



**HAL**  
open science

## **Stock assessment and management of cephalopods: advances and challenges for short-lived fishery resources**

Alexander Arkhipkin, Lisa Hendrickson, Ignacio Payá, Graham J Pierce,  
Ruben Roa-Ureta, Jean-Paul Robin, Andreas Winter

► **To cite this version:**

Alexander Arkhipkin, Lisa Hendrickson, Ignacio Payá, Graham J Pierce, Ruben Roa-Ureta, et al..  
Stock assessment and management of cephalopods: advances and challenges for short-lived fishery  
resources. ICES Journal of Marine Science, 2020, 10.1093/icesjms/fsaa038 . hal-02892541

**HAL Id: hal-02892541**

**<https://hal.science/hal-02892541v1>**

Submitted on 3 Sep 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

## **Stock assessment and management of cephalopods: advances and challenges for short-lived fishery resources**

Arkhipkin, A.I.<sup>1\*</sup>, Hendrickson, L.C.<sup>2</sup>, Payá, I.<sup>3</sup>, Pierce, G.J.<sup>4</sup>, Roa-Ureta, R.<sup>5</sup>, Robin, J.P.<sup>6</sup>, Winter, A.<sup>1</sup>

<sup>1</sup>Fisheries Department, Bypass Road, Stanley, FIQQ 1ZZ, Falkland Islands

<sup>2</sup>U.S. National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA, 02543 USA

<sup>3</sup>Fisheries Development Institute (IFOP), Blanco 839, Valparaíso, Chile

<sup>4</sup>Instituto de Investigaciones Marinas, Consejo Superior de Investigaciones Científicas, Eduardo Cabello 6, 36208 Vigo, Spain / CESAM and Departamento de Biología, Universidade de Aveiro, 3810-193 Aveiro, Portugal / School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, AB24 2TZ, Aberdeen, UK

<sup>5</sup>King Fahd University of Petroleum & Minerals, Center for Environment & Water, 31261, Dhahran, Saudi Arabia

<sup>6</sup> Borea (Biologie des Organismes et des Ecosystèmes Aquatiques) Normandie Université, UniCaen, CNRS, Esplanade de la Paix CS 14032, 14000 Caen, France

\*Contact author: A.I. Arkhipkin, email: aarkhipkin@fisheries.gov.fkAbstract

Cephalopods have become an important global food source, but their sustainable management is challenged by unique life history characteristics associated with short lifespans and semelparous reproduction, high natural mortality rates, rapid and often non-asymptotic growth, and complex population structures. Weak stock-recruitment relationships together with the time-consuming work required for age validation and high-volume annual age determinations make traditional age-based modelling impractical. We propose that the best method for cephalopod assessment involves innovative depletion models, fitted with in-season data on catch numbers and fishing effort, to produce realistic estimates of stock biomass. A ‘fast lane’ assessment approach is suggested that includes high-frequency data collection for separate, in-season stock assessments of each cohort to ensure sustainable exploitation of these short-lived resources. However, most cephalopod fisheries are data-poor and/or lack the infrastructure and resources needed to apply depletion methods; therefore we also present alternative assessment methods that have been recently applied worldwide. We also offer suggestions for further research on the remaining challenges of cephalopod stock assessment and management.

**Keywords:** cephalopods, short-lived species, stock assessment models, fisheries management

## Introduction

Cephalopods (Mollusca) are key ecosystem components of the World Ocean (e.g. Gasalla et al., 2010) as they occupy a broad range of trophic positions in marine food webs and have a high production to biomass ratio (Boyle, 2002). The species diversity of cephalopods is relatively low, with about 800 pelagic and demersal species belonging to three main Orders, Teuthida (squid), Octopoda (octopuses) and Sepiida (cuttlefish and sepiolids). Cephalopods are also important commercial resources, landings of which have been increasing rapidly in recent decades (Hunsicker et al., 2010; Arkhipkin et al., 2015). Several dozen medium to large-sized cephalopod species are subject to large-scale exploitation due to their muscular bodies having both flavour and texture acceptable for human consumption (Jereb and Roper, 2010). Cephalopod fisheries contributed a small percentage (2% to 5%) of the global landings of marine species relative to fish during 1960 to 2014. Nevertheless, their contribution to world fisheries production gradually increased from 0.5 million tonnes in 1950 to a peak of 4.85 million tonnes in 2014. After 2014, cephalopod landings levelled off then decreased to 3.77 million tonnes in 2017, mainly due to decreases in the landings of the two most abundant squid species; jumbo flying squid, *Dosidicus gigas*, in the eastern Pacific and Argentine shortfin squid, *Illex argentinus*, in the Southwest Atlantic (FAO, 2019).

The general increasing trend in cephalopod landings in recent decades was partially due to the increased market demand and corresponding increase in fishing effort (Arkhipkin et al., 2015). The increase in fishing effort was attributable to increased numbers of large jigging vessels fishing on the high seas, mainly for *I. argentinus*, *Todarodes pacificus*, *Ommastrephes bartramii* and *Nototodarus gouldi*, and increased numbers of small artisanal boats catching *D. gigas* near-shore with hand jigs (Arkhipkin et al., 2015). Another cause of the increased landings of cephalopods could be an overall increase in their abundance worldwide. Cephalopods may benefit both from the decrease in competitive pressure for

ecological niche space, due to overexploitation of finfish competitors and prey, and to the high flexibility of their populations when facing changes in the environment (Caddy and Rodhouse, 1998; Doubleday et al., 2016).

The objective of a stock assessment is to provide fishery managers with stock status estimates to support management decisions; e.g., on catch or effort, with the management aim of ensuring that stock biomass and fishing mortality estimates are below stock-specific reference point thresholds (Boyle and Rodhouse, 2005). In the case of data-poor situations, the aim is to avoid a decline in stock size that can be attributed to fishing mortality as opposed to emigration from the fishing grounds. However, in spite of our increased knowledge about cephalopod biology and ecology in recent decades, many fished stocks are not assessed, and some assessments use methods not well adapted to cephalopod life history and ecology (Pierce and Guerra, 1994; Boyle and Rodhouse, 2005; Arkhipkin et al., 2015). Most traditional stock assessment models were developed for longer-lived fish and invertebrate species, and are not appropriate for short-lived cephalopods because such models assume the existence of multiple year classes and population dynamics associated with iteroparity. In addition, the type of reference points, and hence the assessment method, may need to be based on the requirements of national laws and fishery management plans. In the U.S., reference points must be MSY-based or proxies thereof and an expert scientific review panel determines the assessment's acceptability for management use. In Europe, cephalopod fishing is not covered by the Common Fisheries Policy, which specifies which fisheries must be managed in the EU, although many coastal small-scale fisheries for cephalopods are managed nationally or regionally. Overall in Europe, the low priority assigned to these fisheries, the difficulty of applying common assessment methods and the data-poor nature of the stocks are thus mutually reinforcing barriers (Boyle and Rodhouse, 2005). Cephalopod fisheries are routinely assessed and managed in several other countries, including Argentina,

Australia, Canada, Chile, Falkland Islands, Japan, Mexico, New Zealand, Peru, Russia and South Africa – but many important cephalopod fisheries in other parts of the world are not assessed or managed (Arkhipkin et al., 2015).

In 1983, the FAO published an account of the state-of-the-art in cephalopod biology, ecology and stock assessment (Caddy, 1983a). Within that volume, Caddy (1983b) described aspects of cephalopod biology relevant to assessment. He mentioned the use of production models for assessment of West African trawl fisheries for cephalopods as well describing the principles of what are now known as depletion models, also highlighting the difficulty of estimating natural mortality. Pierce and Guerra (1994) reviewed methods of stock assessment then in use for cephalopods, following Hilborn and Walters' (1992) classification of assessment approaches, as well as recapping relevant aspects of cephalopod biology. Boyle and Rodhouse (2005) reviewed stock assessment models as well as management practices applied to the main cephalopod fisheries around the world. Further, Rodhouse et al. (2014) examined advantages and limitations of using surplus production models, depletion methods, age-structured models and two-stage models, analyzed various types of fishery-dependent and –independent data incorporated into these models, and discussed possible ways forward in forecasting and assessing cephalopod stocks. Arkhipkin et al. (2015) summarized biological characteristics and fishery management for the main exploited squid species around the world.

The aims of the present paper are to (a) review the particularities of cephalopod life cycles and population parameters that pose challenges to using conventional stock assessment methods; (b) discuss the methods that have been used for cephalopod stock assessment, especially those in current use, and assumptions of specific methods, (c) describe the most appropriate methods for cephalopod stock assessment and (d) recommend management measures applicable to the use of these methods for cephalopod fisheries.

## **Biological challenges for cephalopod stock assessment**

Cephalopods have an array of life cycle characteristics that differ from other commercially exploited marine species, and several aspects of cephalopod biology and ecology present particular challenges for their assessment and management (Boyle and Rodhouse, 2005). Cephalopods are characterized by short lifespans, high metabolic rates, and rapid growth. Their growth rates and maturation, as well as life cycle phenology, are highly variable. While much of this variation seems to be environmentally driven, it also reflects phenotypic plasticity and possibly a genetic component (McKeown et al., 2019). As a consequence of these characteristics, abundance and distribution can vary widely from year to year. Many cephalopods have relatively high fecundities and prolonged spawning periods with intermixing seasonal cohorts that contribute to the effective use of available food resources, resulting in rapid abundance fluctuations and facilitating fast recovery of populations after years of poor recruitment or heavy exploitation (Arkhipkin, 2013; Boyle and Rodhouse, 2005). These characteristics are briefly reviewed below.

### *Short life cycles*

The life cycles of commercially exploited cephalopod species vary from six months in small sepiolids and subtropical squids (Czudaj et al., 2012; Arkhipkin et al., 2000) to two years in the large-sized jumbo squid *D. gigas* (Arkhipkin et al., 2015), large temperate sepiids (*Sepia officinalis*, Challier et al., 2005), and octopods (*Octopus tetricus*, Leporati et al., 2015). The majority of fished cephalopod species have a life cycle of about one year (Boyle and Rodhouse, 2005). Some of the variation in lifespan, both within and between species, is related to ambient temperature, with tropical and subtropical populations living for about six months while many of their temperate counterparts live about one year (e.g., broadtail

shortfin squid, *Illex coindetii*, Arkhipkin et al., 2000; González et al., 1996). However, some temperate cephalopod species, such as *I. illecebrosus* and *Doryteuthis pealeii*, live less than one year (Brodziak and Macy 1996; Macy and Brodziak, 2001; Hendrickson 2004). For *D. gigas*, water temperatures encountered at the juvenile stage had the strongest effect on lifespan. Together with other environmental factors, water temperature determined whether adults would have a 1-year life cycle, having experienced higher temperatures, or a 1.5 - 2-year life cycle having experienced lower temperatures during the juvenile stage (Arkhipkin et al., 2015).

To undertake real-time assessment, the short lifespan of cephalopods requires a more data-intensive approach to monitoring, with high population sampling frequency over short time periods. Age-structured population dynamics models that involve projections of population abundance-at-age for each cohort through time could be applied to seasonal cohorts (groups of similar-age individuals each approximately one year younger than the previous group for species that live beyond one year, such as cuttlefish) or to so-called “micro-cohorts” (groups of similar-age individuals recruiting within the same fishing season each typically 2 to 3 months younger than the previous age group such as most squid species) (Rodhouse et al., 2014). However, this would require the collection of fortnightly or even weekly fisheries and age data to produce a time series long enough to estimate the fishing mortality and stock abundance of each cohort or micro-cohort. In addition to these difficulties, age-structured models are in general inappropriate for cephalopod stock assessment because these methods assume a constant value of natural mortality ( $M$ ) for all sizes and years. The data requirements and model assumptions in age-structured models are difficult to accommodate to the rapid life history and high variability that characterize cephalopod population dynamics.



### *Time-consuming ageing techniques*

Cephalopods possess several increment-bearing hard structures that can be used to determine their age, such as statoliths, gladii, beaks, stylets and possibly eye lenses (recently reviewed in Arkhipkin et al., 2018). The formation of increments in these structures is validated to be daily for many cephalopod species, thus enabling age estimates with a high rate of precision. However, despite progress in cephalopod ageing techniques, they are not typically used in stock assessments for two reasons. First, it is a time-consuming job that requires a skillful and dedicated person to prepare the sections to read. Unlike fish, in which is it possible to embed several otoliths on one slide for ‘mass production’, cephalopod statoliths, stylets and beaks require processing of a single structure at any one time, making the procedure much more time-consuming (Arkhipkin et al., 2018). Second, the advantage of determining ages of cephalopods with daily precision is associated with the disadvantage of having to read several hundred daily growth increments per individual, as compared to single- digit (or at worst low double-digit) numbers of annual rings in fish otoliths. Furthermore, the narrowness of the growth increments in statoliths and stylets (~1-5  $\mu\text{m}$ ) may confound the interpretation of alternating dark and translucent increments since optical diffraction can produce false lines (Arkhipkin and Shcherbich, 2012).

The time-consuming nature of processing and reading daily increments on cephalopod hard structures and the high growth rate variability make age-based models impractical for real-time stock assessment. However, age data are a potentially important component of cephalopod stock assessments. For example, age data rather than length data should be used to identify seasonal cohorts and to estimate growth rates because cephalopod growth rates show high plasticity and individuals of the same length can be from different seasonal cohorts (Arkhipkin et al., 2000). Some of the age-based assessment methods that have been utilized for cephalopods are summarized below.

### *Extensive ontogenetic migrations*

The majority of commercially exploited species of squid and sepiids have distribution ranges structured into spatially different spawning and feeding grounds, less so in octopods (Boyle and Rodhouse, 2005). Depending on the species and its swimming abilities, distances between spawning and feeding grounds may vary from tens of kilometers for nearshore sepiids to hundreds of kilometers for offshore loliginids and even thousands of kilometers in nektonic ommastrephid and gonatid squids (Arkhipkin, 2013). Migrations of sepiids and loliginids are usually inshore-offshore, whereas nektonic squid can cross the boundaries of several large oceanic ecosystems to fully exploit resources and take advantage of favourable environmental conditions in various climatic zones at different phases of their ontogenies (Boyle and Rodhouse, 2005, Arkhipkin, 2013). Cephalopods can also exhibit vertical ontogenetic migrations. Sepiids and loliginids usually move from shallow water spawning grounds to deep-water areas of continental shelves to feed, and upon maturation the adults migrate back to shallow waters to spawn (Jereb and Roper, 2010). In contrast, juveniles of neritic ommastrephids move from oceanic spawning grounds located off continental slopes onto continental shelves where they feed, mature and then migrate back to deep waters to spawn (Arkhipkin, 2013).

Some cephalopods (e.g., many squid species) are targeted by the fishery only during certain periods of their life stages, when they occupy one particular habitat. For example, *Doryteuthis gahi* is exploited mainly in its offshore feeding grounds, whereas other loliginids such as *Doryteuthis opalescens* and *Loligo reynaudii* are fished in their inshore spawning grounds prior to spawning (Rosa et al., 2013). These area-restricted fisheries may create challenges for monitoring the full range of a species' life stages, because intensive survey sampling to complement the fishery is difficult to organize given the short duration of the

species' life cycle. Other cephalopod fisheries, like the U.S. *Illex illecebrosus* bottom trawl fishery, occur on the spawning grounds near the edge of the continental shelf and upper slope (Hendrickson, 2004; Hendrickson and Hart, 2006) where all life cycle stages except the eggs, paralarvae and individuals < 3 cm ML have been found. Migrations to and from the fishing grounds pose certain restrictions on the use of models with a “closed population” assumption (e.g., classical depletion models) because it may not be clear whether a sudden decrease in CPUE is due to fishery exploitation (fisheries depletion) or emigration of the target species from the fishing area.

### *Complex population structure*

Cephalopods have evolved protracted, often year-round spawning. This feature helps cephalopods to withstand unfavourable environmental conditions or heavy fishing pressure that would otherwise lead to population crashes in species having short seasonal spawning periods as well as short life cycles. Cephalopods commonly have several cohorts that spawn in different seasons (e.g., autumn-spawning and spring-spawning cohorts of *D. gahi* on the Patagonian Shelf (Patterson, 1988)), or have several successive micro-cohorts. In the South Pacific, *D. gigas* size compositions in commercial catches depend on the availability of different phenotypes by area. These phenotypes reach small, medium and large body sizes before spawning depending on environmental conditions (Keyl et al., 2008). All three phenotypes occur in Peruvian waters, while the large one occurs in Chilean waters and the small one occurs in the convention area of the SPRFMO (Payá, 2016). The protracted spawning periods of cephalopods can result in the simultaneous presence of individuals in the same area which belong to different intra-annual cohorts/generations. Without time-consuming population age studies to reveal the cohort structure, cohort assignment based on modal lengths may be misleading (Caddy, 1991). Thus, tracking modal groups in a time

series of length-frequency distribution samples, even with monthly periodicity (Pierce et al., 1994), is questionable because it does not take into account variable growth rates and ignores possible emigration/immigration through the sampling area, as in the case of jumbo squid *D. gigas* (Keyl et al., 2008). Time series analyses that extrapolate cohort numbers from population size structures should therefore not usually be used in cephalopod stock assessments. However, there may be populations with intra-annual cohorts sufficiently separated in time that a length-based approach could work for *Loligo forbesii*, which has a lifespan longer than one year (Collins et al., 1999), and indeed in cuttlefish (which has a lifespan of two years) two annual cohorts may coexist, but can also be separated by size (see Gras et al., 2016).

### *Rapid growth rates*

Cephalopods are characterized by rapid growth rates, with some species reaching a size of 1 kg in just one year. The jumbo squid *D. gigas* has one of the fastest growth rates among cephalopods, attaining several kg in one year and up to 30-50 kg in two years (Jereb and Roper, 2010). The form of cephalopod growth (i.e., asymptotic versus non-asymptotic length) has been debated in the literature (Jackson, 1994) and the latest recommendation uses a Schnute growth model to describe their growth (Arkhipkin and Roa-Ureta, 2005). To our knowledge, no cephalopod species conforms to the von Bertalanffy growth function; commonly used for fish. Thus, assessment models are inappropriate for cephalopods if they use von Bertalanffy parameters or do not account for a semelparous life history.

### **Logistical challenges for stock assessment**

Many cephalopod catches derive from small-scale fisheries which are intrinsically difficult to monitor and, at least in Europe, most landings of cephalopods in large-scale

fisheries are taken as a bycatch rather than the main target. In such cases, fishers and authorities may have little interest in monitoring or assessing stock status. While cephalopod landings at European ports are normally recorded, a large proportion of these cephalopods are identified only to family level. Under the EU's fishery data collection framework, no northern European countries collect biological data on fished cephalopods. While the circumstances may vary, limited monitoring of cephalopod fisheries is almost certainly a global problem, as is reliable identification of those cephalopod landings that are recorded in official statistics.

Consequently, some fairly basic life cycle and fishery data are often missing, such as size-at-maturity, the timing and location of spawning, the relationship between CPUE and abundance, and estimates of natural mortality. In addition, except for a few studies (see Lipinski, 1994; Hastie, 1996; Tokai and Ueta, 1999; Akiyama et al. 2004; Hendrickson, 2011), the gear selectivity of cephalopods is poorly known.

## **Stock assessment approaches**

### *Definitions and preliminary assessment steps*

Stock assessments can have different functions, albeit with the ultimate aim of facilitating sustainable exploitation. Thus, both retrospective assessments and forecasting can be used to plan future fishing – although the former is perhaps the least useful approach for species which show wide year-to-year fluctuations in abundance. Real-time (in season) assessment can be used by managers to decide on the time of closure of a fishery.

Many cephalopod stock assessments are considered data-poor (Table 1). The term 'data-poor' is most often applied when only catch or landings data are available, plus assumptions that can be made about a species' life-history characteristics (IOTC, 2016; Zhou et al., 2018). In this paper we apply the term 'data-poor' to any situation in which lack of data

impedes the use of population models to determine stock status and estimate biomass and fishing mortality reference points. Data-poor assessments may lack the input data to address the factors that make cephalopod stock assessments difficult, e.g., high and variable natural mortality rates, semelparous reproduction, protracted spawning periods resulting in multiple seasonal micro-cohorts within a single year – which differ from one another in terms of growth and maturation rates, immigration/emigration schedules and environmental influences on biomass/abundance (e.g., Brodziak and Hendrickson, 1999; Macy and Brodziak, 2001).

Due to the short, primarily annual life cycles of exploited cephalopods, most stock assessment models require short time-steps (daily, weekly or bi-weekly) and input data of high temporal and spatial resolution. Thus, cephalopod stock assessments tend to use fishery-dependent data (catch, effort and biological data). Regardless of the type of assessment method used, cohorts or micro-cohorts must be identified, except when there is a single cohort per year, and successive cohorts are non-overlapping. In squid, this should be done with a baseline age determination study using statoliths. Length data are not sufficient for cohort identification because individuals from different cohorts can be of similar size (or conversely, individuals from the same cohort can show a range of sizes), due to growth rate plasticity (Arkhipkin and Laptikhovsky, 1994). Differences in growth and maturation rates between cohorts require each cohort to be assessed as if it were a separate stock.

Preliminary assessment steps may include the description of exploitation patterns in time, in space, by gear, etc. (e.g. Dunn, 1999), or examination of trends in relative exploitation rates (i.e., catch/survey biomass), by seasonal cohort. Emigration/immigration patterns are also important considerations. Maturity and length composition data (by cohort) can be examined to assess trends in recruitment and length at 50% maturity (L50). Results from fishery and research survey data may be compared (see ICES, 2010).

## *Natural mortality estimation*

Most stock assessment models require an estimate of natural mortality that is either estimated external to the model based on empirical data, estimated within the model (e.g. Roa-Ureta, 2012) or assumed. Natural mortality rates are especially difficult to estimate for cephalopods because empirical data are difficult to obtain (e.g., tagging studies) and because most species are semelparous, so natural mortality is an increasing function of age for spawning individuals. Despite this fact, natural mortality rates for cephalopod stocks with concurrent fishing and spawning mortality are usually assumed to be constant for all individuals of commercial size (an inherent assumption of production models). Neither of the two commonly used methods for estimating the natural mortality of cephalopods, Pauly (1980) and Caddy (1996), account for the increase in natural mortality that occurs following spawning in these semelparous species. To address this issue, Hendrickson and Hart (2006) developed a weekly, age-based cohort model for an unfished *I. illecebrosus* cohort that was used to estimate the maturation and natural mortality rates of non-spawners and spawners and which incorporated age-determination error. The same study showed that fishing and spawning mortality occur concurrently during the *I. illecebrosus* fishery in U.S. waters.

Output from the maturation-natural mortality model was incorporated into weekly yield- and eggs-per-recruit models that were used to estimate and compare MSY-based and %MSP-based Biological Reference Points (Hendrickson and Hart, 2006). When age determination error was unaccounted for in the model, the proportion of squid-at-age that were mature, and hence also the maturation rate, were underestimated for the older age groups. This resulted in underestimation of natural mortality rates-at-age because the percentage of individuals that suffered spawning mortality was lower. When statolith-based aging error was unaccounted for in the natural mortality estimates included in per-recruit models, reference points such as the example of  $F_{50\%}$  were underestimated by 41%. This

finding emphasizes the importance of computing age-estimation error and incorporating it in age-based assessment models of semelparous cephalopod species.

### *Determination of population trends and exploitation rates*

Various published examples have used analyses of commercial CPUE or catch data in place of formal assessments to provide information on abundance trends in cuttlefish (e.g.,

Dunn, 1999; Denis and Robin, 2002), octopods (e.g., Lourenço and Pereira, 2006; Orsi-Relini et al., 2006), squids (e.g. Zuur and Pierce, 2004; Chen et al., 2006; Georgakarakos et al., 2006), or cephalopods globally (Doubleday et al., 2016). In Europe, such exercises are undertaken regularly by the ICES Working Group on Cephalopod Biology and Life History (WGCEPH). Evidently, CPUE may not always be a good indicator of abundance, especially in species with patchy distributions, like many squids (Winter and Arkhipkin, 2015). On the other hand, where cephalopods are taken as bycatch, and provided that the spatiotemporal distribution of fishing effort is independent of the distribution of cephalopod abundance, a good relationship between abundance and CPUE is possible.

In 2013, Zhou et al. developed a catch-only method for finfish stocks (later published in Zhou et al., 2018), which was applied to *D. gigas* fishery in Chile by Clark et al. (2014). The model reconstructs possible trajectories of stock change from the beginning of the fishery, given possible ranges of carrying capacity and population growth rate, assumed stock status (proportion of depletion), and historical catch data. A Graham-Schaefer surplus production model was used, with a wide range of initial parameters. The carrying capacity  $K$



was set from maximum catch  $C_{\max}$  to 50 times  $C_{\max}$ ; the intrinsic population growth rate  $r$  set from 0.8 to 1.5 (based on  $r = 0.85$  for *I. illecebrosus* and  $r = 1.19$  for *O. bartramii*, Ichii et al., 2006); and the depletion at the end of the time series ( $D = B_{\text{end}}/K$ ) from 0.1 to 0.8 at a step of 0.05. Since the end point for each assumed  $D$  was fixed, the biomass trajectories were determined by only two variables: the initial biomass at the beginning of the fishery  $K$ , and the population growth rate  $r$ . The combination of these two parameters was found by minimizing the difference between simulated biomass and assumed biomass at the end of the period ( $B_{\text{end}} = D \cdot K$ ). After running the model and obtaining all possible  $[K, r]$  pairs, unlikely pairs were eliminated. Because the catch-only method uses Graham-Schaefer surplus production model, biological reference points ( $B_{\text{MSY}}$  and  $F_{\text{MSY}}$ ) and catch quota can be easily computed.

### *Stock assessment methods based on survey data*

Data from fishery-independent surveys have been used to derive recruitment indices and/or estimates of adult abundance/biomass for a number of cephalopod stocks, including squid stocks in the USA, South Africa, New Zealand, Argentina, and the Falkland Islands (NEFSC, 2011; Rowell et al., 1985; Augustyn et al., 1992; Sato and Hatanaka, 1983; Roa-Ureta and Arkhipkin, 2007; Roa-Ureta and Niklitschek, 2007). Absolute abundance or biomass estimates are typically based on swept-area calculations from data collected during bottom trawl surveys, but they require estimates of catchability ( $q$ ) determined from empirical data. Index-based cephalopod assessments utilize relative abundance or biomass indices when  $q$  is unknown (Hendrickson and Showell, 2016). As noted by Caddy (1983b), cephalopod biomass/abundance can be difficult to estimate by swept-area when recruitment occurs over a prolonged period and when multiple intra-annual cohorts exist. Thus, age-based cohort identification and determination of the timing of recruitment pulses are needed to

avoid such pitfalls. As noted above, distributions of some cephalopods may be patchy, resulting in survey abundance estimates that are more likely to be inaccurate. In these cases, stratified, random bottom trawl surveys conducted throughout the species geographic range reduce this possibility. Given the absence of year-to-year stability, the potential for survey abundance estimates being inaccurate is arguably greater for annual species. However, survey-based abundance estimates are commonly used for cephalopod stocks because adequate fishery CPUE data are frequently lacking.

Stock assessments for both commercial squid species in the Northwest Atlantic; *D. pealeii* (longfin inshore squid) and *I. illecebrosus* (northern shortfin squid), are data-poor with respect to the temporal and spatial resolution of available CPUE and biological data, which limits the types of stock assessment methods that can be used. However, data from stratified, random research bottom trawl surveys, conducted during spring and fall, are available and these data are used in *D. pealeii* assessments. For each of the two seasonal cohorts (Macy and Brodziak, 2001), data from these surveys were used to derive annual, swept-area biomass and abundance estimates (NEFSC, 2011). Based on “non-informative” uniform prior distributions for each underlying factor (e.g., effective trawl width and capture efficiency), survey catchability uncertainty was characterized by means of a composite prior distribution. Instead of using diel conversion factors to standardize survey catch rates, GAMs and a grid-search procedure were used to find objective criteria for defining “daytime” tows (a time when the species is most available to bottom trawl gear) based on solar zenith angle (Jacobson et al., 2015). Swept-area abundance estimates based on daytime tows were more precise than estimates based on diel conversion factors. Relative exploitation rates were also computed for the cohorts caught in the spring and fall surveys as the January-June catch / spring survey biomass estimate and the July-December catch / fall survey biomass estimate, respectively. In order to provide assessment results that conformed to the required annual-

based, fixed quota management framework, a two-year moving average of the annual means of the spring and fall survey biomass estimates was compared to the target and threshold survey-based  $B_{MSY}$  proxies to determine stock status with respect to biomass. The target biomass proxy assumed that biomass was at 90% of the carrying capacity ( $K$ ), and  $K$  was computed as the time series median of the averages of spring and fall  $q$ -adjusted biomasses. The threshold  $B_{MSY}$  proxy was computed as 50% of the biomass target. However, data were not available to compute MSY-based fishing mortality reference points, so the overfishing status of the stock could not be determined.

Another example of a data-poor squid assessment based on survey data involved the northern component of the *I. illecebrosus* stock which inhabits international waters located off the east coast of Canada, and which is regulated by the Northwest Atlantic Fisheries Organization (NAFO). Only landings and survey data are available. Annual relative biomass and mean body size indices were derived using data from a stratified, random bottom trawl survey that is conducted on the Scotian Shelf near the start of the fishery (Hendrickson and Showell, 2016). Relative exploitation rates were also computed as the nominal catch for this portion of the stock divided by the survey biomass index. Each year, all three variables were compared to their respective time-series means during the low and high productivity periods to determine productivity regime. The northern stock component collapsed in 1982 following the period of highest catches (and biomass indices), resulting in a shift from a high productivity period to low productivity period that has lasted for 34 years. The Total Allowable Catch (TAC; synonymous with NAFO's Limit Reference Point proxy) is established annually based on productivity regime. The higher of the two proposed proxies was chosen by the NAFO Scientific Council as the TAC for the low-productivity regime, and was computed as: the 1979 peak in nominal catch multiplied by the 1982-1997 mean

biomass index for the low-productivity period, then this value was divided by the 1979 biomass index.

### *Production models*

Biomass dynamics or production models in their simplest form require only fishery catch and effort data. This is both a strength and a weakness and various historical (finfish) fishery collapses were at least partly due to inappropriate use of production models, notably those models which assume that the fishery and stock are at equilibrium (see Hilborn and Walters, 1992). At first sight, these models seem unsuitable for cephalopods, given that they assume a constant carrying capacity, which is unlikely for species whose abundance varies widely according to environmental conditions (Rodhouse et al., 2014). On the other hand, as long as they are not severely overfished, cephalopod stocks may show rapid recovery from overexploitation so that equilibrium between the fishery and stock is arguably more plausible than in many longer-lived species. Production models are arguably inappropriate for semelparous species because they assume that natural mortality is constant throughout an individual's lifespan. However for an annual species, when the year is the time step of the assessment and fishing tends to follow the same seasonal cycle every year, within-year variation in natural mortality is not very relevant. Another issue is that production models require an abundance index, some pitfalls of which are discussed below.

Production models have been used routinely for Saharan Bank cephalopod stocks including octopus, squid and cuttlefish (e.g. Sato and Hakanaka, 1983; Bravo de Laguna, 1989) as well as Mauritanian octopus stocks (Meissa and Gascuel, 2015). They have also been applied to European cephalopod fishery data under the auspices of ICES WGCEPH, most recently a Stochastic Surplus Production Model in Continuous Time (SPiCT) used for European Atlantic squid and cuttlefish stocks. This approach is based on the Pella and

Tomlinson (1969) production model and incorporating errors on catches and biomass indices (after Pedersen and Berg, 2017).

ICES (2016, 2017) fit a classical Graham-Schaefer surplus production model to fishery catch and effort data from the English Channel fishery for loliginid squid (1994-2015). The model was fitted separately for *Loligo vulgaris* and *L. forbesii* and for both species together, following a two-step procedure with initial values estimated by non-equilibrium multiple linear regression followed by nonlinear estimation using time-series fitting (as described by Hilborn and Walters, 1992). Input data were total catch by France and UK vessels and a series of abundance indices derived from French bottom trawl LPUE, standardized with Delta-GLM (Gras et al., 2014). Results obtained in 2015 suggested contrasting year-to-year abundance trends in *L. vulgaris* and *L. forbesii*. However, re-analysis in 2016 resulted in unrealistic values of population parameters  $r$  and  $K$  and the model based on combined abundance of both species is considered to be more robust. Given their ecological similarity, a joint carrying capacity for both species might be more realistic. The combined assessment for both *Loligo* species suggested that, in a constant environment, MSY for this resource in the English Channel is 4,600 tonnes.

In a separate analysis, ICES (2014) applied a Bayesian state-space version of the Graham-Schaefer model that incorporated both observation and process error to *L. vulgaris* and *L. forbesii* in the Bay of Biscay (1997-2013). In general, estimated annual biomass was always above  $B_{msy}$ , with  $B/B_{msy}$  generally around 1.7, while annual fishing mortalities were mostly slightly above  $F_{msy}$ . However, there was considerable uncertainty around both estimates.

A possible mechanism to improve model fit is to incorporate environmental variables. ICES (2014) fitted a surplus production model to fishery and survey data for *Octopus vulgaris* in the Gulf of Cadiz using landings data for 1993 to 2013. Four abundance indices

were tested: LPUE from the trawl fleet and three abundance indices from surveys (November survey, March survey and the survey average). Results were generally similar (MSY between 1950 and 2350 t) although the LPUE index resulted in the best fit. Sobrino et al. (2002) found that octopus abundance in the Gulf of Cadiz was highly correlated with rainfall in the previous years and ICES (2014) therefore incorporated this variable into the production model. The annual rainfall factor ( $R_f$ ) was defined as  $R_f = 1/(\text{Annual rain period}/\text{mean rain period})$ . This multiplier was applied to annual carrying capacity ( $K$ ) and growth rate ( $r$ ) values or only to carrying capacity ( $K$ ). In combination with landings or survey abundance indices, the models with variable MSY all had somewhat better fits than those with fixed MSY. The best fit was obtained using the LPUE index and allowing variation in both  $r$  and  $K$ . Under these scenarios carrying capacity varied approximately threefold following the wettest and driest years.

ICES (2017) extended the analysis of English Channel squid data using the classical Graham-Schaefer model (Schaefer, 1954) complemented by an environmental effect on stock parameters ( $r$  and  $K$ ) as described by Barros (2007). The environmental variable was a linear combination of several hydroclimatic variables that had previously been found useful to predict peaks of recruitment. While the basic Schaefer model for both *Loligo* species suggested an MSY of 4600 t, the model including environmental variation indicated that annual MSY varied between 2880 and 7430 t. By taking environmental variation into account, a better fit was obtained. Annual catches were generally below MSY, suggesting an absence of overexploitation, although estimated biomass relative to  $B_{msy}$  varied between 0.4 and 1.0 and may be unrealistically low.

In the northwest Pacific, Wang et al. (2016) calculated the abundance of the western winter-spring cohort of *O. bartrami* by a surplus production model with carrying capacity ( $K$ ) proportioned to sea-surface temperature in the spawning habitat and growth rate ( $r$ )

proportional to sea-surface temperature in the feeding habitat. Including the environmental variable of seas-surface temperature was again found to improve model fit, with more conservative management reference points than the conventional surplus production model.

### *Cohort models*

Statistical catch-at-age models and yield- or SSB-per-recruit models form the basis of most data-rich finfish stock assessments, relying on the existence of multiple year classes and a fixed age-length relationship which together allow the decline in abundance of individual age-classes to be tracked over time. For short-lived species present as a single cohort at any one time, such models reduce to a simple population dynamics equation whereby catch over a time period can be related to population size if values for fishing and natural mortality rates are known. Expressing fishing mortality as a function of effort and catchability gives an equation that can be solved by non-linear regression – an approach that has been used for the *I. argentinus* fishery in the Falkland Islands (Rosenberg et al., 1990). Expressing abundance in terms of biomass rather than numbers leads to yield-per-recruit models. Yield- and eggs-per-recruit models developed for semelparous species have been applied to the *I. illecebrosus* stock component in U.S. waters to estimate Biological Reference Points (Hendrickson and Hart, 2006).

In the English Channel, cohort models have been applied on a monthly time-scale to *L. forbesii* and *L. vulgaris* (Royer et al., 2002). Historical data sets of catch-at-age were estimated from catch-at-length data and applying published growth curves. Cohort analysis and depletion models gave broadly similar estimates for the number of recruits (i.e. the peak numerical abundance of the annual cohort taking into account its recruitment spread over several months), with population size varying by up to a factor of 5 from year to year. Note that in the case of a single annual cohort both cohort and depletion methods tended to

describe the same dynamic (e.g., Pierce and Guerra, 1994). Royer et al. (2002) additionally used a Thomson and Bell model to simulate production and biomass of the exploited populations. They found that estimated exploitation levels were above optimum for both species, but argued that reduced fishing mortality would not have led to significantly higher yields. The most striking result of Thomson and Bell projections was to reveal over-exploitation in abundant cohorts and under-exploitation in less abundant ones. This apparent contradiction was considered to be a result of the changing status of a resource fished by multispecies trawlers: targeted when abundant, and only a by-catch species when scarce. Cohort analysis was updated in English Channel *L. forbesii* using statolith based age determination (Challier et al. 2005). Population estimates in 13 fishing seasons did not show significant stock-recruitment relationship but underlined the influence of environment in the period preceding the recruitment peak. A similar approach was applied to cuttlefish *Sepia officinalis* in the same area by Royer et al. (2006). Again, catch-at-age was estimated from catch-at-length data and applying published growth curves. In this case, recruitment varied by a factor of 2 between years. Exploitation patterns appeared to be stable: each cohort was fully exploited but there was no evidence of recruitment over-fishing. The timing of cuttlefish recruitment was based on the observation of small specimens (<100 g.) in landings. A phenomenon that occurred in two pulses related to the migration cycle (i.e. late summer-autumn catches in the inshore fishery and late winter in the offshore fishery). After 2006 the lack of separation of these two pulses did not allow updating the assessments.

Another example of monthly cohort analysis applied to a cephalopod stock involved *O. vulgaris* in Senegalese waters (Jouffre and Caverivière, 2005). The assessments used growth data based on tagging experiments (Domain et al, 2000) and age structure based on landings by commercial categories (weight categories that match with monthly growth). This



analysis was useful for management strategy evaluation in an area where variations in upwelling intensity generate recruitment fluctuations (Faure, 2000).

Although such models are normally applied to longer-lived species to estimate year-to-year abundance changes, and hence at first sight appear unsuitable for cephalopods, the application of cohort models to monthly data seems promising for this species. However, most assessment exercises have been based on historical data sets (cohorts entirely exploited and not alive at the time of the assessment). The application of diagnostics to future cohorts assumes that both population parameter estimates and exploitation pattern remain valid. The main issue for such a cohort model is whether assessments can be carried out in a timeframe sufficient to apply management measures that protect stocks from overfishing.

### *Empirical models, hybrid models, and other approaches*

Based on the high sensitivity of cephalopod abundance to environmental conditions and the absence of a “buffer” of older individuals, annual abundance could arguably be predicted from environmental conditions alone. Fogarty (1989) reviewed such “heuristic” approaches for fished invertebrates, while several other authors have pointed to relationships between squid abundance and sea temperature (e.g. Dow, 1976; Coelho and Rosenburg, 1984; Brodziak and Hendrickson, 1999; Bellido et al., 2001; Agnew et al., 2002; Waluda and Rodhouse, 2006).

One example of using environmental data to forecast cephalopod recruitment involves *O. vulgaris*. In Galicia (NW Spain), productivity was strongly related to the strength of upwelling. Variables related to wind stress, which may affect egg development, the planktonic stage and subsequent recruitment explained up to 90 % of the interannual variability of catches of adult octopus in the region (Otero et al., 2008).

Another cephalopod forecast model by Sobrino et al. (2020) also reported on a forecasting model for *O. vulgaris*, but in the Gulf of Cadiz. Their model combined environmental and survey data, using rainfall in the previous year, a survey recruitment index, and a correction factor to account for the number of survey hauls that fell within the known recruitment area. One limitation with such approaches is the need for an environmental predictor available before the start of the fishery, which could thus be used to set catch or effort limits at the start of the fishing season. Despite the encouraging performance of the above-mentioned forecasting models for predicting catches, empirical relationships do not normally explain the mechanisms underlying statistical relationships and efforts are thus needed to elucidate the underlying processes. Cautioning against such approaches, Solow (2002) pointed out the sometimes “fleeting nature” of time series correlations, noting that high correlations observed between gadid recruitment indices and the North Atlantic Oscillation index during 1973 to 1995 had not been evident over two decades prior to 1972.

Various approaches are adapted to the circumstances of particular cephalopod stocks. Mehanna et al. (2014) used exploitation ratios derived from length-frequency analyses to estimate biomass of the data-limited cuttlefish stock (*Sepia pharaonis*) in Omani coastal waters. Ichii et al. (2006) compared a depletion model with commercial driftnet swept-area and surplus production estimation for the autumn cohort of neon flying squid (*O. bartramii*), and concluded that swept-area had the most realistic assumptions and lowest uncertainty. Area methods based on large-scale commercial catch distributions may be advantageous as they utilize the most extensive data, but require additional procedures if distributions of either the stock or the fishery are heterogeneous.

For highly migratory *I. argentinus* in the south-west Atlantic, Chang et al. (2016) used geostatistical techniques and Chiu et al. (2017) used generalized additive models to

characterize spatial and temporal variability from the Taiwanese jigging fleet. Cephalopod stocks that in contrast have several, but partial, fishery indices have been assessed with biomass models that include a recruit stage followed by an exploitation stage. These two-stage models address the importance of recruitment dynamics for short-lived animals, and have been implemented for chokka squid (*Loligo vulgaris reynaudii*) in South Africa (Roel and Butterworth, 2000; Glazer and Butterworth, 2006) and cuttlefish (*Sepia officinalis*) in the English Channel (Gras et al., 2014; Alemany et al., 2017).

### *Depletion methods*

Given the short life cycles of cephalopods, assessment methods are poorly suited that are based on a spawning stock carry-over from year to year (Rosenberg et al., 1990). For many squid fisheries, the assessment methods used instead are depletion models, because depletion models can be calculated using only in-season time series of catch and effort to estimate levels of abundance which would sustain the observed rate of catch. However, the intensive requirements for these data qualify depletion methods as data-rich (Table 1).

In its basic form (Leslie and Davis, 1939; De Lury, 1947; Chapman, 1974), the depletion model assumes for the duration of assessment a homogenous cohort forming a closed population, linear relationship between catch rate and abundance, constant catchability, constant natural mortality, and actual decline of the catch rate (McAllister et al., 2004). Unlike population dynamics models, depletion models proceed at short time-steps such as daily or weekly. This feature makes them apt for the fast dynamics of cephalopod life histories, and depletion models have been commonly used to assess squid stocks exploited by fishing fleets from the 1980s onwards (Erhardt et al., 1983 – *D. gigas*, Gulf of California; Murata, 1989 – *T. pacificus*, Japan; Rosenberg et al., 1990 – *I. argentinus*, Falkland Islands; Brodziak and Rosenberg, 1993 – *L. pealei*, northwest Atlantic; Alvarez Perez, 2002 – *L. plei*,

southern Brazil; Royer et al., 2002 – *L. forbesi* and *L. vulgaris*, English Channel; Roa-Ureta and Arkhipkin, 2007, Arkhipkin et al., 2008, Roa-Ureta 2012, Winter and Arkhipkin, 2015 – *D. gahi*, Falkland Islands;; Chen et al., 2008 – *O. bartramii*, northwest Pacific; Morales-Bojórquez et al., 2008 – *D. gigas*, Gulf of California; McGregor and Tingley, 2016 – *Nototodarus gouldi* and *N. sloanii*, New Zealand, 2016; Medellín-Ortiz et al., 2016 – *D. gigas*, Baja California). Young et al. (2004) applied depletion modelling to Scottish *L. forbesi* fisheries with monthly landings and effort by trawlers and monthly biological data from market samples. Given the low temporal resolution in this case the approach was necessarily retrospective, but nevertheless highlighted wide inter-annual variations in abundance and in catches of the squid. Depletion models running at monthly time steps have also been applied to the cuttlefish, *Sepia officinalis*, fished by the coastal fishery off Catalonia (Maynou, 2015). The interesting variation in this case was that the model was run multi-annually, to a 14-years long monthly time series, and included data from two fleets.

For a fishery CPUE time series, a depletion model can predict the point at which the population would be reduced to a pre-determined stock size threshold, and, after accounting for growth and natural mortality, the initial population size can be back-calculated. Applied in-season, an important management application of the model is to avoid overfishing, and specialized software packages have been developed, e.g. MSQUID (Holden et al. 1990) and CEDDA (Holden et al., 1995). In Mediterranean states where cephalopods are sampled as part of the EU fishery Data Collection Framework, it has been argued that better focus of sampling effort, including during the post-recruitment period, could allow the use of depletion methods (Keller et al., 2015).

Depletion modelling has long been used for the Falkland Islands *D. gahi* assessment (Rosenberg *et al.*, 1990; Payá, 2009). The decrease of abundance during a fishing season is modeled as:

where  $t$  represents the time interval (here weeks),  $N$  the abundance in number of individuals,  $C$  the catch in number of individuals (catch weight divided by mean individual weight  $W_i$ ), and  $M/52$  is weekly natural mortality. Abundance at the week of arrival (i.e. when the squid migrate into the fishing area) is a parameter to be estimated. The model predicts the abundance index, as:

where  $q$  is the catchability coefficient and is also a parameter to be estimated. For simplicity this formulation includes one index of abundance only, but can easily extend to include several indices with their own catchability coefficients. The observed abundance index in numbers of individuals,  $I$ , is calculated as standardized CPUE divided by mean individual weight. Standardization may be calculated after the fishing season, when the complete data are available for this purpose. If the model is fit during the fishing season (in-season assessment) abundance indices can be replaced by nominal CPUE of different vessel categories (tonnage, vessel length, etc.) that should be related with the vessels' fishing powers.

The model is then optimized by maximizing the likelihood of the data, or minimizing the negative lognormal difference between and  $I$  over the time series  $t$ . The relative simplicity of the depletion model can make in-season cephalopod CPUE difficult to parameterize effectively (e.g., a given time series of decreasing catches could computationally represent high catchability acting on a low abundance, or low catchability acting on a high abundance), so a number of assessments have been formulated in Bayesian frameworks to improve estimation. Prior distribution for catchability and squid abundance have been developed from previous years in the fisheries (McAllister et al., 2004; Robert et al., 2010; Cao et al., 2015; Ding et al. 2019), or from surveys preceding a fishing season (Payá, 2009; Winter, 2019a).

Because of the uncertainty of the natural mortality  $M$ , Payá (2009) also added a prior distribution  $M_{prior}$ , and the lognormal difference between  $M$  and  $M_{prior}$  was added to the minimization of the model. An important function of depletion modeling is estimation of fishery escapement for setting a pre-determined sustainable biomass threshold, e.g., 10,000 tonnes per season in the Falkland Islands *D. gahi* fishery (Barton, 2002). Percent escapement (also known as %MSP) is calculated as the ratio between biomass in week  $t_{fin}$  and the potential biomass that would have existed without fishing,  $PB_{fin}$ :

### *Depletion model with successive cohorts*

For squid stocks, the depletion model assumption of a closed population is unlikely to be met. For example, analyses of the Falkland Islands *D. gahi* fishery have repeatedly shown that squid groups arrive in successive pulses after the start of the season, identified by sudden increases in CPUE and changes in squid size distributions (Roa-Ureta and Arkhipkin, 2007; Roa-Ureta, 2012; Winter and Arkhipkin, 2015). Therefore, a depletion model with successive pulses of recruitment was developed to account for this population pattern (Payá, 2009). Successive pulses were included in the abundance equation by adding the numbers of new recruits to the previous stock size:

where  $N_{t,ng}$  is the abundance of the new recruits (ng) in week  $t$ . For simplicity, the formulation above shows only one new group of recruits, but can be extended to add as many new groups as indicated. The estimation of the rest of the variables and model-fitting is done the same way as for a single group of squid. The model has also been applied to *D. gigas* in the Chilean fishery (Payá, 2018), using the program CHUSMODEL (Chilean HUmboldt Squid Depletion Model) written by Payá (2016).

Less frequently, *D. gahi* can disappear from the fishing zone to an extent not accountable by regular depletion. In a recent season (Winter, 2019a), average catches dropped by nearly half after a single day of bad weather, suggesting the squid had emigrated or irreversibly dispersed. The depletion model was then re-parametrized to account for a negative pulse on that date. While computationally equivalent to a positive pulse, Roa-Ureta (2012) cautioned that inferring a negative pulse risked counting animals twice if they subsequently returned to the fishing grounds. The difference between in-season pulses (positive or negative) and random catch variation can in any case be somewhat subjective, so further analysis of this issue is needed.

Ecosystem changes can bring additional complexity to the depletion model. In the summer season of 2015, the Falkland Islands fishing zone for *D. gahi* experienced an unusual incursion of the larger ommastrephid squid *I. argentinus* (Arkhipkin et al., 2016). As *I. argentinus* are both predators and competitors (Arkhipkin and Middleton, 2002), the population of *D. gahi* was quickly impacted. As *I. argentinus* are commercially valuable (Barton, 2002), vessels started to switch from targeting *D. gahi* to targeting *I. argentinus*, and ultimately the switch was made compulsory to protect the *D. gahi* stock. The depletion model was adapted to this situation by having two catchability coefficients  $q$ , applicable to days of respectively high and low *I. argentinus* proportions in the catch. Both catchability coefficients were freely estimated parameters in the model, as was the switch between them; i.e., the model itself selected the optimum threshold of what proportion of *I. argentinus* in the catch triggered a different catchability. In this manner, the depletion model could more accurately track the abundance of the *D. gahi* stock in-season.

A different sort of incursion occurred in the *D. gahi* fishery two years later. South American fur seals (*Arctocephalus australis*) and South American sea lions (*Otaria flavescens*) are resident species around the Falkland Islands, but during the winter fishing

season of 2017, both species appeared in the fishing zone in unprecedented numbers (Arkhipkin et al., 2018). To mitigate the risk of bycatch mortality for these pinnipeds, vessels were instructed to either avoid high density areas or fit their trawl nets with Seal Exclusion Devices (SEDs). As vessels complied, the depletion model was adapted based on the assumption that trawl nets with SEDs had a different average catchability than trawl nets without SEDs. The depletion model was again designed with two catchability coefficients, but differently from the *I. argentinus* influx, as SED and non-SED trawls were explicitly distinct and could be taken on the same days while fishing on the same stock. The quantitative difference between SED and non-SED catchabilities then included not only the technical efficacy of either gear, but all fishing-related aspects attributable to the gear (e.g., that vessels fishing under SED ‘conditions’ might be taking shorter trawls than otherwise, or switching fishing locations more frequently or moving them farther from the pinnipeds).

### *Generalized depletion model*

The basic form of the depletion model was further generalized by Roa-Ureta (2012). In addition to successive cohorts, the generalized depletion model includes a second modification for nonlinear processes in the relationships between catch rate and abundance  $N$  ( $\beta$ ) and catch rate and fishing effort  $E$  ( $\alpha$ ):

In this way, the model can consider phenomena such as hyper-stability and hyper-depletion (Harley et al., 2001) and saturability and synergy (Bannerot and Austin, 1983). The former ( $\beta$ ) is a continuum that represents mechanisms of fishing that keep the catch rate high when the stock declines (hyper-stability), makes the catch rate track the size of the stock (proportionality) or makes the catch rate decline more rapidly than the stock declines (hyper-depletion). The latter ( $\alpha$ ) is a second continuum that represents mechanisms making the catch



rate decline faster than the fishing effort expended (saturability), keep track of the effort expended (proportionality) or having the catch rate increase faster than the effort expended (synergy). Generalized depletion models permit modelling the data from several fleets simultaneously (Maynou, 2015). Multi-fleet versions make all parameters, except initial abundance and natural mortality, fleet-specific. Generalized depletion models can be intra-annual (or intra-season) or multi-annual. Intra-annual versions assess the stock with data from a single fishing season at daily or weekly time steps while multi-annual versions assess the stock with data from multiple years or seasons at monthly time step. Multi-annual models can handle long time series of monthly catch and effort involving years or decades (Maynou, 2015).

While the usual purpose of using catch and effort data in stock assessment is the generation of relative indices of abundance from linear approximations applied to CPUE (Maunder and Punt, 2004; Venables and Dichmont, 2004), generalized depletion models are mechanistic models where catch is the response variable resulting from effort, abundance and natural mortality. Fishing effort as a predictor allows nonlinear phenomena, namely the saturability-synergy continuum, to be modeled and parameterized. The mechanistic equations for expected catch by day, week or month can be calculated by maximum likelihood statistical inference in the R package CatDyn (Roa-Ureta, 2018), which also estimates the annual exploitation rate, instantaneous catch rate, and fishing mortality per time step.

### *Integrated Ecosystem Assessment*

Given the importance of cephalopods as forage species and predators in marine ecosystems, cephalopod fisheries should be managed in a sustainable manner that takes into account their impact on the ecosystem as a whole, preferably in the context of ecosystem-based fishery management (Link, 2010). One way to accomplish this objective is to include

cephalopods in ecosystem-based stock assessments (e.g., based on Ecopath models) and another way is to be more precautionary when setting catch limits. This might include notionally setting aside a portion of the quota that is based on a single-species cephalopod assessment for its consumption by marine predators. Ecosystem-based assessments have been conducted for two of the NAFO-managed Large Marine Ecosystems (Koen-Alonso et al, 2019). Given the complexities of marine ecosystems, analytical ecosystem-based stock assessments require large amounts of data, portions of which are often lacking, requiring their values to be assumed. Another challenge to implementing ecosystem-based assessments is that the amount of error inherent such models is generally much higher than it is for single-species assessment models (Link et al., 2012).

In Europe there is interest in a broader view of Integrated Ecosystem Assessment (IEA), whereby stocks and fisheries are assessed in the context of outcomes for the ecosystem, the economy and society. This is reflected in the current ICES Advisory Plan (ICES, 2019) and in recent calls for large-scale collaborative research proposals under the European Union's H2020 funding programme. It is evident that analytical solutions may be almost impossible to achieve due to the likely complexity and enormous data demands of models capable of incorporating all the wider and indirect effects of a fishery on the socio-ecological system. An alternative may be a semi-quantitative indicator, expert opinion and stakeholder-based approach.

Also in the European context, the fishery monitoring, assessment and management system designed to implement the Common Fisheries Policy has never been extended to cephalopod stocks. This raises the interesting possibility of including cephalopods in integrated assessments and integrated management without them ever having passed through a phase of routine stock assessment and quota management. Consequently, the starting point for developing IEA for cephalopod fisheries in Europe is essentially a clean slate. Possible

approaches to IEA might involve integrating environmental assessments derived from implementation of the Marine Strategy Framework Directive and/or applying principles proposed by fishery certification bodies (e.g. the Marine Stewardship Council's principles for sustainable fish stocks, minimising environmental impact and effective fisheries management). Alternative modelling approaches might include the use of Models of Intermediate Complexity for Ecosystem assessment (MICE) (e.g. Scott et al., 2016) and economic models (e.g. Colla-De-Robertis et al., 2019).

## **Fisheries management**

Given the distinctive characteristics of their short life cycles, cephalopods require a 'fast lane' approach to managing their fisheries, different from the approach taken with most finfish fisheries. For such short-lived animals, population size may vary seasonally and, regardless of whether it has been measured reliably, population size may be a poor predictor of the subsequent year's recruitment (Caddy, 1983; Boyle, 2002). In this event, information about the potential size of the exploitable stock will only be available shortly before recruitment (Roa-Ureta and Arkhipkin, 2007). Large-scale pre-recruitment surveys may help estimate recruitment abundance (e.g., *I. argentinus* and *D. gahi* in the Southwest Atlantic, Arkhipkin et al., 2015), but surveys need to be timed for when recruits are large enough to be caught by the fishing gear. Retrospective assessments could have a sentinel role (warning of unusually low biomass), but real-time assessments using depletion methods can be used to control fishing to allow sufficient escapement (as in the Falkland Islands fisheries for *I. argentinus* and *D. gahi*) or could also be used for in-season adaptive quota management. However, effective control generally requires the cephalopod to be the target of the fishery, natural seasonality of abundance (timing of migrations) to be sufficiently well-known, and licencing conditions that allow a fishery to be closed early.

In the Falkland Islands *D. gahi* fishery, the occurrence of successive recruitment pulses (micro-cohorts) during a fishing season has introduced an extra complexity in the fishery management, which is the possibility that new micro-cohorts could arrive after a season has been closed early for stock conservation. To address this possible outcome, a combined risk analysis was developed multiplying the probability that biomass was below the escapement level by the probability that no more micro-cohorts will arrive after the date of an early closure (Payá, 2007). Since then, the Falkland Island Fisheries Department has discussed early closure decisions with stakeholders based on the combined risk.

For the implementation of *D. gigas* management in the SPRFMO area, the Scientific Committee (SFRFMO\_SC, 2017) noted that SPRFMO is required to follow annual cycles in stock assessment and decision making. These annual cycles could result in up to 2 years' delay from the time a severe decline is detected and assessed (by the Scientific Committee) to the time a management decision may be taken and implemented (by the Commission). This delay would be too long for squid that have a 1- to 1.5-year lifespan. Essentially, SPRFMO management decisions would need to be based on recruitment projections since all squids die within 1 to 2 years. The risk of applying longer-lived finfish management frameworks to *D. gigas* should be evaluated, giving proper consideration to the possible implementation of an in-season framework in the SPRFMO. This type of management issue is a common problem for cephalopod stocks without adaptive, in-season management.

### *Reference Points*

Cohort-specific stock assessments and reference points (RPs) are required to determine the stock status of cephalopod species with annual lifespans because maturation and growth rates of intra-annual cohorts can exhibit a high degree of seasonal and inter-annual variability (Arkhipkin and Laptikhovsky, 1994). The types of data available for stock

assessments determine which methods can be used for reference point estimation, but equally important is the appropriateness of the reference points to the short lifespan, semelparous reproduction and environmentally-driven recruitment variability of cephalopods. Data-rich stocks for which catch, effort and biological data are available to conduct a weekly, in-season depletion models (e.g., *D. gahi*, Arkhipkin et al., 2008; Roa-Ureta, 2012; *I. argentinus*, Rosenberg et al., 1990; Winter, 2019b) have straightforward RP estimation. However, most managed cephalopod stocks are limited to landings data and possibly an annual survey abundance or biomass index (usually not from a survey designed to capture cephalopods). For stocks like these without analytical assessments, RPs are more difficult to estimate.

Globally, many marine stocks are managed using  $F_{MSY}$  and  $B_{MSY}$  reference points (Zheng et al., 2019). However, the overfishing definition for an annual cephalopod stock should minimize the risk of recruitment overfishing by ensuring that spawner escapement during year  $t$  exceeds a threshold minimum spawning stock biomass ( $SSB_{min}$ ) to ensure a high probability of adequate recruitment in year  $t+1$ . To satisfy this objective, percent maximum spawning potential (%MSP) RPs are recommended over MSY-based RPs (Basson et al., 1996). Drawbacks to per-recruit models is that they require cohort-specific, age-based input data that are frequently not available for cephalopods, and traditional per-recruit models assume that natural mortality is constant with age. For cephalopods, natural mortality rates included in per-recruit models that do not account for both spawning and non-spawning natural mortality and for species-specific aging error, can substantially underestimate both %MSP and MSY-based RPs (Hendrickson and Hart, 2006).

Reference points used for data-poor stocks without analytical assessment models tend to be biomass-based because data for fishing mortality rate estimation are generally not available (Table 1). For example, the simple method previously described for estimation of a  $B_{Lim}$  RP for the NAFO-regulated northern stock component of *I. illecebrosus*. The method

does not assume any specific underlying stock dynamics and is considered more appropriate than production model-based RPs given that the assumptions of such models are not met for semelparous cephalopods (e.g., constant natural mortality) and the major influence of environmental variability on the availability and abundance of this squid resource to the northern fisheries. Another advantage of this  $B_{Lim}$  RP is that it accounts for *I. illecebrosus* biomass during low productivity periods and can be re-estimated for use under a high productivity regime when necessary. A second RP estimation method that accounts for shifts in squid stock productivity regimes involves the *T. pacificus* stocks managed by Japan. MSY-based RPs were computed annually for each cohort based on Beverton-Holt stock-recruit relationships and survey indices reflecting the environmental regimes to which the stocks were subject (Kidokoro and Mori, 2004).

### *Effort-based management*

Effort-based management of cephalopod stocks was first proposed by Caddy (1983b) who suggested using effort limitation with short-term adjustments to allow a maximum percentage (40%) of the available biomass to be taken by the fishery every year. The Falkland Islands fisheries for *I. argentinus* and *D. gahi* were the first to adopt and refine this approach (Beddington et al., 1990; Rosenberg et al., 1990; Rodhouse et al., 2013). Depletion of the stock was monitored in-season on a weekly basis and management was initially TAC-based. During years of low recruitment, fishing was stopped on the date when predicted spawning stock biomass fell below the fixed minimum management target for biomass (now set at 10,000 t for each cohort of *D. gahi*, Barton, 2002). Constant proportion spawner escapement (F40%) was managed for *I. argentinus* by setting a limit of allowed fishing days estimated from prior catchability and the estimated time spent fishing by commercial fleets (Beddington et al., 1990, Rosenberg et al., 1990). Management by total allowable effort,

TAE), has the advantage of reducing catch misreporting (Beddington et al., 1990) and the race to fish. This approach has not been widely adopted elsewhere due to difficulties in obtaining real-time fishery-dependent data necessary for incorporation into a depletion model (Brodziak and Rosenberg, 1999; Augustyn et al., 1992).

### *Catch-based management*

Management based on total allowable catch (TAC) has traditionally been more widely used for managing cephalopod stocks than TAE management (Baudron et al., 2010). For example, the Peruvian fishery for *D. gigas* is managed by setting quotas based on acoustic survey estimates and a surplus production model (Csirke et al., 2019). The Chilean fishery for *D. gigas* is also managed by setting quotas and restricting access to the fishery for different types of fleets (Rosa et al., 2013). By law, these quotas must be within the range of quotas that are annually fixed by a scientific technical committee, taking into account the stock assessment conducted by the Chilean Fisheries Development Institute. The stock assessment includes different models (catch-only method, surplus production model and depletion model with successive pulses) in order to cover the high uncertainty produced by the different hypotheses of stock structure and abundance indices (Payá, 2016).

In the U.S., stock assessment results feed into a resource management framework established by federal law. The stock status determination is a comparison of the terminal-year biomass and fishing mortality rate estimates in relation to  $B_{MSY}$  and  $F_{MSY}$  target and threshold Biological Reference Points or proxies thereof. The *D. pealeii* stock in the Northwest Atlantic is managed by a U.S. management body, but the broader-ranging ommastrephid species, *I. illecebrosus*, is a transboundary stock that is managed separately, as stock components, by the U.S., Canada and NAFO. The *I. illecebrosus* fishery in NAFO waters is regulated by an annual TAC, fishery start date, and minimum codend mesh size, but

the jig fishery in Canadian waters is unregulated. Annual quotas with the implementation of trip limits following fishery closures are the primary management measures for the *D. pealeii* and *I. illecebrosus* fisheries in U.S. waters, but many other measures have been adopted for both stocks as part of their respective Fishery Management Plans. For example, the *D. pealeii* fishery is also managed based on trimester quotas, a minimum codend mesh size and a bycatch quota for a co-occurring finfish species. Although both species have sub-annual life cycles, neither species is assessed annually in the U.S.. Instead, catch, survey relative abundance/biomass indices and other relevant data are provided annually to a scientific committee which recommends whether the Acceptable Biological Catch, which is used to compute the quota (after subtracting discards), should be adjusted.

#### *Additional management measures*

In conjunction with TAC and TAE, additional management measures are also used in cephalopod fisheries. These include spatial and seasonal fishing restrictions, mesh size restrictions and individual transferable quotas (ITQs) to decrease the level of “competitive” fishing (Boyle and Rodhouse, 2005). U.S. fisheries for *D. pealeii* and *I. illecebrosus* were the first cephalopod fisheries to become certified by the Marine Stewardship Council; a non-profit organization which sets fishery-specific standards for sustainable fishing and regularly audits the certified fisheries. However, the current list of parameters used to evaluate fishery impacts on resource sustainability were not adopted with short-lived, semelparous species in mind. Spatial restrictions are used in the Falkland Islands to prevent fishing on juvenile squid in their nursery grounds, as well as spawning squid in their spawning grounds. The locations and timings of closed areas may vary inter-annually depending on environmental conditions, which influence the distribution of squid (Arkhipkin et al., 2008). However, inshore spawning and nursery grounds are permanently closed to commercial fishing as marine



protected areas (MPA). These management practices keep the *D. gahi* stock at a sustainable level and prevent its overfishing in years of low abundance (Arkhipkin et al., 2015).

## Conclusions

The ICES symposium on the legacy of Johan Hjort, held in June 2019 in Bergen, Norway, has brought into perspective the rapid evolvement of fisheries science as a modern discipline, in response to the economic demands of fishing industries. During his time, Hjort focused on finfish, whale, and shrimp fisheries, but in the decades since, cephalopods have become an increasingly vital component of marine resources. Equally important, the economic demands for fishing are nowadays associated with social and environmental concerns on a global scale.

The legacy of Hjort continues to be upheld; fisheries science based on rigorous quantitative methods. For cephalopod stocks, this has required the adaptation of stock assessment methods to the unique characteristics of short-lived animals and highly variable abundance of their populations (Table 1). The most comprehensive and versatile models for cephalopod fisheries have so far proven to be the depletion models, and advances of these models continue to be developed. The application of depletion models requires catch and effort data collected at short time steps, which allows biomass estimates to be calculated iteratively during a fishing season. Given cephalopods' rapid life history and terminal spawning it would be desirable to use reference points connected to escapement biomass levels that would secure sufficient spawning. Depletion models are particularly useful for fisheries managed with these reference points because of their rapid dynamics. Reference points based on fishing mortality levels that account for natural mortality differences between non-spawning and spawning parts of the life cycle are also well adapted and useful when ageing data are available to conduct pre-recruit calculations.

However, the data-rich requirement of high-frequency catch and effort reporting may not be met in all types of cephalopod fisheries, so diverse alternative methods have been put into practice. For example, various squid fisheries use catch-only and surplus production methods to determine RPs of  $B_{MSY}$  and  $F_{MSY}$ , swept area methods to determine proxy  $B_{MSY}$ , or index-based methods for RPs  $B_{lim}$  or  $F_{50\%}$  (Table 1). Our review presents a synthesis of these methods, while anticipating that further work is required on uncertainty estimation. Future research is also needed on the appropriateness of the various RPs, and on the frequency required for RP estimation given the complex life histories of cephalopods, their short lifespans, and their rapid recruitment responses to changing environmental conditions.

## References

- Agnew, D. J., Baranowski, R., Beddington, J. R., des Clers, S., and Nolan, C. P. 1998. Approaches to assessing stocks of *Loligo gahi* around the Falkland Islands. *Fisheries Research*, 35: 155–169.
- Agnew, D. J., Beddington, J. R., and Hill, S. L. 2002. The potential use of environmental information to manage squid stocks. *Canadian Journal of Fisheries and Aquatic Sciences*, 59: 1851–1857.
- Akiyama, S., Kaihara, S., Arimoto, T., and Tokai, T. 2004. Size selectivity of a trammel net for oval squid *Sepioteuthis lessoniana*. *Fisheries Science*, 70: 945–951.
- Aleman, J., Rivot, E., Foucher, E., Vigneau, J., and Robin, J.-P. 2017. A Bayesian two-stage biomass model for stock assessment of data-limited species: An application to cuttlefish (*Sepia officinalis*) in the English Channel. *Fisheries Research*, 191: 131–143.
- Alvarez Perez, J.A. 2002. Biomass dynamics of the squid *Loligo plei* and the development of a small-scale seasonal fishery off southern Brazil. *Bulletin of Marine Science*, 71: 633–651.

- Arkhipkin, A. I., 2013. Squid as nutrient vectors linking Southwest Atlantic marine ecosystems. *Deep-Sea Research. Part II: Topical Studies in Oceanography*, 95: 7–20.
- Arkhipkin, A. I., Bizikov, V. A., Doubleday, Z. A., Laptikhovsky, V. V., Lishchenko, F. V., Perales-Raya, C., and Hollyman, P. R., 2018. Techniques for Estimating the Age and Growth of Molluscs: Cephalopoda. *Journal of shellfish research*, 37(4), 783–793.
- Arkhipkin, A.I., Blake, D., and Iriarte, V. 2018. Introduction of seal exclusion devices to avoid seal bycatch in squid trawling fishery in the Falkland Islands. *ICES CM 2018/N: 33*.
- Arkhipkin, A. I., P. Jereb and S. Ragonese, 2000. Growth and maturation in two successive seasonal groups of the short-finned squid, *Illex coindetii* from the Strait of Sicily (central Mediterranean). *ICES Journal of Marine Science*, 57: 31–41.
- Arkhipkin, A.I., and Laptikhovsky, V.V. 1994. Seasonal and interannual variability in growth and maturation of winter-spawning *Illex argentinus* (Teuthida, Ommastrephidae) in the Southwest Atlantic. *Aquatic Living Resources*, 7: 221–232.
- Arkhipkin, A.I., and Middleton, D.A.J. 2002. Inverse patterns in abundance of *Illex argentinus* and *Loligo gahi* in Falkland waters: possible interspecific competition between squid? *Fisheries Research*, 59: 181–196.
- Arkhipkin, A., Middleton, D. A. J., and Barton, J. 2008. Management and conservation of a short-lived fishery resource: *Loligo gahi* around the Falkland Islands. *American Fisheries Society Symposium*, 49: 1243–1252.
- Arkhipkin, A.I., and R. Roa, 2005. Identification of ontogenetic growth models for squid. *Marine and Freshwater Resources*, 56: 371–386.
- Arkhipkin, A. I., Rodhouse, P. G., Pierce, G. J., Sauer, W., Sakai, M., Allcock, L., ... and Chen, C. S. 2015. World squid fisheries. *Reviews in Fisheries Science and Aquaculture*, 23(2): 92–252.

Arkhipkin, A. I., and Shcherbich, Z. N., 2012. Thirty years' progress in age determination of squid using statoliths. *Journal of the Marine Biological Association of the United Kingdom*, 92(6), 1389–1398.

Arkhipkin, A., Zawadowski, T., Shcherbich, Z., and Winter, A. 2016. Predatory impact on Patagonian squid after sudden range expansion of Argentine squid. *ICES CM* 2016/D: 137.

Augustyn, C.J., Lipiinski, M., Sauer, W., 1992. Can the *Loligo* squid fishery be managed effectively? A synthesis of research on *Loligo vulgaris reynaudii*. *South African Journal of Marine Science*, 12, 903–918.

Bannerot, S. P., and Austin, C. B. 1983. Using frequency distributions of catch per unit of effort to measure fish-stock abundance. *Transactions of the American Fisheries Society*, 112: 608–617.

Barros, P., 2007. Biomass dynamic model with environmental effects-User instructions. Report of the FAO Working Group on the Assessment of Small Pelagic Fish off Northwest Africa. Agadir, Morocco, 17–26.

Barton, J. 2002. Fisheries and fisheries management in Falkland Islands Conservation Zones. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 12: 127–135.

Basson, M., J.R. Beddington, J.A. Crombie, S.J. Holden, L.V. Purchase and G.A. Tingely. 1996. Assessment and management techniques for migratory annual squid stocks: the *Illex argentinus* fishery in the southwest Atlantic as an example. *Fisheries Research*, 28 (1): 3–27.

Baudron, A., Ulrich, C., Nielsen, J.R., and Boje, J. 2010. Comparative evaluation of a mixed-fisheries effort-management system based on the Faroe Islands example. *ICES Journal of Marine Science*, 67: 1036–1050.

Beddington, J. R., Rosenberg, A. A., Crombie, J. A., & Kirkwood, G. P. 1990. Stock assessment and the provision of management advice for the short fin squid fishery in Falkland Islands waters. *Fisheries Research*, 8(4): 351-365.

Bellido, J.M., Pierce, G.J. and Wang, J., 2001. Modelling intra-annual variation in abundance of squid *Loligo forbesi* in Scottish waters using generalised additive models. *Fisheries Research*, 52, 23–39.

Boyle, P.R. , 2002. Cephalopod biomass and production. *Bulletin of Marine Science*, 71: 13–16.

Boyle, P.R. and P.G. Rodhouse, 2005. *Cephalopods: ecology and fisheries*. Blackwell, Oxford, 452 pp.

Bravo de Laguna, J. 1989. Managing an international multispecies fishery: the Saharan trawl fishery for cephalopods. In *Marine Invertebrate Fisheries: Their Assessment and Management*, pp. 591–612. Ed. by J. F. Caddy. John Wiley and Sons, New York. 752 pp.

Brodziak, J. K. T. and L. C. Hendrickson. 1999. An analysis of environmental effects on survey catches of squids *Loligo pealei* and *Illex illecebrosus* in the northwest Atlantic. *Fishery Bulletin U.S.*, 97: 9–24.

Brodziak, J. K. T., and Macy, W. K. 1996. Growth of long-finned squid, *Loligo pealei*, in the northwest Atlantic. *Fishery Bulletin U.S.*, 94: 212–236.

Brodziak, J.K.T. and Rosenberg, A.A., 1993. A method to assess the squid fisheries in the northwest Atlantic. *ICES Journal of Marine Science*, 50: 187–194.

Caddy, J. F. (Editor), 1983a. *Advances in assessment of world cephalopod resources*. FAO Fisheries Technical Papers, 231, Rome.

Caddy, J. F., 1983b. The cephalopods: factors relevant to their population dynamics and to the assessment and management of stocks. In: *Advances in assessment of world cephalopod resources*. FAO Fisheries Technical Papers, 231: 416–457, Rome.

Caddy, J.F. 1991. Daily rings on squid statoliths: an opportunity to test standard population models? In: *Squid age determination using statoliths*. Eds. P.Jereb, S.Ragonese and S. von Boletzky. N.T.R.-I.T.P.P. Special publ., Mazara del Vallo, Italy, pp. 53–66.

Caddy, J.F., 1996. Modelling natural mortality with age in short-lived invertebrate populations: definition of a strategy of gnomonic time division. *Aquatic Living Resources*, 9: 197–207.

Caddy, J. F., and P. G. Rodhouse, 1998. Cephalopod and groundfish landings: evidence for ecological change in global fisheries? *Reviews in Fish Biology and Fisheries*, 8: 431–444.

Cao, J., Chen, X, and Tian, S. 2015. A Bayesian hierarchical DeLury model for stock assessment of the west winter-spring cohort of neon flying squid (*Ommastrephes bartramii*) in the northwest Pacific Ocean. *Bulletin of Marine Science*, 91: 1-13.

Challier, L., Dunn, M. R., and Robin, J. P. 2005. Trends in age-at-recruitment and juvenile growth of cuttlefish, *Sepia officinalis*, from the English Channel. *ICES Journal of Marine Science*, 62(8): 1671–1682.

Chang, K.-Y., Chen, C.-S., Chiu, T.-Y., Huang, W.-B., and Chiu, T.-S. 2016. Argentine shortfin Squid (*Illex argentinus*) stock assessment in the Southwest Atlantic using geostatistical techniques. *Terrestrial, Atmospheric and Oceanic Sciences*, 27: 281–292.

Chapman, D.G., 1974. Estimation of population size and sustainable yield of sei whales in the Antarctic. *Reports of International Whaling Commission*, 24: 82–90.

Chen, C.S., Pierce, G.J., Wang, J., Robin, J.-P., Poulard, J.C., Pereira, J., Zuur, A.F., Boyle, P.R., Bailey, N., Beare, D.J., Jereb, P., Ragonese, S., Mannini, A. Orsi-Relini, L. 2006. The apparent disappearance of *Loligo forbesi* from the south of its range in the 1990s: Trends in *Loligo* spp. abundance in the northeast Atlantic and possible environmental influences. *Fisheries Research* 78: 44–54.

Chen, X., Chen, Y., Tian, S., Liu, B., and Qian, W. 2008. An assessment of the west winter-spring cohort of neon flying squid (*Ommastrephes bartramii*) in the Northwest Pacific Ocean. *Fisheries Research*, 92: 221–230.

Chiu, T.-Y., Chiu, T.-S., and Chen, C.-S. 2017. Movement patterns determine the availability of Argentine shortfin squid *Illex argentinus* to fisheries. *Fisheries Research*, 193: 71–80.

Clark W, M. Dorn, M. Dunn, C. Fernández, M. Haddon, N. Klaer, M. Sissenwine and S. Zhou. 2014. Review of Biological Reference Points for main Chilean fisheries. Report of the Second International Workshop. Annex IV in Payá et al., 2014. Revisión de los puntos biológicos de referencia (Rendimiento Máximo Sostenible) en las pesquerías nacionales. (Review of Biological Reference Points for main Chilean fisheries). Instituto de Fomento Pesquero. Chile. 51 pp + 8 Annexes. <https://doi.org/10.13140/RG.2.1.3048.0246>.

Coelho, M.L. and Rosenberg, A.A., 1984. Causal analysis of some biological data for *Illex illecebrosus* from the Scotian Shelf. *NAFO Scientific Council Studies*, 7: 61–66.

Colla-De-Robertis, E., Da-Roch, J.-M., García-Cutrín, J., Gutiérrez, M.-J. and Prellezo, R., 2019. A Bayesian estimation of the economic effects of the Common Fisheries Policy on the Galician fleet: A dynamic stochastic general equilibrium approach. *Ocean and Coastal Management*, 167: 137–144.

Collins, M. A., Boyle, P. R., Pierce, G. J., Key, L. N., Hughes, S. E., and Murphy, J. 1999. Resolution of multiple cohorts in the *Loligo forbesi* population from the west of Scotland. *ICES Journal of Marine Science*, 56: 500–509.

Csirke, J., Argüelles, J., Alegre, A., Ayón, P., Bouchon, B., Castillo, G., Castillo, R., Cisneros, R., Guevara-Carrasco, R., Lau, L., Mariátegui, L., Salazar, C., Tafur, R., Torrejón, J., Yamashiro, C. 2018. Biology, population structure and fishery of jumbo flying squid (*Dosidicus gigas*) in Peru. *Boletín Instituto del Mar del Perú*, 33(2): 302–364.

- Czudaj, S., Pereira, J., Moreno, A., Costa, A. M., Saint-Paul, U., and Rosa, R. 2012. Distribution, abundance, reproduction and ageing of the common bobtail squid *Sepietta oweniana* (Sepiolidae, Cephalopoda) from the Portuguese Coast. *Marine Biology Research*, 8(1): 74–86.
- Dawe, E. G., and Beck, P. C. 1997. Population structure, growth, and sexual maturation of short-finned squid (*Illex illecebrosus*) at Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 137–146.
- De Lury, D.B., 1947. On the estimation of biological populations. *Biometrics*, 3: 145–167.
- Denis, V., and Robin, J-P. 2002. Present status of the French Atlantic fishery for cuttlefish (*Sepia officinalis*). *Fisheries Research*, 52: 11–22.
- Ding, Q., Cao, J., and Chen, X. 2019. Stock assessment of the western winter-spring cohort of *Ommastrephes bartramii* in the Northwest Pacific Ocean using a Bayesian hierarchical DeLury model based on daily natural mortality during 2005-2015. *Scientia Marina*, 83: 155–166.
- Domain, F., Jouffre, D., and Caverivière, A. 2000. Growth of *Octopus vulgaris* from tagging in Senegalese waters. *Journal of the Marine Biological Association of the United Kingdom*, 80(4): 699–705.
- Doubleday, Z.A., Prowse, T.A.A., Arkhipkin, A., Pierce, G.J., Semmens, J., Steer, M., Leporati, S.C., Lourenço, S., Quetglas, A., Sauer, W. and Gillanders, B.M., 2016. Global proliferation of cephalopods. *Current Biology*, 26: R406–R407.



Dow, R.L., 1977. Effects of climatic cycles on the relative abundance and availability of commercial marine and estuarine species. *ICES Journal of Marine Science*, 37(3): 274–280.

Dunn, M. R. 1999. Aspects of the stock dynamics and exploitation of cuttlefish, *Sepia officinalis* (Linnaeus, 1758), in the English Channel. *Fisheries Research*, 40: 277–293.

Ehrhardt, N.M., Jacquemin, P.S., Garcia, F.B., Gonzalez, G.D., Lopez, J.M.B., Ortiz, J.C., and Solis, A.N., 1983. On the fishery and biology of the giant squid *Dosidicus gigas* in the Gulf of California, Mexico. In: Caddy, J.F. (Ed.), *Advances in Assessment of World Cephalopod Resources*. Fisheries Technical Paper No. 231, FAO, Rome, pp. 306–340.

Falkland Islands Government, 2019. Fisheries Department Fisheries Statistics, Volume 23, 2018: 102 pp. Stanley, FIG Fisheries Department.

FAO, 2019. FAO Yearbook 2017. *Fishery and Aquaculture statistics*. Rome, FAO.

Faure, V. 2000. Dynamiques spatiale et temporelle des populations de poulpes (*Octopus vulgaris*) en Afrique de l'Ouest: Influence des fluctuations environnementales et des relations interspécifiques. Thèse doc., univ. Montpellier-II, 403 p.

Fogarty, M. J. 1989. Forecasting yield and abundance of exploited invertebrates. *Marine Invertebrate Fisheries: Their Assessment and Management*. Wiley, 701724.

Gasalla, M.A., Rodrigues, A.R., Postuma, F.A., 2010. The trophic role of the squid *Loligo plei* as a keystone species in the South Brazil Bight ecosystem. *ICES Journal of Marine Science*, 67(7), 1413–1424.

Gavaris, S. 1988. An adaptive framework for the estimation of population size. CAFSAC Research Documents, 88/129 (mimeo).

Georgakarakos, S., Koutsoubas, D., and Valavanis, V., 2006. Time series analysis and forecasting techniques applied on loliginid and ommastrephid landings in Greek waters. *Fisheries Research*, 78: 55–71.

Glazer, J.P., and Butterworth, D.S. 2006. Some refinements of the assessment of the South African squid resource, *Loligo vulgaris reynaudii*. Fisheries Research, 78: 14–25.

González, A. F., B. G. Castro, and A. Guerra. 1996. Age and growth of the short-finned squid *Illex coindetii* in Galician waters (NW Spain) based on statolith analysis. ICES Journal of Marine Science, 53: 802–810.

Gras, M., Roel, B.A., Coppin, F., Foucher, E., and Robin, J.-P. 2014. A two-stage biomass model to assess the English Channel cuttlefish (*Sepia officinalis* L.) stock. ICES Journal of Marine Science, 71: 2457–2468.

Gras, M., Safi, G., Lebretonchel, H., Quinquis, J., Foucher, E., Koueta, N., and Robin, J. –P. 2016. Stock structure of the English Channel common cuttlefish *Sepia officinalis* (Linnaeus, 1758) during the reproduction period. Journal of the Marine Biological Association of the United Kingdom, 96(1): 167–176.

Harley, S. J., Myers, R. A., and Dunn, A. 2001. Is catch-per-unit-effort proportional to abundance? Canadian Journal of Fisheries and Aquatic Sciences, 58: 1760 – 1772.

Hastie, L.C., 1996. Estimation of trawl codend selectivity for squid (*Loligo forbesi*), based on Scottish research vessel survey data. ICES Journal of Marine Science, 53: 741–744.

Hendrickson, L. C. and M. A. Showell. 2016. Assessment of Northern Shortfin Squid (*Illex illecebrosus*) in Subareas 3+4 for 2015. Northwest Atlantic Fisheries Organization Serial No. 6577 SCR Doc. 16/34REV, 28 p.

<https://www.nafo.int/Portals/0/PDFs/sc/2016/scr16-034.pdf>.

Hendrickson, L. C. 2004. Population biology of northern shortfin squid (*Illex illecebrosus*) in the Northwest Atlantic Ocean and initial documentation of a spawning area. ICES Journal of Marine Science, 61: 252–266.

Hendrickson, L. C. 2011. Effects of a codend mesh size increase on size selectivity and catch rates in a small-mesh bottom trawl fishery for longfin inshore squid, *Loligo pealeii*. *Fisheries Research*, 108: 42–51.

Hendrickson, L. C., and D. R. Hart. 2006. An age-based cohort model for estimating the spawning mortality of semelparous cephalopods with an application to per-recruit calculations for the northern shortfin squid, *Illex illecebrosus*. *Fisheries Research*, 78: 4–13.

Hilborn, R., Walters, C., 1992. *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*. Springer, Chapman and Hall, New York.

Holden, S., Bravington, M. and Kirkwood, G.P., 1990. MSQUID—software for fitting a Delury model to multiple fleets using a maximum likelihood method. Renewable Resources Assessment Group, Imperial College, London.

Holden, S., Kirkwood, G., Bravington, M.V., 1995. *Catch Effort Data Analysis*. The CEDA Package Version 2.01. MRAG Ltd., London.

Hunsicker, M.E., Essington, T.E, Watson, R., and Sumaila, U.R. 2010. The contribution of cephalopods to global marine fisheries: can we have our squid and eat them too? *Fish and Fisheries*, 11: 421–438.

ICES. 2010. Report of the Working Group on Cephalopod Fisheries and Life History (WGCEPH), 9–11 March 2010, Sukarrieta, Spain. ICES CM 2010/SSGEF:09. 95 pp.

ICES. 2014. Report of the Working Group on Cephalopod Fisheries and Life History (WGCEPH), 16–19 June 2014, Lisbon, Portugal. ICES CM 2014/SSGEF:02. 353 pp.

ICES. 2016. Interim Report of the Working Group on Cephalopod Fisheries and Life History (WGCEPH), 8–11 June 2015, Tenerife, Spain. ICES CM 2015/SSGEPD:02. 127 pp.

ICES. 2017. Report of the Working Group on Cephalopod Fisheries and Life History (WGCEPH), 14–17 June 2016, ICES Headquarters, Copenhagen, Denmark. ICES CM 2016/SSGEPD:03. 111 pp.

ICES. 2019. Advisory Plan. <http://doi.org/10.17895/ices.pub.5468>.

Ichii, T., Mahapatra, K., Okamura, H., and Okada, Y. 2006. Stock assessment of the autumn cohort of neon flying squid (*Ommastrephes bartramii*) in the North Pacific based on past large-scale high seas driftnet fishery data. *Fisheries Research*, 78: 286–297.

IOTC. 2016. Assessment of Indian Ocean Indo-Pacific king mackerel (*Scomberomorus guttatus*) using data poor catch-based methods. Indian Ocean Tuna Commission. IOTC–2016–WPNT06–21. 25 p.

Jackson, G. D. 1994. Application and future potential of statolith increment analysis in squids and sepioids. *Canadian Journal of Fisheries and Aquatic Sciences*, 51(11): 2612–2625.

Jacobson, L. D., L. C. Hendrickson and J. Tang. 2015. Solar zenith angles for biological research and an expected catch model for diel vertical migration patterns that affect stock size estimates for longfin inshore squid (*Doryteuthis pealeii*). *Canadian Journal of Fisheries and Aquatic Sciences*, 72(9): 1329–1338.

Jereb, P. and C.F.E. Roper, (eds), 2010. Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 2. Myopsid and Oegopsid Squids. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO.

Jouffre, D., and Caverivière, A. 2005. Combining fishing closure with minimum size of capture to improve octopus production in senegalese waters: an evaluation using analytical modelling. *Phuket Marine Biological Center Research Bulletin*, 66: 307–319.

Keller, S., Robin, J.P., Valls, M., Gras, M., Cabanellas-Reboredo, M., and Quetglas, A. 2015. The use of depletion models to assess Mediterranean cephalopod stocks under the current EU data collection framework. *Mediterranean Marine Science*, 16: 513–523.

Keyl, F., M. Wolff, J. Arguelles, L. Mariategui, R. Tafur, and C. Yamashiro, 2008. A hypothesis on range expansion and spatio-temporal shifts in size-at-maturity of jumbo squid (*Dosidicus gigas*) in the Eastern Pacific ocean. *CalCOFI Reports*, 49: 119–128.

Kidikoro, H., Mori, K. 2004. Stock assessment method and management procedure used for the *Todarodes pacificus* fishery in Japan. ICES CM2004 / CC: 02.

Koen-Alonso, M., Pepin, P., Fogarty, M. J., Kenny, A., and Kenchington, E., 2019. The Northwest Atlantic Fisheries Organization Roadmap for the development and implementation of an Ecosystem Approach to Fisheries: structure, state of development, and challenges. *Marine Policy*, 100: 342–352.

Leporati, S. C., Hart, A. M., Larsen, R., Franken, L. E., and De Graaf, M. (2015). Octopus life history relative to age, in a multi-gear developmental fishery. *Fisheries Research*, 165: 28–41.

Leslie, P.H., Davis, D.H.S., 1939. An attempt to determine the absolute number of rats on a given area. *Journal of Animal Ecology*, 8: 94–113.

Link, J.S. 2010. *Ecosystem-based Fisheries management: confronting tradeoffs*. Cambridge University Press, New York.

Link, J.S., Ihde, T.F., Harvey, C.J., Gaichas, S.K., Field, J.C., Brodziak, J.K.T., Townsend, H.M., and Peterman, R.M. 2012. Dealing with uncertainty in ecosystem models: The paradox of use for living marine resource management. *Progress in Oceanography*, 102: 102–114.

Lipinski, M.R. 1994. Differences among basic biological parameters in a population of chokka squid *Loligo vulgaris reynaudii* (Cephalopoda: Loliginidae) sampled by three methods. *South African Journal of Marine Science*, 14: 281–286.

Lourenço, S., and Pereira, J., 2006. Estimating standard landings per unit effort for an octopus mixed components fishery. *Fisheries Research*, 78: 89–95.

Macy, W. K. III, and J. K. T. Brodziak. 2001. Seasonal maturity and size at age of *Loligo pealeii* in waters of southern New England. *ICES Journal of Marine Science*, 58: 852–864.

Maunder, M. N., and Punt, A.E. 2004. Standardizing catch and effort data: a review of recent approaches. *Fisheries Research*, 70: 141–159.

Maynou, F. 2015. Application of a multi-annual generalized depletion model to the assessment of a data-limited coastal fishery in the western Mediterranean. *Scientia Marina*, 79: 157–168.

McAllister, M.K., Hill, S.L., Agnew, D.J., Kirkwood, G.P., and Beddington, J.R. 2004. A Bayesian hierarchical formulation of the De Lury stock assessment model for abundance estimation of Falkland Islands' squid (*Loligo gahi*). *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 1048–1059.

McKeown, N.J., Arkhipkin, A.I., and Shaw, P.W. 2019. Genetic analysis reveals historical and contemporary population dynamics in the longfin squid *Doryteuthis gahi*: implications for cephalopod management and conservation. *ICES Journal of Marine Science*, 76: 1019–1027.

McGregor, V., and Tingley, G.A. 2016. A preliminary evaluation of depletion modelling to assess New Zealand squid stocks. *New Zealand Fisheries Assessment Report 2016/25*. 28 p.

Medellín-Ortiz, A., Cadena-Cárdenas, L., and Santana-Morales, O. 2016. Environmental effects on the jumbo squid fishery along Baja California's west coast. *Fisheries Science*, 82: 851–861.

Mehanna, S.F., Al-kharusi, L., and Al-Habsi, S. 2014. Population dynamics of the pharaoh cuttlefish *Sepia pharaonis* (Mollusca: Cephalopoda) in the Arabian Sea coast of Oman. *Indian Journal of Fisheries*, 61: 7–11.

Meissa, B., and Gascuel, D. 2015. Overfishing of marine resources: some lessons from the assessment of demersal stocks off Mauritania. *ICES Journal of Marine Science*, 72: 414–427.

Morales-Bojórquez, E., Hernández-Herrera, A., Cisneros-Mata, M.A., and Nevárez-Martínez, M.O. 2008. Improving estimates of recruitment and catchability of jumbo squid *Dosidicus gigas* in the Gulf of California, Mexico. *Journal of Shellfish Research*, 27: 1233–1237.

Murata, M., 1989. Population assessment, management and fishery forecasting for the Japanese common squid, *Todarodes pacificus*. In: Caddy, J.F. (Ed.), *Marine Invertebrate Fisheries: Their Assessment and Management*. Wiley, New York, pp. 613–636.

NEFSC. 2011. Part B: *Loligo* assessment for 2010. In 51st Northeast Regional Stock Assessment Workshop (51st SAW) Assessment Report. Northeast Fisheries Science Center Ref. Doc. 11-02. Available from <http://www.nefsc.noaa.gov/publications/crd/crd1102/loligo.pdf>.

Orsi-Relini, L., Mannini, A., Fiorentino, F., Palandri, G., and Relini, G. 2006. Biology and fishery of *Eledone cirrhosa* in the Ligurian Sea. *Fisheries Research*, 78: 72–88.

Otero, J., Álvarez-Salgado, X. A., González, A. F., Miranda, A., Groom, S. B., Cabanas, J. M., Smyth, T., et al. 2008. Bottom – up control of *Octopus vulgaris* abundance in a wind-driven upwelling ecosystem (NE Atlantic). *Marine Ecology Progress Series*, 362: 181–192.

Patterson, K.R, 1988. Life history of Patagonian squid *Loligo gahi* and growth parameter estimates using least square fits to linear and von Bertalanffy models. *Marine Ecology Progress Series*, 47: 65–74.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *ICES Journal of Marine Science*, 39(2): 175–192.

Payá, I. 2007. Fishery Report *Loligo gahi*, First Season 2007. Fishery Statistics, Biological Trends and Stock Assessment. Technical Document, Falkland Islands Fisheries Department. 36 pp. <https://doi.org/10.13140/RG.2.2.16389.76006>

Payá, I. 2009. Fishery Report, *Loligo gahi*, Second Season 2009. Fishery Statistics, Biological Trends, Stock Assessment and Risk Analysis. Falkland Islands Fisheries Department, Stanley, Falkland Islands, 48 p.

Payá, I. 2016. Informe 1 de Estatus. Estatus y posibilidades de explotación biológicamente sustentables de los principales recursos pesqueros nacionales año 2017: Jibia 2017. Instituto de Fomento Pesquero, Chile. Subsecretaría de Economía - IFOP. 95 pp + 4 Anexos. <https://doi.org/10.13140/RG.2.2.26341.81128>.

Payá I., C. Canales, D. Bucarey, M. Canales, F. Contreras, E. Leal, R. Tascheri, A. Yáñez, M. Zúñiga, W. Clark, M. Dorn, M. Dunn, C. Fernández, M. Haddon, N. Klaer, M. Sissenwine and S. Zhou. 2014. Revisión de los puntos biológicos de referencia (Rendimiento Máximo Sostenible) en las pesquerías nacionales. (Review of Biological Reference Points for main Chilean fisheries). Instituto de Fomento Pesquero. Chile. 51 pp + 8 Annexes. <https://doi.org/10.13140/RG.2.1.3048.0246>.

Pedersen, M. W., & Berg, C. W. 2017. A stochastic surplus production model in continuous time. *Fish and Fisheries*, 18(2): 226-243.



Pella, J. J., & Tomlinson, P. K. 1969. A generalized stock production model. *Inter-American Tropical Tuna Commission Bulletin*, 13(3): 416-497.

Pierce, G.J., Boyle, P.R., Hastie, L.C., and Key, L., 1994. The life history of *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. *Fisheries Research*, 21: 17–41.

Pierce, G.J., and Guerra, A., 1994. Stock assessment methods used for cephalopod fisheries. *Fisheries Research* 21, 255–285.

Pierce, G.J., Allcock, L., Bruno, I., Bustamante, P., González, A.F., Guerra, A., Jereb, P., Lefkaditou, E., Malham, S., Moreno, A., Pereira, J., Piatkowski, U., Rasero, M., Sánchez, P., Santos, M.B., Santurtún, M., Seixas, S., Sobrino, I. and Villanueva, R. (Editors), 2010.

Cephalopod biology and fisheries in Europe. Cooperative Research Report 303, International

Council for the Exploration of the Sea, 175 pp. ISBN 978-87-7482-078-9.

Roa-Ureta, R.H. 2012. Modelling in-annual pulses of recruitment and hyperstability-hyperdepletion in the *Loligo gahi* fishery around the Falkland Islands with generalized depletion models. *ICES Journal of Marine Science*, 69: 1403–1415.

Roa-Ureta, R. 2018. CatDyn: Fishery Stock Assessment by Catch Dynamics Models version 1.1-1. <https://cran.r-project.org/web/packages/CatDyn/>

Roa-Ureta, R., and Arkhipkin, A. 2007. Short-term stock assessment of *Loligo gahi* at the Falkland Islands: sequential use of stochastic biomass projection and stock depletion models. *ICES Journal of Marine Science*, 64: 3–17.

Roa-Ureta, R., and Nikitschek, E. 2007. Biomass estimation from surveys with likelihood-based geostatistics. *ICES Journal of Marine Science*, 64: 1723–1734.

Roa-Ureta, R.H., Molinet, C., and Bahamonde, N. 2015. Hierarchical statistical framework to combine generalized depletion models and biomass dynamic models in the stock assessment of the Chilean sea urchin (*Loxechinus albus*) fishery. *Fisheries Research*, 171: 59–67.

Robert, M., Faraj, A., McAllister, M. K., and Rivot, E. 2010. Bayesian state-space modelling of the De Lury depletion model: strengths and limitations of the method, and application to the Moroccan octopus fishery. *ICES Journal of Marine Science*, 67: 1272–1290.

Rodhouse, P.G.K., Pierce, G.J., Nichols, O.C., Sauer, W.H.H., Arkhipkin, A.I., Laptikhovskiy, V.V., Lipinski, M.L., Ramos, J., Gras, M., Kidokoro, H., Sadayasu, K., Pereira, J., Lefkaditou, E., Pita, C., Gasalla, M., Haimovici, M., Sakai, M. and Downey, N., 2014. Environmental effects on cephalopod population dynamics: implications for management of fisheries. *Advances in Marine Biology*, 67: 99–233.

Roel, B.A., and Butterworth, D.S. 2000. Assessment of the South African chokka squid *Loligo vulgaris reynaudii*. Is disturbance of aggregations by the recent jig fishery having a negative impact on recruitment? *Fisheries Research*, 48: 213–228.

Rosa, R., R. O’Dor, and G. J. Pierce (Eds), 2013. *Advances in squid biology, ecology and fisheries. Part I. Myopsid squids*. New York: Nova Science Publishers, Inc.

Rosenberg, A.A., Kirkwood, G.P., Crombie, J.A., and Beddington, J.R. 1990. The assessment of stocks of annual squid species. *Fisheries Research*, 8: 335–350.

Rowell, T.W., Trites, R.W., and Dawe, E.G., 1985. Distribution of shortfinned squid (*Illex illecebrosus*) larvae and juveniles in relation to the Gulf Stream Frontal Zone between Florida and Cape Hatteras. *NAFO Scientific Council Studies*, 9: 77–92.

Royer, J., Périès, P., and Robin, J.P. 2002. Stock assessments of English Channel loliginid squids: updated depletion methods and new analytical methods. *ICES Journal of Marine Science*, 59: 445-457.

Royer, J., Pierce, G.J., Foucher, E., and Robin, J.-P., 2006. The English Channel stock of *Sepia officinalis*: modeling variability in abundance and impact of the fishery. *Fisheries Research*, 78: 96–106.

Sato, T., and Hatanaka, H., 1983. A review of the assessments of Japanese distant-water fisheries for cephalopods. In: Caddy, J.F. (Ed.), In: *Advances in Assessment of World Cephalopod Resources*, Fisheries Technical Paper No. 231, FAO, Rome, pp. 145–203.

Schaefer, M.B., 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. *Bulletin of the Inter-American Tropical Tuna Commission*, 1: 27–56.

Scott, F., Jardim, E., Millar, C.P. and Cerviño, S., 2016. An applied framework for incorporating multiple sources of uncertainty in fisheries stock assessments. *PLoS ONE*, 11 (5): e0154922. doi:10.1371/journal.pone.0154922.

Sobrino, I., Silva, L., Bellido, J.M., and Ramos, F., 2002. Rainfall, river discharges and sea temperature as factors affecting abundance of two coastal benthic cephalopod species in the Gulf of Cadiz (SW Spain). *Bulletin of Marine Science*, 71 (2): 851–865.

Sobrino, I., Rueda, L., Tugores, M.P., Burgos, C., Cojan, M., and Pierce, G.J., 2020. Abundance prediction and influence of environmental parameters in the abundance of Octopus (*Octopus vulgaris* Cuvier, 1797) in the Gulf of Cadiz. *Fisheries Research*, 221: 105382.

Solow, A.R., 2002. Fisheries recruitment and the North Atlantic Oscillation. *Fisheries Research*, 54: 295–297.

SPRFMO\_SC, 2017. Report of the 5th Scientific Committee meeting. SPRFMO. 51 pp. <https://www.sprfmo.int/assets/Meetings/Meetings-2013-plus/SC-Meetings/4th-SC-Meeting-2016/SC04-report/SC-04-FinalReport-Rev1-25Oct2016.pdf>.

Tokai, T., and Ueta, Y. 1999. Estimation of size selectivity for oval squid *Sepioteuthis lessoniana* in the squid jigging fishery of Tokushima Prefecture. *Fisheries Science*, 65: 448–454.

Venables, W.N., and Dichmont, C.M. 2004. GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. *Fisheries Research*, 70: 319–337.

Waluda, C. M., and Rodhouse, P. G., 2006. Remotely sensed mesoscale oceanography of the Central Eastern Pacific and recruitment variability in *Dosidicus gigas*. *Marine Ecology Progress Series*, 310: 25–32.

Waluda, C. M., Rodhouse, P. G., Podestá, G. P., Trathan, P. N., and Pierce, G.J. 2001. Surface oceanography of the inferred hatching grounds of *Illex argentinus* (Cephalopoda: Ommastrephidae) and influences on recruitment variability. *Marine Biology*, 139: 671–679.

Wang, J., Yu, W., Chen, X., and Chen, Y. 2016. Stock assessment for the western winter-spring cohort of neon flying squid (*Ommastrephes bartramii*) using environmentally dependent surplus production models. *Scientia Marina*, 80: 69–78.

Winter, A. 2019a. Falkland calamari (*Doryteuthis gahi*) stock assessment, 2<sup>nd</sup> season 2019. Falkland Islands Fisheries Department, Stanley, Falkland Islands, 36 p.

Winter, A. 2019b. Shortfin squid *Illex argentinus*, Joint survey and stock assessment. Falkland Islands Fisheries Department, Stanley, Falkland Islands, 17 p.

Winter, A., and Arkhipkin, A. 2015. Environmental impacts on recruitment migrations of Patagonian longfin squid (*Doryteuthis gahi*) in the Falkland Islands with reference to stock assessment. *Fisheries Research*, 172: 85–95.

Xinjun, C., Yong, C., Siquan, T., Bilin, L., and Weiguo, Q. 2008. An assessment of the west winter – spring cohort of neon flying squid (*Ommastrephes bartramii*) in the Northwest Pacific Ocean. *Fisheries Research*, 92: 221–230.

Young, I.A.G., Pierce, G.J., Daly, H.I., Santos, M.B., Key, L.N., Bailey, N., Robin, J.-P., Bishop, A.J., Stowasser, G., Nyegaard, M., Cho, S.K., Rasero, M., and Pereira, J.M.F. 2004. Application of depletion methods to estimate stock size in the squid *Loligo forbesi* in Scottish waters (UK). *Fisheries Research*, 69: 211–227.

Zheng, N., Wang, S., and N. Cadigan, N. 2019. Local sensitivity equations for maximum sustainable yield reference points. *Theoretical Population Biology*, 130: 143–159.

Zhou, S., Punt, A.E., Smith, A.D.M., Ye, Y., Haddon, M., Dichmont, C.M., and Smith, D.C. 2018. An optimized catch-only assessment method for data poor fisheries. *ICES Journal of Marine Science*, 75: 964–976.

Zuur, A.F. and Pierce, G.J., 2004. Common trends in Northeast Atlantic squid time series. *Journal of Sea Research*, 52: 57–72.