5-5-2019

A Review of the Global Commercial Cephalopod Fishery, with a Focus on Apparent Expansion, Changing Environments, and Management

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NSUWorks Citation

Corey Clark. 2019. *A Review of the Global Commercial Cephalopod Fishery, with a Focus on Apparent Expansion, Changing Environments, and Management.* Capstone. Nova Southeastern University. Retrieved from NSUWorks, . (343) https://nsuworks.nova.edu/cnso_stucap/343.

Capstone of
Corey Clark

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science

M.S. Marine Biology

Nova Southeastern University
Halmos College of Natural Sciences and Oceanography

May 2019

Approved:
Capstone Committee

Major Professor: Charles Messing, Ph.D.

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HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

A Review of the Global Commercial Cephalopod Fishery, with a Focus on Apparent Expansion, Changing Environments, and Management

By
Corey James Clark

Submitted to the Faculty of
Halmos College of Natural Sciences and Oceanography
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:

Marine Biology

Nova Southeastern University

05/31/2019

A Capstone Paper

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4. Abstract

Cephalopods are both important predators and prey in many marine environments and important fishery resources in many countries. The global fishery has expanded almost continuously from landings of 580,000 metric tonnes in 1950 to over 4 m.t. in 2007. Cephalopods are ecological opportunists with highly plastic biological characteristics and varied population dynamics. Nearly all commercially harvested species are short-lived and can reproduce quickly, enabling them to evolve more rapidly under high selection pressure relative to many fish competitors and predators. As a result, they may have the biological means to be successful under conditions of long-term global climate change. This capstone reviews current information on cephalopod life history, morphology and taxonomy, population dynamics, and recruitment as they relate to fishery assessments, proper management, associated gear, and the impacts of their proper or improper use. Despite the adaptive capabilities of cephalopods, the sustainability of heavy fishing effort will be questioned in the future as the impacts of socio-cultural values and economic importance continue to rise across the globe. The correlation between increased oceanic temperatures and the global proliferation of cephalopods may be inferred from the literature; however, this does not provide direct causality, nor does it suggest that cephalopods may be fished extensively without proper management and guidance. Future endeavors to promote stock and population sustainability via proper management and assessments will increase the likelihood of enjoying cephalopod products in all of their forms across the globe.

Keywords

Cephalopods, biology, trophic relationship, commercial fisheries, artisanal fisheries, fishing gear, assessments, management, sustainability.

5. Introduction

Cephalopods are market and restaurant mainstays in many countries. Many restaurants in coastal cities and states offer cephalopod appetizers and entrees. Fried squid and octopus are served in a variety of soups, salads, and other dishes. In Barcelona, Spain, I noticed that nearly every restaurant had either squid or octopus as a seafood option, while La Boqueria seafood vendors offered fresh or frozen cephalopod for purchase. I began to wonder whether such fishing pressure was sustainable, as I only visited one coastal city in one country, without looking into the imports and exports of the nation. The cephalopods I saw in Spain may have arrived from Morocco or from the Spanish Galician fleet, but I began to question whether such harvest is sustainable long-term, especially because Paqoutte and Lem (2008) state that Spain is one of the largest global seafood markets.

Aside from the import and export side of marine fisheries, assessment and stock management of commercially valuable cephalopods have become important. Fisheries data are critical for understanding whether a specific cephalopod stock has been over-exploited or proliferating. Such data from regulated targeted fishing and bycatch are "generally noted as one catch" (Keledhjian et al. 2014, p. 15). However, cephalopod fisheries continue to run into problems typical of any fishery. For example, Pope (2009) reported that fisheries have become subject to political pressures depending upon their implementation of more effective management techniques during closed season and alternative import methods.

Arkhipkin et al. (2015) stated that commercially caught cephalopods are grouped in to three categories that basically, although not precisely, reflect current taxonomy of the subclass Coleoidea: squid, octopus, and cuttlefish. The biology section of this capstone will describe the differences among these categories, including subsections covering life histories, morphology and taxonomy, migration, population dynamics, trophic relationships, and recruitment, particularly with reference to how they vary among fisheries, e.g., longevities vary substantially: 1-2 years for the common jumbo squid, *Dosidicus gigas* (Nigmatullin et al. 2001), and 6-9 months for the California market squid, *Doryteuthis opalescens* (Butler et al. 1999).

Variations among species within commercially important zones, assessments, and management of resources will be treated in both the biology and fishery sections. In addition, catch data may include species misidentifications due to morphological variations. For example, Amor et al. (2017) noted *Octopus sinensis* was labeled incorrectly as commercially valuable *O. vulgaris*, despite morphological differences.

The fisheries section will cover subjects ranging from bycatch and targeted fishing, to assessment of cephalopod stocks within fisheries and appropriate gear usage per region fished. Management of fisheries will also be discussed, due to the potential impact of fisheries upon worldwide stocks. Included data will demonstrate fisheries gear and trends across the globe and possible implications of gear use, fishery overhauls, and cephalopod importance (e.g., Arkhipkin et al. 2015). Artisanal fishery and global fishery catch data will be discussed. However, in order to draw correlations between fishing efforts and environmental changes, data will be limited to US commercial landing records, as these data are the most complete and up to date.

This capstone will review the biology, population dynamics, and fisheries of commercially caught cephalopods both worldwide and regionally, with a focus on how an increased understanding of their biology has increased over the last few decades via molecular genetics, improvements in assessments, gear, and stock management techniques. The work will discuss how stock assessments, import and export trade, and government regulations affect both domestic and global fisheries, and it will explore how global climate change may affect these organisms and their fisheries. Gear updates and models from data have permitted the development of hypotheses about cephalopod population dynamics and future sustainability (Arkhipkin et al. 2015).

6. Cephalopod Biology

Differences in the biology of the major groups of commercially caught cephalopods will be summarized as they are relevant to today’s global economy, active fisheries, and environmental impacts of changing oceans. This capstone focuses on the subclass Coleoidea, which is characterized by two bipectinate gills and no external shell. It omits consideration of the few extant species of subclass Nautiloidea, which have an external, chambered shell, and four bipectinate gills, and are not commercially fished. Subsections treated in order are life history, morphology and taxonomy, population dynamics, and recruitment.

6a. Life Histories

Doubleday et al. (2016) pointed out that unique features of cephalopod life histories, including short lifespans, rapid growth, and developmental plasticity, permit rapid adaptation to changing environmental conditions, both natural and anthropogenic. They reported that cephalopod populations have increased over the last six decades. Caddy and Rodhouse (1998) reported cephalopod landing increases relative to groundfish landings from 25 years of data. They hypothesized that the shorter life cycles and rapid turnover of cephalopods gave them an advantage over longer-lived finfish species. Rodhouse et al. (2014) stated that exploited species of cephalopods in particular have short life cycles of at most one to two years, associated with the high plasticity in life history characteristics of fast growth and high metabolic rates. Such plasticity refers to potentially wide variations in all components of phenotypic expression (e.g., morphology, development, physiology, behavior, recruitment, population structure) induced by changes in the environment (Price et al. 2003). Anderson et al. (2011) noted that increased trends in invertebrate fisheries may be partly explained by increasing precision in reporting and that clear trends in fishery expansion by catch, country, and taxa are underlying factors.

Rodhouse et al. (2014) stated that external factors such as temperature fluctuations may be the most important factors to which cephalopods may have to adapt. Internal body functions such as metabolism and growth rates increase with temperature as it rises from the critical thermal minimum to the critical thermal maximum temperature that cephalopods can handle. Most coleoid squids are short-lived and exhibit life cycle changes with changing temperatures and other external factors. Melzner et al. (2007) reported that when the cuttlefish *Sepia officinalis* is exposed to critically high or low temperatures, certain important muscle tissues transition to anaerobic energy production. They found that the metabolic response differed at high versus low temperatures, with the former due to circulatory failures but the latter associated with the function of the blood pigment hemocyanin.

Changes in temperature can dictate life cycle changes as well as internal and homeostatic functions in cephalopods. Rodhouse et al. (2014) noted that temperature directly impacts growth rates, settlement, reproduction, and paralarval survival. At higher temperatures, mortality due to starvation is more likely if food sources are scarce. Arkhipkin (2000) pointed out that some short-finned squid (*Illex coindetii*, Ommastrephidae) populations have shown such extreme sensitivity to temperature, that any change directly determines whether they exhibit an annual or sub-annual life cycle. Note that post-hatching cephalopods are referred to as paralarvae rather than larvae, as they do not undergo the true metamorphosis that characterizes the latter.

Rosa et al. (2012) discovered that raising the temperature by predicted near-future oceanic warming (+2°C) would be above the optimal thermal tolerance of *Loligo vulgaris*. Results showed a 2-8% increase in premature hatching at elevated temperatures and up to a 50% chance of hatchling deformity at the treatment temperature. The authors noted that they did not entirely understand the underlying causes of premature death. However, temperature did have a concomitant negative effect on growth and survival success.

The combined efforts of Boletzky (1987, 1988) and Laptikhovsky et al. (2003) provided insight into the potential extension of the adult phase due to increased temperature, which may lead to a great increase in fecundity and thus in recruitment strength. This is particularly true for cuttlefish (*Sepia officinalis*), which have highly flexible reproductive strategies that range from a single batch of eggs to multiple spawning sessions within the same population.

Future research and development of models should provide more insight into life history changes that may be applied to longer-lived species (Rodhouse et al. 2014). Graphs and models resulting from studies of life history variations may predict population changes currently and in the future.

Salinity effects embryonic development similarly to temperature: development proceeds normally within an optimal range but diminishes to zero outside minimum and maximum limits (Rodhouse et al. 2014). Although ocean currents and upwelling generate broader ranges in salinity than storms and anthropogenic emissions, all of them contribute to fluctuations in water column salinity. Nabhitabhata et al. (2001) experimentally discovered that higher salinity promoted premature hatching of embryos of two neritic cephalopods—bigfin squid (*Sepioteuthis lessioniana*) and pharaoh cuttlefish (*Sepia pharaonis*)—while low salinity created developmental abnormalities that impacted survival. Sen (2004) also studied the effects of salinity on the development and incubation of European squid (*Loligo vulgaris*) eggs and estimated that hatching rates were 88.5% at 37‰, 60% at 34‰, and that below 34‰ the eggs died at very early stages. In addition, Dupavillon and Gillanders (2009) stated that, when a desalination plant discharged brine back into the environment, it negatively affected the breeding aggregations of giant cuttlefish (*Sepia apama*).

Dissolved oxygen levels not only change the population dynamics within an ecosystem through migration to more habitable regions, higher levels encourage spawning and migration for spawning events. Cephalopods actively search for areas of high oxygen content required for their metabolic processes. Rodhouse et al. (2014) discussed the differences in the effects of oxygen tension on eggs, egg masses, and hatchlings of octopus and squid egg masses. Lower levels of oxygen within the brood can create development problems and negatively affect survival rates. Octopod egg clusters avoid oxygen deprivation, or hypoxic conditions, due to extensive maternal care, during which brooding mothers regularly aerate the egg clusters. However, loliginid squid produce egg masses that have increased chances of developmental abnormalities because of their larger egg sizes and reduced water flow throughout the egg mass, particularly at the attachment point (Gowland et al., 2002; Rosa et al., 2012; Steer and Moltschaniwskyj, 2007).

Climate change generates fluctuations in both oxygen and dissolved carbon dioxide, the latter leading to ocean acidification, which may have drastic impacts upon cephalopod survival. Several experiments have been conducted on epipelagic squid (e.g., in the oegopsid families Ommastrephidae, Gonatidae, and Loliginidae) because of their higher metabolic rates compared to those of other aquatic organisms (Rodhouse et al. 2014). After hypothesizing that increased carbon dioxide would create oxygen binding issues on the gills of these epipelagic squid, Rosa et al. (2008) found that activity levels of *Dosidicus gigas* diminished when subjected to projected elevated levels of dissolved carbon dioxide, presumably through lower oxygenation. Similarly, Kaplan et al. (2013) reported that *Doryteuthis pleii* eggs subjected to elevated dissolved carbon dioxide levels were smaller and developed more delicate and irregularly organized statoliths.

Because cephalopods are visual predators, they are also affected by light and photoperiods. They need light to hunt, especially if their prey lack photophores or other bioluminescence (Rodhouse et al. 2014). Of several experiments conducted on the cuttlefish *Sepia officinalis*, Koueta and Boucaud-Camou (2003) found that specimens which remained in complete darkness died of starvation, even with sufficient available active prey, and the authors recorded increased mortality rates in juveniles subjected to shorter photoperiods.

Thus, temperature, oxygen, salinity, light levels, and ocean acidification all play important roles in cephalopod development and life histories and will likely have increased effects as the environment continues to change.

6b. Morphology and Taxonomy

Multiple recent studies have revised the taxonomy of various cephalopod taxa, including commercial species, and illustrate the importance of detailed morphological and molecular data for accurate identification of commercially fished cephalopods (e.g., Söller et al. 2000; Espiñera et al. 2010; Kaneko et al. 2011; Wakabayashi et al. 2001; Granados-Amores et al. 2014; Lü et al. 2013). Lima et al. (2017, p. 2) succinctly summarized the need for better understanding taxonomy in general: "Misidentification of morphologically similar species can also affect our understanding of the ecological and evolutionary processes in marine communities (Knowlton 2000). The consequences of these mistakes can lead to misinterpretation of biological indicators of environmental quality (Gabrielsen et al. 2012), under or overestimation of the species richness (Bortolus 2008), and generate biologically and ecologically inappropriate information. This then hinders the development of effective policies for the protection of ecosystems (Knowlton 1993, 2000)."

Lima et al. (2017) noted the treatment of genus *Octopus* as a "catch-all" due to morphological similarities among specimens. In a phylogenetic study of cephalopods in tropical western Atlantic fisheries (Brazil to Mexico) due to possible misidentification and overexploitation, they found that 21 GenBank sequences from Tropical Northwestern Atlantic specimens identified as *Octopus vulgaris* grouped within the *Octopus insularis* clade and were most likely that species. Their mitochondrial (cytochrome oxidase I) analysis revealed that 18 individuals collected in landings and fish markets, and previously identified as *O. vulgaris,* had the identical haplotype of *Octopus maya* collected as the controls from the Universidad Nacional Autónoma de México (UNAM) cultivation center. Their results expanded the known distribution of *O. insularis* into the Caribbean Sea.

In establishing a basis for diversifying the fishery of commercially important chokka squid (*Loligo reynaudii*) in South African waters, van der Vyver et al. (2016) analyzed 43 morphometric characteristics among 1,079 specimens collected off the southern and western coasts of South Africa, and off southern Angola. Although they found no significant differences in hard body parts, all four types of morphometric attributes (soft body parts, beaks, statoliths, sucker rings) revealed some separation among the three regions, generating correct classification rates of 0.68–0.99 for males and 0.7–0.99 for females in all three regions. Some variability thus exists within this species, creating potential problems for stock assessments and management.

The examples above demonstrate the need for further accurate identification of species, and sometimes genera. Technological advances such as molecular genetics have allowed data to be collected more accurately, providing scientists and fisheries managers appropriate data for conservation and fishing.

6c. Migration

Cephalopods exhibit a wide spectrum of diurnal and ontogenetic migrations (Rodhouse et al. 2014). Diurnal migrations are associated with feeding behavior. Ontogenetic migrations occur with a splitting of the range occupied into feeding grounds and a separate spawning or nursery area while maximizing resources of both based on favorable environmental conditions (Nesis 1985, in Rodhouse et al. 2014). Both predator-prey interactions and external factors play vital roles in shaping cephalopod migrations. As an example, warmer temperatures induce earlier migrations in *Doryteuthis gahi* and colder water delays them (Arkhipkin et al. 2004). The major taxonomic cephalopod groups also differ in migratory behavior, with *Nautilus* species, benthic octopods, and cuttlefish migrating little in comparison with most, if not all, squid species.

Nautilus species exhibit complicated diurnal behavior but little to no ontogenetic migrations and have the shortest spatial migration among all cephalopods. Dunstan et al.'s (2011) study on the vertical migrations of *Nautilus pompilius* suggested nearly continuous, nightly movement between depths of 130 and 700 m, with daytime behavior split between either virtual stasis at 160–225 m or active foraging between 489 and 700 m.

Both benthic octopods and cuttlefish generally remain close to their places of birth, within ten kilometers for the former. Scheel and Bisson (2012) monitored movements of forty Pacific giant octopus (*Enteroctopus dofleini*) and found that they remained stationary or in hiding 94% of the time with maximum movement of 4.8 km over a 3-month period by the largest female, reinforcing Rodhouse et al. (2014).

Cuttlefish generally have offshore feeding grounds and inshore spawning grounds (Rodhouse et al. 2014). Bloor et al. (2013) reported that, of eight some adult and sub-adult European common cuttlefish (*Sepia officinalis*), some might stay within a small spawning area for weeks, while others might travel some 20–35 km for several weeks if not longer during the spawning season. Cuttlefish movements appear to span greater distances than those of *Nautilus* species and benthic octopods, but they do not move nearly as much as members of either major group of squids, the neritic suborder Myopsida and chiefly oceanic suborder Oegopsida.

Nesis (1985) noted that squids have the longest migrations among cephalopods, with myopsids migrating shorter distances between spawning and feeding grounds. Oceanic oegopsids such as ommastrephids and onychoteuthids travel much farther (Nesis 1985), and exhibit well differentiated spatial migratory ranges by using various ecosystems for spawning, nursing, and feeding (O'Dor and Coelho, 1993).

Gilly et al. (2006) tagged and tracked seven *Dosidicus gigas* (Oegopsida) and discovered that horizontal movements over three days amounted to nearly 100 km, while the complex diel vertical migrations ranged from the surface to 500 m. In a trawl-based survey on the Patagonian shelf in the Falkland Islands, Hartfield et al. (1990) caught over 10,000 *Loligo gahi* (Myopsida) between 50 and 400 m. They deduced that the squid migrate down the shelf as they grow, a shorter migratory pattern than found in *D. gigas*. These examples permit us to infer that migrational differences among species of the two groups may affect population dynamics.

6d. Population Dynamics

Turchin (2003, p. 19) defined a population as: "…a group of individuals of the same species that live together in an area of sufficient size to permit normal dispersal and migration behavior, and in which population changes are largely determined by birth and death processes", and population dynamics (p. 3) as: "the study of how and why population numbers change in time and space, documenting empirical patterns of population change and attempting to determine the mechanisms explaining the observed patterns."

In introducing population ecology, Boyle and Rodhouse (2005) wrote that population biology of a defined group of animals includes those quantitative aspects of its biology leading to understanding changes in the scale and distribution of their biomass. They added an addendum specific for cephalopods (p. 221) that: “The life cycle characteristics and ecology of the oceanic and mesopelagic cephalopod fauna, in particular, need to be established before current estimates for global cephalopod biomass can be reconciled with their biological productive capacity and that of the marine ecosystem in total. We must begin to understand whether the life cycle features established for the coastal species represent special cases, or the degree to which they may be generalized to the much greater oceanic and deepwater fauna.”

The cornerstones of population dynamics—stability and oscillations—together define population regulation through the equation $r_t = \ln(N_t/N_{t-1})$, where N is the population at time t and $\ln(N_t)$ is the natural logarithm of population density over time t (Rodhouse et al. 2014). This population regulation equation is the realized per capita rate of population change, which only provides a framework for quantifying wild populations because of the vast array of variations in population stability and oscillations (Rodhouse et al. 2014).

Fisheries population dynamics currently use a mix of field observation and laboratory data, often from rodents (Turchin 2003) or insects (e.g., *Drosophila* and *Tribolium*; Mueller and Joshi 2000), or from fisheries stock assessment research (Quinn and Deriso, 1999). The latter authors noted that spatial aspects of population dynamics are often omitted in fisheries science.

Assessment of cephalopod population dynamics fall prey to difficulties similar to those of other marine fisheries, particularly because standardized data must be collected over long time series that span many generations, which may or may not overlap due to the typical short life span of most cephalopods (Rodhouse et al. 2014). Life stage survival rates provide empirical data to include in prediction models. Rodhouse et al. (2014) noted that, for species with rapid growth rates and short lives, increased population stability is typically noted when larvae have higher levels of food availability and adults have lower available levels of food; departures from population equilibrium arise from the reverse situation.

Cephalopod migrations as described above by Rodhouse et al (2014) also create significant variability within populations, whether they are diurnal, ontogenetic, or seasonal. These migrations can be vertical or horizontal, or both, which makes tracking and researching cephalopod populations over a long time series a major challenge. Rodhouse et al. (2014) noted that environmental changes during travel at any point during ontogenetic migration may cause changes in mortality rates and alter population dynamics. However, repeated seasonal assessments can record variability in abundances due to migrations between spawning and feeding sites.

Squid migrations are difficult to observe and map over long time series as the oceans undergo change, so it is difficult to identify population increases versus declines or longer term trends. Without observing populations and subpopulations throughout the day/week/month/year, migrations become harder to define and model, which may generate conflicting information about population variations (e.g., increases or declines) all spatial scales. These difficulties notwithstanding, fisheries pressures on cephalopod populations are often more obvious.

Most population dynamics assessments of fish and cephalopods focus on harvesting, management goals, policy impact, and research, while trophic relationships are often ignored (Rodhouse et al. 2014). Ecological differences between fish and cephalopods provide different challenges that must be addressed when discussing fisheries and effective management strategies. Saville (1987) and Lipinski et al. (1998) provided generalized but qualitative reviews of the differences in questions, methods, approaches, and difficulties of theoretical ecology between fish and cephalopod fisheries. Lipinski et al. (1998) identified life-cycle understanding, spatial distribution, stock-recruitment relationship, and age determination/growth studies as priorities for research, while stating that management strategies for short-lived fish species could be applied effectively for cephalopods.

The tables summarizing these data in Rodhouse et al. (2014) show 59 cephalopod species that have been researched relatively well of the (current) total of ~800 and are therefore suitable candidates for population dynamics analysis. Another table displayed the level of knowledge at the time of trophic and environmental relationships at the family level. O’Brien et al.’s (2018) more recent update indicated that biology, ecology, and physiology are known for about 60 species—8% of the total number of extant cephalopod species (Jereb and Roper 2005, 2010; Norman et al. 2014).

Population dynamics would be best analyzed using species collected on a large scale over a long time frame in order to create the best possible map of interactions between the animals and the environment. Boyle and Rodhouse (2005) stated that only *Todarodes pacificus* has been researched well enough to meet the standards described above. They identify Ommastrephidae (including the genera *Illex, Dosidicus, Todarodes, Ommastrephes,* and *Nototodarus*) as the largest family of commercially targeted cephalopods globally.

Understanding population overlap is important in investigating population dynamics. In the past, theoretical ecologists took little interest in cephalopods due to the degree to which consecutive generations overlap, a feature that remains poorly understood even in some of the better-studied families (e,g., chokka squid, Loliginidae) (Melo and Sauer 1999, 2007). Generational overlap cannot be clearly defined by one statement. However, Nunney (1993) provided some basic assumptions to outline factors influencing overlap: adult numbers are constant, fecundity is age-independent, survival is age-independent, and maturity is achieved at age one. Nevertheless, these assumption work under ideal conditions and rarely exist in the real world, especially for mobile cephalopod populations.

Cephalopod spawning periods dictate generational overlap, which determine a starting point for population research. The spawning periods of some cephalopods are quite prolonged, particularly in warmer climates, while others in colder regions may be abbreviated, which generates different degrees of overlap (Rodhouse et al. 2014). Squid in particular have prolonged spawning periods. As examples, Melo and Sauer (1999, 2007) discussed several studies of chokka squid (*Loligo vulgaris reynaudii*) (e.g., Augustyn 1990; Augustyn et al. 1992 1994), in which they confirmed that females appear to be serial spawners capable of spawning a number of times over several weeks once they reach the spawning grounds. Young and Mangold (1994) discovered that the small mesopelagic squid, *Abralia trigonura* may spawn every three days during its average life span of six months.

Caddy et al. (1983) stated that nonsynchronous spawning events create and contribute to generational overlap, which creates a buffer against recruitment failure. Rodhouse et al. (2014) added that generational overlap can be difficult to determine due to the occurrence of multiple discrete spawning events over a period of years. As an example of the difficulties recognizing generational overlap, Yatsu et al. (1998), Nagasawa et al. (1998), and Chen (2010) collected fisheries and biological data over vast areas during more than 20 years of exploitation of *Ommastrephes bartramii* and found that the northern Pacific contains four separate groups.

Katugin (2002) confirmed that at least two of these groups are clearly distinct populations (eastern and western) and noted that distinguishing factors included hatching time and area, length–frequency data, maturities, paralarval occurrence, parasitic infestation, fleet operations, and environmental factors. However, different generations still could not reliably be distinguished. Spawning periods and life cycle plasticity have been previously noted in the biology section and will remain important factors throughout this review.

In attempting to determine whether cephalopod populations are proliferating or decreasing over time, it is important to incorporate the effects and roles of oceanic currents and migration. Oceanic currents and upwelling may alter population dynamics and affect recruitment, and the effects can be recognized immediately. Some cephalopod species that spawn in upwelling regions exhibit positively increased survival rates and retention of paralarvae due to the enrichment and potential mixing and dispersal through the water column (Rodhouse et al. 2014). Gonzalez and Guerra (2013) noted incredibly high levels of abundance of the short-finned squid, *Illex coindeti*, in Galician waters at the beginning of upwelling season. Sauer et al (2013) similarly found the abundance of *Loligo reynaudii* to be positively influenced by upwelling season off of the South African coast.

The retention of paralarvae promotes competition for food but will more likely increase the stock of juveniles and adults. However, cephalopod stocks can expand their distribution, and populations can be established in new areas if paralarvae are transported to areas with conditions favorable to growth and proliferation (Rodhouse et al. 2014). The perfect example of this is the Humboldt squid, *Dosidicus gigas*, in which the described range has recently expanded, and stock structure has changed (Rosa et al. 2013; Waluda and Rodhouse 2006; Waluda et al. 2004). Rodhouse et al. (2014) claimed that this species abundance is strongly correlated and driven by ENSO (El Niño-Southern Oscillation) events around the Peruvian coastal upwelling system. As these early life history stages normally exhibit high mortality rates, transport to an unfavorable area increases the already negative impact on the parent stock due to losses through transport alone (Rodhouse et al. 2014).

6e. Trophic Relationships

Trophic relationships are defined by the interactions among predators and prey in a food web. McQueen et al. (1986) described two models in freshwater pelagic systems as representative of trophic relationships in general. The producer-controlled (bottom-up) model controls the maximum biomass at each step from the bottom of the web via nutrient availability and weakens upward at each trophic level by a factor of two, so that interactions at any step become less predictable at higher levels. In the consumer-controlled (top-down) model, predator-prey interactions are strong at higher trophic levels with relatively little variation but become weaker at every step down the food web. Carpenter et al. (1985) referred to this top-down model as a cascading trophic interaction concept, the bottom-up model as nutrient-loading, and noted that they are complementary rather than contradictory. Note, however, that both papers only discussed freshwater pelagic trophic systems, which differ from marine systems in both environmental parameters and their effects on resident organisms.

Cephalopods often occupy similar trophic niches to fish, as all cephalopods, like many commercial fish species, are active predators. Cephalopods are also important prey of organisms at higher trophic levels due to their generally high biomass ratios (Clarke 1996; Croxall and Prince 1996; Klages 1996; Smale 1996). Gasalla et al. (2010) noted that recent ecological modelling work has highlighted the fact that cephalopods can be keystone species. The authors applied an Ecopath model to *Doryteuthis* (previously *Loligo*) *pleii* in the South Brazilian Bight and looked at mixed trophic impact and "keystoneness" for all associated groups and species. *Doryteuthis pleii* had the third highest "keystoneness", that is, it has a disproportionately strong effect on the abundances of other species and on food web structure relative to its low biomass. They also found that it has a high overall mixed trophic impact, in that it is negatively affected by multiple higher-level predators (e.g., weakfish, cutlassfish, whales, large pelagic fish, and mackerel) via top-down effects, and positively affected (often indirectly) by multiple lower-levels (e.g., producers and plankton, small pelagic fish, and carangids) via bottom-up effects. "Squid on squid" effects, i.e., likely cannibalism, are also important (Figure 1: Figure 2.11 in Rodhouse et al. (2014, p. 137), from Gasalla et al. 2010.)

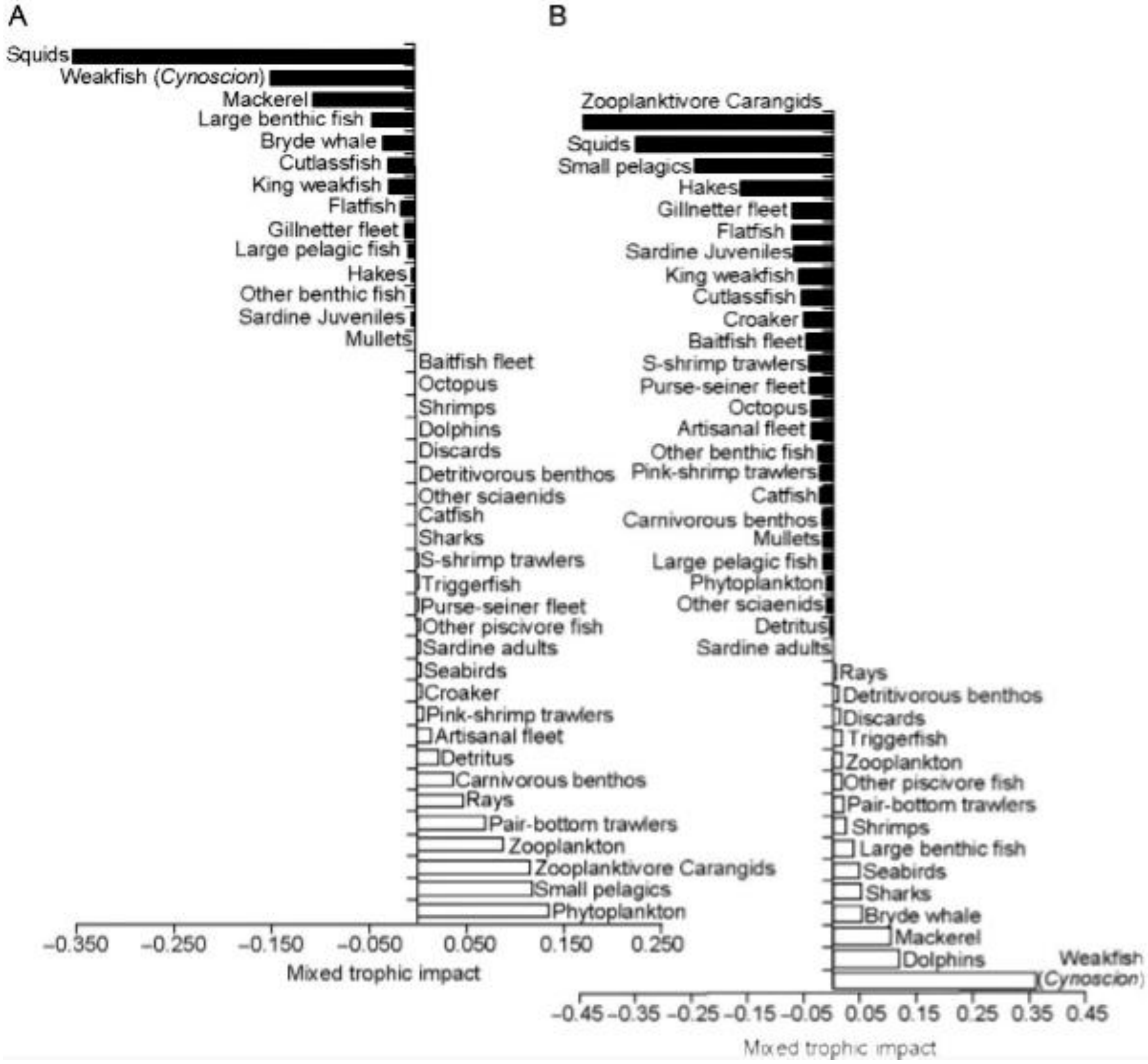


Figure 1. Trophic role of *Doryteuthis pleii* in the South Brazilian Bight based on a mixed trophic impact matrix analysis. (A) Impacts of other groups upon squid impact squid positively via bottom-up process. (B) Squid as impacting species upon other groups or species. Negative impacts are seen for several prey species such as zooplanktivorous carangids and small pelagic fish. Positive impacts are seen among "predators" of squid and/or as indirect links. From Gasalla et al. (2010), Figure 2.11 in Rodhouse et al. (2014, p. 137).

Trophic relationships of cephalopods are well known and extensively covered in the literature, primarily from a classical descriptive point of view (e.g., Amaratunga 1983; Dawe and Brodziak 1998; Jackson et al. 2007; Lipinski 1987, 1992; Lipinski and David 1990; Lipinski and Jackson 1989; Lipinski et al. 1992; Lordan et al. 1998; Pierce et al. 1994; Rodhouse and Nigmatullin 1996), although more recent work has extracted trophic information from stable isotope analyses of beaks (e.g., Jackson et al., 2006; Cherel and Hobson 2005). All cephalopods are active predators, but their trophic relationships become more complex with growth and depend upon life-history stage; paralarvae, juveniles, and adults have different diets and are preyed upon by different species. Similarly, between ontogenetic changes and ecological differences, the different squid species in a single community may span three trophic levels (Cherel and Hobson 2005).

Guerra (2006) noted that, with few exceptions (e.g., Australian weasel shark *Hemigaleus australiensis* (Taylor and Bennet 2008)), no known fish specialize on cephalopods as prey, although most predatory fishes, and many pelagic sea birds and marine mammals, include cephalopods in their diets (Benjamins 2000), and some, such as beaked whales and the sperm whale, feed exclusively (or almost so) on cephalopods (Benjamins 2000). Figure 2 from Gasalla et al. (2010) reflects how diverse the trophic relationships of a single species (*Doryteuthis* (formerly *Loligo*) *pleii*) may be.

Octopods are quite opportunistic, and their diets vary depending upon seasons and prey availability. Mather (1991) wrote about the specialized predation techniques (e.g., boring/drilling, splitting) of the common commercial octopus, *Octopus vulgaris*, on small crustaceans and mollusks. Saunders et al. (1991) noted that octopods in the Admiralty Islands, Papua New Guinea, prey on the two native nautilus species, *N. pompilius* and *N. scrobiculatus*, by boring through their shells. As prey, octopods have been found as stomach contents in whales, sharks, dolphins, and even skates. Stomach contents of 446 thorny skates from the Northwest Atlantic included cephalopods (e.g., octopus and the squids *Gonatus fabricii* and *Illex illecebrosus*) among other marine organisms (Templeman 1982).

Cuttlefish are also trophic opportunists (Guerra 2006). The diet of *Sepia officinalis* includes crustaceans, bony fishes, mollusks, polychaetes, and nemertean worms (Nixon, 1987; Castro and Guerra, 1990; Pinczon du Sel, et al., 2000). *Sepia officinalis* has been found in stomachs of elasmobranchs (e.g., *Prionace glauca* (Clarke and Steven 1974), *Scyliorhinus canicula, Mustelus mustelus* (Morte et al. 1997), and *Galeus melastomus* (Velasco et al. 2001)); teleosts (e.g., *Merluccius merluccius* (Larrañeta 1970; Velasco et al. 2001)), and even Risso's dolphin (*Grampus griseus*) (Clarke and Pascoe 1985).

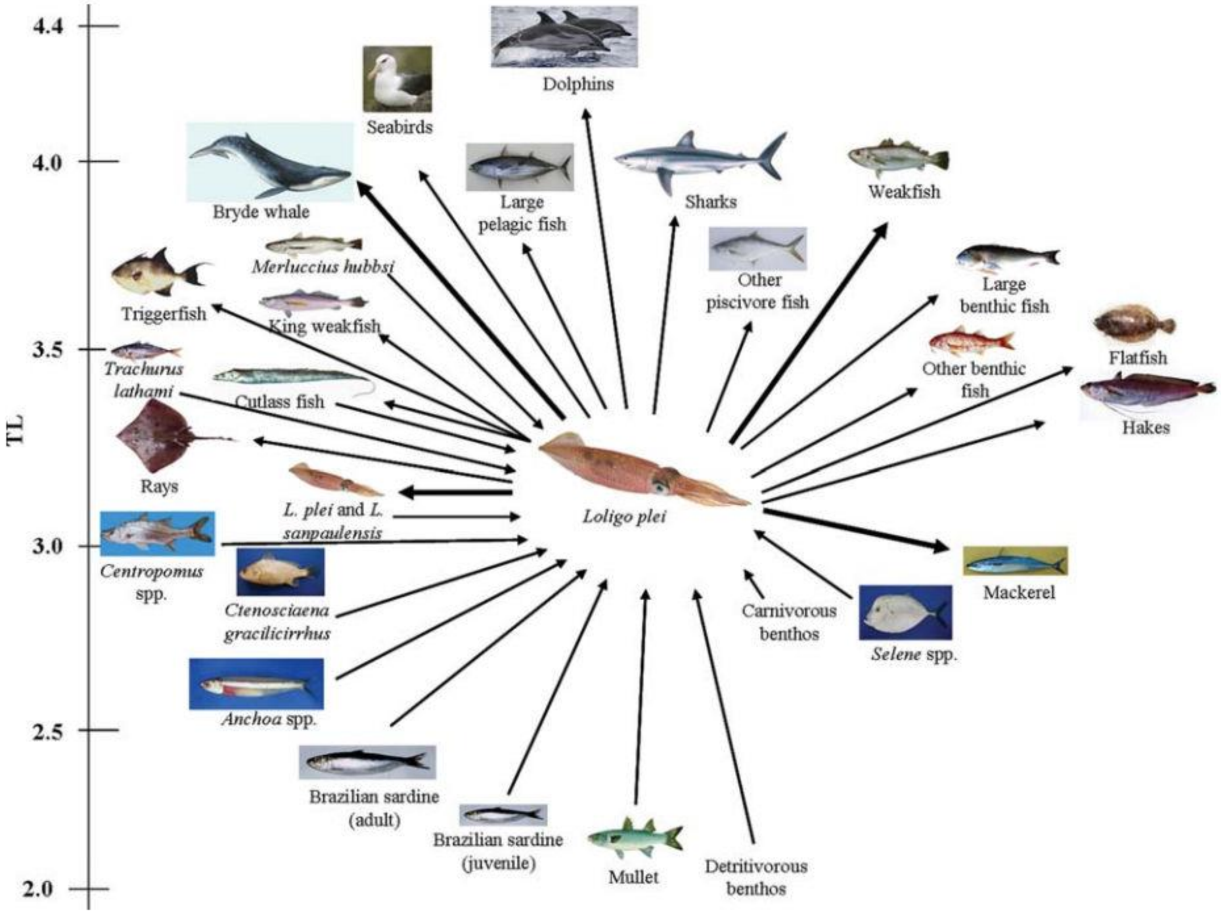


Figure 2. Trophic interactions of *Doryteuthis pleii* in the South Brazilian Bight. Arrows pointing to the central squid are its prey. Arrows leading away point to its predators. The y-axis is the trophic level (TL); arrow width indicates importance in the diet (Fig. 7 in Gasalla et al. 2010).

Cannibalism—the consumption of a member of the same species (Ibáñez and Keyl 2010)—is common among cephalopods but depends upon food availability. Roel (1998) identified cannibalism as density-dependent and an important role in predation on spawners and eggs of chokka squid (*Loligo reynaudii*). Ibáñez and Keyl (2010) concluded that cannibalism is common in most cephalopod species for which diet has been studied and reaffirmed that cannibalism in cephalopods is density-dependent due to their aggressive predatory behavior and, in case of octopuses, territoriality. They noted that cannibalism was particularly important in the genera *Illex, Octopus, Sepia*, *Dosidicus*, *Onychoteuthis*, *Todarodes*, *Ommastrephes and Loligo*.

6f. Recruitment

Recruitment has been difficult to label and define, as it may be based on a strict biological definition or upon gear selection used in particular fisheries (Rodhouse et al. 2014). An argument has been made that biological definitions ignore the reality of gear selectivity removal of the smallest fish (Boletzky 2003; Quinn and Deriso 1999). Here, I use a widely accepted definition: the addition of new juveniles to a population that will be taken by a particular gear (Rodhouse et al. 2014).

Pierce et al. (2008) wrote that there has been an increased emphasis on the apparently strong links between recruitment and favorable oceanographic conditions (e.g., wind, currents, and temperature). Strong links may contribute to predictive models. However, even the models have flaws as described through Solow's (2002) warning about the transience of trophic relationships and short time-series observations (Rodhouse et al. 2014).

Recruitment studies have also incorporated trophic relationships as a dominant factor in population dynamics. Roel (1998) identified predation and cannibalism as two primary mechanisms of trophic relationships detrimental to recruitment and provided evidence that cephalopod life stages and overlapping generations are dependent upon starvation and predation at various points from conception. The biological need to feed seems to precede any gear removal of new recruits, further diminishing the populations.

Studies on *Illex argentinus* have shown that winter cohort recruitment is strongly influenced by retention or transport of eggs within the spawning grounds (Rodhouse et al. 2013; Waluda et al. 1999, 2001). Sakurai et al. (2000, 2013) also noted a similar case in varied recruitment of *Todarodes pacificus* over the continental shelf during the autumn and winter spawning events. Waluda et al. (2001) reported the interactions of the Brazil and Falkland Currents on the *Illex argentinus* hatching area during the early life stages, stating the importance of environmental conditions on recruitment size for the year.

Winter and Arkhipkin (2015) studied data from thirteen fishing seasons of *Doryteuthis gahi* and concluded that size distributions are influenced by environmental variables such as wind, sea surface temperatures, and geostrophic currents. Waluda et al. (1999) showed that sea surface temperature variations during early life stages appear to be an important factor in determining recruitment in another commercially valuable squid, *Illex argentinus*. They noted that sea surface temperatures in the hatching grounds during the hatching period (particularly June and July) negatively correlated with fishery catches the following season.

7. Fisheries

As major finfish stocks have been depleted and industrial-scale exploitation has expanded over the last several decades, interest in alternative resources, such as cephalopods, has increased correspondingly, a circumstance first predicted by Voss (1973) (Jereb et al., 2005). The U.N. Food and Agriculture Organization (FAO) first published records of the total world cephalopod catch in 1950 (580,500 metric tonnes) (1 mt = 10^3 kg). Since then, the catch has increased almost continuously every year, to consistently over 1 million mt in 1972, over 2 million in 1987, and generally over three million since 1996 (FAO, 2000; Jereb et al., 2005). By 2010, the total catch had reached 3.6 million (FAO, 2012; Jereb and Roper, 2014), with a peak in 2007 of 4 million mt (Jereb et al., 2010). In parallel, the number of commercially exploited cephalopod species has increased since 1984, as demand has increased, and fishing efforts have expanded to new areas and into deeper waters (Jereb et al., 2005). However, Pauly and Zeller (2016) created figures of reconstructed fisheries landing data and suggested that all global commercial fishing peaked in 1996 and has been declining since.

Although octopuses and cuttlefish are regionally important targets, squids represent the great majority of the world catch, accounting for ~74% of the total in the 2007 peak year (FAO, 2000). As examples of how the squid fishery has expanded, Jereb et al. (2010) point to three species in particular. The catch of *Illex argentinus* in the southwestern Atlantic and sub-Antarctic surpassed 1 million mt in 1999; the region accounts for ~30% of the global squid catch. The eastern Pacific catch, dominated by *Dosidicus gigas*, contributes ~20% of the total, and the northwestern Pacific, chiefly *Todarodes pacificus*, ~13%. For the other two major cephalopod categories, Jereb et al. (2005) noted that the world cuttlefish harvest increased from ~150,000 mt in the early 1970s to over 500,000 mt in 2001, and octopods from ~200,000 to ~300,000 mt over the same period, but with substantial interannual variations. However, many of the stocks have had limited assessment or none at all (Doubleday et al., 2016; Rodhouse et al., 2014). Most targeted species tend to be the short-lived, 1-year life cycle species, which grow rapidly and spawn before death (Rodhouse et al., 2014). Norman and Finn (2014, in Jereb et al., 2014) listed 59 harvested octopod species (including uncertain taxa, e.g., *Octopus vulgaris* I, II, III, and IV, each fished in different regions, and *Cistopus* sp.), of which eleven are treated as “major” harvests. However, Jereb et al. (2014) noted that global summary statistics list only four species: common octopus (*Octopus vulgaris*), Mexican four-eyed octopus (*O. maya*), horned octopus (*Eledone cirrhosa*), and musky octopus (*E. moschata*). The remaining species are at best listed as “unidentified Octopus”. Jereb et al. (2005) listed 50 harvested cuttlefishes (family Sepiidae) with about a dozen of at least local, sometimes artisanal, fisheries, but the majority taken as bycatch. Jereb and Roper (2010) indicated that over 300 squid species are currently recognized. Of these, Arkhipkin et al. (2015) listed between 30 and 40 species of substantial commercial value, with 17 species spread among four families: Ommastrephidae, Loliginidae, Onychoteuthidae, and Gonatidae. Smaller, chiefly local fisheries also exist for bobtail squid (suborder Sepiolida) (Czudaj et al., 2012), although catches are recorded with cuttlefish (Hastie et al. 2009).

According to Mouritsen and Styrbæk (2018), southern Europe and east Asia, particularly China and Japan, have the richest traditions for consuming cephalopods. Morocco and Mauretania are largest producers and exporters of octopus, while Japan consumes more per capita than any other country. They also stated that supplies of *Sepia*-like species chiefly come from China and Thailand, while Spain, China, Thailand, Argentina, and Peru are the world's largest exporter of squid-like species.

Understanding, identifying, and assessing cephalopod fisheries is complicated by a combination of factors that can under- or overestimate stocks and mask trends over time, whether increases or declines; these factors include, in particular, the combination of taxonomic uncertainties, lack of precision in reporting catches, and lack of substantial information on the biology of all but a few harvested taxa. In FAO (2000), “unidentified squids” contributed anywhere from 10% to 48% of the global squid catch between 1950 and 2001, and “unidentified cephalopods” contributed as much as 7.8% of the world total (in 2000), with the percent increasing substantially from the 1970s onward. As noted above, global statistics distinguish only four octopus species, but the status of octopus taxonomy is historically poor, and some countries report only total cephalopod catches, or “catch-all” identifications (Loew, 2017), if they do so at all (Jereb et al. 2014). Variations in life history traits and abundances relative to distributions and environmental factors contribute uncertainties as well (Loew, 2017; Rodhouse et al., 2014).

Cephalopod fisheries tend to be at extremes: they are either cycling boom and bust dynamics or relatively stable (Rodhouse et al., 2014). However, any fishery landing decreases are less likely to be a direct consequence of gear effectiveness and use, and far more likely to be the indirect result of a combination of cephalopod dynamics and fishery demand.

Fishery management systems vary with location due to country of origin and availability of resources. Pierce and Guerra (1994) reported, for instance, that European fisheries tend to be less regulated than those of the United States and even the Falkland Islands, due to a lack of routine assessments and management specifications via Common Fisheries Policy. They also noted that targeted species can be identified using three different approaches: depletion methods, boat-based surveys, and production models. Depletion methods derive from Leslie and Davis (1939) and De Lury (1947) and assume a closed population declines because of fishing mortality, recognition of which requires data on catches, fishing effort, and abundance estimates (e.g., catch per unit effort). Boat-based surveys require an onboard observer to determine environmental/fisher factors (e.g., boat speed and direction, precipitation, sea state, wind direction, and wind force) and targeted species information (e.g., total number of species, number of adults and juveniles, behavior and direction of travel, as well as any large congregations of birds seen in close proximity to the sighting and their approximate number and behavior) (Wildlife Trust of South and West Wales, n. d). Pierce and Guerra (1994) defined a surplus production model as the difference between production and natural mortality. They noted that application of this model requires time-series data on catches and abundance, the latter normally expressed as an index of stock biomass. Carruthers et al. (2014) discussed additional models and noted one that adjusts historical catches by using assumptions of historical depletion ("depletion methods"), those that rely on a time series of catches ("catch based"), and those that rely on current estimates of absolute abundance ("abundance-based methods").

Cadarin et al. (2013) wrote that populations or segments of those populations are assumed to be of a single unit stock with spatially homogenous production (e.g., recruitment and mortality) within spatial boundaries, within which the assumptions allow for processing of fisheries management and stock assessments. They also noted that the stock boundaries are often based upon delineated fisheries territories instead of the natural distributional range of the cephalopods. The range reduction via fisheries territory only provides a small sample of the stock as a whole.

7a. Markets

Markets are a complex aspect of marine fisheries that substantially affect both humans and the marine organisms fished. Markets are heavily driven by fisheries landings and fishing effort and chiefly rely on fishery-dependent data reported by both commercial and recreational sources. Data may include biological information (e.g., characteristics of target species such as identification, maturity, weight, and length), effort information (e.g., catch/landing totals, location, season, gear type, costs), bycatch, and discards. Fishery-independent data, typically from longer-term scientific surveys, are incorporated into market analyses but can usually be restricted to assessments and external factors of socio-cultural value (e.g., providing employment and income in coastal fishing communities) (Pierce, 1999; Pierce et al., 2010; Shaw, 1994). Fisheries and markets are not as straightforward as providing a product and getting paid for it. Fisheries do not typically include overfishing and non-reporting in their business models, but Belhabib et al. (2014) noted that non-reporting seems more prevalent than misreporting and discussed some implications of this in the example of Senegalese illegal unregulated and unreported fishing activities.

7b. Assessment

Global cephalopod fishery data collection from different countries is important for the comparison of stocks, stock management, gear selection or updates, and models for future fisheries. A disconnect currently exists between what scientists and fishery managers versus the fishers who are recording the data regard as targeted catch versus incidental bycatch (Davies et al., 2009). Fishers are more likely to consider any species that has commercial or economic value as a targeted catch rather than as bycatch. As different species of cephalopods become commercially valuable, less valuable species or misidentified species are considered as bycatch by the fisher and recorded as such.

When discussing marine fisheries and their commercially viable species, management and stock assessment of populations of targeted and non-targeted species and the data following are invaluable in forming educated decisions regarding the fisheries. Cephalopod stock identification has become complicated due to confusion about life history traits and plasticity relative to environmental factors (Boyle and Boletzky, 1996). Since 1966, many advances in genetic techniques have been applied to identifying cephalopod stocks and understanding of their structure (Semmens et al., 2007; Shaw et al., 2010). Stock identification and its associated research are critical to assessing these valuable marine fisheries (Rodhouse et al., 2014). A caveat for assessments is that they are based only on whatever data, however limited, is available.

Many authors have noted the importance of appropriate fishing levels and the relationships between the stock abundance and recruitment in order to maintain a sustainable cephalopod fishery (Boyle and Rodhouse, 2005; Caddy, 1983; Pierce and Guerra, 1994). The stock assessments and forecasting for cephalopods are basically the same methods widely used for fish stocks. However, accurately estimating and forecasting cephalopod abundances may be difficult due to their life history plasticity, fast growth, and quick maturation, which together result in short recruitment periods (Boyle and Rodhouse, 2005; Caddy, 1983; Pierce and Guerra, 1994). Most cephalopod stock assessment models tend to avoid age-structure models because of the uncertainty in age estimation from growth patterns and highly variable maturation processes due to environmental conditions (Royer et al., 2002). The assessment of cephalopods stocks is generally categorized based upon the timing of their observation or experimentation relative to the fishing season: preseason, in-season, and postseason (Boyle and Rodhouse, 2005; sensu Pierce and Guerra, 1994). However, the application of finfish assessment models to cephalopods does provide some insight into whether or not the fishing of cephalopod stocks may be sustainable in the long run.

Preseason assessments forecast stock size and future management of cephalopod stocks based upon one-year lifespans and assume that the targets for the fished stock are composed of newly recruited individuals into the population (Rodhouse et al., 2014). Such assessments usually require special sampling gear in order to catch and measure the abundance of smaller pre-recruit stages, which require enough time just before the fishing season opens (Rodhouse, 2001). As a result of this preseason timing issue, less effort is generally put into this category of stock assessment, although preseason data, e.g., juvenile and paralarval densities, are used to forecast stock sizes using suitable models (Rodhouse et al., 2014). However, preseason assessments using methodologies such as midwater trawls to collect abundance data run into the difficulty of determining the values of paralarval and juvenile densities and their relation to the spawning stock and what it could mean for future generations. Both Boyle and Rodhouse (2005) and Wormuth and Roper (1983) provided insight into how midwater trawl surveys may seriously underestimate densities in oceanic cephalopod assessments. Kidokoro et al. (2014) discovered that *Todarodes pacificus* juveniles between 8 and 205 mm were caught in 267 out of 331 midwater trawls using a trawl net with a 7-mm mesh cod end, reinforcing the idea that surveys are not always diminished through net avoidance. This study did not acknowledge net avoidance, nor did it discuss the smaller specimens (<7 mm) that may have slipped through the cod end without active avoidance behaviors. Human observational errors and experimental errors (e.g., net placement, collection, observation, data collection) can create unreliable forecasting models, although such models may be suitable for fisheries that have never been assessed before.

In-season assessment data usually derives from recruited individuals captured by commercial fisheries (Rodhouse et al., 2014). These data may also use biological reference points (e.g., fishing mortality, biomass, spawning-recruitment) to compare against the commercial data to make informative management decisions regarding thresholds for each fishery (Mace, 1994; Rodhouse et al., 2014). One of many benefits of in-season assessments is that timely updates permit recognition of population growth or decline as the season progresses. Such information allows fisheries managers, e.g., in the Japanese *T. pacificus* fishery, to understand seasonal shifts and migration patterns that can be used in forecasting catches and abundances at particular fishing grounds (Okutani, 2017). However, Rodhouse et al. (2014) stated that in-season assessments are only used for a few of the most commercially important cephalopod fisheries (e.g., Falkland Islands *Illex* fishery (Arkhipkin et al., 2013; Basson et al., 1996; Rosenberg et al., 1990)) due to the highly migratory and adaptive nature of those species. They also noted that data collected from assessments combined with knowledge of migratory patterns can reinforce fishery focus in particular fishing grounds.

The widely available oceanic dynamics models (e.g., Regional Oceanic Modeling System (DMCS Ocean Modeling Group, n.d.; Research Institute of Applied Mechanics Ocean Model, n.d., in Rodhouse et al. 2014)) enable commercial fisheries to forecast potential movement of stock caused by environmental change, mainly temperature (Rodhouse et al. 2014). DMCS Ocean Modeling Group (n.d.) allows the user to input any available physical aspect of the environment into the algorithms to create and follow the pathway needed. Shifts in stocks can be calculated on a weekly or even monthly basis due to known interactions between cephalopods at the species level and the oceanic conditions (Rodhouse et al. 2014). An example of this forecasting system using empirical models based on oceanographic conditions is the distribution map of *T. pacificus* in Figure 3 (Figure 2.14 in Rodhouse et al., 2014). The map demonstrates the use of oceanic temperatures and known squid density correlations to show which fishing grounds may be more viable seasonally. Models such as these can provide educated assumptions about population dynamics and oceanic impacts, although Rodhouse et al. (2014) noted that detailed recruitment data are necessary for more reliable forecasting of cephalopod populations. These authors provide a caution for the use of empirical based models incorporating environmental conditions to create stock forecasts without the use long time series. The effects of oceanic change upon cephalopods is still being studied, and fisheries require detailed forecasts to maximize yield and minimize loss for future endeavors. Thus, more studies are needed to thoroughly and accurately develop forecasts for any particular cephalopod fishery.

Postseason methods rely on data collected from former generations of cephalopod stocks using one or more of the methods and models described below (Rodhouse et al., 2014). Several authors (e.g., Arkhipkin et al., 2013; Roa-Ureta and Arkhipkin, 2007) noted the importance of using multiple methods to assess cephalopod fisheries due to variability across stocks and availability. The first production model, the Surplus Production Model (SPM), also known as a Biomass Dynamic Model, essentially provides the simplest version of a stock assessment (Rodhouse et al., 2014). In theory, the SPM estimates the biomass of the cephalopod stock for the year by adding the biomass for the calculated year plus the estimated catch (an aggregated parameter of the recruitment and the growth) and then subtracting the actual catch (Graham, 1935; Schaefer, 1954). Rodhouse et al. (2014) noted that this is considered an overly simplified model due to the lack of age or spatial structure consideration into the population dynamics, and therefore the stock assessment. The SPM additionally assumes that the stock is at equilibrium, a situation is rarely encountered in cephalopod assessments, and which may lead to the overestimation of a stock (Hilborn and Walters, 1992). As an example, the developed SPM for the cephalopod fishery of the Saharan Bank indicated that both octopus, squid, and cuttlefish stocks were overexploited in those areas (Bravo de Laguna, 1989; Sato and Hatanaka, 1983). This overly simplified model may suggest that a stock has been over- or under-fished, but the results are subject to uncertainties. The lack of spatial temporal population dynamics means that this overly simplified model will not provide all the information needed to properly assess a cephalopod Fishery.

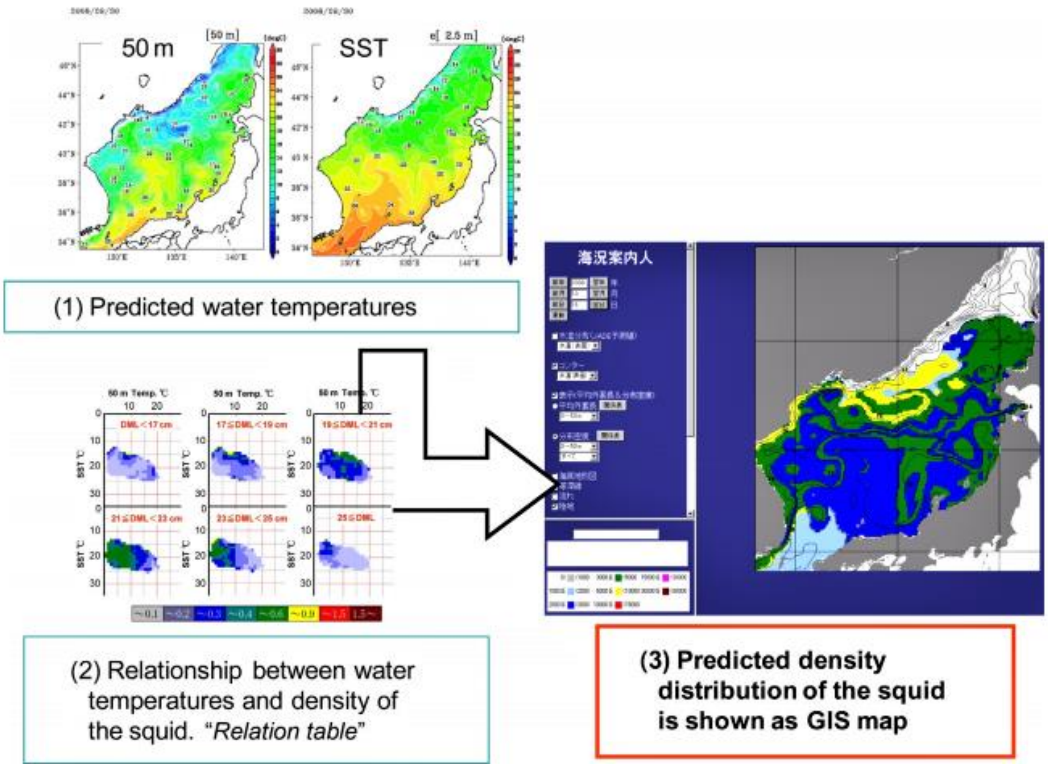


Figure 3. Predicted density for *Todarodes pacificus* in the Sea of Japan using an oceanic dynamics model to forecast favorable sea surface temperatures based upon the temperature-density relationship. Density map from the Research Institute of Applied Mechanics Ocean Model (n.d.), in Rodhouse et al. (2014).

The second method is the depletion method, which is commonly used to assess marine fisheries stocks, including those of cephalopods (Rodhouse et al., 2014). This method, mentioned above and derived from Leslie and Davis (1939) and De Lury (1947), essentially states that the model will estimate the potential consequences of removing individuals from the population; it determines the size of the population without the fishery activity (Hilborn and Walters, 1992). Although this model is favored, the limitations of randomly distributed populations of cephalopod stocks with a constant catchability mean that this method cannot determine with 100% accuracy whether a stock is growing or declining exponentially. As an example, this method was used to assess *D. gigas* stock in the Gulf of California by modeling three different fleets operating in the same area (Ehrhardt et al., 1983).

Virtual Population Analysis (VPA) is the most broadly-used, age-structured method for assessing long-lived finfish stocks (Hilborn and Walters, 1992). Several authors (Jouffre et al., 2002; Royer et al., 2002, 2006; Thiaw et al., 2011) noted that application of this method to cephalopods suffers from the brief nature of their life histories. As cephalopods generally live for only one to two years, the VPA must be completed every few months instead of years to calculate the initial cohort population, with each stock consisting of multiple annual cohorts. To determine numbers of cephalopods per cohort via this method, numbers lost to natural mortality and capture during a year are added to the number remaining at year's end to estimate the number of individuals in the cohort or stock at the beginning of the year (Rodhouse et al., 2014).

Finally, Collie and Sissenwine (1983) described two-stage models, which are used when the data are not accurate enough to implement VPA but are accurate enough to determine the recruitment period and a fully recruited phase of the population. The theory behind this population model is that abundance of a recruited stage can be estimated by adding the recruitment strength to fully recruited individuals (Rodhouse et al., 2014). The equation for populations dynamics designed by Collie and Sissenwine (1983) was adapted by Mesnil (2003), and is as follows:

$$N_{t+1} = (N_t + R_t)\, e^{-M} - C_t\, e^{-M(1-\tau)}$$

where N_t is the population size in number of fully recruited animals at the beginning of the year t; R_t is the population size based on recruits at the beginning of the year t; C_t is the catch number throughout the year t; M is the instantaneous natural mortality rate assumed to be equal for the different stages, and τ is the pulse in which the catch is assumed to occur during a fraction of the year (Rodhouse et al., 2014).

The first trial to determine cephalopod stocks took place in the 1980's off the coast of South Africa (Roel and Butterworth, 2000). The method was updated by adding the process error through Bayesian methodology to the observation error (Rodhouse et al., 2014). Rodhouse et al. (2014) added that the International Council for the Exploration of the Sea (ICES) Working Group on Cephalopod Fisheries and Life History created an application software for this methodology to perform routine assessments of cephalopod stocks. The stock assessments do provide management details pertaining to the stock in question. Forecasting of stock population changes does impact how fisheries determine gear use and where to actively fish. Rodhouse et al. (2014) described the fishery-dependent data collection and gear differentiation amongst fleets, which impacts stock and management of cephalopod stocks, while fishery-independent data collection, such as paralarval surveys, trawls, and active jigging, provide non-fishery related data to be used and repurposed for healthy population management.

Fishery management and assessment issues rise from varying abundance, stock identification, and damage to known spawning grounds. As noted above, the fluid state of cephalopod taxonomies, compounded by a systemic failure to record landings at the species level, if anything is recorded at all, creates challenges for stock identification. Cephalopods exhibit wide natural variations in abundance. As a result, understanding escapement – the percent or actual numbers of individuals not captured (Roper et al., 2010) – is critical to estimating stock size, as is also true with short-lived, synchronous spawning species that lack any buffer to prevent recruitment failure and population collapse (Rodhouse et al., 2014; Caddy, 1983). Rodhouse et al. (2014) also discussed clear social and economic challenges to declining cephalopod fisheries. Contingency plans for both large-scale and small-scale fisheries are needed for economic necessity, while the social impact of failure is high. Coastal cities and regions that depend upon cephalopod fisheries for food and economic trade feel the loss of populations or stocks the most, while commercial fisheries that catch cephalopods as by-catch have a hard time regulating mortality rates.

The need to manage cephalopod fisheries has become increasingly apparent because global fishery data (FAO, n.d.-a) suggest that cephalopod fishery landings peaked in 2007, and overexploitation of cephalopod stocks may already be taking place. Rodhouse et al. (2014) explained that climate change and the ever-growing human population will continue to diminish food supply, so cephalopods are likely to become a prized commodity as fish become scarcer due to these conditions. In addition, global climate change and ocean acidification have also directed scientists to begin research into using environmentally sensitive mollusks as sentinels for future changes.

7b(1). Assessment Gear

The gear used in the assessment methods mentioned above vary with biology and targeted life stages. Benthic versus pelagic species require different methodologies. The most precise means of estimating squid abundances and distribution is to collect early paralarvae via net sampling, as these early life history stages are less capable than older stages of avoiding or escaping from net openings. Plankton collecting gear works well for paralarvae, e.g., ring net, Nansen net, bongo net, neuston net, multilayer sampling MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System), and BIOMOC (BIOlogical Multiple Opening/Closing) nets (Rodhouse et al. 2014). Jigging and acoustic surveys provide additional assessment method options, but typically for larger specimens of juveniles and adults. Examples of paralarval sampling nets follow.

Although FAO (2001b) described a ring net as a hybrid surrounding net intermediate between a purse seine and a lampara net, the midwater ring nets used for capturing paralarvae are plankton nets (e.g., ICES, 2013) (Figure 4). Vertically-towed Nansen nets are similar (Figure 5).

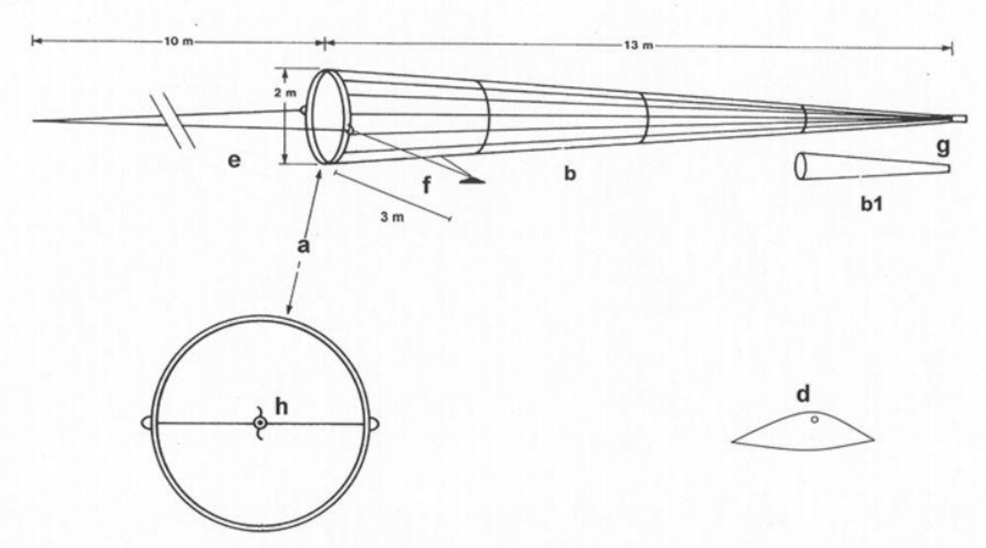


Figure 4. Construction and rigging of a midwater ring, or plankton, net (ICES, 2013, p. 8). a) steel ring, 2 m diameter; b) black net, 1.6 mm mesh, 13 m long, strengthened by nylon or canvas straps, with (b1) 500-µm mesh net in the last meter; d) saddle-shaped weight or depressor, ~25 kg or more when necessary, depending upon weight of 2-m ring; e) pair of 10-m-long bridles; f) pair of 3-m-long bridles to weight/depressor; g) cod end collecting bucket (11 cm diam.); h) flowmeter (best accompanied by acoustic depth sounder) centrally mounted on line within ring, positioned ~0.5 m inside the net. From ICES (2013).

Figure 5. Nansen Closing Net is a vertically deployed plankton net with messenger-operated closing mechanism. A 70-cm-diameter stainless steel ring with a 3-m-long net bag, made of Tetex, gauze of 100 µm (upper conical part), and gauze of 55 µm (lower conical part and side window of Netbucket). From Hydro-Bios, (n.d.-b).

Bongo nets are paired plankton nets. The double ring with central attachment of the towline eliminates turbulence cause by the bridle of a single net, which may contribute to net avoidance by organisms, and also permits simultaneous use of nets with two different mesh sizes (Figure 6). Bower et al. (1999) used 70-cm diameter paired nets with 334-µm mesh equipped with paired flowmeters and a time-depth recorder to sample *T. pacificus* paralarvae. Various modifications of the nets, e.g., ring diameter and mesh size, depend upon biotic and abiotic factors.

Figure 6. Bongo paired net with two rings . From Hydro-bios, (n.d.-a).

Neuston nets are low profile, rectangular-mouthed nets with a rigid frame opening for collecting small organisms on or just under the seas surface film (Koslow & Allen, 2011) (Figure 7).

Figure 7. Neuston net. From Neustons nets. (n.d.)

The MOCNESS consists of a sturdy rectangular frame that carries sensors (e.g., for conductivity/salinity, temperature, depth, chlorophyll, oxygen, and light levels), controls 6 to 20 nets that can be opened and closed from the surface, and is towed slowly (<3 knots) (Wiebe, n.d.) (Figure 8). The cable connecting ship and instrument allows scientists to control sampling depth. MOCNESS nets are long and tapered; frame size (0.25-20 m^2) and mesh size (64 µm to 3 mm) vary with the intended catch size of specific kinds of plankton. The slow towing speed creates problems with escapement or avoidance, producing less reliable estimates for larger organisms. The BIOMOC multilayer sampling mechanism (Voss et al., 2007) is a modified MOCNESS net that can be adjusted with smaller micrometer netting and is deployed horizontally.

Figure 8. MOCNESS launched from the research vessel Ronald H. Brown during the Census of Marine Zooplankton in April 2006. (Photo by Madin, L (2006)). From Wiebe,(n.d.).

Gear is deployed either horizontally, vertically, or obliquely, depending upon the stock assessment requirements (Rodhouse et al., 2014). Flowmeters permit quantification of water volume sampled and thus paralarval densities. However, it is crucial to understand the biological and morphological characteristics of cephalopod paralarvae and identify them to species level before creating management systems, whereas other sampling methods for juveniles and adults require specific modifications for behavior and distributional errors.

Jigging surveys are a dominant method of assessment for juvenile and adult squids and cuttlefish (Rodhouse et al., 2014). A jig is a vertical fishing line with a sinker and one or more hooks. Squid-specific jigs have a special set of squid jiggers called ripped hooks, which are mounted one after the other with monofilament line at certain intervals. The line, weighed down by sinkers, can be lowered to 200 m depth and is hauled up with jerky movements (FAO, 2001d) (Figure 9). Jigging has been proven to catch commercially important species of squids and cuttlefish, but is not commonly used for estimating biomass, because different jig colors and sizes determine which species will be caught (Mercer and Bucy, 1983). Kidokoro and Mori (2004) created an index of abundance from the results of their jigging survey for the Japanese common squid (*T. pacificus).*

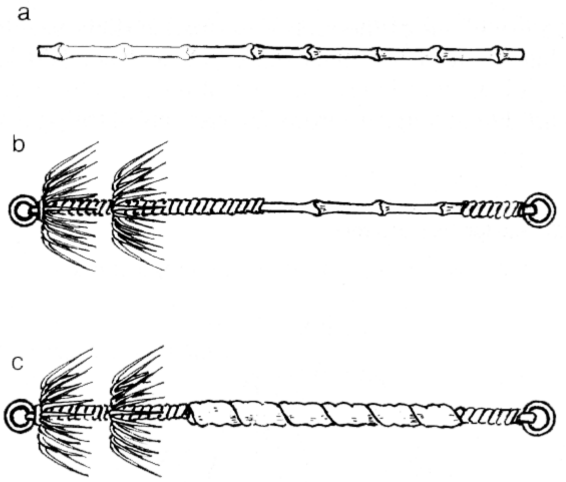


Figure 9. Constructing a handmade squid jigger with bamboo stem. From Bjarnason, (1992).

Acoustic surveys can also produce large aggregate data sets, although several early studies produced results that were more qualitative rather than quantitative (Shibata and Flores, 1972; Starr and Thorne, 1998; Suzuki et al., 1974). More recently, quantitative acoustic studies have proven useful in determining abundance estimations when paired with catch rate indices of fisheries. As an example, Goss et al. (2001) conducted two-frequency acoustic surveys for *D. gahi* around the Falkland Islands. Limitations of acoustic assessments include the lack of species level identification, which, however, can be avoided by pairing acoustic methods with trawl surveys and addition of known biological requirements for the targeted species (e.g., location, depth, temperature) (Rodhouse et al., 2014). Advances in broadband acoustic systems permit more accurate classification techniques (e.g., acoustic signal characteristics of live *D. pealeii* (Lee et al., 2012)), along with modern modifications such as the optical-acoustic platforms that incorporate cameras to provide simultaneous target acquisition (Imaizumi et al., 2008; Stanton et al., 2010).

7c. Fishing Gear

The forecasting of cephalopod stocks and assessment techniques discussed above are used chiefly for fishery-independent surveys and provide only a fraction of the "whole picture" for cephalopod fishery sustainability. The equipment described below is that used by fisheries and provides data for fishery-dependent assessments and management. Rodhouse et al. (2014) provided several tables (Tables 1 and 2), which discuss management of small-scale and industrial-scale fisheries, respectively. Some equipment used in artisanal fisheries described below has been updated to promote higher catch rates for targeted species while reducing unwanted by-catch or species caught in mixed-species fisheries. Some squid and cuttlefish large-scale fisheries use bottom trawls and purse seines to capture their quota (Arkhipkin et al. 2015).

Octopuses are traditionally caught by pots or traps, although handheld harpoons and gaffs are frequently used by recreational and local fishers on tidal flats or shallow reefs. Clay pots are the traditional artisanal gear for local and small-scale fisheries globally. The octopus fishery in Gulf of Cadiz off Spain uses species-specific clay pots, locally called *alcatruces* or *cajirones* (Sobrino et al., 2011). An *alcatruz* is simple, easy to deploy along a long line, and can be left unattended for extended periods of time. It is used specifically for the common octopus fishery based on a close knowledge of octopus behavior and needs. Sobrino et al. (2011) used four kinds of pots to identify cephalopod selectivity; some were made of clay or plastic and came in different shapes and volumes (Figure 10).

Trammel nets (FAO, 2001c) are stationary walls of one to three layers of vertically hanging mesh. Fish (or cephalopods) are entangled in a slack inner net between the vertical netting walls (Figure 11). They can be used either anchored to the sea floor or as drift nets. This gear is inexpensive but inefficient as it is more likely to capture non-target species.

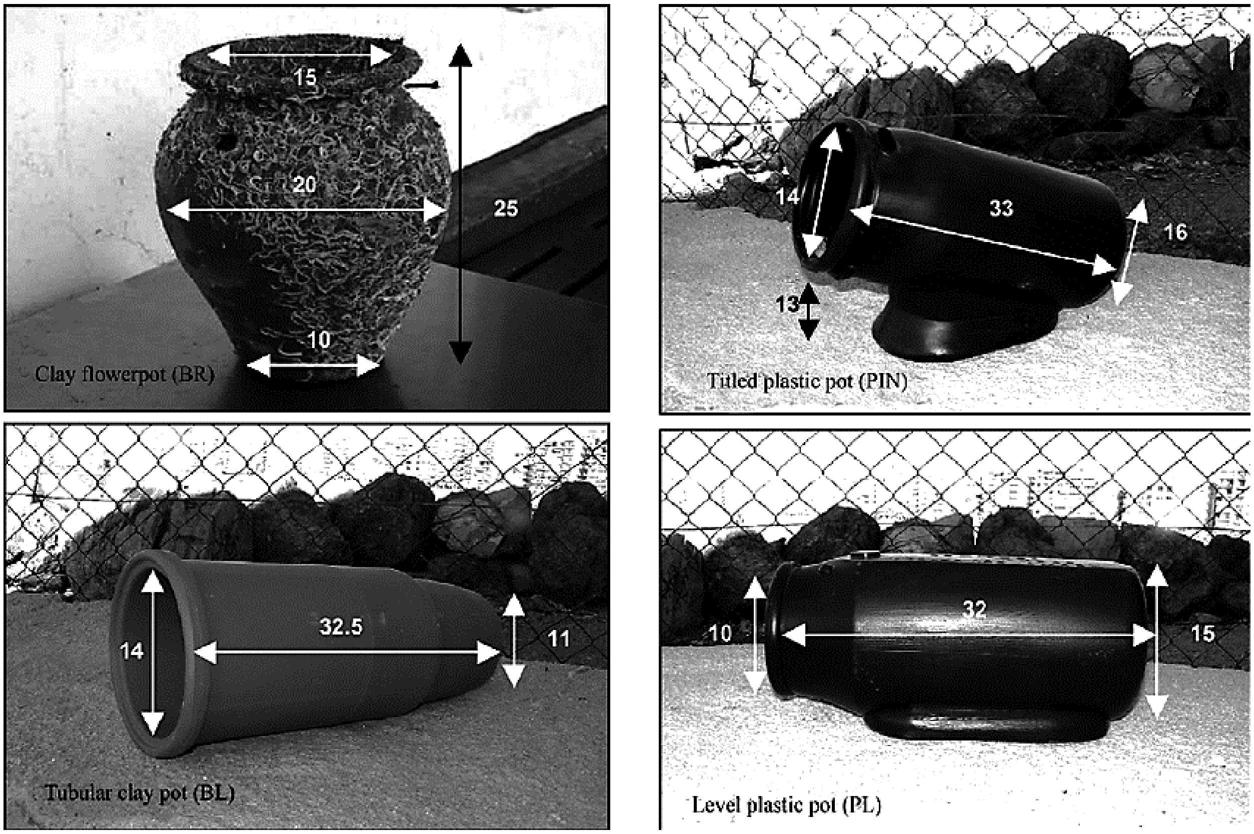


Figure 10. Examples of the four types of pots used by Sobrino et al. (2011). Clay flowerpot (BR), 4.4 L volume; plastic pot (PIN), 6.5 L with a tilting and cement-filled bottom; tubular clay pot (BL), 3.7 L, and level plastic pot (PL), 6.3 L with a flat and cement-filled bottom for stabilization.

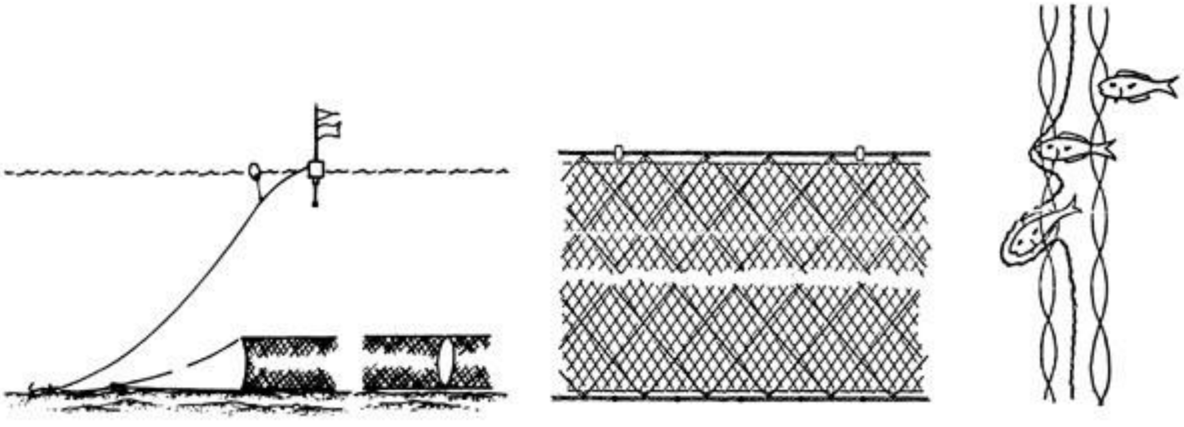


Figure 11. Trammel net. From FAO, (2001c).

A fyke net is cylindrical or cone-shaped net bag mounted on rings or other rigid structures with wings or leaders to guide the fish towards the entrance of the bag (FAO, 2001a)

(Figure 12). This gear may or may not work on soft bodied cephalopods, which may be able to squeeze their way out of the nets. Fyke nets also run into the problem of incidental by-catch, but non-target species capture is likely to be less, because the gear is a one-way fish trap rather than a wall of impassable nets.

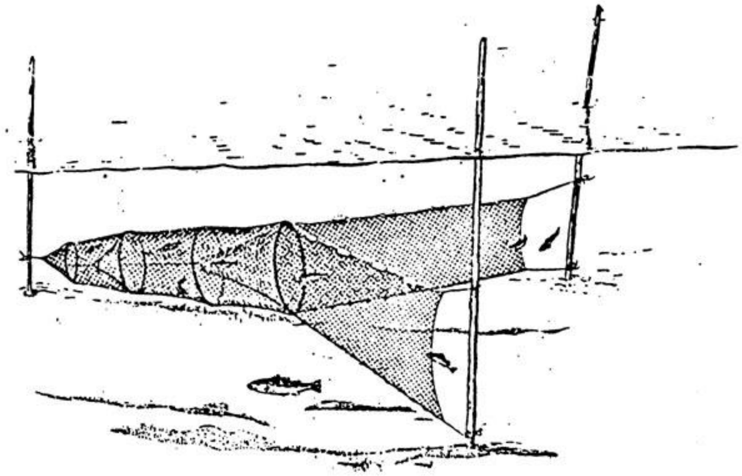


Figure 12. Standard fyke net anchored to substrate . From FAO, (2001a).

With many gear choices and the ability to use them for assessments and/or fishing, managing the fishery effort is the next step in both industrial and small-scale fisheries.

7d. Management

The tables in Rodhouse et al. (2014) provide some insight into what management solutions were in place prior to the fishery declines in 2016 and 2017 (Globefish, 2019). Earlier, Boyle and Rodhouse (2005) had mentioned that cephalopod landings were on the rise and seemed to be one of the few remaining marine resources available for expanded exploitation. However, Globefish (2019) stated that supplies of octopus and squid that were already low were becoming tighter, and prices were expected to continue to skyrocket as commercial fisheries struggle to meet quotas for import and export. The FAO is urgently requesting better management for overfished stocks along national Exclusive Economic Zones (EEZ), particularly for the three most important squid species (jumbo flying squid, Argentine shortfin squid, and Japanese flying squid) stocks. One of the problems is that those three important squid species all span EEZs of multiple nations as well as the high seas, which allows vessels to fish for these species without quota enforcement, resulting in overfishing and the possible depletion of the resource. Some medium to small operators in the octopus sector quit the fishery due to tight supplies and slim return margins.

Before the declines, Arkhipkin (2016) noted that, despite the increase in cephalopod landings and stock increases, management solutions were being investigated as a component of food security, because humans have always gone above and beyond sustainable fishing. Rodhouse et al. (2014) noted that management strategies included standard finfish stratagems, not only those restricted to those suited to cephalopod biology. These included top-down, co-management, and even rights-based strategies.

Rights-based strategies are now broadly accepted as the most successful management tools. These include rights for both access and withdrawal (Rodhouse et al., 2014). Charles (2009) summarized access rights as including territorial use rights (TURFs) and limited entry rights to provide only a limited amount fishing licenses or assigned rights for restricted locales. Rodhouse et al. (2014) defined withdrawal rights as quantitative rights based upon input data and effort rights, and effort rights as the rights assigned to each fisher to use a specific amount of gear for a particular time period. The quantitative input data comes from harvest quotas and require the total allowable catch (TAC) data to be input and allocated to several sectors in the fishery. While management of cephalopod fisheries requires time and effort while also presenting its own limitations, efforts-based management schemes seem to work well on both small-scale and large-scale fisheries.

Co-management systems are popular for resources users, governments agencies, and sometimes other parties affiliated with management of the fishery (Gutiérrez et al., 2011; IUCN, 1996). Such arrangements may increase the responsibility of the fisher towards the stock, while decreasing the skepticism of the fishers towards policies and legislations that may interfere with fishing effort. Rodhouse et al. (2014) stated that one of the major selling points for co-management is the “voice”, or input, that every party involved can provide for appropriate fishery management. However, Mikalsen and Jentoft (2008) noted that true-co management rarely exists, and that fishers often have little to no “voice” in fishery matters.

In top-down management, a governing body, such as a governmental agency, attempts to achieve a unified successful management consensus for a particular stock that may be over- or underexploited, but this approach is generally unsuccessful (Arceo et al., 2013; Caddy and Seijo, 2005; Gaymer et al., 2014). All of the literature consulted for summarizing this approach were the top results of the search for top-down fishery management, and all three were from after the year 2000. However, Gaymer et al. (2014) provided some merit for in-depth and well-informed top-down management that may provide useful guidelines for productive co-management; they suggested that many top-down management systems are merging with bottom-up systems to essentially create co-management systems.

Several challenges and limitations exist for each management system, which create difficult challenges for non-finfish fisheries (Rodhouse et al., 2014). Key factors for cephalopod fisheries include misidentification of species in official reports and statistics, the relatively short-lived nature of the target species, their changing trophic roles with growth within an ecosystem, and the determination of boundaries for specific fisheries (Rodhouse et al. 2014 and references therein). Cephalopods migrate depending upon their physiological needs, and some fisheries straddle international and political boundaries, creating additional hoops for management with mixed species fisheries (e.g., *D. gigas*, which is exploited in the Peru, Mexico, and Chile Exclusive Economic Zones (EEZs) (Pope, 2009). The comprehensive knowledge of a targeted species is invaluable in determining gear restrictions, closures and restrictions of fishing grounds, and the interactions of the species with other fisheries (Rodhouse et al., 2014). Mixed fisheries and by-catch species cause problems for commercial or large-scale fisheries (e.g., trawling and long-line fishing for cephalopods). In a broad sense, management generally aims to sustain the fish stock, sustain the fishery, and sustain fishery-related employment.

A global problem for marine fisheries beyond the cephalopods themselves is their economic and social impacts upon the human population (Rodhouse et al., 2014). Countries that rely heavily on marine resources to feed their populations require measures to prevent stock collapses when populations boom and bust as cephalopods tend to do. Pita et al. (2015) described the challenges Portugal faces in governing their own small-scale fishery, because it is excluded from quota regulations under the European Common Fisheries Policy, and concerns have risen over its long-term sustainability. European nations (e.g., Spain, Portugal, Italy, Greece, France, and the United Kingdom) constitute the most important market in the world for imported cephalopod resources (Pierce et al. (2010).

Rodhouse et al. (2014) stated that the recent bump in cephalopod landings (again, before the declines of 2016 and 2017) was due to the changes in gear described above, generally moving away from "traditional and old-fashioned" inefficient gear towards modernized gear. The literature mentions the illegal, unreported and unregulated (IUU) fishing activity that plagues fisheries globally. A major component of IUU is the artisanal and locally-resourced fishing activity that is hard to track and becomes expensive to maintain governance over (Rodhouse et al., 2014). The long-term impacts of IUU are beginning to appear, as FAO (2019) reported that the markets are struggling to keep up with demand, while artisanal fisheries are meeting around 99% of their quotas.

The tables in Rodhouse et al. (2014) are not entirely comprehensive nor exhaustive of the all cephalopod fisheries management globally, but they do synthesize and shape currently applied management initiatives. However, they do not include data from recreational fisheries, which exist primarily in countries where cephalopods are a common meal. The FAO (1996) published a set of guidelines for artisanal and developing fisheries that included limiting risk by use of closed areas, delegating some management decisions to the community, limiting industrial fishery influence on resources, and investigating social and economic impacts of the fisheries. FAO (1996) also published cephalopod-relevant precautionary guidelines for responsible equipment use and implementation of management systems and development, using the best scientific evidence available for adoption or creation of management: 1) developing effective communication for all parties associated (e.g., international and co-management regimes), 2) aiming to reduce or eliminate mis-reporting or non-reporting, 3) expanding biological and ecological models of the fishery through environmental and technological interactions, 4) using technology "responsibly" in support of conservation and promotion of environmental "friendliness," 5) recognizing that gear consideration should incorporate biological/environmental factors as well as socio-economic constraints, and 6) providing sufficient data on the impacts of a new or updated gear selection to all parties. The application of these principles could provide some coastal cities or countries with unmanaged fisheries to develop more sustainable fisheries for future generations of stock and human-environment interactions.

Marine Protected Areas are often contentious methods for management. Rodhouse et al. (2014) stated that MPA's have been used as management systems and do work as seen in Portugal and Spain, although they are typically associated with small-scale fisheries or even to-take zones. They noted that these protected zones are controlled by stricter legislation and require better enforcement of policy.

Lack of enforcement of regulations on both large-scale and small-scale fisheries has prevented the proper management of cephalopod fisheries. Rodhouse et al. (2014) provided examples of overexploited cephalopod stocks (e.g., neon flying squid *O. bartramii*, jumbo flying squid *D. gigas*, Japanese common squid *T. pacificus*, and Argentine short-fin squid *I. argentinus*) within underdeveloped or developing countries that do not have the means to monitor, control, and surveil (MCS) their management systems, as well as open seas fisheries outside of an EEZ.

Rodhouse et al.'s (2014) recommendations on management can be summarized by the following principles: (1) explore the use of the ecosystem approach to cephalopod fisheries (EAFC) as described by FAO (2003); (2) reduce the uncertainties in how fisheries interact with specific ecosystems; (3) recognize that fisheries production and yield are constrained by factors that can be classified as biological, ecological and environmental, technological, social and cultural, and economic; (4) strive for more complex adaptive management systems to include large abundances of finfish and cephalopods; (5) identify the social and economic importance of European fisheries; (6) promote and maintain small-scale and artisanal fisheries; (7) carry out research into cephalopod by-catch reduction; and (8) recognize and act on the need for more effective, monitoring, and control over management systems. Management systems will continuously need to be revisited as time and environmental change alter population dynamics of both finfish and cephalopod resources and fisheries.

7d(1). United States Management

The United States is seen globally as relatively well managed for fisheries in general (D. Kerstetter, personal communication), relative to the number of global fisheries that combine all take levels from small- to large-scale. Its fisheries are legislatively required under the Magnuson-Stevens Fishery Conservation and Management Act to uphold specific fishing standards for effort and management and fishery-independent standards (NOAA 2007). By contrast, countries with poor economic conditions and barely functioning or stabilized government may not allocate sufficient funds, effort, and expertise to management. A case study from Matić-Skoko et al. (2010) on the Croatian artisanal fisheries and the data collection advised by the European Union (EU) provides some insight into management difficulties with an almost entirely gear-based management system. The authors concluded that the proper recording, analyzing, and interpreting fishers' knowledge coupled with marine protected areas (MPA) would greatly improve the currently unsustainable fishing situation. Croatia has not been admitted into the EU due to a lack of proper data collection frameworks.

The United States has data collection frameworks in place, both dependent and independent of fisheries and now even has at least one certified sustainable cephalopod fishery: the Marine Stewardship Council (MSC) (2018) in May described at length the world's first certifiably sustainable squid fishery for longfin inshore squid (*Doryteuthis (Amerigo) pealeii)*. MSC certifications are awarded to fisheries with well documented sustainability, minimized environmental impact, and effective fisheries management (Marine Stewardship Council, n.d.). Cephalopod fishers operating such certifiable sustainable fisheries under long-term assessment can become highly valued across the market as a higher quality product that can demand a premium price. The United States as a case study offers an example to management regimes around the world, which will continue to require updating and adjusting management regimes as climate change continues to shape our planet and the organisms within it.

After looking the projected abundance levels of cephalopods, I created Figure 13 based on the National Marine Fisheries Service's (NMFS) commercial landings data for all U.S. states between 2000-2016 (NOAA National Marine Fisheries Service, n.d.) Figures 13A and C show all squid and octopus annual landings, respectively, for all states; Figure 13B shows squid landings minus California Market Squid to provide an improved visual of tons landed for the other species landings under 20,000 tons. Figure 13A illustrates the precipitous decline in California market squid from 2000 to 2003, its recovery from 2008 to 2010, and its decline again from 2014 to 2015. The longfin squid and shortfin squid landings (Figure 13B) inversely alternate in decline and recovery from 2000 to 2016, through prominently in 2004 to 2013, with both recovering after 2016, and the "squids" relatively stable from 2004 onward with a slight peak in 2015. Figure 13C illustrates relatively stable landings until the dramatic increase between 2009 and 2011, a decrease again from 2011 to 2013, a nearly two-fold recovery in one year, then a similar decline from 2014 to 2016.

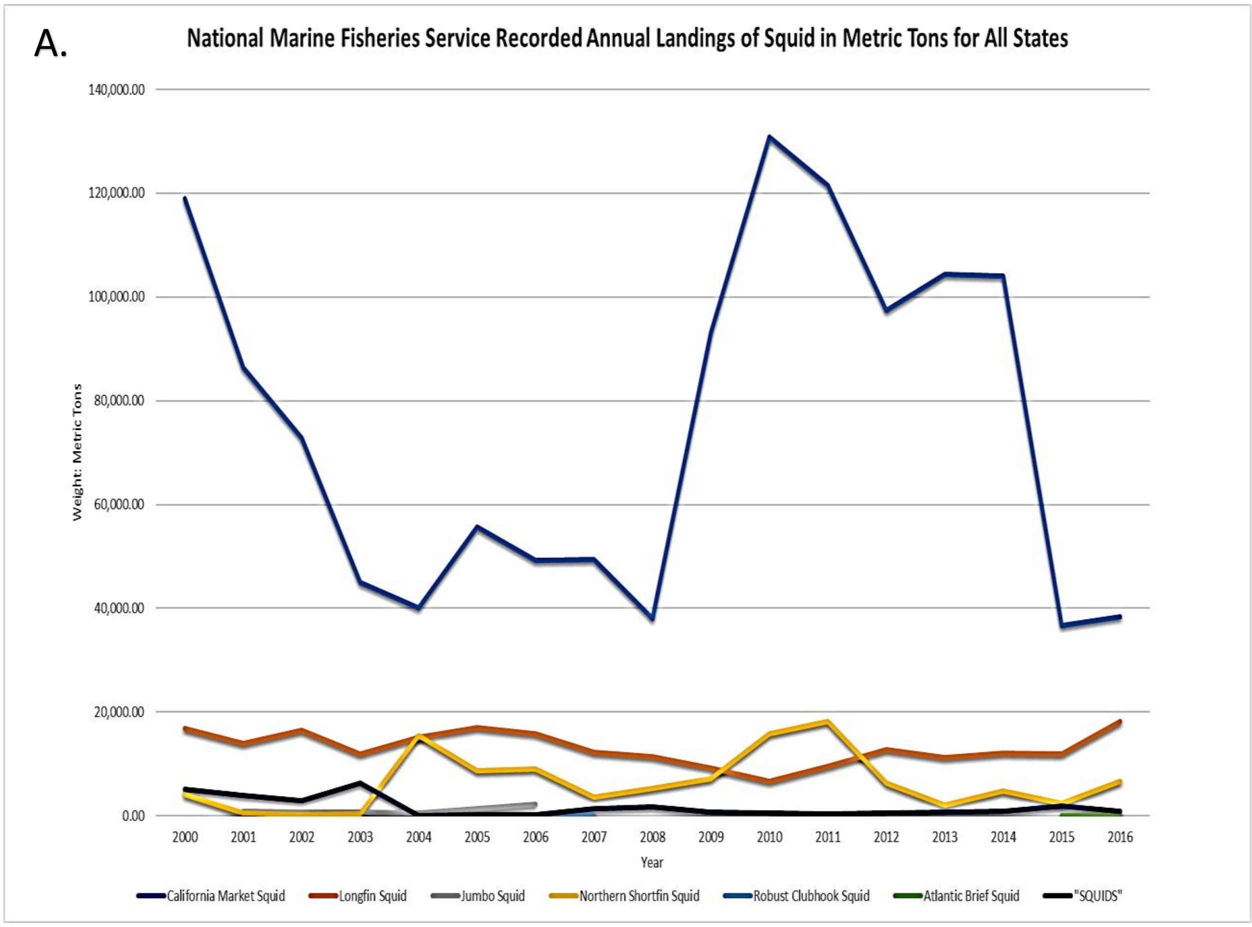
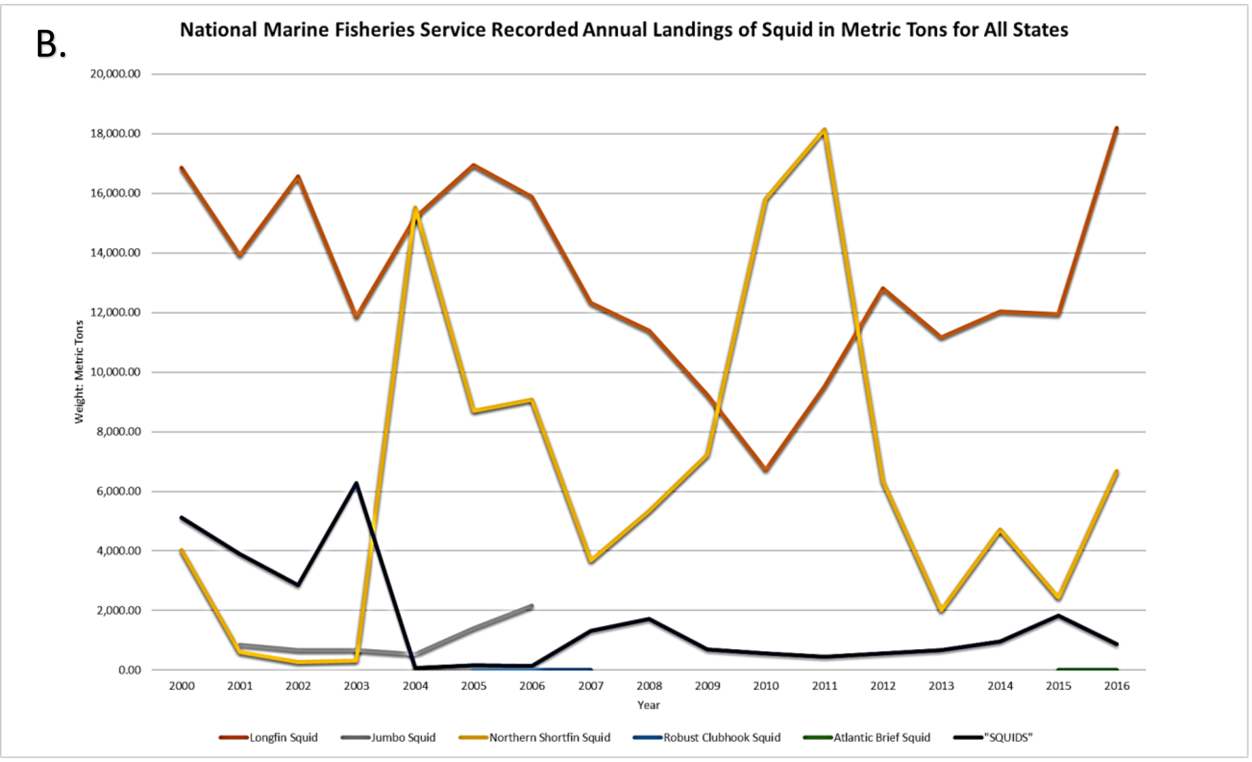


Figure 13. (A) Shows all squid annual landings in metric tons for all states between 2000-2016. Data from NOAA National Marine Fisheries Service, (n.d.).


National Marine Fisheries Service Recorded Annual Landings of Squid in Metric Tons for All States

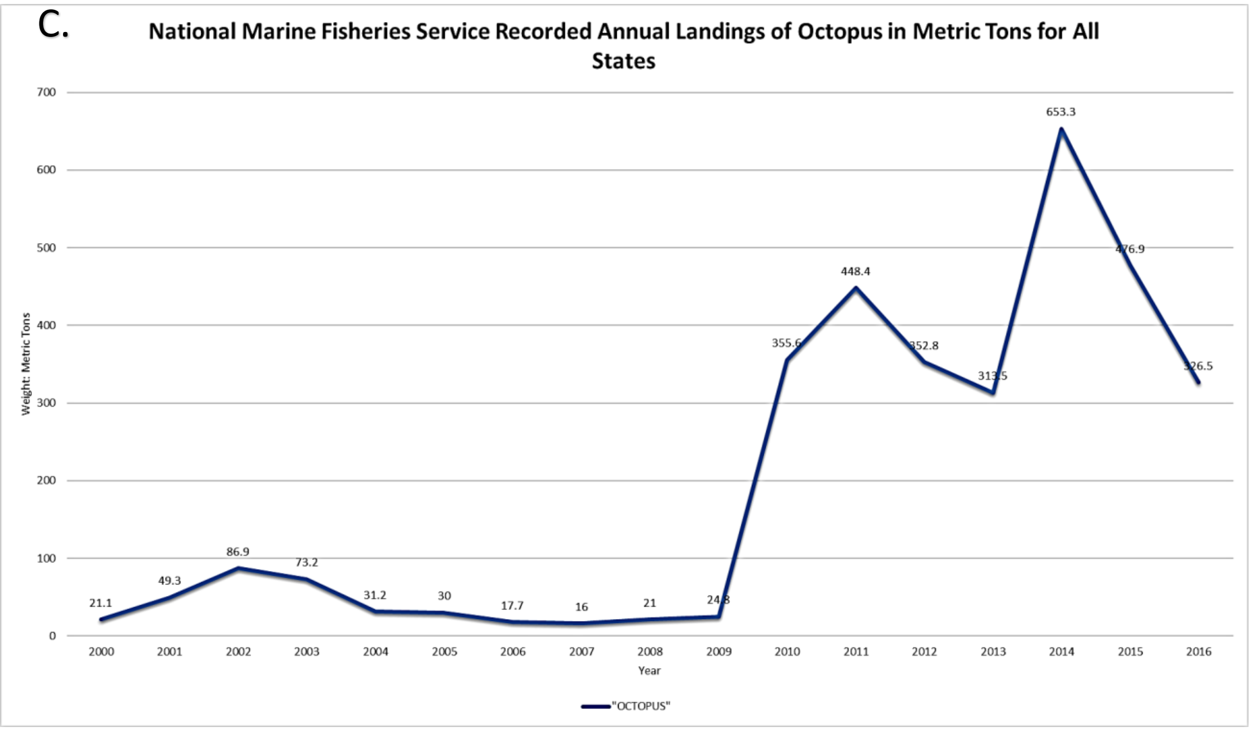

National Marine Fisheries Service Recorded Annual Landings of Octopus in Metric Tons for All States

Figure 13, continued. (B) Shows squid annual landings in metric tons for all states between 2000-2016 minus California Market Squid; (C) shows the annual landings for octopus in metric tons for all states between 2000-2016. Data from NOAA National Marine Fisheries Service, (n.d.).

8. Data

The first step in using data and models to describe population dynamics and trophic relationships is to decide which model benefits the research question. Five common models used to describe cephalopod growth and maturity rates include 1) primitive linear three-stage, 2) ontogenetic growth, 3) bioenergetic, 4) physiological, and 5) maturity. Each provides a different aspect crucial to fisheries management. Possible explanations for observed changes during research can be tested using these models (Rodhouse et al. 2014).

Rodhouse et al. (2014) argued that difficulties inherent in using traditional population dynamics approaches to assess cephalopod stocks may be due to life cycle complexities and external factor sensitivity. Cephalopods are particularly susceptible to changes in their physical environment. Published models detail the direct relevance of environmental conditions, primarily temperature, upon cephalopod growth rates, mantle lengths, maturity, and fecundity (Forsythe 1993, 2004). Forsythe (2004) hypothesized that higher temperatures during hatching would allow monthly cohorts of squids to grow faster, and perhaps larger, than older, earlier-hatched cohorts. The effect, the Forsythe Effect, has been laboratory and field tested with results supporting the hypothesis. However, Reiss et al. (2014) created the first age-based, temperature dependent model for any squid population with results that contradicted Forsythe's hypothesis (Figure 14). This figure demonstrates that growth rate is negatively related to temperature and is generally predictable from the hatch month sea surface temperature. The authors explained the results of the figure as follows: "A linear regression, fit to the combined data of growth rates versus mean monthly temperature during the hatch month and derived from monthly composite satellite data for the SBC, yielded a strong negative relationship between temperature and growth rate: ($GR = 1.18 – 0.0395 * T$) and ($R2 = 0.67$, $df = 14$, $p < 0.0001$)." Reiss et al. (2004) concluded that external factors such as dramatic changes (El Niño vs. La Niña) will impact populations through ecosystem changes (e.g., temperature, habitat). The model proposed that the relationships between cephalopods and their environment reflect trade-offs between physical environmental changes and associated food availability. The effects of environmental factors upon cephalopods and their responses to climate change require more research, particularly as the biology and population structures of oceanic squids (e.g., Reiss et al. 2004) versus, say, octopus (e.g., Andre et al. 2010) differ substantially.

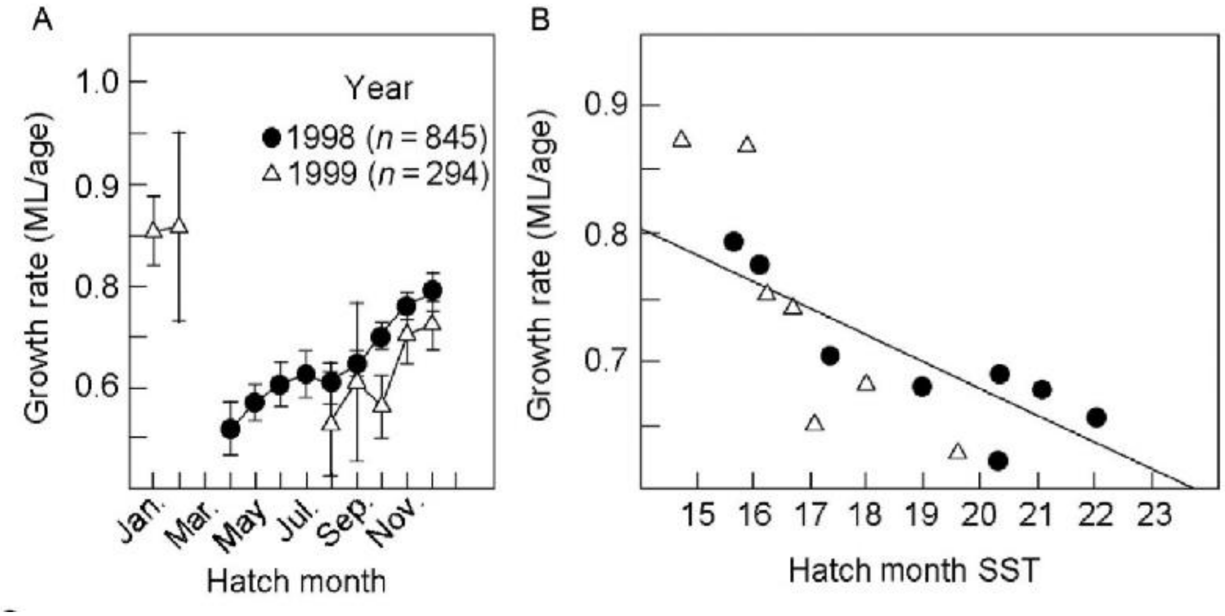


Figure 14. (A) Mean growth rate (1SE) of mature *Loligo opalescens* from the Southern California Bight commercial fishery in 1998 and 1999 plotted by month of hatch; (B) means of growth rates in relation to hatch-month SST (sea surface temperature) as calculated from the monthly mean temperature recorded at Scripps Pier (California, USA) (From Reiss et al. (2004) in Rodhouse et al. (2014)).

Rodhouse et al. (2014) noted that many empirical models that link environmental variables with cephalopod distributions, abundances, and recruitment acknowledge the impact of the environment upon life cycles and trophic relationships. Trophic relationships are known chiefly for the better-known cephalopod species but are primarily classically descriptive, with rare use of biological data (e.g. age, length, and maturity). As an example, Arkhipkin et al. (2015) provided a thorough treatment of the global squid fishery, including its history, details by region and species, and interactions between fisheries and ecosystems. Cashion et al. (2018) summarized catches by fishing gear from 1950-2014 and categorized those efforts by country, taxon, year, and gear. They analyzed gear used in both large, industrial-scale, and small artisanal sectors via reconstructed catch data composed of millions of catch records. As discussed in the fisheries section, gear may be altered in response to changes in stocks, fishery regulations, or even distribution of vessels dependent upon local or international fishing efforts. Understanding such changes may allow managers to predict how gear and fisheries will change in the future.

Tables 1 and 2 (In Rodhouse et al. 2014, Tables 2.3 and 2.4) below provide the data on the gear discussed in the assessment and fishing gear subsections above. They are not comprehensive but do offer an idea of global fisheries management trends. It is important to note that 13 large-scale fisheries included in the tables listed nothing for management regime, due to any one of many possible reasons described in the fisheries section above.

Table 1. Management initiatives for small-scale cephalopod fisheries worldwide (from Rodhouse et al. 2014, Table 2.3).

Table 2.3 Current management initiatives for small-scale cephalopod fisheries

Species	Location/country	Targeted/ by-catch	Gear type	Management regime	Management measures	References
Cuttlefish						
Sepia officinalis	Greece, Aegean and Ionian Seas		Trammel nets			Pierce et al. (2010)
Octopus						
Enteroctopus megalocyathus	Southern Chile, southeastern Pacific	Target and by-catch	Free divers using gaffs and by-catch in crab traps	Co-management	Four-month seasonal bans, minimum catch weight (1 kg), 3-year ban (2008–2011)	IInstituto de Fomento Pesquero (2010), Castilla (2010)
Enteroctopus megalocyathus	Patagonian Gulfs and Shelf, SW Atlantic	Targeted	Scuba diving and gaffs	No management		Ortiz et al. (2011)
Octopus insularis	Rio Grande do Norte State, northeastern Brazil, SW Atlantic	Targeted in summer, by-catch in winter	Free diving and compressor-aided diving (illegal) from small boats	Top-down management, no enforcement	Diving with air compressor forbidden, no enforcement of legislation	Vasconcellos et al. (in press)
Octopus insularis	Northeastern Brazil, SW Atlantic	Targeted	Walking on the reef flats in the low tide with gaffs	Top-down management, no enforcement		Vasconcellos et al. (in press)
Octopus insularis	Fernando de Noronha Islands, northeastern Brazil, SW Atlantic	Targeted	Free divers using gaffs	Co-management	Limited number of licences, minimum DML (80 mm)	Leite et al. (2008)
Octopus maya (and *O. vulgaris*)	Mexico: Yucatan Shelf	Targeted	Baited lines		Static 6.5-month closed season, minimum size (110 mm ML), prohibition of commercial diving and hooks	Diaz-De-León and Seijo (1992)
Octopus mimus	Northern Chile, southeastern Pacific	Targeted	Free divers using gaffs	Rights-based and co-management	Four-month closed season, minimum landing size (MLS: 1 kg), territorial use rights for fisheries (TURFs), exclusive fishing rights, extraexclusive fishing rights allocated to subsistence and small-scale artisanal communities	Rocha and Vega (2003)
Octopus tehuelchus	Nuevo and San Jose Northern Patagonian Gulfs, SW Atlantic	Targeted	Fishing with gaffs during low tide	No fisheries management but access restricted by MPA		Narvarte et al. (2007)

Table 2.3 Current management initiatives for small-scale cephalopod fisheries—cont'd

Species	Location/country	Targeted/ by-catch	Gear type	Management regime	Management measures	References
Octopus vulgaris	Asturias, Spain	Targeted	Traps	Rights-based and co-management	TURFs, exclusive fishing rights, territorial use rights, sea zoning, closed seasons, MLS	Fernández-Rueda and García-Flórez (2007)
Octopus vulgaris	Greece, North Aegean Sea (NE Mediterranean)		Plastic/PVC pots		<1500 pots/vessel, MLS (individual weight, >500 g), fishing ban: July–September, fishing depth > 10 m	Pierce et al. (2010)
Octopus vulgaris	Greece, North Aegean Sea (NE Mediterranean)	Targeted	Fyke nets		<1500 pots/vessel, individual weight >500 g, fishing ban: July–September, fishing depth > 10 m	Pierce et al. (2010)
Octopus vulgaris	Portugal	Targeted	Pots and traps		MLS (main measure, 750 g), technical measures regulating gear	Pereira (1999)
Squid						
Dosidicus gigas	Eastern Pacific Mexico EEZ and Gulf of California	Targeted	Hand jigging		Sonora (Mexico): effort control	Morales-Bojórquez et al. (2001b)
Loligo reynaudi	South Africa	Targeted	Hand-held jigs	Rights-based	Limited number of vessels, limits to number of crew depending on vessel size, 6-week annual closed season during peak spawning period	Sauer (1995)
Todarodes pacificus	Northwest Pacific off Japan and Sea of Japan	Targeted	Jigging machine and squid fishing light		Japan: Restricted by fishing areas, season and fishing light intensity. Allocation of TAC based on ABC.	Kiyofuji and Saitoh (2004)

DML: dorsal mantle length, ML: mantle length, MLS: minimum landing size, TAC: total allowable catch, ABC: available biological catch.

Table 2. Management initiatives for industrial cephalopod fisheries worldwide (from Rodhouse et al. 2014, Table 2.4).

Table 2.4 Current management initiatives for industrial cephalopod fisheries

Species	Location/country	Targeted/ by-catch	Gear type	Management regime	Management measures	References
Cuttlefish						
Sepia officinalis	Lower Normandy, France	Targeted	Trawl and trap fish	Co-management	Closed season, limited licences, fishing seasons, MLS, technical measures (mesh size, number of pots and traps), control number of vessels operating (a limit of 180 trap vessels and 140 coastal trawlers), regulating trawling within the 3 mile limit (Normandy regional orders)	Pierce et al. (2010)
Sepia officinalis	Portugal	Targeted	Unbaited jigs		MLS, technical measures (type of mesh, mesh size)	Pierce et al. (2010)
Octopus						
Octopus insularis	Ceará state, northeastern Brazil, SW Atlantic	Targeted	Pots longlines	Co-management	15 boats under 15 m total length, 5000 pots per boat. Individual mean weight around 600 g	Vasconcellos et al. (in press)
Octopus vulgaris	Galicia, Spain	Targeted	Traps	Co-management	Technical measures (mesh size, number of vessels, number of pots/traps per vessel), time and area restrictions, limitation on the number of licences, MLS, closure period	Pierce et al. (2010), Bañón Diaz et al. (2006)
Octopus vulgaris	Southern Brazil, SW Atlantic	Targeted	Pots longlines		28 boats with up to 20000 pots each. Individual ML over 11 mm, around 1 kg	Barahona et al., 2010
Octopus vulgaris	Greece	Targeted	Traps and fyke nets		Technical measures (number of pots/traps per vessel), time restrictions, MLS, closure period	Pierce et al. (2010)
Octopus vulgaris	Gulf of Cadiz, Spain	Targeted	Pots and traps		Technical measures (number of pots/traps per vessel, length of line), area restrictions, MLS, closure period, ban on sport fishing for octopus	Pierce et al. (2010)
Squid						
Berryteuthis magister	Russia, northwest Pacific	Targeted	Bottom trawl		Technical measures (restricted areas and periods), TACC at about 45–55% of the total assessed biomass	Katugin et al. (2013)
Doryteuthis opalescens	California, United States	Targeted	Purse seine nets	Rights-based	Technical measures (closed or restricted areas), limitations to fishing effort and minimum sizes of mesh and species	California Department of Fish and Game (2007)
Doryteuthis pealeii	United States	Targeted	Trawl		ABC and DAH, fishery closure threshold, trip limits	Mid-Atlantic Fishery Management Council (2011)

Continued

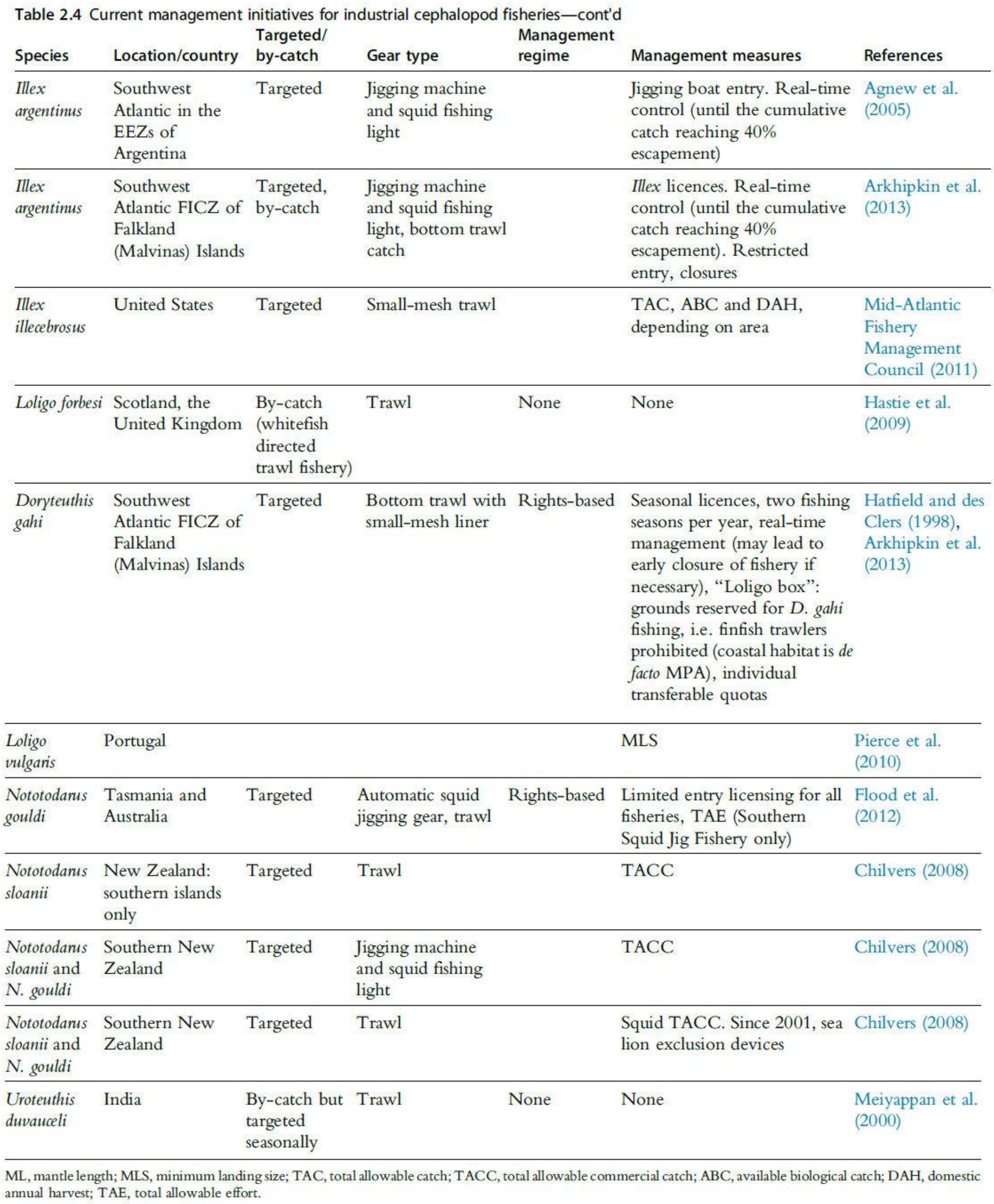


Table 2.4 Current management initiatives for industrial cephalopod fisheries—cont'd

Species	Location/country	Targeted/ by-catch	Gear type	Management regime	Management measures	References
Illex argentinus	Southwest Atlantic in the EEZs of Argentina	Targeted	Jigging machine and squid fishing light		Jigging boat entry. Real-time control (until the cumulative catch reaching 40% escapement)	Agnew et al. (2005)
Illex argentinus	Southwest Atlantic FICZ of Falkland (Malvinas) Islands	Targeted, by-catch	Jigging machine and squid fishing light, bottom trawl catch		*Illex* licences. Real-time control (until the cumulative catch reaching 40% escapement). Restricted entry, closures	Arkhipkin et al. (2013)
Illex illecebrosus	United States	Targeted	Small-mesh trawl		TAC, ABC and DAH, depending on area	Mid-Atlantic Fishery Management Council (2011)
Loligo forbesi	Scotland, the United Kingdom	By-catch (whitefish directed trawl fishery)	Trawl	None	None	Hastie et al. (2009)
Doryteuthis gahi	Southwest Atlantic FICZ of Falkland (Malvinas) Islands	Targeted	Bottom trawl with small-mesh liner	Rights-based	Seasonal licences, two fishing seasons per year, real-time management (may lead to early closure of fishery if necessary), "Loligo box": grounds reserved for *D. gahi* fishing, i.e. finfish trawlers prohibited (coastal habitat is *de facto* MPA), individual transferable quotas	Hatfield and des Clers (1998), Arkhipkin et al. (2013)
Loligo vulgaris	Portugal				MLS	Pierce et al. (2010)
Nototodarus gouldi	Tasmania and Australia	Targeted	Automatic squid jigging gear, trawl	Rights-based	Limited entry licensing for all fisheries, TAE (Southern Squid Jig Fishery only)	Flood et al. (2012)
Nototodarus sloanii	New Zealand: southern islands only	Targeted	Trawl		TACC	Chilvers (2008)
Nototodarus sloanii and *N. gouldi*	Southern New Zealand	Targeted	Jigging machine and squid fishing light		TACC	Chilvers (2008)
Nototodarus sloanii and *N. gouldi*	Southern New Zealand	Targeted	Trawl		Squid TACC. Since 2001, sea lion exclusion devices	Chilvers (2008)
Uroteuthis duvauceli	India	By-catch but targeted seasonally	Trawl	None	None	Meiyappan et al. (2000)

ML, mantle length; MLS, minimum landing size; TAC, total allowable catch; TACC, total allowable commercial catch; ABC, available biological catch; DAH, domestic annual harvest; TAE, total allowable effort.

Additional important data is available through Arkhipkin (2016), who summarized the paper he published with Doubleday et al. (2016), in which he stated that cephalopod populations have been booming over the last six decades as a result of the absence of top predators and vacant niches. Cephalopods grow rapidly and adapt quickly; they may proliferate faster than the environment can accommodate them (Doubleday et al., 2016). The authors continued to discuss the negative impacts of rapid population growth, stating that cephalopods could drastically impact many prey species, including but not limited to commercially valuable fish and invertebrates. They generated abundance graphs by using 67 time-series of cephalopod catch rates (catch data standardized to fishing or survey-sampling effort) from both fisheries-dependent and fisheries-independent sources. The time-series ranged from 10 to 61 years, which provided them with abundance growth forecasting via trendlines from generalized additive mixed models (GAMMs) to investigate temporal trends in cephalopod abundance fitted within the R computing environment (version 3.2.0) (Doubleday et al., 2016).

The National Marine Fisheries Service (NMFS) published commercial landings data for all U.S. states between 2000-2016, but none for 2017-2019, no landings data for cuttlefish, and none for octopus landings by species (i.e., only "octopus" in general) (See Figure 13A-C above) (NOAA National Marine Fisheries Service, n.d.). Data caveats (NOAA National Marine Fisheries Service, 2009) for the published data include: "(1) published data is non-confidential data or confidential data labeled with quotations marks (e.g., "squids" or "octopus") as unclassified; (2) landings do not indicate the physical location of harvest; (3) landings are reported in pounds of round (live) weight for all species or groups…; (4) many fishery products are gutted or otherwise processed while at sea and are landed in a product type other than round (whole) weight, and (5) landing data is unavailable for some of the listed species, because these species or market categories were used as identifiers in other data bases such as the processed product survey or our monthly report of the volume of fishery products held in cold storage." The inclusion of the caveats provides insight into the complexity of recording and publishing landing data, while Figure 13 in the fisheries section provides a more complete look at landing data available for public use. We can infer that the oceanic temperature increase of 2016 (NOAA National Centers for Environmental Information, 2017) had an impact on population growth based upon the landing increases across all squid species around the United States, whereas octopus landings were low for the year. This decrease in octopus landings does not necessarily mean that octopod populations did not grow. The decreased landings could be from various environmental conditions or even socio-economic difficulties ranging from fishers to management systems and regimes.

NOAA's climate monitoring sector publishes environmental data for public access and use. I used the data (e.g., NOAA National Marine Fisheries Service, n.d.) and a figure from the Climate-at-a-Glance section (NOAA National Centers for Environmental Information, 2019), observing global oceanic temperature changes through time. Figure 15 matches the time frame for the commercial landing data above in Figure 13A-C. The trend line demonstrates the overall increase in ocean temperatures since the turn of the century. This supplemental information demonstrates the well-known trend of oceanic warming and reflects the difficulties cephalopods will likely continue to face, especially in terms of reduced growth as temperature increases.

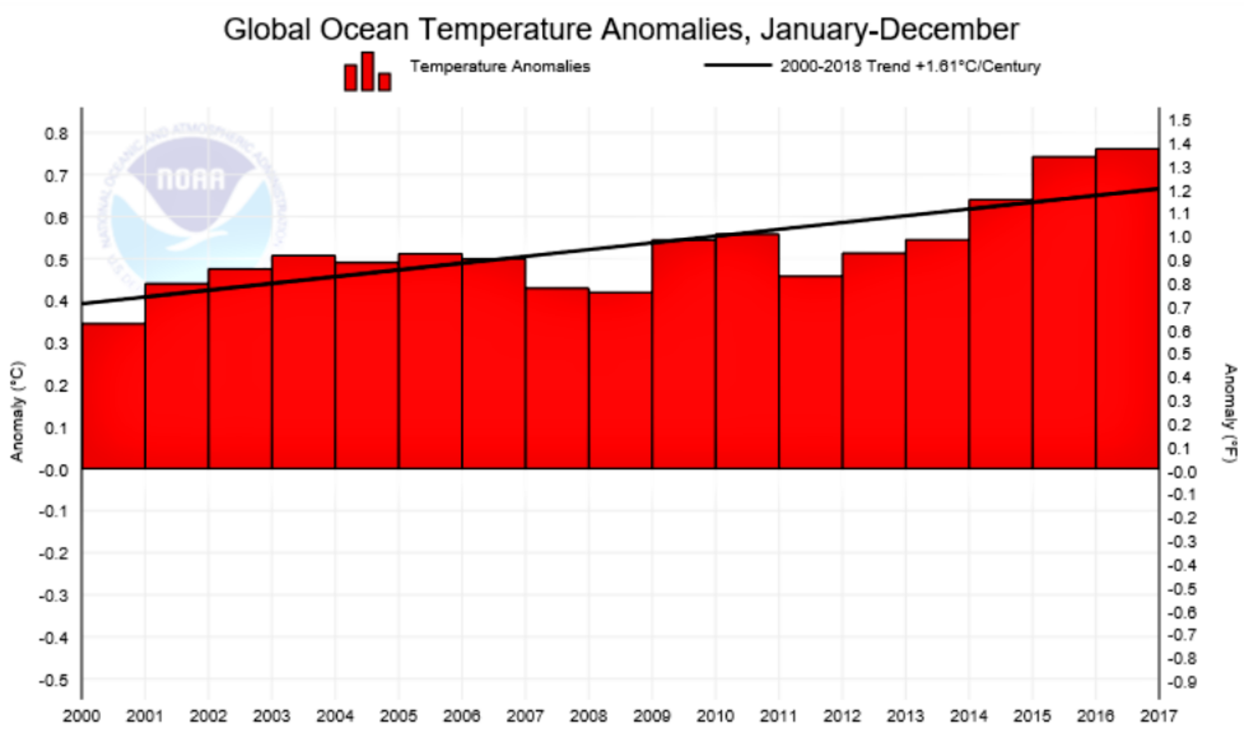


Figure 15. Annual Global Ocean Temperature Anomalies from 2000-2017 in both Celsius and Fahrenheit. From NOAA National Centers for Environmental Information, (2019).

9. Conclusion

The importance of cephalopods to marine communities should not be underestimated, as they are relevant to today's global economy, active fisheries, and environmental impacts of the changing oceans. Cephalopod biology and fisheries directly correlate with the success rates of boom and bust dynamics noted in recent literature. Doubleday et al. (2016) described cephalopod populations as booming in the absence of top predators and vacant niches as a result of overfishing of higher-level predators. Cephalopods grow rapidly, adapt quickly, and their populations can rebound after overexploitation (Rodhouse et al. 2014; Arkhipkin, 2016).

FAO Globefish market reports from 2017 noted the dramatic decrease in both squid and octopus landings in 2016, while cuttlefish landings remained primarily the same in the latter part of the year (Globefish, 2019). This data lightly touched on tons landed and primarily focused on tons traded commercially among nations.

NOAA's State of the Climate reports from 2016 provided a more comprehensive look into what environmental factors (omitting fisheries activity) may have led to the apparent decline in the last two quarters of 2016. The 2016 State of the Climate Global Anomalies webpage provided the data that land masses and oceanic regions experienced higher than average temperatures, becoming "the warmest year in NOAA's 137-year series" (NOAA National Centers for Environmental Information, 2017). NOAA's data also identified a high number of oceanic storms (i.e., 18 hurricanes, 13 cyclones, 13 typhoons, and 93 other storms) influenced by a strong El Niño season. NOAA's graph of increasing oceanic temperatures from 2000-2016 (Figure 15) displayed a trend line of increasing temperatures forecasted to continue in the future. Although at least some cephalopods grow more rapidly at higher temperatures (e.g., Reiss et al. 2014), populations and landings may increase with improved techniques and management, and as finfish predators continue to be overexploited, continued rising ocean temperatures generally bode ill as cephalopods have demonstrated extreme sensitivities to changing temperatures, e.g., greater likelihood of starvation when food is scarce (Rodhouse et al. 2014), altered life cycles (Arkhipkin 2000), and diminished growth rates as SST of hatch month increases (Reiss et al. 2014).

Understanding of cephalopod population dynamics is largely based on commercially exploited coastal and shelf species, which may not be applicable to oceanic and benthic taxa (Rodhouse et al. 2014). Exploited species exhibit complex population structures directly impacted by abiotic factors (e.g., temperature, salinity, dissolved oxygen, oceanic acidification, and photoperiods) as well as predatory behaviors and food availability, including but not limited to cannibalism. The ability to accurately identify cephalopod species can prevent over-exploitation of targeted species and provide more precise estimates of population sizes through accurately recorded inclusive fishing efforts (both targeted and bycatch). Migration and trophic relationships directly affect population dynamics, but most studies only provide short-term data.

Rodhouse et al. (2014) contradicted the earlier literature and noted that trophic relations are poorly understood and disregarded within stock assessments. This information illustrates that, although basic classical descriptions of trophic interactions exist, relationships change over time and updated data will be relevant for the future. As a result, population variability research, which depends on understanding trophic interactions over a cephalopod's entire life cycle, is limited, as are the life cycles themselves of many cephalopod species. These relationships are no less important than the physical parameters of the environment around the organism; trophic relationships require more effort to incorporate into assessments due to the vast challenges with the biology and life histories of cephalopods. Rosa et al. (2012) provided clear data on hatchlings and the direct impacts of future predicted elevated temperatures, demonstrating the struggle cephalopods will have in the warmer oceans of the future. The literature places heavy importance on the influence of temperature upon cephalopods; however, ocean acidification, oxygen tension, salinity, and photoperiods also affect cephalopod life histories at various stages as well as driving change in the whole ecosystem.

Rodhouse et al. (2014) concluded that cephalopod populations have the potential to be good indicators of short-term environmental variability, but this means they are likely to be poor indicators of long-term variables due to their responses in the short-term. The ability to predict environmental change through cephalopods will help future assessments and management of stocks that may or may not do well under specified future conditions. The sustainability of stocks and cephalopod populations globally will benefit from a better understanding of the biology and trophic dynamics derived from future studies.

Assessment methods of cephalopod stocks have the same problems as those of other marine fisheries but also vary with the targeted cephalopod and the resources available. Rodhouse et al. (2014) argued that combining appropriate stock assessment methods with environmental parameters will build a better understanding of the relationship mechanisms and then may be applied in the future. Effective communication and involvement of all affected parties (i.e., from governments to fishers) will provide better management results and more sustainable cephalopod stocks. The assessments and management regimes associated with cephalopods provide insight into their potential sustainability long-term, with a case study of the innovative United States' first certified sustainable squid fishery leading the way.

Cephalopod biology and life histories have provided these animals with the means to be winners under conditions of long-term global climate change. They are ecological opportunists with highly plastic biological characteristics and varied population dynamics. Nearly all cephalopods are short-lived and can reproduce quickly, permitting them to evolve more rapidly under high selection pressure relative to many fish competitors and predators. This capstone looked into cephalopod life history, morphology and taxonomy, population dynamics, and recruitment of this increasingly valuable class of marine organisms.

Despite the adaptive capabilities of cephalopods, the sustainability of heavy fishing effort will be questioned in the future as the impacts of socio-cultural values and economic importance continue to rise across the globe. The correlation between increased oceanic temperatures and the global proliferation of cephalopods may be inferred from the literature; however, this does not provide direct causality, nor does it provide the notion that cephalopods may be fished extensively without proper management and guidance. Future endeavors to promote stock and population sustainability via proper management and assessments will increase the likelihood of enjoying cephalopod products in all of their forms into the future across the globe.

10. Acknowledgements

I would like to first and foremost thank my committee for the vast amount of work they put in over a short amount of time. Dr. Messing spent countless hours editing and providing criticism to help create this review of cephalopod fisheries. Dr. Riegl provided the opportunity to create and complete this capstone as required per program requirements.

I would like to thank my friends and family for their support during the extensive process of completing this degree. I would like to thank Nick Bender and his wife for the opportunity to stay at their home in Barcelona, Spain, for two weeks during the summer of 2018. Without this

opportunity, I would not have seen the vast amount of cephalopods for sale at La Boqueria, and I would not have begun to worry about sustainability of cephalopod fisheries without that experience.

Thank you to any and all who have read through this capstone review of cephalopod fisheries and allocated time towards the sustainability and future of cephalopods.

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