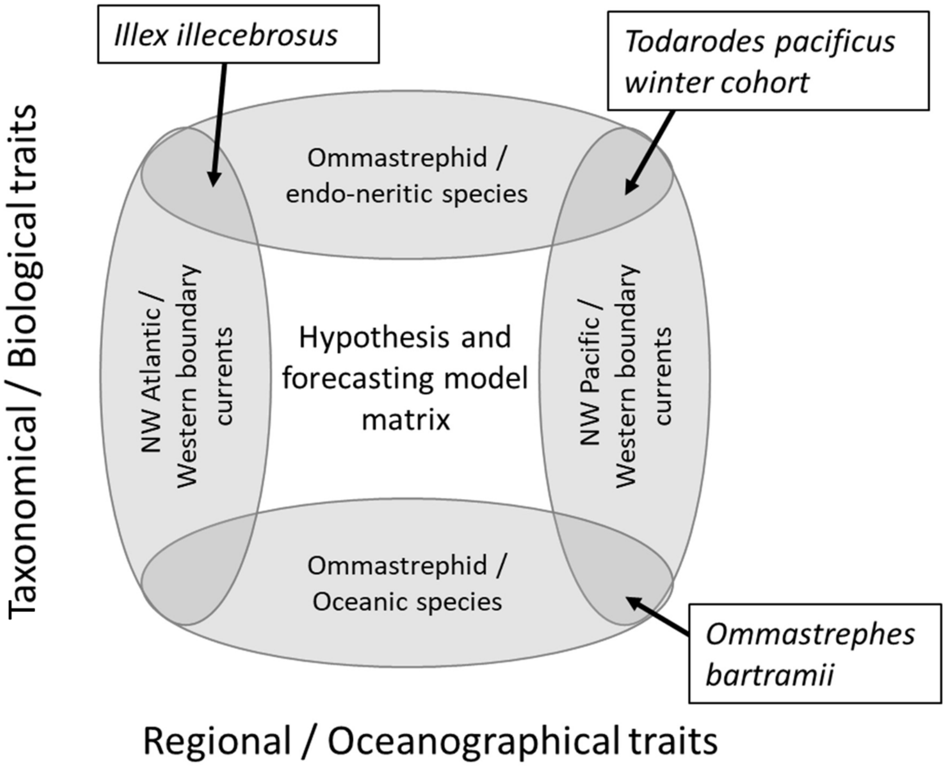

Figure 2. Schematic diagram of the inter-regional and inter-species relationships among the stock dynamics and forecasting models of ommastrephid squids.

(including on the East Coast shelf) have increased significantly, most noticeably in the retroflection area (Rouault et al. 2009). This has in turn caused an increase in the transport of warm, high-salinity water into the Atlantic Ocean (Durgadoo et al. 2013; Loveday et al. 2014).

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

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

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

Environmental variability and climate change impacts on cephalopods

Sensitivity of cephalopods to environmental variability and climate change

It is generally recognized that cephalopods, especially oceanic squid, are sensitive to environmental variability, as a consequence of their "live fast, die young" life history (e.g. Summers 1985; O'Dor 1992; Hanlon & Messenger, 1996; Jackson and O'Dor 2001; Pierce

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

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	*Illex illecebrosus*	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
	Todarodes pacificus	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;
	Illex argentinus	Western South Atlantic	Brazil-and Falklands current		SAMOC (South Atlantic Meredional Overturning Circulation)	Wind-stress curl	Chlorophyll
	Nototodarus gouldi	Western South Pacific	East Australian current				
EBCs	*Illex coindetii*	Eastern North Atlantic, Mediterranean	North Atlantic Current near Iberian Peninsula, Canary and Benguela currents	Eddies, currents, upwelling		NAO, Winds	
	Dosidicus gigas	Eastern Pacific	Humboldt Current, CCS (California Current System)	Northern California to Southern Chile	Upwelling	ENSO	Oxygen Minimum Zone (Ocean Acidification (OA))
Open/ Mixed System	*Loligo forbesii*	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
	Loligo reynaudii	South Indian/South Atlantic (South African Waters)	Agulhas Current (WBC) + Benguela Current (EBC)	Wind driven upwelling	Indian Ocean Overturning Circulation	Wind-stress Curl	OA

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	*Loligo forbesii*, in captivity	Forsythe and Hanlon (1989)
Higher proportion of hatching area with favorable SST leads to higher abundance	Temperature	*Illex argentinus*, Falkland Islands	Waluda et al. (2001)
Earlier migration at higher SST	Temperature	*Loligo forbesii*, English Channel	Sims et al. (2001)
Modified population trajectories showing complex nonlinear dynamics, mediated by effects of incubation time, survivorship and phenology	Temperature	*Octopus pallidus*, model-based	J. André, et al. (2010)
Extended distribution by several hundred kilometers pole-wards, associated with the southwards extension of the warm East Australian Current along south-eastern Australia	Temperature	*Octopus tetricus*, 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	*Todarodes pacificus*, laboratory	Sakurai et al. (1996)
The lifespan may be halved under conditions of higher than normal temperatures. Higher temperatures also seemed to favor faster growth rates with earlier maturation – but also reduced survival.	Temperature	*Todarodes pacificus*, laboratory	Takahara et al. (2017)
Low salinity produces abnormal embryonic development and reduced survival	Salinity	*Todarodes sagittatus*, in captivity	Furukawa and 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-CO2 surface waters will impair predator–prey interactions with cascading consequences for growth, reproduction, and survival.	$[CO_2]$	*Dosidicus gigas*	Rosa and Seibel (2008)
High turbidity forces spawners to lay eggs in deeper waters, reducing squid availability to jig fishing	Turbidity	*Loligo reynaudii*, South Africa	Roberts and Sauer (1994)

et al. 2008; Rodhouse et al., 2014). Their fast growth and rapid maturation, fueled by a high metabolic rate and high food consumption, contribute to individual sensitivity to environmental changes (e.g. changes in seawater temperature and food availability). In many cephalopod species, their short lives and the seasonality of the lifecycles ((e.g. a defined spawning season) result in non-overlapping annual generations and, consequently, no “buffer” of older animals to maintain populations in years of poor recruitment. They are, thus, in some respects typical *r*-selected species and have been described as pioneer species which can move in and replace overfished teleosts (Caddy and Rodhouse 1998; Balguerias et al., 2000; Jackson and O’Dor 2001; Hunsicker et al. 2010) and which generally appear to be increasing in abundance globally (Caddy and Rodhouse 1998; Doubleday et al. 2016). It should be noted that many cephalopods of shelf waters have relatively low fecundity, show complex behavior and apparently high intelligence (Mather and Dickel 2017), and some species display what could be characterized as parental care (i.e. egg-guarding) (Robison et al. 2014). These are all characteristics more typical of *k*- selected species.

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

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

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

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

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

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

Studies under controlled conditions, normally in captivity, have demonstrated a range of environmental effects on cephalopod growth, maturation and survival (not always in squid since octopus and cuttlefish tend to be easier to maintain in captivity) and, importantly, helped to elucidate the mechanisms. For example, multiple studies have confirmed the effects of seawater temperature on growth, maturation, fecundity and adult body size as well as embryonic developmental abnormalities and mortality at various life history stages (e.g. Forsythe et al. 1993; Sakurai et al. 1996). For squid, studies have documented the adverse effects of carbon dioxide concentration on blood oxygen transport (Pörtner & Reipschläger, 1996), a 50% reduction in lifespan associated with high seawater temperatures (Takahara et al. 2017), and adverse effects of low salinity on embryonic development and survival (Furukawa and Sakurai 2008). Increases in ocean acidification affect statolith microstructure of paralarvae, which consequent adverse effects on their behavior (Kaplan et al. 2013) and ocean noise such (e.g. arising from seismic surveys) can lead to mortality (M. André et al 2011). In addition, several studies of climate change impacts on cephalopods were based on mathematical models (e.g., J. André et al. 2010), incorporating empirical data and published climate change projections.

Important inferences about environmental relationships also arise from the detailed description of life-cycle biology and migrations, for example studies on *Illex argentinus* and *Doryteuthis gahi* in the southwest Atlantic and *Loligo reynaudii* in South Africa (Sauer et al. 1991; Sauer et al. 1997). Indeed, the successful application of "depletion models" for stock assessment of *Illex argentinus* in the Falkland Islands followed from an understanding of the migrations and stock structure of this species in the southwest Atlantic. Based on this knowledge it is also makes clear that sustainable fishing of *Illex argentinus* cannot be achieved by effective management of Falkland Islands and Argentinean fisheries alone and a major factor in collapse of catches in 2016 is likely to have been high and unregulated catches in the High Seas.

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

Oceanographic parameters are to different degrees influenced by both natural and anthropogenic processes. Even under directional climate change, the expected nature and direction of change of many of these parameters will continue to vary in space and time (for example under the el Niño-la Niña cycle), with patterns contingent on changes in air circulation, rainfall patterns, ocean currents and human activities. For example, Wei et al. (2018) found that the ENSO events played crucial effects on the incubating and feeding conditions of the winter cohort of Japanese squid during the spawning season and ultimately affected its abundance.

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

Progress on relating squid population dynamics to environmental variability

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

Environmental effects on the spawning grounds

Pelagic egg masses of ommastrephid squid are protected from pelagic zooplankton, hence their survival depends on environmental conditions. Squid actively choose the most appropriate locations to extrude their egg masses (Puneeta et al. 2017). Although the temperature tolerance for normal embryonic development is quite wide (e.g., between 4 and 20 °C for *Illex illecebrosus* squid (Hendrickson and Holmes 2004)), the optimum temperature range is usually narrower (∼ 3 °C). Therefore, embryonic survival rates depend on ambient water temperatures which vary depending on transport of the pelagic egg masses by currents, whereas recruitment levels depend on the optimal conditions (i.e. temperature that drive growth rate), on spatial extent of the spawning grounds and spawning stock size, and on the food supplies available to young squid, and on whether there is much predation. For example, the spawner-recruitment relationship for *Todarodes pacificus* changes with environmental conditions; in particular, decadal or inter-decadal changes are assumed to influence the stock status (Kidokoro et al. 2014). A shift in the location of the spawning grounds may affect the survival rate of paralarvae which will translate to a change in recruitment abundance. An analysis of variability in the size and location of *Todarodes pacificus* spawning areas during 27 spawning seasons (September–April 1978–2006) in the Sea of Japan and East China Sea showed that changes in importance of the local spawning grounds around Kyushu Island and decreased size of the main spawning ground in the East China Sea during the winter spawning period were associated with a decrease in catches of this squid by both the Japanese and Korean fleets. The decrease in size of the spawning grounds may act as an obstacle for adult squid to reach the most southern grounds, or adversely affect abundance of paralarvae that might not be able to survive the early stages of the feeding migrations (Rosa et al. 2011). Another study also showed that that when the winter-spawning areas in the East China Sea shrank, recruitment decreased during a cool oceanographic regime. During a warm regime, the autumn and winter-spawning areas increased in size and overlapped in the Sea of Japan and East China Sea, resulting in increased recruitment (Sakurai et al. 2000).

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

Environmental effects on paralarvae

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

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

Environmental effects on migrations to and within the feeding grounds

Juveniles and subadults actively move to and within their feeding grounds. For example, *Illex argentinus* greater than 20 cm mantle length have relatively low natural mortality (Arkhipkin and Roa, 2005). Their presence and abundance in specific areas of their feeding grounds mainly depends on availability of the optimum environment. Immature subadults of *Illex argentinus* migrate and inhabit shelf water mass on the Patagonian Shelf with relatively high sea surface temperatures (>10 °C). In cold years (like 2002) sea surface temperatures are lower (8-9 °C) than those preferred by the squid in the southern part of the Patagonian Shelf around the Falkland Islands. In these cold years, immature squid of the winter spawning cohort may not migrate further south to cold parts of the Patagonian Shelf, staying mainly to the north of 45°S. Obviously, at these times catches of *Illex argentinus* around the Falkland Islands are very low (Rodhouse et al. 2013).

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

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

Environmental effects on migrations to the spawning grounds

Adult and mature squid take advantage of certain environmental conditions when migrating from the feeding grounds to the spawning grounds. In *Illex argentinus* the outflows of less dense Patagonian Shelf Waters over the slope may act as proxies for determining the pathways of migrations from the shelf to the slope. During maturation, *Illex argentinus* buoyancy doesn't change much, but the females are slightly more buoyant with depth. Subsequent movement of mature individuals to denser Sub-Antarctic Superficial waters located at deeper depths (600-700 m) enable them to approach near-neutral buoyancy and therefore facilitate the lengthy northward pre-spawning migrations (Arkhipkin, Rodhouse, et al., 2015).

Sudden environmental changes can lead to the appearance of migrating, pre-spawning squid in the areas where they have not previously been observed. For example, in the austral autumn of 2015, warmer than usual shelf waters spread to a typical areas on the Patagonian Shelf that are usually occupied by colder waters of Subantarctic origin. This situation caused changes in migration routes of the pre-spawning winter group of *Illex argentinus* which led them to unexpectedly appear in the nursery and feeding grounds of the Patagonian longfin squid, *Doryteuthis gahi*. This resulted in dispersal of commercial aggregations of *Doryteuthis gahi* and caused an early closure of the summer-autumn fishing season. Stomach analysis of *Illex argentinus* collected in the nursery grounds showed that they mainly preyed on *Doryteuthis gahi* adults from the summer cohort, but also fed on small individuals that normally recruit to the fishery during the following winter. Consequently, recruitment to the winter fishery was very low and the fishery had to be closed a month early. All of these impacts were initially triggered by atypical water temperatures which produced a domino effect that led to changes in the distribution and migration routes of ommastrephid squid (Arkhipkin et al., 2016).

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

Which environmental variables suitable for squid ecological-fishery forecasting?

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

The present paper considers the marine environment in relation to the annual squid life cycle. O'Dor (1998) noted that, globally, most squid (especially Ommastrephid nerito-oceanic squid) fisheries are associated with powerful boundary currents as previously mentioned, and squid phenology is adapted to take advantage of annual production events such as blooms. Under this view the interactions between squid and the marine environment can be viewed as operating in four dimensions (the three dimensions of space and the one dimension of time) and at a range of spatial and temporal scales as the animals pass through egg, paralarval, juvenile and adult stages, and interacting with life history and behavior. A key difference between loliginids and ommastrephids is that the former attaches their eggs to the substrate while eggs of the latter float free. Behaviors such as vertical migration can determine whether squid are retained in an area or carried away with the currents. Certainly, it should not be assumed that cephalopods are passive users of current systems. In Northwest Spain, cephalopod paralarvae seem to be able to use current systems in order to avoid (most species) or undertake (Octopus) movements between inshore and

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

Species	Predictor variable	Response variable	Time scale	Spatial scale	Life history	Reference
Loligo forbesii	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 and Boyle 2003
	NAO	LPUE, CPUE	Monthly, Annual	Northern North Sea	Adult	Pierce and Boyle 2003; Pierce et al. 2005; Zuur and Pierce 2004
Loligo reynaudii	SST	Biomass, catch	Annual	South Africa	Adult	Roberts, 2005; Sauer et al. 2013
	Oxygen BST SST	Abundance	Monthly	South Africa	Adult Eggs	Roberts and Sauer 1994;
	SOI	Catch	Annual	South Africa	Adult	Roberts and Sauer 1994
Illex illecebrosus	BST, NAO, SSF	Catch	Annual	NW Atlantic	Adults	Dawe et al. 2000, 2007
Illex argentinus	SST, SOI, TPI	CPUE	Annual	Falkland Islands	Adults	Waluda et al. 1999; 2004; Laptikhovsky et al. 2001
	Thermal gradients	Vessel number, CPUE	Weekly	Falkland Islands	Adults	Waluda et al. 2001
Todarodes pacificus	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
Dosidicus gigas	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)

offshore areas (Roura et al. 2016). Recent observations in the Mediterranean Sea evidenced correlations between Illex *coindetii* life cycle and several environmental parameters (Jereb et al. 2017), even though the mechanisms underlying these correlations are unclear. Recruitment seems to be affected by environmental conditions (Jereb et al. 2001, Ceriola et al. 2007, Lefkaditou et al. 2008, Cuccu et al. 2009) because of egg masses properties and main basic requirements of hatchlings.

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

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

Challenges and opportunities for forecasting squid stock size

Forecasting squid stock size requires knowledge of the species biology and life history, population dynamics, environmental drivers of stock size and fishery

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
Illex illecebrosus[a]	Y	East Coast USA Canada and international waters	USA, shelf/slope (June-Sept/Oct)	Only the winter cohort	115-215 days (144 days)	Bottom trawl
	Y		CA, Scotian Shelf and slope (June-Sept/Oct)	N	Mated females are rare	no fishery since 1999
	Y		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
Illex argentinus	Y	Falklands, Argentina, Brazil and international waters	International waters (Dec-May/June)	Y		Automated jigging machines
	Y		Falklands shelf (Feb-May/June)			
	Y		Within Argentine EEZ (Feb to June-Sept)			
Todarodes pacificus	Y	Japan and Korea	Sea of Japan (winter)	Y		Jig, trawl, set net and purse seine
	Y		Sea of Japan and Pacific Ocean (fall)			
Nototodarus gouldi		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
Dosidicus gigas	Y	Mexico, Chile, Peru and international waters		Y		
Loligo forbesii		United Kingdom	Inshore (fall), offshore (summer)	N		Bottom trawl
Loligo reynaudii		South Africa		Y		Hand Jig

[a] Hendrickson (2004) and Hendrickson and Showell (2019).

characteristics, and how forecast results will feed into the stock assessment and satisfy the needs of fishery managers.

Background stock-specific information pertinent to forecast modeling of squid species reviewed in this paper is summarized in Table 4.

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

Research survey data for stock size estimation are often lacking for squid stocks or stock size is estimated from multispecies survey data for which the survey

Table 4. 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?
Illex[a] *illecebrosus*	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
		No fishery since 1999						
	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
Illex argentinus	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	
Todarodes pacificus	Fall cohort: research jig survey. Winter cohort: jig fishery CPUE	CPUE	Catch and survey length data	Catch and survey data	Y	Y	Y, annually	Y
	Jig and parlarvae surveys	CPUE	Catch and survey length data	Catch and survey data	Y	Y	Y, annually	Y
Nototodarus gouldi	None	CPUE		None				N
Dosidicus gigas		CPUE			Y	Y		Y, biomass only
Loligo forbesii		CPUE	Landings and survey length data		Y	Y		N
Loligo reynaudii		CPUE	Catch and survey length data		Y	Y		

[a] Hendrickson (2004) and Hendrickson and Showell (2019).

timing and/or gear types may not be ideal for catching squid (e.g., the survey may occur when the species is migrating on or off the continental shelf and/or the survey is not synoptic across the geographic range of the stock, and in some cases there is no ideal timing because recruitment extends over an extended period). As a result, standardized fishery catch-per-unit-effort (CPUE) indices are often utilized to estimate stock size. The validity of the assumption that CPUE data are proportional to stock size must be examined prior to the use of such data. Pre-recruits (i.e., small squid that have not recruited to the fishery) are often difficult to quantify either because they are found outside the survey sampling area and/or they are not fully available to the survey or fishing gear. Due to (sometimes) year-round recruitment and the highly migratory nature of squid stocks, the model assumption of a “closed population”, relative to the temporal and spatial scales of the stock being assessed, is generally not met and therefore estimates of immigration into and emigration from the fishing grounds are required. An additional challenge is the estimation of cohort-specific natural mortality rates for these semelparous species. Natural mortality increases with age for mature individuals (Hendrickson and Hart 2006) and cannibalism and high predation rates must also be taken into account.

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

Mechanistic models tend to be more complex, requiring more knowledge and often contain more variables. These models may be more informative for understanding population dynamics, though more complex models do not necessarily provide more precise predictions (Payne et al. 2017). Rather, with respect to forecast performance, mechanism-free models that rely on emergent statistical properties of the data are recommended for conducting short-term projections (Schindler and Hilborn 2015). Even if empirical models that link environmental and catch data provide very useful information, their explanatory capacity is limited (Hobday and Hartog 2014). On the other hand, mechanistic models might not make accurate predictions initially, but they are expected to continue improving (Urban et al. 2016). As global environmental conditions continue to change in an unprecedented fashion as previously mentioned, mechanistic models may provide us with more detailed and accurate insights into the impacts of climate change on marine species and ecosystems than statistical models constrained by past observations. Annual forecasting from historical data can be particularly problematic for species like squid which are characterized by "boom-bust" abundance trends. The numerous relationships between recruitment and environmental variables that have broken down when updated with new data (Myers, 1998) are evidence of this need for new approaches to forecasting. It is possible that as climate change forces ecosystems to enter unprecedented territory, the effectiveness of existing metrics may change. The validity of the relationships used in forecasting models and the mechanisms represented or missed in the stock assessment procedures that are continuously operating need to be examined. Testing the relevance and influence of various processes on squid recruitment is a necessity. Comparisons among species and oceanographic conditions are also necessary for constructing robust prediction and forecast models (Nigmatullin 2004a).

Examples of squid ecological-fishery forecasting

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

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

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

The S-R relationship of *Todarodes pacificus* is assumed to change with changes in environmental

Table 5. Regime shift detection methods in the Japanese Todarodes pacificus stock assessment and results using recent data.

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 *(Sardinops melanostictus)*	Kidokoro(2009) Yatsu et al (2013)	Increased to high level	Decreased to low level	Increasing	Positive
Japanese anchovy *(Engraulis japonicas)*	Yatsu et al. (2013)	Decreased to low level	Increased to high level	Decreasing	Positive

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

For the Japanese flying squid (*Todarodes pacificus*), the spawning grounds (Goto 2002), migration routes (Nakata 1993; Kidokoro et al. 2010), and body size (Takayanagi, 1993) were all changed coincide with regime shift. In particular, a shift in the spawning grounds is considered as the most important factor to affect the survival rate of paralarvae accounting for the changing stock size. To detect regime shifts and forecast recruits and stock size, oceanographic indices (Pacific Decadal Oscillation (PDO), SST) and the changes in ecological traits are used in the *Todarodes pacificus* stock assessment method (Kidokoro 2009). This approach may also be useful and feasible for the stock assessment and management of other ommastrephid squids affected by regime shifts.

In the current Japanese stock assessment, it is reported that regime shifts have not occurred yet, while the current regime for *Todarodes pacificus* is viewed as "favorable" (Kaga et al. 2018; Kubota et al. 2018). In recent years (2015-2017) however, the stock size and catch of *Todarodes pacificus* declined abruptly around the Japanese waters. And to verify which variables are useful to understand regime shift have occurred or not a new data have analyzed (?<PICK no=Table 5).

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

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

As previously mentioned, there are many publications that describe how environmental conditions relate to variability in stock size and recruitment of ommastrephid squids. In recent studies, the lifespan of

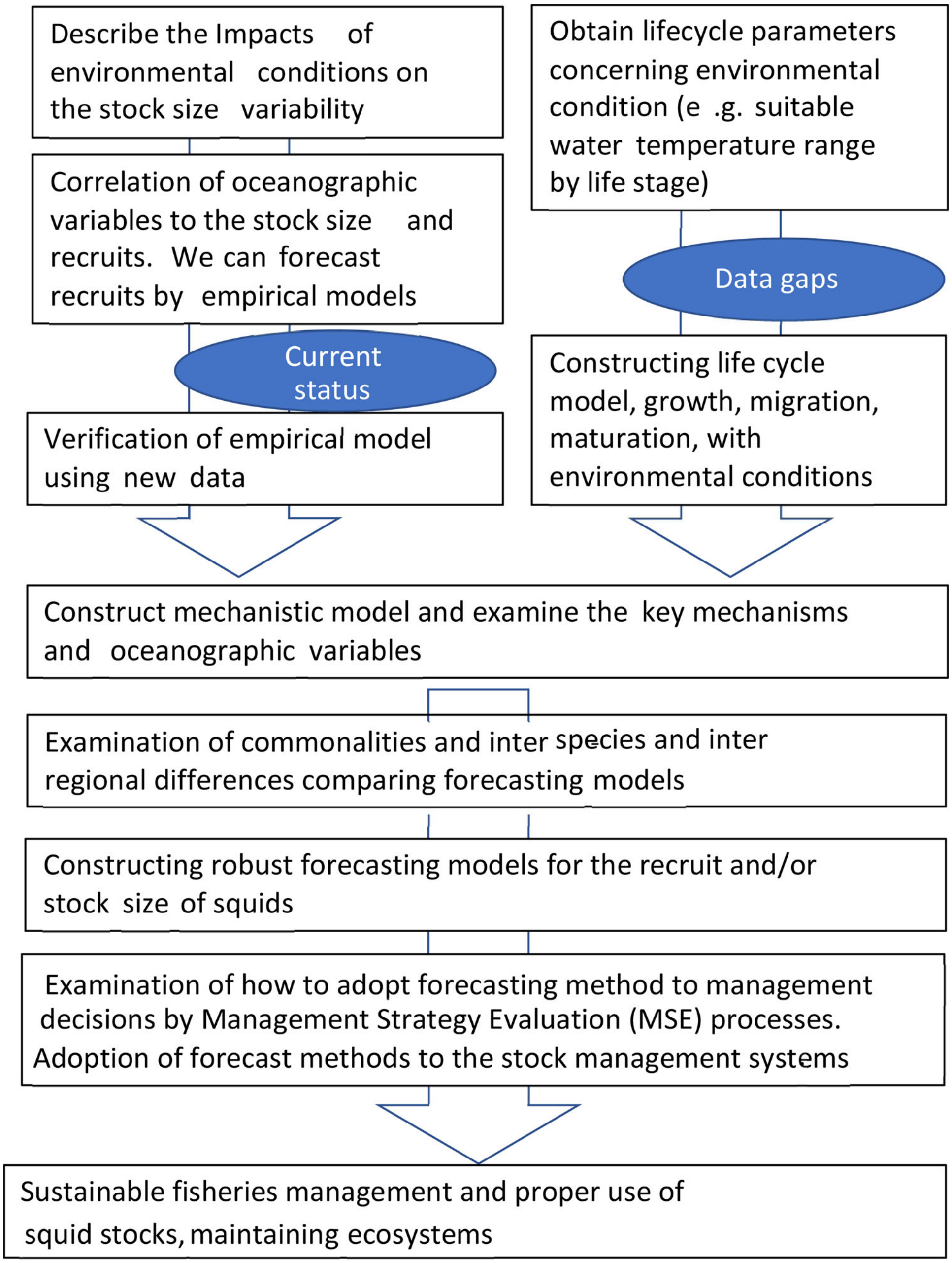

Figure 3. Roadmap to progress ecological-fishery forecast models to support squid fisheries management decisions.

ommastrephid squids is suggested to be rather flexible (Takahara et al. 2017), which may influence how squid stocks are managed. Squid management plans need to incorporate lifecycle parameters concerning environmental conditions (e.g. suitable water temperature ranges for various life history stages). Based on these parameters, mechanistic models could be developed and used to examine the key oceanographic variables that influence stock size and recruitment variability.

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

The relationship between environmental variables and stock size had been identified for most of the squid species considered in this study (Figure 1), and because of gaps in the forecast model input data forecasting was only conducted on a few stocks, (i.e., those that are data-rich and well-studied). In order to increase the number of squid stocks for which forecasting is conducted in the future a roadmap is proposed to improve squid forecasts products (Figure 3). As for the adoption of specific orecasting methods to the operational fishery management process, what is important in forecasting is the relationship between needs, feasibility and clarify to what extent the present prediction level is (Payne et al. 2017, Jacox et al. 2020). The ultimate success of a forecast is determined by whether it is used by end-users.

Conclusions and recommendations

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

1. Ideally, squid fisheries need a forecasting system that includes all time-scales of forecasting, and especially short - and medium-terms. The effective management of squid fishing with their highly variable stock dynamics is possible only with a working set of predictive models providing forecasts at multiple time-scales.
2. More research is needed to move these forecasts products toward more realistic mechanistic representations of distribution such as explicitly incorporating movement and life-cycle with the limitations imposed by habitat. Also exploiting the situations where predictive skill is needed and available and linking them to fishery management systems may lead to valuable new ecological fishery forecast products.
3. Implementation of the Roadmap (Figure 3) through development of demonstration projects that are feasible and end-users driven could help to develop guidelines to adopt and operationalize the ecological-fishery forecasting approaches to inform sustainable squid fisheries management.
4. More efforts are needed to adopt and communicate the forecasts products to stakeholders in term of the limitations and assumptions, its associated levels of uncertainty to minimize misuse.
5. Finally continuous active engagement and collaboration with end-users and stakeholders (fishing industry, fishery and market managers etc.) in designing forecasts that can effectively support their specific decision-making requirements is critical.

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