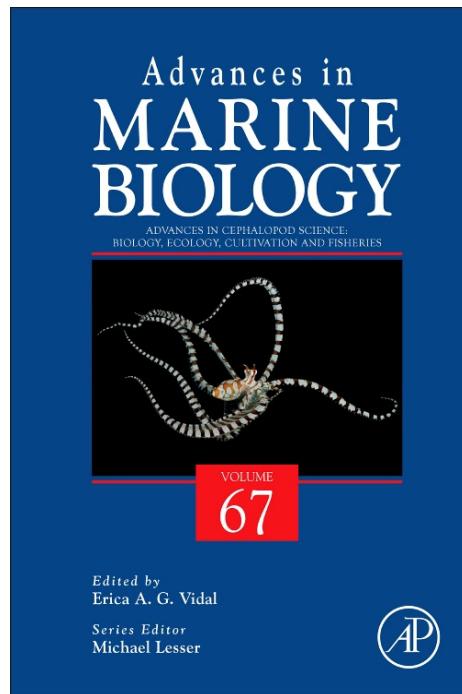


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Environmental Effects on Cephalopod Population Dynamics: Implications for Management of Fisheries

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Abstract

Cephalopods are a relatively small class of molluscs (~800 species), but they support some large industrial scale fisheries and numerous small-scale, local, artisanal fisheries. For several decades, landings of cephalopods globally have grown against a background of total finfish landings levelling off and then declining. There is now evidence that in recent years, growth in cephalopod landings has declined. The commercially exploited cephalopod species are fast-growing, short-lived ecological opportunists. Annual variability in abundance is strongly influenced by environmental variability, but the underlying causes of the links between environment and population dynamics are poorly understood. Stock assessment models have recently been developed that incorporate environmental processes that drive variability in recruitment, distribution and migration patterns. These models can be expected to improve as more, and better, data are obtained on environmental effects and as techniques for stock identification improve. A key element of future progress will be improved understanding of trophic dynamics at all phases in the cephalopod life cycle. In the meantime, there is no routine stock assessment in many targeted fisheries or in the numerous by-catch fisheries for

cephalopods. There is a particular need for a precautionary approach in these cases. Assessment in many fisheries is complicated because cephalopods are ecological opportunists and stocks appear to have benefited from the reduction of key predator by overexploitation. Because of the complexities involved, ecosystem-based fisheries management integrating social, economic and ecological considerations is desirable for cephalopod fisheries. An ecological approach to management is routine in many fisheries, but to be effective, good scientific understanding of the relationships between the environment, trophic dynamics and population dynamics is essential. Fisheries and the ecosystems they depend on can only be managed by regulating the activities of the fishing industry, and this requires understanding the dynamics of the stocks they exploit.

Keywords: Cephalopods, Population dynamics, Environment, Fluctuations, Stock assessment, Forecasting, Management, Governance



1. INTRODUCTION

There around 800 species of cephalopods living today. Fishery exploitation is mainly confined to coastal species of squid, cuttlefish and octopus and those oceanic squids whose migration routes regularly bring them within range of commercial fleets (see [Fries, 2010](#)).

Like most cephalopods, the exploited species typically live only 1 or 2 years, living fast and dying young. Their short life cycles, high metabolic rates and fast growth are associated with high plasticity in life history characteristics and marked sensitivity to environmental variation, reflected in large year-to-year fluctuations in population abundance. Cephalopod population dynamics are surprisingly poorly understood.

Empirical relationships between distribution or abundance and environmental conditions are widely documented (see [Pierce et al., 2008](#) for a review), and some of these empirical relationships appear to be sufficiently predictable to be used for fishery forecasting (see [Otero et al., 2008; Sobrino et al., 2002; Waluda et al., 2001a](#)). However, caution is necessary before recommending such approaches. As [Solow \(2002\)](#) observed, relationships between time series have a habit of unravelling when longer time series become available. In short, there is no substitute for understanding the underlying mechanisms, in relation both to population dynamics and to how environmental variation effects change in dynamics.

Some authors (e.g. [Pauly, 1998](#)) have drawn attention to parallels with small pelagic fish, but many researchers working on cephalopods highlight the difference between fish and cephalopods (e.g. [Boyle and Knobloch, 1983](#)). It is, however, difficult to draw clear conclusions since cephalopods display a complex mixture of *r*- and *k*-selected traits, the balance varying

between species (see [Caddy, 1996](#)). Some cephalopods produce relatively small numbers of eggs, for example, around 2500 eggs in *Eledone cirrhosa* ([Regueira et al., 2013](#)) and up to 8000 in *Sepia officinalis* ([Laptikhovsky et al., 2003](#)). In other species, tens or hundreds of thousands of eggs are produced: up to 74,000 eggs in *Loligo vulgaris* ([Laptikhovsky, 2000](#)), up to around 550,000 in *Octopus vulgaris* ([Cuccu et al., 2013](#)) and up to 800,000 in *Illex coindetii* ([Laptikhovsky and Nigmatullin, 1999](#)). Some species brood the eggs until hatching (e.g. *O. vulgaris* and *Gonatus onyx*) ([Mangold and Boletzky, 1973; Seibel et al., 2000](#)). All cephalopods lack true larval stages, but some have planktonic paralarvae, while in others, the hatchlings both are extremely similar in form to the adults and live in the same habitats.

Cephalopods can occupy similar trophic niches to fish, all commercial species being active predators, and they are also important prey of higher trophic levels, their significance accentuated by the high production to biomass ratio—see the series of reviews by [Clarke \(1996\)](#), [Croxall and Prince \(1996\)](#), [Klages \(1996\)](#) and [Smale \(1996\)](#), as well as many other papers by the late Malcolm Clarke. Recently, ecological modelling work has highlighted the fact that cephalopods can be keystone species (e.g. [Gasalla et al., 2010](#)).

1.1. Fisheries

The importance of cephalopods as fishery resources has risen dramatically since 1950. World cephalopod landings rose from around 500,000 t annually to a peak of over 4 million t in 2007. The most recent annual total (for 2010) is around 3.5 million t, an apparent decrease that is evident in trends from several regions ([FAO, 2011](#)). There are three main types of cephalopod fisheries: large-scale directed fisheries (e.g. jig fishing for ommastrephid squid), by-catch fisheries (e.g. a substantial proportion of landings of loliginid squids arise as by-catch from demersal trawling) and small-scale directed fisheries that use a range of gears to catch squid, cuttlefish and octopus. Cephalopods vary in their importance as fishery resources in different global regions and remain less important in the northeast Atlantic than in many other regions (see [Caddy and Rodhouse, 1998](#); [Hunsicker et al., 2010](#)). Globally, the most important fisheries have been those for ommastrephid squid; while some are relatively stable, others (e.g. for *Dosidicus gigas* on the Pacific coast of the Americas) seem to be characterized by boom and bust dynamics.

Many cephalopod fisheries are regulated; again, Europe is something of an exception, with no routine assessment and no management specified by

the Common Fisheries Policy, although local and regional regulatory systems are in place for some artisanal fisheries. Although biological characteristics such as the short life cycle and fast and variable growth rate, plus the difficulty of obtaining accurate age estimates, mean that some approaches to stock assessment (e.g. age-based methods) are unsuitable, a range of approaches, including in-season depletion methods, boat-based surveys and even production models, have been successfully applied (see [Pierce and Guerra, 1994](#)) and at least some cephalopod fisheries are routinely (and well) managed.

Particular issues arising in relation to assessment and management include stock identification, variability in abundance (and how to predict it) and prevention of damage to spawning areas. Globally, the comparatively fluid state of cephalopod taxonomy, as new molecular studies challenge (or sometimes support) traditional taxonomic units, and relatively slow progress of genetic stock identification studies also create challenges, compounded in many regions by a systemic failure to record fishery landings to species level.

We have already highlighted the environmental sensitivity of cephalopods and the fact that many if not all species show wide fluctuations in abundance and that this is most evident in the oceanic squid. For the demersal and benthic species that attach their eggs to the seabed or structures thereon, protection of spawning areas and eggs is critical. The use of fixed gear in spawning areas can be problematic in both squids and cuttlefish, with substantial losses of eggs when the gear is hauled, as seen for cuttlefish that lay eggs on cuttlefish traps in the English Channel and loliginid squids that lay their eggs on gill nets off western Portugal.

Management also presents particular challenges. Essentially, the main biological issue is one of escapement. In short-lived species, especially those with nonoverlapping generations, there is no buffer against recruitment failure ([Caddy, 1983](#)). In practice, cephalopods usually show nonsynchronous spawning and recruitment, which may help protect against total loss. The flip side of this coin is that cephalopod stocks are generally seen as resilient, rapidly bouncing back after overexploitation. However, it is also possible that the large natural fluctuations have obscured collapses caused by overfishing, even (or perhaps especially) in the ommastrephids.

There are also clear technical, social and economic challenges. Where cephalopods are taken as a by-catch of multispecies fisheries for demersal fish, regulating fishing mortality is difficult. In the case of the large-scale directed fisheries and indeed the small-scale directed fisheries, contingency plans are needed for low abundance years. Small-scale fisheries are probably

more adaptable, since they routinely exploit a range of target species—but the social cost of failure is high due to the dependence of many small coastal communities on cephalopod fishing.

These challenges are increasingly relevant, not least because global fishery data ([FAO, 2011](#)) suggest that cephalopod fishery landings peaked in 2007 and overexploitation of cephalopod stocks may already be taking place.

1.2. Future challenges and the rationale for a new review

While nowadays cephalopods are routinely fished in coastal waters of most regions of the world, our knowledge of many aspects of their taxonomy, biology and ecology remains limited. The need to manage those cephalopod fisheries that are presently unregulated is becoming increasingly apparent; it is also evident that the toolbox of assessment methods and management measures—and even governance systems, traditionally used to ensure sustainability, needs to be updated to accommodate cephalopods.

An additional driver, which is already changing the way we manage fisheries, certainly in the European Union (EU), is the adoption of the so-called ecosystem approach, enshrined in the EU's revised Common Fishery Policy and supported by a range of other marine-related legislations including the (EU) Marine Strategy Framework Directive. The new paradigm includes the following:

1. Evaluation of effects of fishing on nontarget species and the wider ecosystem
2. Explicit consideration of social and economic consequences of possible management actions and accounting for implementation issues
3. Placing fisheries in the broader context of integrated marine management, for example, recognizing the impacts of multiple stressors on marine ecosystems, evaluating their effects on ecosystem function and ecosystem services and assessing the status of marine ecosystems through the Integrated Ecosystem Assessment, definition of Good Environmental Status and development of monitoring and management systems to deliver action

Such considerations are central to the new Science Plan (due in 2014) of the International Council for the Exploration of the Sea (covering the North Atlantic and its fisheries) but to a greater or lesser extent are also achieving global recognition.

Finally, we must consider the background of global climate change and the ever-rising human population of the world. Well-managed fisheries

represent just one component of food security. Fisheries must currently provide both protein for direct human consumption and the base of much of the world's aquafeed, although the latter challenge falls beyond the scope of this chapter. While still a small component of global fisheries production, cephalopods are likely to be increasingly targeted unless overexploited finfish stocks are allowed to recover. Even in the relatively well-managed fisheries of the eastern North Atlantic, the collapse of traditional stocks like hake or cod is leading fishermen to target squid.

The warming and acidification of the oceans, falling salinity due to melting ice, shoaling of the oxygen minimum layer and changes in current systems are expected to have profound effects on marine ecosystems. As environmentally hypersensitive species, cephalopods may be seen as sentinels of future change. As fast-growing molluscs with calcareous statoliths and a high demand for oxygen, the effects of acidification and ocean warming may be significant, as a range of studies are already beginning to suggest (e.g. [Rosa and Seibel, 2008](#)).

This chapter arises from a workshop held at the 2012 CIAC (Cephalopod International Advisory Council) conference on *population dynamics, environmental effects, stock assessment and management*. The purpose of the workshop and review was to synthesize the state of the art, identify knowledge gaps and look forwards to the future of cephalopod fisheries, taking into account the many and demanding challenges that lie ahead.



2. POPULATION DYNAMICS

Currently, population dynamics mainly uses large-scale field observations 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](#)). Spatial aspects of population dynamics are rarely considered in fisheries science ([Quinn and Deriso, 1999](#)).

[Turchin \(2003\)](#) defined a population as a group of individuals of the same species living together in an area of sufficient size to permit normal dispersal and migration behaviour and in which population changes are largely determined by births and deaths. This definition stems mainly from experience with terrestrial animals and does not provide much information on how to differentiate between populations. "Living together" in the context of mobile marine animals might imply a high probability of reproducing together and being together for important large-scale events (e.g. feeding

and migration). Population dynamics is thus “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” ([Turchin, 2003](#)), including consideration of population numbers and structure, population stability, temporal change, spatial change and demographic and genetic effects.

2.1. Population dynamics theory

Population dynamics research requires comparable and standardized data collection over many subsequent generations and long time series, which are not always available in a fisheries context.

A central point in population regulation is the realized per capita rate of population change, $r_t = \ln(N_t/N_{t-1})$, where $\ln(N_t)$ is the natural logarithm of population density at time t . Change is inversely related to population density and/or time-lagged density, but this function may be complex and nonlinear. Analogous to chemical reactions, population growth can be viewed as a zero-order (exponential), first-order (logistic) or second-order (cyclic, e.g. Lotka–Volterra-type equations) process (see [Quinn and Deriso, 1999](#); [Turchin, 2003](#)).

Stability and oscillations in nature (a cornerstone of population dynamics science, representing two sides of the same coin) are invariably linked to trophic interactions: specialist predation is considered to be the most frequent cause of second-order oscillations in natural populations, with the second being food availability. Nevertheless, within this basic framework, there is no universal mechanism underlying population cycles.

Common questions in population dynamics (quoted from [Mueller and Joshi, 2000](#)) include the following:

- Are generations discrete or overlapping? If the latter, are cohorts segregated in space?
- What kinds of interactions exist among life stages? Which life stages are likely to be the triggers of density-dependent regulatory mechanisms? Often, the trigger stage is the primary consumer of resources.
- Which life stages are the likely targets of density-dependent regulatory mechanisms? If the target is the first juvenile stage, does the regulatory mechanism act primarily through fecundity or mortality?
- How do the trigger and target map onto the ontogeny, especially in the context of whether cohorts are spatially segregated? What are the time delays between the triggering of a regulatory mechanism and its effect

on the target and between the effect on the target and its final effect on the triggering life stage?

- If fecundity and mortality are density-independent, what is the magnitude of each?
- What is the census life stage? If this stage is not the trigger life stage, how does it map onto the ontogeny, relative to the trigger life stage, and the first juvenile stage to which recruitment is governed through fecundity?

Models and empirical studies of *Drosophila* populations suggest that the relative levels of food given to larval and adult stages are crucial for the ultimate stability of the populations. High levels of food for larvae and low levels of food for adults favour stability; the reverse situation leads to cycles and other departures from stable-point equilibria. Model results show that time delays in density dependence destabilize populations when generations overlap ([Mueller and Joshi, 2000](#)).

Because of its commercial and applied significance, the study of fish population dynamics has developed a huge literature and a multitude of approaches. However, much of this research focuses on harvesting, and indeed fisheries management goals and policies' impact on the research approach. This is unfortunate, because trophic relationships, the dominant issue of theoretical ecology (see above, in third chapter of this section), are more often than not ignored. An exception is the multispecies approach, which is however generally regarded as too complicated and parameter-hungry for most practical applications ([Quinn and Deriso, 1999](#)). The recent consideration of trophic relationships in modelling of harvesting options ([Overholtz et al., 2000, 2008; Tyrrell et al., 2008, 2011](#)) is a step in the right direction although it also suffers from a weak link to theoretical ecology.

2.2. Recruitment

In fisheries science, the use of the term “recruitment” is often at odds with its usual meaning in ecology. While some authors propose purely biological definitions, for example, “an addition of new fish to the vulnerable population by growth from among smaller size categories” ([Ricker, 1975](#); see also [Boletzky, 2003](#); [Quinn and Deriso, 1999](#)), others acknowledge the reality that recruitment in fisheries is measured in a way that depends on gear selectivity: new recruits will be the smallest fish taken by a particular gear. Thus, [Bloor et al. \(2013a\)](#) defined recruitment as the renewal of harvestable stages in a population. [O'Dor \(1998a,b\)](#) noted that “from a fisheries perspective recruitment is quantitative, but from a population perspective it is also

qualitative. All genes are not of equal value in all environments". Recruitment may in principle refer to the first or repeated appearance (i.e. at a moment in time linked to the value or characteristics of a given parameter) of a specific life stage, size, weight, age or maturity stage—or indeed when an animal with a specific gene enters the population.

A further theoretical challenge lies in the relationship, if any, between recruitment and spawner abundance. For some short-lived animals, stock-recruitment relationships have been found (e.g. shrimps; Ye, 2000). However, in schooling marine animals, due to density-dependent population regulation, the spawning biomass of a cohort is not necessarily proportional to the numbers recruited (Rochet, 2000).

In the cephalopod literature, there is an emphasis on strong links between recruitment and favourable oceanographic regimes (e.g. temperature, water masses and winds; see review by Pierce et al., 2008). Dawe and Warren (1993) and Dawe et al. (2000) found that *Illex illecebrosus* recruitment was positively related to negative values of the North Atlantic Oscillation index, high water temperatures off Newfoundland and a southward shift in the various water masses associated with the Gulf Stream. Models derived from such empirical relationships (see also Challier et al., 2005b; Garofalo et al., 2010; Nevárez-Martínez et al., 2010; Roberts and van den Berg, 2002; Waluda et al., 1999, 2001a) often have good predictive capability, at least in the short term—although Solow's (2002) warning about the transience of relationships between short time series should be heeded. Links between the recruitment and the trophic relationships are rarely addressed, although Moustahfid et al. (2009) included predation mortality in a surplus production model; see also the very general approach of Gaichas et al. (2010).

2.3. Defining populations: Concepts

The most comprehensive summaries of the population ecology of cephalopods are those by Boyle and Boletzky (1996) and Boyle and Rodhouse (2005). Saville (1987) and Lipinski et al. (1998a) discussed ecological differences between fish and cephalopods related to fisheries. These accounts offer general, descriptive reviews of questions, approaches and difficulties. Out of around 750–800 cephalopod species, of which some are not yet described, 59 have been researched relatively well and are therefore suitable candidates for the analysis of population dynamics (Table 2.1). An assessment of the current level of knowledge of trophic and environmental relationships, summarized by family, appears in Table 2.2.

Table 2.1 Species of cephalopods with sufficient data accumulated to be suitable for population dynamics analysis

Family name	Species name	(1) Taxonomic issues		(2) Exploitation level		(3) Fishery	(4) Ecological information		
		Yes	No	FAO db	Nat. db		Regulated?	Pop. ID	Review
Nautilidae (29%)	<i>Nautilus pompilius</i>	x		No/yes	A, Pa, Ph	No	Yes	Yes	Yes
	<i>Nautilus macromphalus</i>	x		No/no	A, Pa, Ph	No	Yes	Yes	Yes
Sepiidae (6%)	<i>Sepia apama</i>	x		No/yes	A	Partial	Yes	Yes	Yes
	<i>Sepia australis</i>	x		No/yes	SA	No	No	Yes	Yes
	<i>Sepia elegans</i>	x		No/yes	EU	Partial	No	No	No
	<i>Sepia officinalis</i>	x		Yes/yes	EU, M	Partial	Yes	Yes	Yes
	<i>Sepia orbignyana</i>	x		No/yes	EU	Partial	No	No	No
	<i>Sepia esculenta</i>	x		No/yes	J, Ch	No	No	No	Yes
	<i>Sepia pharaonis</i>	x		No/yes	A, J, Ch	Partial	No	No	No
	<i>Sepiella inermis</i>	x		No/yes	I, Th	No	No	No	No
Sepiolidae (5%)	<i>Sepiella oweniana</i>	x		No/yes	EU	Partial	No	No	Yes
	<i>Rossia pacifica pacifica</i>	x		No/yes	None ^a	No	No	No	No
	<i>Heteroteuthis dispar</i>	x		No/yes	None ^a	No	No	No	Yes

Continued

Table 2.1 Species of cephalopods with sufficient data accumulated to be suitable for population dynamics analysis—cont'd

Family name	Species name	(1) Taxonomic issues		(2) Exploitation level		(3) Fishery	(4) Ecological information		
		Yes	No	FAO db	Nat. db		Regulated?	Pop. ID	Review
Loliginidae (20%)	<i>Loligo vulgaris</i>		x	No/yes	EU	Partial	No	Yes	No Yes
	<i>Loligo forbesii</i>		x	No/yes	EU	Partial	Yes	Yes	No Yes
	<i>Loligo reynaudii</i>		x	No/yes	SA	Yes	Yes	Yes	Yes
	<i>Alloteuthis media</i>	x		No/yes	EU	Partial	No	No	No No
	<i>Alloteuthis subulata</i>	x		No/yes	EU	No	No	No	No No
	<i>Doryteuthis plei</i>	x		No/yes	B?	No	No	No	No No
	<i>Doryteuthis gahi</i>		x	Yes/yes	FI, Ar	Yes	Yes	Yes	Yes Yes
	<i>Doryteuthis opalescens</i>		x	No/yes	United States	Yes	Yes	Yes	Yes Yes
	<i>Doryteuthis pealeii</i>	x		Yes/yes	United States	Yes	Yes	Yes	Yes Yes
	<i>Doryteuthis sanpaulensis</i>		x	No/yes	B, Ar	No	No	Yes	No Yes
Loliginidae (20%)	<i>Heteroligo bleekeri</i>		x	No/yes	J	Yes	Yes	Yes	Yes Yes
	<i>Lolliguncula brevis</i>	x		No/no	United States	No	No	Yes	Yes Yes
	<i>Sepioteuthis sepioidea</i>		x	No/yes	United States	No	No	Yes	No No
	<i>Sepioteuthis australis</i>	x		No/yes	A	No	Yes	No	Yes Yes
	<i>Sepioteuthis lessoniana</i>	x		No/yes	J, A, Th	Partial	Partial	No	Yes Yes
	<i>Uroteuthis edulis</i>	x		No/yes	Ch, A, J	Partial	Partial	No	Yes Yes
	<i>Uroteuthis duvaucelii</i> ^b	x		No/yes	I, Th, A	No	Partial	No	No Yes

Gonatidae (10%)	<i>Berryteuthis magister</i>	x	No/yes	R	No	Yes	Yes	No	Yes
	<i>Gonatus fabricii</i>	x	No/yes	None ^a	No	No	No	No	Yes
Lycoteuthidae (17%)	<i>Lycoteuthis lorigera</i>	x	No/no	None ^a	No	No	No	No	No
Ommastrephidae (62%)	<i>Illex illecebrosus</i>	x	Yes/yes	C, United States	Yes	Partial	Yes	Yes	Yes
	<i>Illex argentinus</i>	x	Yes/yes	FI, Ar	Yes	Partial	Yes	Yes	Yes
	<i>Illex coindetii</i>	x	No/yes	EU, M	No	No	Yes	No	Yes
	<i>Ommastrephes bartramii</i> ^b	x	No/yes	J, R, Ch	Partial	Partial	Yes	Yes	Yes
	<i>Dosidicus gigas</i>	x	Yes/yes	Me, United States, J	Partial	No	Yes	Yes	Yes
	<i>Omīthoteuthis antillarum</i>	x	No/yes	None ^a	No	No	No	No	Yes
	<i>Sthenoteuthis oualaniensis</i>	x	No/no	None ^a	No	No	Yes	No	Yes
	<i>Sthenoteuthis pteropus</i> ^b	x	No/yes	None ^a	No	No	Yes	No	Yes
	<i>Todarodes sagittatus</i>	x	No/yes	EU, No	Partial	No	No	No	Yes
	<i>Todarodes pacificus</i>	x	Yes/yes	J, R, Ch	Yes	Yes	Yes	Yes	Yes
	<i>Nototodarus sloanii</i>	x	Yes/yes	NZ	Yes	No	Yes	No	Yes
	<i>Nototodarus gouldi</i>	x	No/yes	A, NZ	Yes	No	No	No	Yes
	<i>Todaropsis eblanae</i>	x	No/yes	EU, SA	No	Yes	No	No	Yes
Thysanoteuthidae (100%)	<i>Thysanoteuthis rhombus</i>	x	No/yes	J	Yes	No	Yes	No	Yes

Continued

Table 2.1 Species of cephalopods with sufficient data accumulated to be suitable for population dynamics analysis—cont'd

Family name	Species name	(1) Taxonomic issues		(2) Exploitation level		(3) Fishery	(4) Ecological information			
		Yes	No	FAO db	Nat. db		Regulated?	Pop. ID	Review	Envir.
Eledonidae (33%)	<i>Eledone cirrhosa</i>		x	No/yes	EU	Partial	No	Yes	Yes	Yes
	<i>Eledone moschata</i>		x	No/yes	EU	Partial	No	No	No	Yes
Enteroctopodidae (7%)	<i>Enteroctopus dofleini</i>	x		No/yes	United States	Yes	No	No	No	Yes
	<i>Enteroctopus megalocyathus</i>		x	No/yes	Ar, CE	No	No	No	No	Yes
Octopodidae (7%)	<i>Octopus vulgaris</i>	x		Yes/yes	World	Variable	Partial	Yes	Yes	Yes
	<i>Octopus maya</i>		x	No/yes	Me	Yes	No	Yes	Yes	Yes
	<i>Octopus pallidus</i>		x	No/no	A	No	No	No	No	Yes
	<i>Octopus bimaculatus</i>		x	No/no	United States	No	No	No	No	Yes
	<i>Octopus cyanea</i>		x	No/no	A	No	No	Yes	No	Yes
	<i>Octopus tehuelchus</i>		x	No/yes	Ar	No	No	No	No	Yes
	<i>Octopus insularis</i>		x	No/no	B	No	No	No	No	Yes
	<i>Octopus mimus</i>		x	No/no	CE	No	No	No	No	Yes

^aNo existing fisheries or by-catch or subsistence (small-scale); therefore, future modelling attempts must be based on research data.

^bSpelt differently in the FAO aquatic species list (e.g. *Uroteuthis diuvauceli*, *Ommastrephes bartramii* and *O. pteropus*).

Percentages in the first column refer to the number of species listed for each family as a percentage of the total number of species in that family. Results on availability of information about each topic are then given by species as follows: (1) The existence of issues with taxonomic status is indicated by yes/no (no = no issues). (2) Availability of information on exploitation level in (a) the Food and Agriculture Organization of the United Nations two databases (FAO db) (yes/no) and (b) national databases (Nat. db). Countries: A, Australia; B, Brazil; CE, Chile; Ch, China; Ar, Argentina; FI, Falkland Islands; M, Morocco; SA, South Africa. (3) Existence of fishery regulation (yes/no/partial). (4) Ecological information: the existence of studies is scored as yes/no. Pop. ID = population identity researched and recognized; Review = broad ecological review published; Envir. = environmental relationships studied; Trophic = trophic relationships studied. Main source of information: FAO, in particular Jereb and Roper (2005, 2010) and references therein, also FAO Aquatic Species Fact Sheets (www.fao.org/fishery/species/search/en) and FAO Aquatic Species Portal (<http://temportal.fao.org/faosas/main/start.do>).

Table 2.2 Level of basic knowledge of trophic and environmental relationships for all cephalopod families

Family name	(1) Number of species			(2) % of species well investigated			(3) Commercial value/potential	(4) Ecological role
	Common	Rare	Undetermined	Trophic	Environmental	Others		
Nautilidae	2	3	2	14	14	14	8	4
Spirulidae	1	0	0	0	0	100	1	2
Sepiidae	55	22	32	3	4	50 ^a	10	10
Sepiolidae	37	10	16	5	3	24 ^a	4	6
Sepiadariidae	3	4	0	29	0	29 ^a	1	2
Idiosepiidae	1	0	7	12	12	12 ^a	1	2
Loliginidae	47	0	0	36	26	47 ^a	10	10
Australiteuthidae	0	1	0	0	0	0	1	2
Gonatidae	14	0	6	40	10	50	5	8
Octopoteuthidae	2	0	6	12	0	25	1	5
Pyroteuthidae	2	0	4	0	0	33	1	5
Ancistrocheiridae	1	0	0	0	0	100	1	3
Enoplateuthidae	11	0	32	1	1	2	5	8
Onychoteuthidae	9	0	6	53	0	60	7	10
Pholidoteuthidae	2	0	0	100	0	100	2	6
Lepidoteuthidae	1	0	0	100	0	100	2	4

Continued

Table 2.2 Level of basic knowledge of trophic and environmental relationships for all cephalopod families—cont'd

Family name	(1) Number of species			(2) % of species well investigated			(3) Commercial value/potential	(4) Ecological role
	Common	Rare	Undetermined	Trophic	Environmental	Others		
Chtenopterygidae	1	2	0	0	0	0	1	3
Batoteuthidae	0	0	1	0	0	0	1	2
Brachioseuthidae	3	? ^b	5 ^c	0	0	0	1	6
Lycoteuthidae	1	3	2	0	0	17	3	7
Histioseuthidae	5	0	12	18	0	18	2	8
Bathyteuthidae	1	0	2	0	0	33	1	3
Psychroteuthidae	1	0	0	100	0	100	3	5
Neoteuthidae	1	0	3	25	0	25	1	5
Architeuthidae	1	0	0	100	0	100	1	7
Ommastrephidae	21	0	0	86	24	90	10	10
Thysanoteuthidae	1	0	0	100	100	100	10	7
Chiroteuthidae	1	7	8	0	0	0	1	2
Mastigoteuthidae	4	0	14	0	0	0	1	3
Joubiniteuthidae	0	1	0	0	0	0	1	1
Magnapinnidae	0	0	3	0	0	0	1	3
Cycloteuthidae	0	0	4	0	0	0	1	2

Promachoteuthidae	0	5	0	0	0	1	1
Cranchiidae	19	1	10	7	0	13	2
Vampyroteuthidae	1	0	0	100	0	100	1
Cirroteuthidae	0	0	3	0	0	33	1
Stauroteuthidae	0	0	2	0	0	0	1
Alloposidae	1	0	0	100	0	100	1
Tremoctopodidae	1	0	3	0	0	25	1
Argonautidae	2	0	2	0	0	50	1
Ocythoidae	1	0	0	0	0	0	1
Eledonidae ^b	6	0	0	33	33	33	7
Octopodidae ^b	24	0	95	8	8	20	10
Enteroctopodidae	4	0	25	3	3	3	7
Bathypolypodidae	2	0	4	0	0	17	2
Megaeledonidae	6	0	24	0	0	10	5
Amphitretidae	3	0	2	0	0	0	1
							3

^aNote: includes species investigated for trophic and environmental relationships.

^bThe number of undescribed species is high.

^cUnder revision.

(1) Number of species refers to the described species only, categorized according to their abundance (common, rare and undetermined). (2) The percentage of species well investigated is given in relation to knowledge of trophic relationships, environmental relationships and other studies. The last two columns indicate the (3) likely commercial value or potential and (4) the ecological importance of the species, in both cases on a scale of 1–10 where a score of 10 indicates the highest potential or importance. Based on [Jereb and Roper \(2005, 2010\)](#).

Boyle and Rodhouse (2005) stated 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 generalised to the much greater oceanic and deepwater fauna”. It might be expected that species exploited commercially on a large scale would be the best candidates for population dynamics analysis. However, of the three dominant species in the world fisheries, arguably only one (*Todarodes pacificus*) has been researched well enough to meet the standards described in the preceding text (see Table 2.1).

Previous reviews identified limitations to understanding of cephalopod population ecology. Boyle and Boletzky (1996) stated that “the study of cephalopod populations currently lacks the means to define populations adequately and to resolve basic systematic confusions”, while Boyle and Rodhouse (2005) indicated that “no cohesive description of cephalopod population ecology is yet available. (...) Modelling of population ecology for fisheries purposes is confounded by a lack of consensus among workers as to the form of the growth model to be applied, and also by a lack of data to define populations”. However, for a number of families and species (Tables 2.1 and 2.2), systematic problems have been largely resolved over the last 20 years, and a wealth of life cycle and ecological data have accumulated as a result of fisheries, fisheries research and biological projects.

Furthermore, Turchin’s (2003) definition of the population requires only that the animals “live together in an area of sufficient size to permit normal dispersal and migration behaviour”, which can be easily investigated (e.g. Augustyn et al., 1992, 1994; Sauer et al., 1992, 2000), and “in which population changes are largely determined by birth and death processes”. The latter statement implies exclusion of situations in which exchange of animals with other areas is known but suggests that useful work could be done even in the absence of stock identification based on comprehensive genetic analysis. However, fine-tuned understanding of population identity and stock structure is possible only by combining multilevel ecological research, well-thought out molecular biology research and modelling. Such research is under way, setting standards (O’Dor, 1998a) for sustainable utilization of these resources.

In the past, there has been limited interest in cephalopods by theoretical ecologists. For example, the degree of overlap between consecutive

generations, crucial in population dynamics analysis, was poorly understood even in the better-known families (e.g. Melo and Sauer, 1999, 2007). In practice, the only biological feature that results in nonoverlapping generations is strict semelparity, when an animal produces offspring and dies before the hatching of its progeny. In most cephalopods (especially squid, not octopods), the spawning period for an individual female can be quite prolonged; certainly, multiple modes in egg size distributions in the ovary suggest that eggs may be spawned in several batches (although it is not certain that all eggs present in the ovary are finally spawned). However, in colder regions, the embryonic phase may be relatively protracted, reducing the likelihood of overlap.

In addition, the lack of synchrony between spawning in different individuals can lead to protracted spawning seasons, evidenced by the existence of several microcohorts, and there may also be multiple spawning seasons, blurring the distinction between different generations (even if individuals do not overlap with their own progeny). This contrasts with the usual situation in fish and other iteroparous organisms, in which overlapping generations are also created by the occurrence of multiple discrete spawning events, often over a period of several years: parents thus coexist with their progeny over an extended period.

In their review, Boyle and Rodhouse (2005) discussed the problem of finding and researching separate populations of the same species, listing 31 species for which some information is available. They mentioned the use of molecular biology, morphometrics and parasite tags, as well as knowledge of “timing and location of breeding or the recruitment of young” (e.g. in *T. pacificus*, *O. vulgaris*, *Sthenoteuthis oualaniensis* and *I. illecebrosus*) and information on population structure, particularly emphasizing size and age.

Some authors (e.g. Yeatman and Benzie, 1993) have questioned the validity of separating populations using a morphological approach such as the one used by Nesis (1993), but see Vidal et al. (2010a). This may be even more relevant for cephalopods than other organisms (especially long-living fish), because of the importance of spatial considerations linked to survival of consecutive generations (Lipiński, 1998; Lipinski et al., 1998b; O'Dor, 1998a,b; Ranta et al., 1997). O'Dor (1998a) felt that “management of squid stocks according to the ‘Precautionary Principle’ requires defining individual microcohorts genetically, temporally and spatially”. This requirement lies at the base of any rigorous ecological testing in the field and in the laboratory. What gives even more credence to this statement is the fact that, in cephalopods, there is a possibility to mistake different (time-, space- or

temperature-wise) groups (broods) for biologically and/or genetically separate populations—see discussions in Boyle and Rodhouse (2005) and Forsythe (1993, 2004). This can arise as a result of intertwined generations with different biological characteristics, either alternating generations, as hypothesized by Mesnil (1977), or when individuals of the same cohort breed at two (or more) different times. This pattern is well documented in the genus *Sepia* (Boletzky, 1983; Hall et al., 2007; Le Goff et al., 1998), in which the only certain method to separate populations is by molecular biological methods, for example, Pérez-Losada et al. (2007). Therefore, simple indicators in isolation (especially length–frequency) are not good enough to diagnose separate populations of cephalopods. Also, while it may be easy to generate consecutive generations in a model (indeed, this is frequently done), it is difficult to identify them in the wild.

2.4. Defining populations: Examples

Yatsu et al. (1998), Nagasawa et al. (1998) and Chen (2010) have provided fisheries and biological evidence, collected over vast area during more than 20 years of exploitation, indicating that *Ommastrephes bartramii* from the northern Pacific comprises four groups. At least two of these groups are clearly distinct populations (eastern and western), as confirmed by Katugin (2002). Discriminating factors included hatching time and area, length–frequency data, maturities, paralarval occurrence, parasitic infestation, fleet operations and environmental factors. However, it is still not possible to distinguish different generations.

On the other hand, numerous studies on three exploited species of squids (*Nototodarus gouldi*, *N. sloanii* and *D. gigas*) revealed no clear differentiation into separate populations, because of the complexity of their distribution and biological characteristics (Jackson et al., 2005; Keyl et al., 2011; Masuda et al., 1998; Uozumi, 1998; Zavala et al., 2012). *D. gigas* has relatively recently expanded its distribution northwards, probably due to a combination of favourable environmental conditions and fishery impacts (Keyl et al., 2008) interacting with physiological mechanisms (e.g. related to oxygen debt; Rosa and Seibel, 2010).

T. pacificus is one of the best-studied squids in the world. There is evidence (Katugin, 2002; Kidokoro et al., 2010) that this huge resource comprises a distinct autumn-spawning population and less distinct non-autumn-spawning population that is dominated by the winter cohort. Both these populations migrate between spawning grounds in the south and

feeding grounds in the north. The biology of the more diverse “non-autumn-spawning population” is especially interesting as it sheds light on how, when and where various splinter cohorts and microcohorts make up one large population, with complicated structure, variable life cycle parameters, long migration pathways and large fluctuations in abundance (Nakata, 1993; Song et al., 2012; Takayanagi, 1993). It is believed that it is possible to track consecutive generations of the winter population by research in the Tsugaru Strait between Honshu and Hokkaido during years of high yield (Takayanagi, 1993). Indexes of maturity may be used for this purpose. In two consecutive years, maturity indexes of the winter population were similar, which indicates stability during which generations may be identified and compared (Figure 2.1).

I. illecebrosus was intensely exploited in the northwest Atlantic in the 1970s, with a subsequent stock collapse, and has never regained its former numbers. Nevertheless, it is one of the best-researched ommastrephid squids

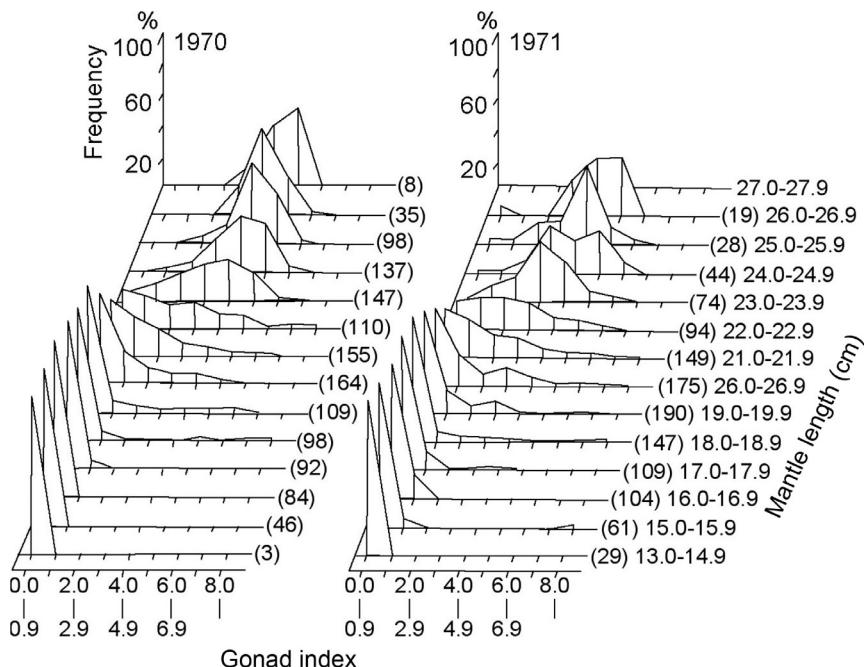


Figure 2.1 Frequency distribution of gonad index (Gl; males only) by mantle length class in *Todarodes pacificus*. Data from two consecutive years of high abundance. Numbers in parentheses refer to the number of squid examined. After Takayanagi (1993).

in the world (O'Dor and Dawe, 1998). Dawe and Hendrickson (1998) and Hendrickson (2004) provided evidence that there is a single population of *I. illecebrosus* extending over a wide area (from Cape Hatteras to Newfoundland). This stock is however very variable and its structure is complicated, so it would be difficult to track consecutive generations in this species.

Illex argentinus is one of the three most abundant squids in the world. It is relatively well researched (Arkhipkin, 1993, 2000; Brunetti et al., 1998; Haimovici et al., 1998; Sacau et al., 2005; Uozumi and Shiba, 1993). It is distributed over a large area and has a complicated population structure with many and variable microcohorts. At present, two populations are recognized: winter spawning and summer spawning; differentiation criteria are temporal, spatial and biological (Sacau et al., 2005). However, such divisions may be transient, and recent work by Crespi-Abril and Baron (2012) and Crespi-Abril et al. (2013, 2014) suggests inshore spawning of *I. argentinus* over a wide area year round. This would most likely create one large panmictic metapopulation. Thus, as in *I. illecebrosus*, it would be difficult to track subsequent generations in *I. argentinus*.

Todaropsis eblanae is an ommastrephid that is bottom-dwelling and not so heavily exploited. Nevertheless, it is relatively well studied (Dillane et al., 2000, 2005; Hastie et al., 1994; Lordan et al., 1998; Rasero et al., 1996; Zumholz and Piatkowski, 2005). Based on the analysis of one minisatellite and four microsatellite loci, Dillane et al. (2005) concluded that there are at least three genetically isolated populations in the east Atlantic. Again as in *Illex*, there is no immediate prospect of tracking consecutive generations in this species.

Berryteuthis magister from the northern Pacific has been well studied, mainly by Russian scientists—see Jelizarov (1996) and Katugin (2002). It is a bottom-dwelling squid, abundant and targeted by a bottom trawl fishery; there are three subspecies and population structure is complicated. One subspecies, *B. magister magister*, has been the object of detailed ecological and genetic analysis and appears to comprise three populations, occurring in the Alaskan Gyre system, the western subarctic gyre and the Sea of Japan, respectively. Variability is clinal (Katugin, 2002). As in the *Illex* spp. and *T. eblanae*, there is no immediate prospect of tracking consecutive generations in this species.

Some squids from the family Loliginidae have also been intensively studied. Accounts of a few of the best known are given in the following text.

Doryteuthis gahi is an unusual loliginid, thriving in cool and relatively deep waters. It is heavily exploited and researched well in a fairly narrow

area around the Falkland Islands (Agnew et al., 1998a,b; Hatfield, 1996; Hatfield and des Clers, 1998; Hill and Agnew, 2002; Patterson, 1988; Shaw et al., 2004). There is one population and at least two cohorts (based on seasonal appearances on the fishing grounds but with inferred separate spawning and recruitment). It is a good candidate for tracing consecutive generations. In fact, a model of optimal harvest strategy proposed by Hill and Agnew (2002) assumes a single generation each year, which undergoes continuous depletion due to natural mortality. The main equation of this model is $C_y/C_x = (1 + aT)e^{-MT}$, where C_y and C_x are catch weights at specific points in time, a is growth rate, $T = y - x$ (in weeks) and M is natural mortality. Figure 2.2 illustrates how this model works. Rates of immigration and emigration are also incorporated in the model.

Doryteuthis opalescens is heavily exploited off California (Fields, 1962; Recksiek and Frey, 1978; Zeidberg et al., 2006). Initial investigations concerning population structure were inconclusive (Ally and Keck, 1978; Christofferson et al., 1978; Kashiwada and Recksiek, 1978). Population structure in this species has also been studied by Jackson (1998), Vojkovich (1998), Jackson and Domeier (2003), Reiss et al. (2004), Macewicz et al. (2004), Maxwell et al. (2005), Brady (2008), Warner et al. (2009) and Dorval et al. (2013) and appears to be complex. A study of microsatellite loci by Reichow and Smith (1999, 2001) concluded that there is a single large, possibly panmictic, population. However, further analysis of local “cohorts” over consecutive spawning cycles would still be useful. Because of the complex population structure, despite the fact that population is apparently genetically uniform, tracing consecutive generations in this species may be difficult.

Loligo vulgaris is one of the most-studied loliginids, but its population structure is still imperfectly known. Most research has focused on particular regions within its distribution (e.g. Coelho et al., 1994; Guerra and Rocha, 1994; Krstulović Šifner and Vrgoč, 2004; Marques Moreno, 2012; Moreno et al., 1994, 2005; Vila et al., 2010). The only large-scale synthesis was that by Moreno et al. (2002), which, by using multivariate analysis of biological indexes, demonstrated significant differences between regions. Existing evidence suggests that these differences may be ascribed to large-scale environmental phenomena. Despite the large number of studies, population structure cannot be confidently described for this species.

Loligo forbesii, another large European loliginid, is probably better studied than *L. vulgaris*. Several studies on both species appeared in a special volume of Fisheries Research (Boyle and Pierce, 1994). Shaw et al. (1999)

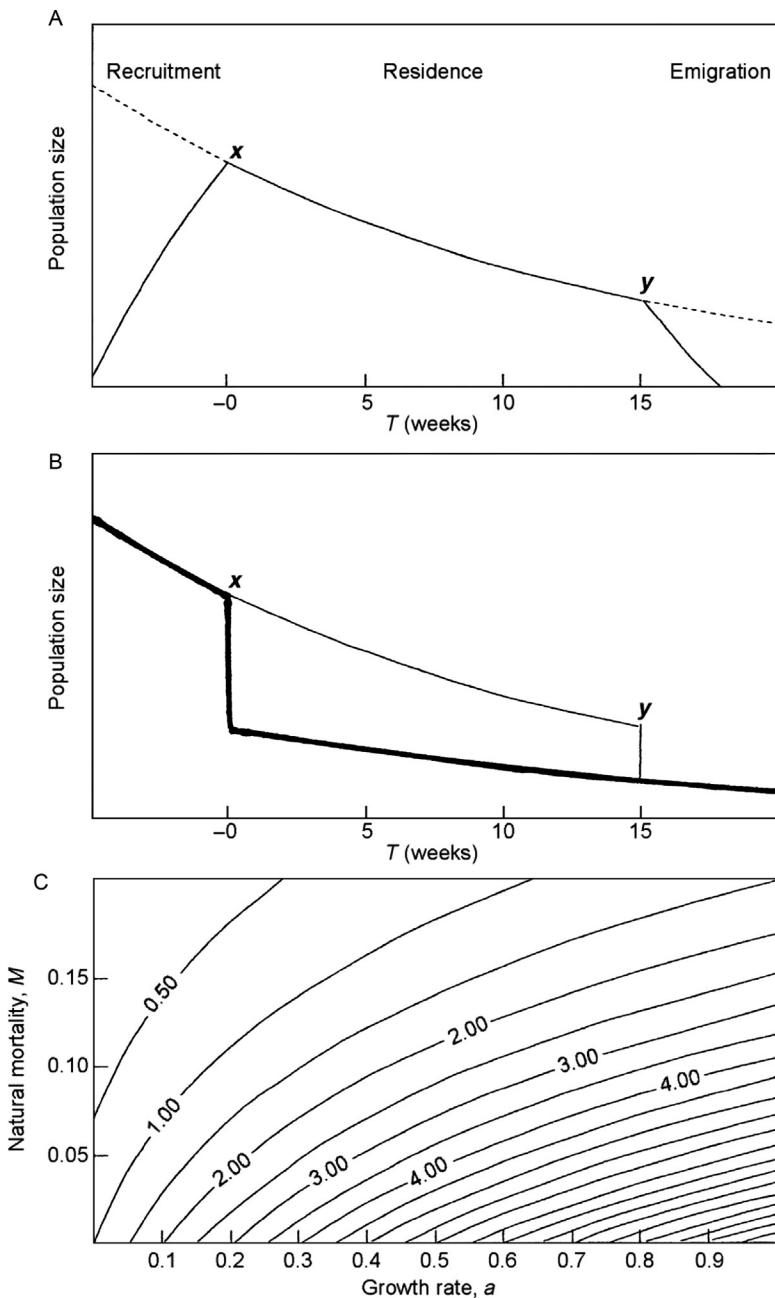


Figure 2.2 (A) A population consisting of a single generation and experiencing constant natural mortality (dotted line). The solid line shows the population vulnerable to fishing, where 100% of the population is resident (between points x and y).

demonstrated the possible existence of three populations: the Azores population (see also Brierley et al., 1993, who considered it might be a separate subspecies), a population inhabiting NE Atlantic offshore banks such as Rockall and Faroe, and the shelf population. Papers that discuss various aspects of its population structure include Holme (1974), Martins (1982), Collins et al. (1995, 1997, 1999), Pierce et al. (1998, 2005), Bellido et al. (2001), Pierce and Boyle (2003), Young et al. (2004), Challier et al. (2005a) and Chen et al. (2006); as in other squids, winter and summer breeders and varying numbers of different microcohorts have been documented. The identification of consecutive generations in this species is most likely to be successful in the isolated parts of the range (e.g. Azores).

Loligo reynaudii is one of the best-studied loliginids in the world. Population structure of this species was reported in a number of studies (Augustyn, 1989; Augustyn et al., 1992, 1993, 1994; Lipinski et al., 1998b; Martins et al., 2014; Olyott et al., 2006, 2007; Roberts, 2005; Roberts and Sauer, 1994; Roberts and van den Berg, 2002; Roel, 1998; Sauer, 1991, 1993; Sauer et al., 1997). However, population differentiation has been studied in detail only recently (Stonier, 2012; van der Vyver, 2013). There are three populations, the first located along the eastern part of the south coast of South Africa, the second from Agulhas Bank and the west coast of South Africa and the third off Angola. The change was clinal, differences increased with the geographic distance. The best candidate for the study of consecutive generations is the most isolated and distant site of the overall distribution, that is, the Angolan population. South African populations have a complicated structure and are subject to mixing of many microcohorts, taking into consideration the dynamic character of each spawning aggregation (Lipinski et al., 1998b; Sauer et al., 2000).

Sepioteuthis australis is relatively well researched; Pecl (2000), Jackson and Pecl (2003), Pecl et al. (2006) and Hibberd and Pecl (2007) all described a complicated population structure in the eastern Tasmanian population. However, Triantafylllos and Adams (2001, 2005) detected two cryptic species

A single instantaneous fishing event may occur at either of these points and will result in the capture of a fixed proportion of the vulnerable population. T is time relative to point x . (B) A population experiencing a fixed fishing mortality at point x (thick line; catch there is C_x) or point y (thin line; catch there is C_y). The number of survivors at time 20 (escapement) is the same under either scenario. (C) Contour lines showing combinations of natural mortality and growth rates that produce various values of the ratio C_y/C_x (increasing in steps of one, left to right). The residence period (T) is 10 weeks for all lines. From Hill and Agnew (2002).

instead of the one previously described, as well as hybrid forms. A similar situation was described for the sister species, *S. lessoniana* (see Cheng et al., 2014). More data are required to explain population structure(s) in these species. Because of the “conveyor belt” of recruits found in an ideal spot for research (Great Oyster Bay), this species is an unlikely candidate to research consecutive generations. The related species, *S. lessoniana*, has been cultured in the laboratory for multiple generations (Lee et al., 1994; Walsh et al., 2002).

Several species of cuttlefish are relatively well studied (Jereb and Roper, 2005), but *S. officinalis* is perhaps the most representative example of this group; research on its population structure is summarized in Guerra (2006) and Pierce et al. (2010). Several authors have detected a multitude of fairly localized separate populations throughout the distribution range (Pérez-Losada et al., 1999, 2002, 2007; Turan and Yaglioglu, 2010; Wolfram et al., 2006). *S. officinalis* offers excellent prospects for investigating consecutive generations both in the field and in the laboratory. The same can be said about the largest cuttlefish in the world, the Australian *Sepia apama* (Hall et al., 2007).

Likewise, several species of octopus are well researched (Roper et al., 1984), but *O. vulgaris* is perhaps the best representative example of this group, despite the fact that there is a view that it may be a large complex of species (Mangold, personal communication). Its population structure was described by Mangold and Boletzky (1973), Hatanaka (1979), Smale and Buchan (1981), Mangold (1983), Sanchez and Obarti (1993), Oosthuizen and Smale (2003) and Robert et al. (2010). Population differentiation has been studied throughout the world, using both genetic and morphological approaches (e.g. Vidal et al., 2010a), most frequently in Europe and in South Africa (Cabranes et al., 2008; Greatorex et al., 2000; Maltagliati et al., 2002; Moreira et al., 2011; Murphy et al., 2002; Oosthuizen et al., 2004; Robert et al., 2010; Teske et al., 2007). A good summary is given by Pierce et al. (2010). All these authors detected a multitude of localized populations throughout the distribution range, similar to that of *S. officinalis*. As in *S. officinalis*, *O. vulgaris* offers excellent prospects for investigating subsequent generations both in the field and in the laboratory.

2.5. Population dynamics of cephalopods: Models

As reviewed in the preceding text, an understanding of the population structure of a species is a fundamental introduction to population dynamics and

involves two steps: the description of the biological parameters (length-frequency, maturity, abundance, age, growth rate, recruitment, environmental relations, trophic relations, etc.) and molecular biological studies of intraspecific variability, to identify populations (e.g. Shaw, 2002; Triantafyllou and Adams, 2001, 2005; Yeatman and Benzie, 1993). An effort to discriminate between consecutive generations is the next logical direction to follow.

The first step requires the choice of model(s) to describe growth and maturity. Existing models include the primitive linear three-stage model (Lipinski, 2001), which was followed by Keyl et al. (2011) and Zavala et al. (2012); the ontogenetic growth model for squids of Arkhipkin and Roa-Ureta (2005), followed by many authors, for example, Schwarz and Perez (2010, 2013); the bioenergetic models of Grist and Jackson (2004) and O'Dor et al. (2005), followed by André et al. (2009); and the physiological model of Moltschanivskyj (1994, 2004), followed by many authors (e.g. Kuipers, 2012; Semmens et al., 2011). The maturity model of Macewicz et al. (2004) has been further developed by Dorval et al. (2013) into a good management tool.

With the basic data available, it is possible to devise a model that addresses the two main issues of population dynamics: *per capita* rate of population change and stability versus oscillations. Models can then be used to test possible explanations of the observed change. In theoretical ecology, more often than not, this explanation lies in trophic relationships (e.g. specialist predation is thought to be the most frequent cause of second-order oscillations). Two older reviews of the population dynamics of cephalopods (Caddy, 1983; Pauly, 1985) underlined the differences and similarities of cephalopod population biology compared with fish, utilizing both the traditional fisheries framework of stock assessment and resource management.

Recently, however, the most frequently pursued direction has been to focus on understanding external effects of environmental systems and variables. Does the environment govern cephalopod life cycles?

Given the apparent unsuitability of traditional approaches to stock assessment arising from the complexity of the squid life cycle and the sensitivity to extrinsic factors touched on in the preceding text, it can be argued (Pierce et al., 2008) that an understanding of the traditional population dynamics parameters (fecundity, mortality and growth) may be fruitless; stock-recruitment relationships are absent and much of the predictability in population dynamics may derive from knowledge of external effects, particularly the physical environment. In fact, there are several examples of models in the published literature, often investigating in detail the impact of temperature

upon growth rate, mantle length at age, maturity and ultimately fecundity described by [Forsythe \(1993, 2004\)](#). There is an inference that higher temperatures may reduce life span, which in turn will result in oscillations of abundance linked only to change in a population structure, but not effected in the long series of subsequent generations ([Pecl and Jackson, 2008](#)); see [Figure 2.3](#). [Roberts \(2005\)](#) presented a simple model whereby he calculated the relationship between maximum summer SST as a monthly average and biomass of squid (*L. reynaudi*) the following autumn (and/or annual catch). The linear relationship obtained ([Figure 2.4](#)) shows a clear problem for rational management of the resource: catch is more strongly correlated with SST the previous summer than with stock biomass. Also, Roberts' model suffers from intense data manipulation (all relationships are based upon pooling massive database and on averages) and simplistic treatment of changes in the population; the model does not consider population structure.

[Reiss et al. \(2004\)](#) constructed an age-based temperature-dependent model of squid (*D. opalescens*) growth and a simple population dynamics model based on the aforementioned to drive the population growth rates. The results of this model are presented in [Figure 2.5](#). A surprising result was that growth rate was negatively related to temperature, contrary to the predictions by [Forsythe \(1993, 2004\)](#). [Jackson and Domeier \(2003\)](#) were first to detect this inverse relationship; they also detected a relationship between the intensity of upwelling and the size and age of squid, as might be expected. Although conceptual or quantitative proof is lacking, they

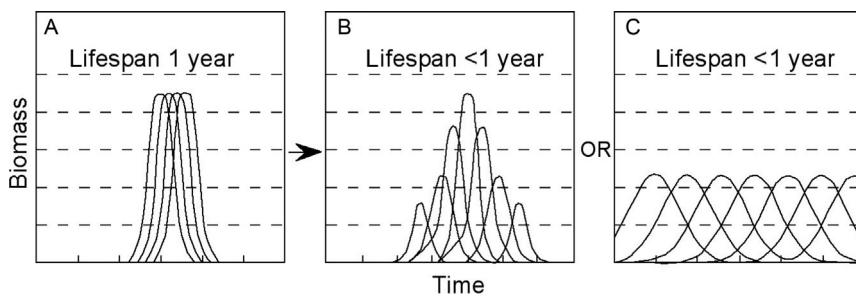


Figure 2.3 Diagrammatic representation of fluctuations in biomass of squid over 1-year period. (A) Aggregative spawning over an extended spawning season of up to several months resulting in successive waves of recruitment, however, a clear peak is present. (B) Breeding season is extended beyond a few months as the lifespan of squid becomes shorter, although seasonal peaks in biomass are still evident. (C) Uncoupling of seasonal and synchronous spawning cues resulting in aseasonal pulses of recruitment with no obvious dominant peak in biomass. *From Pecl and Jackson (2008); adapted from Boyle and von Boletzky (1996).*

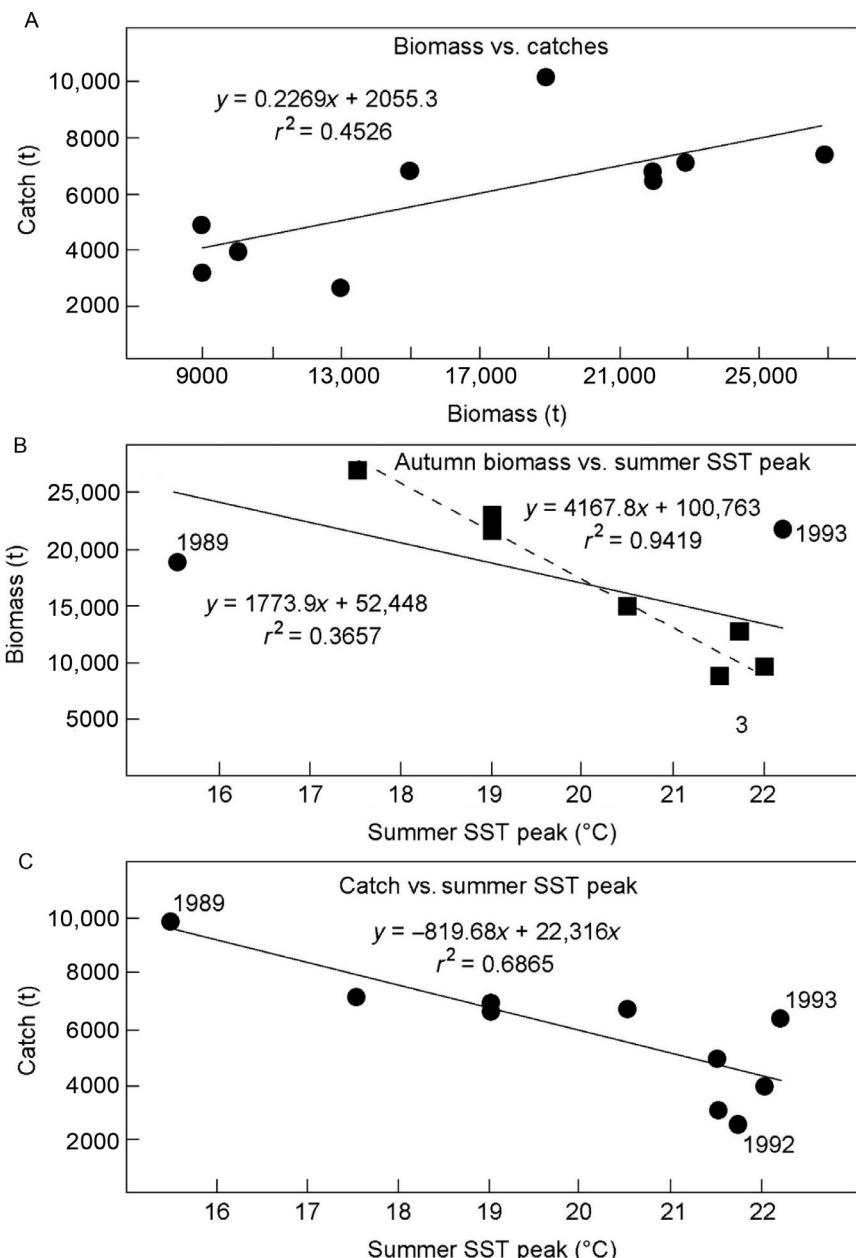


Figure 2.4 (A) Estimated *Loligo reynaudii* biomass versus total annual jig catch (1988–1997). (B) Biomass versus maximum monthly average SST (sea surface temperature). The linear fit is improved (dashed line) if the anomalous years 1989 and 1993 are excluded. (C) Total annual jig catch versus maximum monthly average SST. From Roberts (2005).

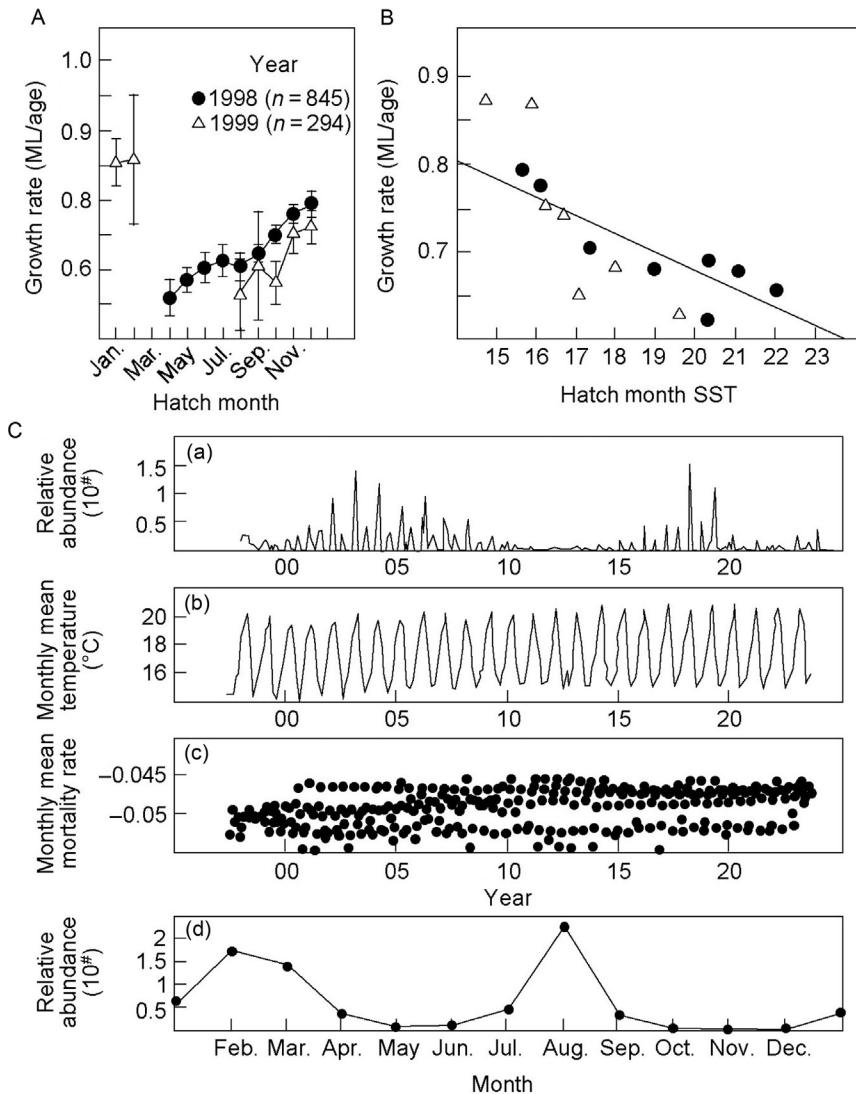


Figure 2.5 (A) Mean growth rate (± 1 SE) of mature *Loligo opalescens* from the Southern California Bight commercial fishery in 1998 and 1999 plotted by month of hatch; (B) means of growth rates in relation to hatch-month SST (sea surface temperature) as calculated from the monthly mean temperature recorded at Scripps Pier (California, USA); (C) 25-year population simulations of using an age-based temperature-dependent growth model. (a) Time series of monthly population abundance; (b) monthly average temperature; (c) monthly mortality rates; and (d) seasonal pattern of recruitment. *From Reiss et al. (2004).*

propose that these relationships reflect a trade-off between physical environmental effects and food availability. [Reiss et al. \(2004\)](#) did not include trophic relationships or density-dependent processes in their model or indeed test their model against real data. However, they suggested that including food in the model would have affected the empirically derived growth relationship. They predicted that this inclusion would shift the period of maximum growth rate from winter to late spring, to coincide with low temperatures and high abundance of prey.

[André et al. \(2010\)](#) used a combination of individual-based bioenergetics and stage-structured population models to describe the capacity of cephalopods (represented by *Octopus pallidus*) to respond to climate change. Results of this model are given in [Figure 2.6](#). This very useful model predicts possible consequences of climate change. The model assumed a linear increase in the mean annual temperature from 17.32 in 2005 to 19.43 °C in 2070. Results indicated that the response of the *O. pallidus* population to climate change would be nonlinear. Assuming the survivorship schedule remained constant, an increase in water temperature could lead to a shift from exponential population growth to exponential decline within a matter of years. Egg incubation period was predicted to fall (from 186 to 95 days), coupled

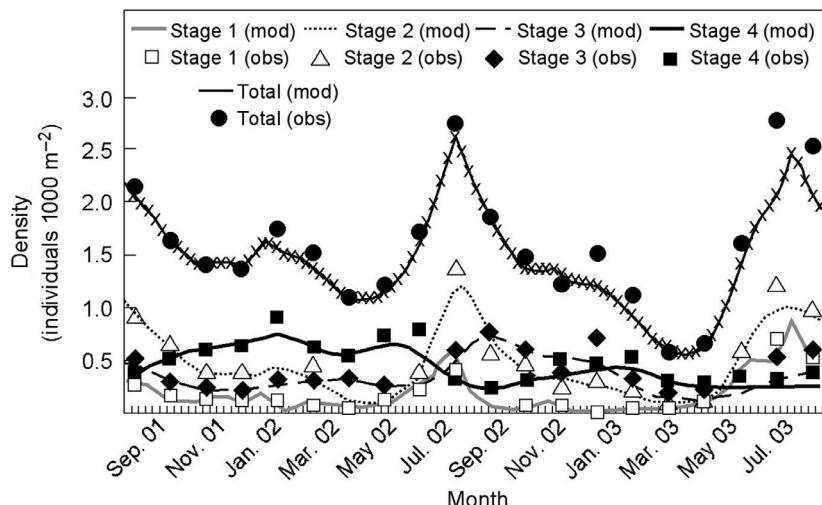


Figure 2.6 Model predictions concerning densities of *Octopus vulgaris* in Greece over time. Predictions start from an initial density vector \mathbf{n}_1 equal to the observed vector at that time. Predictions are compared with observed densities (real data). Lines represent model estimations and markers represent real data. From [Katsanevakis and Verriopoulos \(2006\)](#).

with reduced hatchling size (0.34 to 0.23 g), small weight at reproductive maturity (466.0 to 395.8 g) and a shorter generation time (12 to 9 months). One conclusion, therefore, is that successful adaptation to climate change may come at the cost of substantial change in population structure and dynamics, resulting in a potential decrease in generation time, streamlining of the life cycle, lower fecundity and possible loss of resilience to catastrophic events. Secondly, cephalopods may be bad climate indicators. However, it should be noted that, again, the authors did not include trophic relationships in their model. Instead, they speculated why the exponential growth is not observed in reality and ascribed this to environmental factors (such as extreme weather events and various environmental variations). The lack of exponential growth in the real population can however be related to trophic relationships, and this should be taken into consideration in future research. This is underlined by the fact that the change illustrated in the model can lead theoretically to decoupling of predator–prey relationships. The authors speculated what implications this may have for cephalopods and indeed for whole marine ecosystems.

The existence of numerous empirical models that link environmental variables with distribution, abundance and recruitment of several cephalopod species (e.g. Sobrino et al., 2002; Waluda et al., 1999, 2001a,b; Wang et al., 2003) led Pierce et al. (2008) to acknowledge the environment as a key factor in determining, leading and varying cephalopod life cycles and their population dynamics. However, they also recognized the importance of trophic relationships, specifically the role of prey availability (alongside environmental factors) in determining growth and mortality rates of early life stages. The same view (adding density-dependent effects) is underlined by Otero et al. (2008) who investigated abundance fluctuations of *O. vulgaris* and their possible causes. In addition, Vidal et al. (2006) provided empirical data to demonstrate the importance of prey availability for the survival and growth rates of squid paralarvae.

Katsanevakis and Verriopoulos (2006) constructed a simple model of *O. vulgaris* population dynamics in the eastern Mediterranean. The basis for this model was a monthly visual census (July 2001–September 2003), using scuba diving, of octopus abundance along 14 fixed transects within an area of 1600 m². The census was run monthly from July 2001 to September 2003. All octopuses sighted were assigned to one of four estimated weight classes (<50, 50–200, 200–500 and >500 g). To explain densities by weight class and to estimate life cycle parameters, a time-variant, weight class-based matrix population model was developed. Annual and semiannual

density cycles were found, with the main peak of benthic settlement in summer and a secondary, irregular settlement during late autumn. On the basis of the model, spawning peaks, mortality, lifespan and growth rates for various stages were predicted, and the model achieved good prediction capability (Figure 2.6). However, modelling the complete life cycle would require information on fecundity as well as egg and paralarval densities, parameters that would be difficult to estimate for the population study because of the possible disturbance of the spawning process in octopuses' dens (although literature values of fecundity could be used, e.g. Mangold, 1983d) and because knowledge of hatching success and mortality of paralarval mortality in the plankton is lacking. Other aspects not covered by the model include trophic relationships and environmental influences.

Trophic relationships of cephalopods are 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; Lipiński, 1987, 1992; Lipinski and David, 1990; Lipinski and Jackson, 1989; Lipinski et al., 1991, 1992; Lordan et al., 1998; Pierce et al., 1994; Rodhouse and Nigmatullin, 1996). As can be seen in Table 2.1, trophic relationships are the most often researched topic in the best-known species of cephalopods.

However, the use of these data in the generation of biological ideas and models is rare. Nevertheless, there has been a trend to use the wealth of basic field and laboratory data that are available for some form of ecological modelling. This modelling is based not only on stomach content analyses but also in bioenergetics research (which is mentioned but not reviewed here; see O'Dor and Wells, 1987; Wells and Clarke, 1996). In recent years, some of the first ecosystem models that explicitly examine the importance of squids have been produced, for example, Jackson et al. (2007), Gasalla et al. (2010) and Wangvoralak (2011).

Amaratunga (1983) in his early review of the role of cephalopods in the marine ecosystem presented conceptual models of cephalopod predation for various groups of cephalopods in the form of block diagrams. He mentioned briefly energy requirements, balance and change of generations, but he did not discuss the issue of overlapping generations. His block model of biomass change in a squid (*I. illecebrosus*) is shown in Figure 2.7A. He calculated the prey biomass taken by 1000 g of squid under various assumptions and linked growth rate to feeding rate (Figure 2.7B) following Jones (1976) and O'Dor et al. (1980). He also addressed mortality in a population using yield-per-recruit analysis (after Mohn, 1982). However, this very simplistic description of biomass change, driven by trophic relationships, relies on

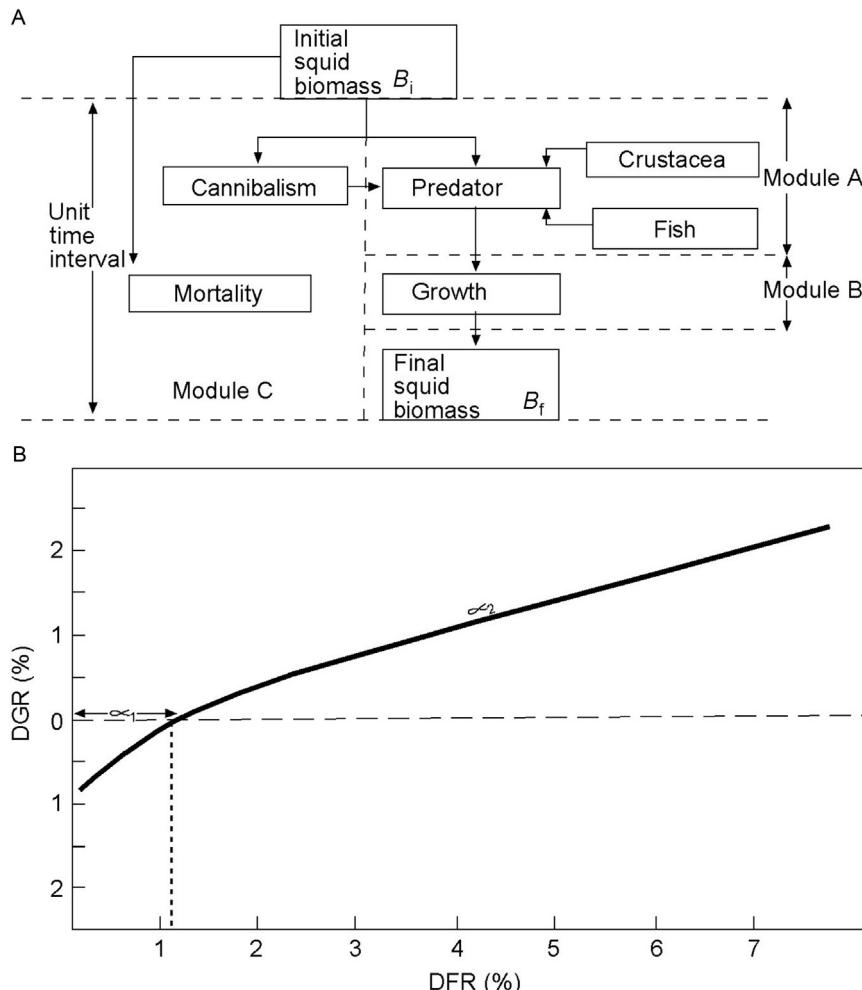


Figure 2.7 (A) Block diagram of the biomass change of *Illex illecebrosus*, affected by trophic relationships. Module A represents predation, module B represents growth. (B) Mean daily growth rate (DGR) plotted against mean daily feeding rate (DFR) for *Illex illecebrosus* maintained in the aquarium. From Amaratunga (1983).

sweeping assumptions about constancy of feeding rate and a linear relationship between the percentage of animals' feeding and time (month).

In a considerable improvement of this approach, Pierce and Santos (1996) modelled month-to-month changes in the population size and amount of different prey species removed, using data on fishery landings, size composition and diet of *L. forbesii* in Scottish waters, along with literature estimates for natural mortality and daily energy requirements.

In their review, [Rodhouse and Nigmatullin \(1996\)](#) not only provided a descriptive reflection of trophic relationships in cephalopods but also covered quantitative impacts on prey populations. Their summary of the life energetics of a squid, specifically the winter-spawning population of *I. argentinus* (the best available at the time), is given in [Figure 2.8](#). In another review (concerning squid of the genus *Illex*), [Dawe and Brodziak \(1998\)](#) listed difficulties in incorporating trophic relationships into quantitative population dynamics analysis of cephalopods, as follows:

- If *Illex* recruitment is substantially influenced by environmental variation, then trophic interactions may be difficult to discern.
- If important trophic interactions occur primarily between the youngest stages of *Illex* and other species during the oceanic phase of the life cycle, then abundance data concerning older life stages may be inadequate to discern the cause of recruitment variability.
- If spatial aggregation and temporal aggregation of relative abundance data conceal the effects of local processes, then correlations based on aggregated data may be impossible to measure.
- If species that interact with *Illex* through competition for prey or through the sharing of predators are not considered, then important indirect trophic effects may be impossible to measure.

Their diagnosis stands firm to the present day. An example of Dawe and Brodziak's approach is given in [Figure 2.9](#).

[Jackson et al. \(2007\)](#) provided a general analysis of the role of squid using the Atlantis model ([Fulton et al., 2004](#)). This is a holistic ecosystem model based on trophic interactions in many modules, including fisheries. An example of the use of this model to assess an impact of fisheries on squids in the Bass Strait is given in [Figure 2.10](#).

[Gasalla et al. \(2010\)](#) included the squid *Doryteuthis plei* within an Ecopath model for which the mixed trophic impact and “keystone ness” were calculated for all component groups and/or species. The main finding was that *D. plei* had the third highest “keystone ness” as well as a high overall mixed trophic effect index. It appears that “squid on squid” effects are very important in these interactions. The interactions matrix (i.e. for mixed trophic impact) for *D. plei* is shown in [Figure 2.11](#).

[Gaichas et al. \(2010\)](#) used a food web model to incorporate data on trophic relationships into stock assessment under an “ecosystem approach to fisheries” (EAF) perspective. They included squids without specifying species and compared resources with high fishing mortality (halibut, skate and walleye pollack) with those that are incidentally fished (squids), noting that

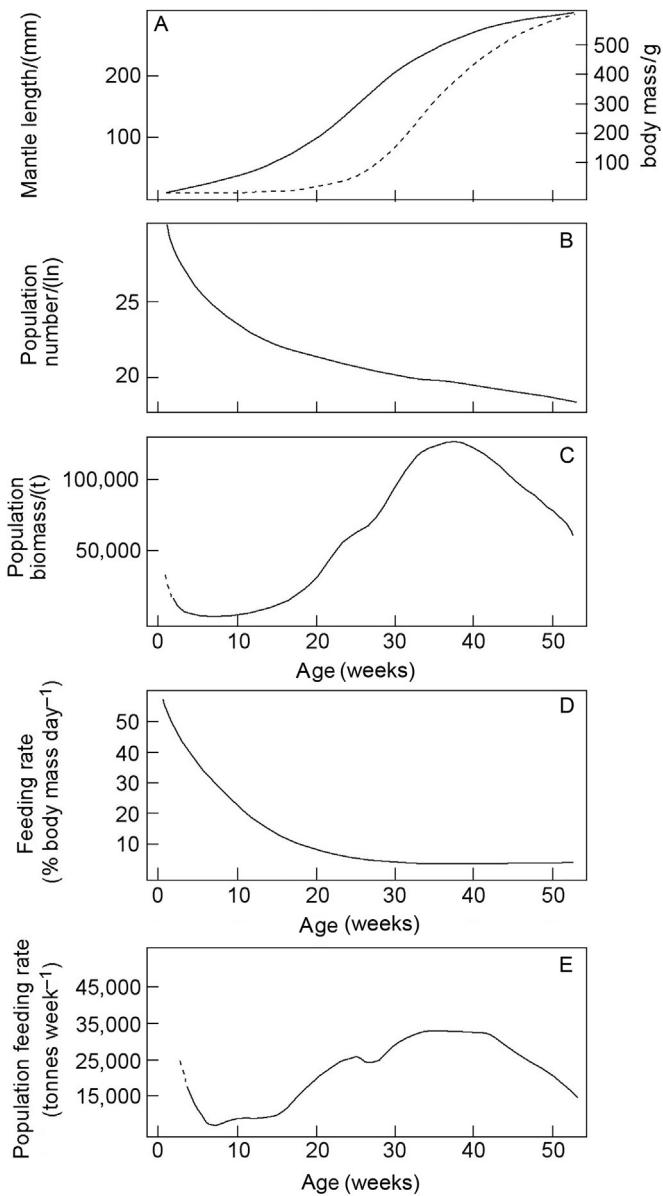


Figure 2.8 Lifetime energetics of an *Illex argentinus* cohort from the winter-spawning southern Patagonian Shelf population. From [Rodhouse and Nigmatullin \(1996\)](#).

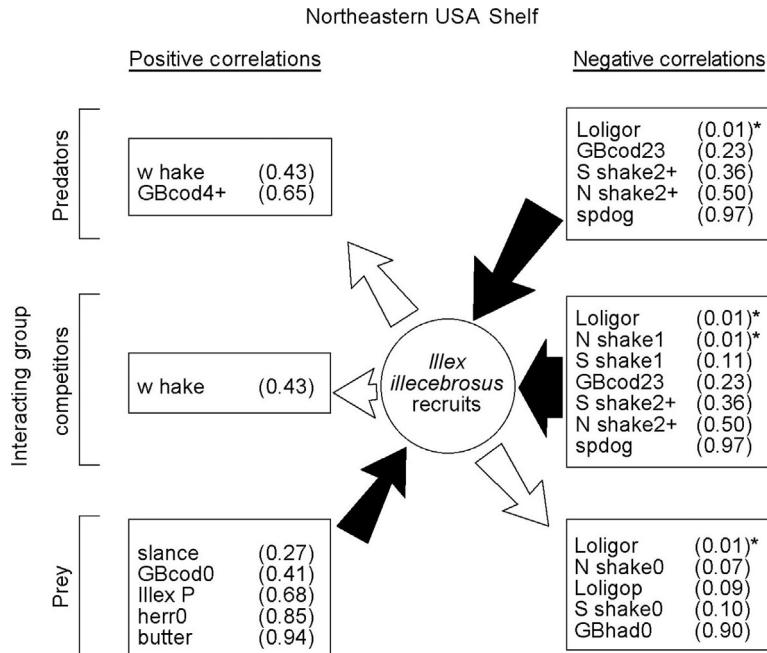


Figure 2.9 Schematic representation of the relative importance of three types of trophic interactions on *Illex illecebrosus* recruitment on the northeastern U.S. shelf, based on the occurrence of positive versus negative correlations with relevant fish stocks and age groups (*p*-values marked by * were judged to be statistically significant); thickness of the dark arrows represents relative importance of interactions which could affect *I. illecebrosus* recruitment. For definitions of interacting groups, see [Dawe and Brodziak \(1998\)](#) p. 131 (Table 7.1) from where this figure was reproduced.

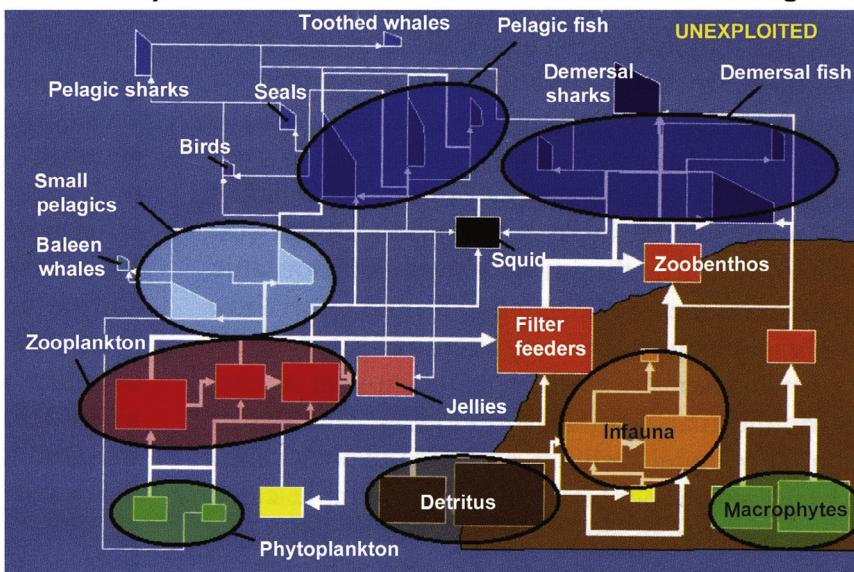
natural predation in squids is much greater than fishing mortality and should therefore be considered in ecosystem modelling.

[Moustahfid et al. \(2009\)](#) concluded that incorporating trophic relationships (predation) into a surplus production model is feasible, providing a demonstration of an alternative to the present approach to management of *Doryteuthis pealeii*.

[Roel \(1998\)](#) identified several mechanisms that play a role in determining recruitment levels in chokka (*L. reynaudii*), for example, predation on the spawners and on eggs and cannibalism. She concluded that cannibalism is likely to be a density-dependent cause of mortality, while environmental events such as the frequency of westerly winds in winter and of upwelling events in summer appear to have a direct influence on the extent of spawning inshore (and are positively correlated with abundance).

A

Atlantis example
Trophic abundance & connections — before fishing



B

Atlantis example
Trophic abundance & connections — after fishing

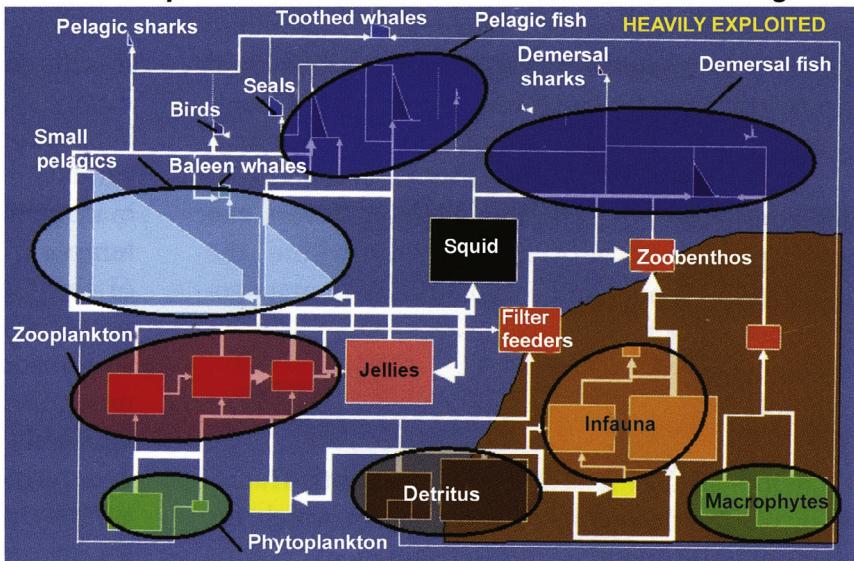


Figure 2.10 The framework of the “Atlantis” model. The framework represents a natural ecosystem using a nutrient-based biogeochemical model that is coupled in the biological/physical sense through differential equations. An assessment, using “Atlantis”, of the potential effect of fishing pressure on trophic abundances and connections in the Bass Strait (Australia), by showing the food web equilibrium before fishing (a) and after fishing (b). From Grist et al. (2007) in Jackson et al. (2007).

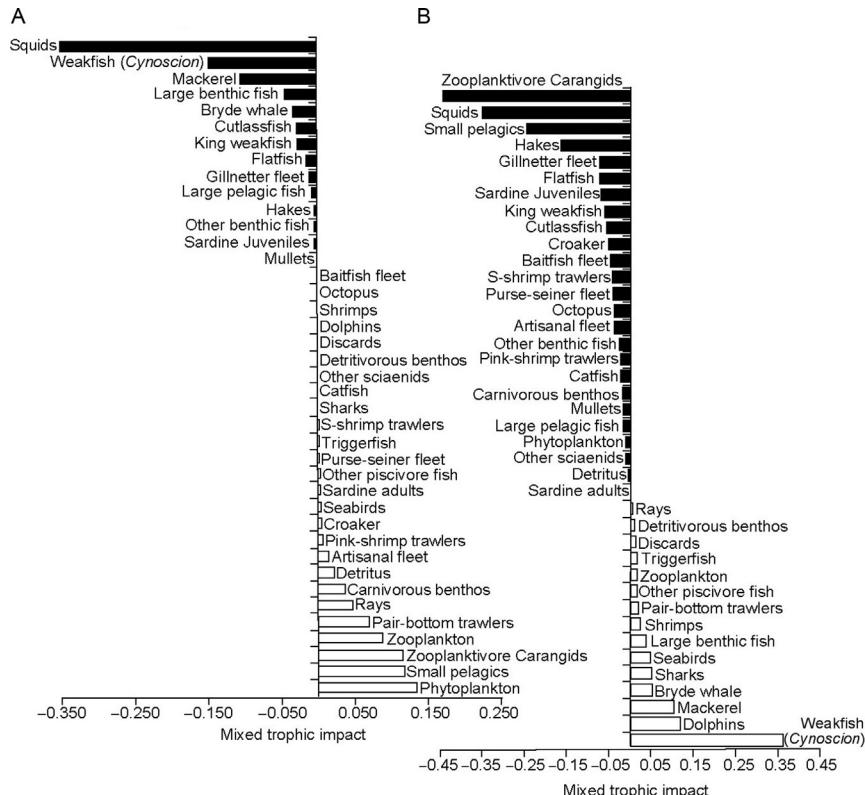


Figure 2.11 Trophic role of the *Loligo plei* in the South Brazilian Bight. The mixed-trophic impact matrix analysis was used. (A) Impacts of other groups upon squid. For example, weakfish, cutlassfish, whales, large pelagic fish and mackerel seem to negatively impact squid as predators or indirectly (top-down). Producers and plankton groups, small pelagic fish and carangids seem to 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. \(2010\)](#).

Fisheries biomass and various aspects of applied population dynamics of cephalopods are covered by a large literature base stretching over many years, probably starting with [Sasaki's \(1921, 1929\)](#) remarks about *T. pacificus* exploitation in Japan. Generally, neither environmental impacts nor trophic relationships are explicitly included in stock assessment models (e.g. Basson et al., 1996; Beddington et al., 1990; Khoufi et al., 2012; Lu et al., 2013; Morales-Bojorquez et al., 2001a, 2008, 2012; Nevárez-Martínez et al., 2006, 2010; Robert et al., 2010; Tomas and Petrere,

2012), except perhaps *T. pacificus* in Japan (see below). Relevant studies on specific cephalopod species include those of Mohamad Kasim (1985), Vidyasagar and Deshmukh (1992), Karnik et al. (2003) and Thomas and Kizhakudan (2011) for *Photololigo duvaucelii*; Sundaram and Khan (2009) for *Sepiella inermis*; Mohamad Kasim (1993) for *Sepia elliptica*; Arreguín-Sánchez et al. (2000) for *Octopus maya*; Alvarez Perez (2002) for *D. plei*; and Augustyn et al. (1993) and Roel (1998) for *L. reynaudii*. A notable exception to this rule is stock assessment for *T. pacificus*, where environmental effects are included (Kidokoro and Mori, 2004; see also Section 4).

There is certainly enough evidence that intrinsic elements and trophic relations are no less important than the environment in shaping cephalopod life cycles and their population dynamics and recruitment in particular. However, their incorporation into workable management strategies is a challenge. At present, empirical models of abundances (or catches) based on external (environmental) factors may appear to be better candidates for fisheries management tools than traditional stock assessment approaches, but our lack of knowledge about underlying mechanisms, rooted in ecological theory, is also a serious weakness.

2.6. Synthesis and the future

Stability, oscillations in abundance and occurrence and chaotic behaviour of populations have been studied only selectively in cephalopods. The linking of population dynamics to molecular biology is at an early stage, although its importance has been recognized.

The problem of overlapping generations has not been solved (neither is it satisfactorily solved in theoretical ecology either). The population biology of octopods offers excellent experimental opportunities in this regard because of their strict semelparity. The understanding of interaction between various life stages in studies on both fish and cephalopods has just only started receiving attention (see Bloor et al., 2013a), with the understanding that larval and paralarval phases are the most vulnerable, and account for the greatest mortality in each generation because of starvation and predation pressure. However, paralarvae and juveniles differ profoundly: newly hatched paralarvae must learn within a very short time period how to catch food (e.g. Chen et al., 1996) and are unable to withstand even short periods of starvation due to their high metabolism and short-lasting yolk reserves (Vidal et al., 2006); they are therefore very prone to death from starvation. Cephalopod juveniles are highly visible, occur together in large numbers and energetically

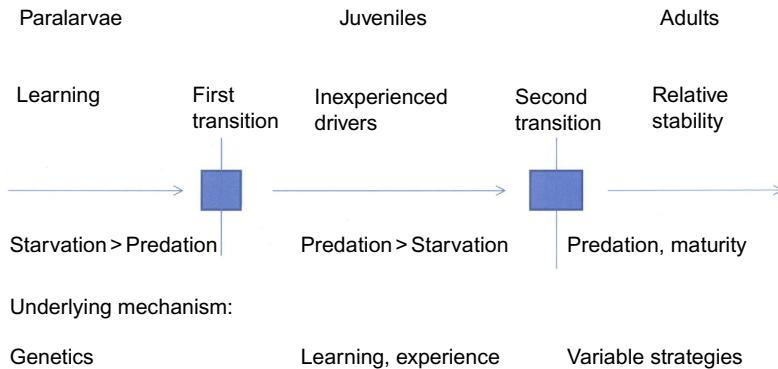
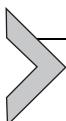


Figure 2.12 Schematic representation of a cephalopod life cycle. Mortality of paralarvae is mainly due to starvation; mortality of the juveniles is mainly due to predation. Transitions are morphological as well as physiological and behavioural.

offer greater energetic rewards for predators than do paralarvae, suggesting that their mortality from predation must be considerable (Figure 2.12).

Pierce et al. (2008) had reviewed the importance of environmental factors for the structure and dynamics of cephalopod life cycles (including population dynamics). Their assessment is corroborated by further research upon several species. This effort makes a strong connection with recent trends in general marine ecology. Indeed, Lehodey et al. (2010) and Buckley and Buckley (2010) had strongly advocated further the development of an approach linking ocean models and environmental effects to population dynamics of large marine predators. However, the cornerstone of the current population dynamics theory–trophic relationships remains to be adequately addressed in cephalopods. This is the most important area for future research and one that could result in an original contribution to theoretical ecology. One of the main inferences from theory is that specialist predation is a key driver of population dynamics of prey. However, predation upon and by cephalopods is a network of opportunistic links, governed by a different set of models (Turchin, 2003). This is untapped research territory in theoretical ecology. Another important area of research is the interplay of temporal and spatial considerations and issues of cephalopod survival (e.g. Challier et al., 2006b; Crespi-Abril and Baron, 2012; Crespi-Abril et al., 2013, 2014; Lipinski et al., 1998a,b; see also Olyott et al., 2006, 2007). Researchers wishing to pursue this line of research have plenty of data (see Table 2.1). Myers (2000) had written about the Ocean Biogeographic Information System (OBIS; <http://www.iobis.org/>), while Turchin (2003) mentioned the Global Population Dynamics Database

(<http://www3.imperial.ac.uk/cpb/databases/gpdd>). There are also the database of the Food and Agriculture Organization of the United Nations (<http://www.fao.org/fishery/en>) and data from various large projects funded by the European Union. There are also large databases of the individual countries (or scores of countries under bilateral and multilateral agreements) at the forefront of exploitation and research of cephalopods (Japan, the United Kingdom and the United States).



3. CAUSES OF FLUCTUATIONS IN POPULATIONS

3.1. Physical and biological effects

3.1.1 Temperature effects on metabolism and survival

Body temperature is perhaps the most important ecophysiological variable affecting the performance of ectotherms. Performance functions including metabolism and growth rates steadily increase with temperature from the critical thermal minimum until achieving the thermal optimum with a further abrupt drop to zero at the critical thermal maximum (Angilletta et al., 2002). Such an asymmetric function, in which performance is maximized at an intermediate temperature, is especially marked in cephalopods because of an incipient oxygen limitation of metabolism at the species-specific thermal maximum (Meltzner et al., 2007).

Cephalopod egg survival seems to be very stable within the thermal optimum (ca. 90–100%), then, either abruptly dropping to zero at thermal limits as in squids *D. gahi* and *D. opalescens* (Cinti et al., 2004; Zeidberg et al., 2011) or gradually decreasing because of a simultaneous increase of developmental anomalies, particularly in the last stages of development as in *L. reynaudi* and *T. pacificus* (Oosthuizen et al., 2002; Sakurai et al., 1996). Fluctuations in temperature have a negative impact on survival of loliginid eggs, and upward fluctuations are comparatively more deleterious than downward fluctuations. Earlier stages of embryonic development are more sensitive to such temperature variability (Gowland et al., 2002; Oosthuizen et al., 2002; Segawa, 1995).

Within the optimum thermal range for reproduction, populations reproducing at lower temperatures (e.g. winter vs. summer), or in higher latitudes, produce eggs of larger size (Laptikhovsky, 2006). Because of this higher amount of yolk in the egg, squids and cuttlefish hatched at lower temperatures not only are larger but also have a proportionally larger yolk sac, so increase in hatching size is not coming at the cost of diminishing of yolk reserves (Bouchaud, 1991; Vidal et al., 2002; Villanueva et al., 2011). Taking

into account the fact that lower temperature also invokes lower rates of metabolism, survival on yolk reserves is longer at lower temperatures (Vidal et al., 2005), and these hatchlings possibly have more time to find a suitable stable food source before their yolk reserves run out and they die (Bouchaud, 1991). Therefore, lower temperatures within the optimum species-specific range might generally be more favourable for recruitment survival and cohort strength. However, it was demonstrated under experimental conditions that temperature might have negative impact on hatchling survival within normal developmental temperature range (Vidal et al., 2002), so this supposition should be taken cautiously. Hatchlings of *S. officinalis* are known to vary in weight from 0.053 to at least 0.180 g (Bloor et al., 2013a), so differences in size-related survival rates might be quite important.

Temperature has a crucial impact on paralarval survival, growth rate, age of juvenile benthic settlement and timing of reproduction. Recruitment strength (hence commercial catch) of cephalopods is often related to environmental temperatures during the first months of life (Caballero-Alfonso et al., 2010; Pierce and Boyle, 2003; Vargas-Yáñez et al., 2009), but it is not clear if this is a direct temperature impact or whether temperature acts as an indicator of some other environmental changes influencing survival at early stages. At lower temperatures, growth rates are reduced, increasing size-dependent mortality by predation, while high temperatures increase growth rate, reducing size-dependent mortality but will tend to increase mortality due to starvation if food is scarce. These relationships are not straightforward due to numerous other factors, in turn affected by temperature, impacting recruitment strength.

Generally, once cohort strength is established, stock size depends mostly on growth rates and mortality. Squids grow faster at higher temperatures within the optimum range, and because of this, squids hatched at different times from the same population achieve different adult sizes. Beyond this range, at the thermal limits of the species survival, growth is slower.

At higher temperatures, cephalopods also mature faster, so their growth rates slow down at an earlier age. However, this earlier start of reproductive activity might not always impact on the population-specific duration of the life cycle, but rather, it will extend the duration of the adult phase (Arkhipkin and Laptikhovsky, 1994; Forsythe, 2004; Forsythe et al., 2001; Rodhouse and Hatfield, 1990). Extension of the adult phase might support a manyfold increase in fecundity and thus in recruitment strength, particularly in cuttlefish with their highly flexible reproductive strategies ranging from a single batch to multiple spawning within the same population

(Boletzky, 1987, 1988; Laptikhovsky et al., 2003). However, populations of some squids with wide temperature tolerance might exhibit either an annual or a half-annual life cycle (Arkhipkin et al., 2000) depending mostly on environmental temperatures, thus making this factor very important in determining the entire life cycle.

As oceans warm, marine species that live near their upper thermal limit are likely to undergo changes in distribution as they follow their optimum thermal window (Parmesan and Yohe, 2003; Pinsky et al., 2013; Sunday et al., 2012). Most coleoid cephalopods are short-living species (Boyle and Rodhouse, 2005) with annual or subannual life cycles. This has recently raised the interest of studying them as models to examine possible changes in the life histories of long-lived range-shifting species (Hoving et al., 2013).

3.1.2 Other physical environmental effects

The effect of salinity on embryonic development is generally similar to that of temperature: hatching rates are close to 90–100% within the normal environmental range quickly dropping to zero beyond its limits, where metabolic processes slow down and embryos develop malformations (Paulij et al., 1990). Generally, salinity fluctuations in the natural environment are less than those of seasonal temperature. However, some short-term large-scale changes caused by torrential rains in coastal areas are possible, particularly in closed bights and bays used by many cephalopod species for spawning. Human-induced effects can also occur. It was shown that a desalination plant, which discharges concentrated brine into the vicinity of *S. apama*'s breeding aggregation, could possibly be detrimental to the future survival of the population (Dupavillon and Gillanders, 2009). Survival changes during gradual changes in salinity are to those following sudden change. Outside the optimum range, the salinity tended to cause premature hatching and death of the embryos before organogenesis at high salinity and abnormal development at low salinity (Nabhitabhata et al., 2001).

Oxygen tension is important for egg development and survival. It is not usually a problem for octopod egg clusters that are brooded and aerated by the female, but in loliginid squids, the large size of egg masses is likely to restrict water flow causing hypoxic conditions and higher occurrence of developmental abnormalities. Egg mortality is higher in large egg masses, as well as in embryos located near the attachment point where oxygen is likely to become most depleted (Gowland et al., 2002; Murray, 1999; Steer and Moltschanowskyj, 2007). Biofouling has been shown to have an interactive effect with egg position (thus oxygenation) on egg survival. In

heavily fouled masses, egg survival on the distal end of a strand was lower, and on a proximal end, higher than in clean egg masses ([Steer and Motschaniwskyj, 2007](#)).

Light and photoperiod might also have the impact on survival and growth of cephalopods, which are visual predators especially if their prey lacks photophores and therefore cannot be seen in darkness. Adult cuttlefish *S. officinalis* died of starvation in experiments in complete darkness even when enough prey was available, and mortality of juveniles was higher at the shortest light period ([Koueta and Boucaud-Camou, 2003; Richard, 1975](#)).

Changes in dissolved carbon dioxide content and related acidification of oceanic waters might have an intensive impact on cephalopod survival and evolution as in the geologic past, they caused numerous mass extinctions of ammonites and belemnites including final extinction ([Arkhipkin and Laptikhovsky, 2012](#)). Epipelagic squids (e.g. Ommastrephidae, Gonatidae and Loliginidae) are hypothesized to be most severely impacted by the interference of CO₂ with oxygen binding at the gills, because their metabolic rates are higher than other aquatic animals ([Seibel, 2007; Seibel and Drazen, 2007](#)). [Rosa and Seibel \(2008\)](#) subjected the squids (*D. gigas*) to elevated concentrations of CO₂ equivalent to those likely to be found in the oceans in 100 years due to anthropogenic emissions. They found that routine oxygen consumption rate was reduced under these conditions and their activity levels declined, presumably enough to have an effect on their feeding behaviour. [Kaplan et al. \(2013\)](#) reported on their experiments hatching Atlantic long-fin squid, *D. pealeii*, in both regular ocean water and acidified ocean water, mimicking the conditions likely to be seen in the oceans in 100 years. The squid eggs placed in the acidified water hatched later were smaller and their statoliths were smaller, more porous and less dense, and the small crystals that comprise the statolith were organized more irregularly than those in a normal squid.

3.1.3 Oceanographic effects: Currents/transport and upwelling

Paralarval dispersal plays an important role in the population dynamics and survival of a generation. On one hand, it permits a species to occupy new habitats and expand its range wherever and whenever it is possible while simultaneously diminishing intraspecific competition at early stages of the life cycle. On another hand, it invokes critically high mortality when paralarvae are transported into area with unfavourable environmental conditions.

A particular case is a situation when a substantial proportion of the generation might be carried away from the normal population range into

remote areas where the environment is still favourable for growth and reproduction. Even if these squids survive and spawn, they are lost from the original stock, which thus declines. In some years, offshore feeding aggregations of immature *D. gahi* are transported by the Falkland Current >500–700 km from their usual feeding ground to the east of the Falkland Islands (51–52°S) to the high seas area (46–47°S) off the Patagonian Shelf. These squids do not migrate back to the Falkland Islands to spawn, which causes a decrease in parent spawning stock. Due to changes in the position and intensity the Falkland Current is thus responsible for major variability in the recruitment of this species to the fisheries ([Arkhipkin et al., 2006](#)).

Recruitment strength of the winter-spawning cohort of the squid *I. argentinus* is strongly influenced by retention/transport of eggs within the spawning grounds off Uruguay and adjacent waters. Recruitment is stronger when the suitable SST habitat around spawning and nursery grounds increases in area ([Rodhouse et al., 2013](#); [Waluda et al., 1999, 2001a](#)), thus diminishing intraspecific competition and possibly predation because of wider dispersal. A similar cause of recruitment variability was recorded in another ommastrephid squid, *T. pacificus* ([Sakurai et al., 2000, 2013](#)). Since the late 1980s, the autumn- and winter-spawning areas of this species have expanded over the continental shelf and slope in the East China Sea, promoting an increase in abundance with respective expansion of the summer feeding grounds.

In upwelling areas, oceanographic events can be an important factor determining cephalopod distribution and abundance. For example, the short-fin squid *I. coindeti* appeared in Galician waters at very high level of abundance in 1987, when the upwelling season was a particularly favourable ([Gonzalez and Guerra, 2013](#)). Similarly, the abundance of the squid *L. reynaudi* in waters of the South Africa seems to be influenced by upwelling intensity ([Sauer et al., 2013](#)). For species spawning in upwelling areas, paralarval retention is a crucial factor of survival of a generation. In a common octopus, *O. vulgaris*, retention in coastal waters appears to be a key factor for the recruitment success off the Arguin Bank (Mauritania). Paralarvae have been shown to benefit from increased retention in spring due to enrichment and limited mixing and dispersion, whereas hatching in autumn is less beneficial to the recruitment because at the beginning of the upwelling season, there is less coastal retention and only weak wind-induced turbulence ([Demarcq and Faure, 2013](#); [Faure et al., 2000](#)). Wind stress structure and related upwelling intensity were found to affect the early life phase of

this species off Galicia and explain up to 85% of the total variance of the year-to-year variability of the adult catch (Otero et al., 2008).

The range of the Humboldt squid, *D. gigas*, has recently expanded and stock structure has changed. This is a species in which abundance is strongly driven by ENSO events around the Peruvian coastal upwelling system. Abundance is at a maximum when temperature anomalies are moderate, and decreases during intense warm and cold events, probably because of lower survival of early stages and adult spawning outside areas of optimal conditions (Rosa et al., 2013; Waluda and Rodhouse, 2006; Waluda et al., 2004).

Cold upwelling water might block distribution of warm water species in the area, and occasional intensive inflows of anoxic waters with sporadic occurrence of high H₂S concentrations might be deleterious for entire cephalopod groups. Over a huge area of intensive upwelling in Namibian waters, between 21°S and 27°S outbreaks of toxic H₂S gas are a seasonally recurrent feature (Emeis et al., 2004) poisoning near-bottom layers, whereas surface layers remain clean. Only those cephalopods with small pelagic eggs are able to reproduce there (Ommastrephidae, Enoplateuthidae and *Lycoteuthis diadema*), whereas to the north and to the south of this area, large-egged bottom dwellers laying eggs on the sea floor (Sepiida, Sepiolida and *L. vulgaris reynaudii*) are very common (Laptikhovsky et al., 2013).

3.2. Migrations

Migrations cause a significant source of population variability among cephalopods. They may be a reflection of population redistribution, when animals move either diurnally or throughout their life cycle during ontogenetic migrations. Diurnal and ontogenetic migrations may take place either horizontally or vertically or both. Diurnal migrations mainly reflect changes in feeding behaviour with alternating periods of feeding activity and resting at different times of the day. Ontogenetic migrations happen when the species range (or population area) is separated into spawning/nursery grounds and feeding grounds to take an advantage of favourable environmental conditions for the development of egg masses and juveniles and maximally exploit food resources, therefore releasing some competitive pressure between different ontogenetic stages (Nesis, 1985). Changes in environmental conditions at any ontogenetic stage may cause changes in natural mortality resulting in variability in population abundance. Various cephalopods are characterized by a wide spectrum of both diurnal and ontogenetic migrations (Boyle and Rodhouse, 2005; Nesis, 1985; Roper and Young, 1975).

The chambered *Nautilus* spp. do the shortest spatial migrations among all recent cephalopods. The animals exhibit complicated diurnal behaviour, with continuous movement and feeding at night between depths of 130 and 700 m and with some animals resting during the day at relatively shallow depths and others actively forage in the deep. There is no separation between nursery and feeding grounds, as juveniles are distributed within the same habitat as adults (Dunstan et al., 2011). Tagging studies have revealed some long-term movements of up to 150 km in 332 days by living nautiluses (Saunders and Spinosa, 1979).

Benthic species of octopods have limited migrations, generally moving no more than tens of kilometres during their whole life. The largest species, the Pacific giant octopus *Enteroctopus dofleini*, remains stationary or hiding for 94% of the time with maximum movement being 4.8 km in a 3-month period (Scheel and Bisson, 2012). In Hokkaido waters, giant octopuses make short distance offshore–inshore nondistant migrations twice a year. These movements probably coincide with active choice of optimum ambient temperature inshore, when they avoid water that is too cold (in winter) and too warm (in summer) (Rigby and Sakurai, 2004).

Cuttlefish (Sepiida) are characterized by separate feeding grounds, which are usually offshore, and the inshore spawning grounds. Their ontogenetic migrations are quite short (tens to low hundreds of kilometres) but could result in a strong seasonal variability in abundance especially in their localized spawning grounds. Dense breeding aggregations are formed by the Australian cuttlefish *S. apama* during the austral winter when mature animals converge in a highly localized area (60 ha) of rocky reef in the northern Spencer Gulf (South Australia) to breed. For the rest of the year, young and juvenile cuttlefish disperse and forage over a much wider area of the gulf (Hall and Hanlon, 2002). The European cuttlefish *S. officinalis* has extensive offshore feeding grounds around Hurd Deep (100–170 m depth) in the English Channel, where juveniles and subadults spend the autumn and winter months in deeper and warmer waters. In spring, maturing and mature adults move to their spawning grounds located along the French coasts of Normandy, with mature males arriving there about a month earlier than females. Mating and spawning occur in summer in shallow water where the warmest ambient conditions for egg development are found. In inshore waters, some adult cuttlefish might stay within a small spawning area for weeks, while others might travel some 20–35 km in 2–6 weeks during the spawning season (Bloor et al., 2013b). Mass postspawning mortality drastically reduces the biomass of cuttlefish in inshore waters until the next

spawning migration the following year (Boletzky, 1983). A similar pattern of ontogenetic migration was also revealed for the abundant Pacific cuttlefish in Japanese waters. Mature adults of *Sepia esculenta* and *Sepiella japonica* migrate to shallow bays and inlets from their offshore feeding grounds in summer to spawn and lay their eggs in the warmest time of the year (May–July) (Natsukari and Tashiro, 1991).

Squids (Teuthida) have the longest migrations among cephalopods. Among them, neritic squids of the suborder Myopsida migrate shorter distances between their spawning and feeding grounds than some large nerito-oceanic and oceanic squids of the suborder Oegopsida families Ommastrephidae and Onychoteuthidae (Nesis, 1985).

The nearshore species *Sepioteuthis* (Loliginidae) have a similar lifestyle to cuttlefish, including relatively short migrations. Southern calamari *S. australis* moves extensively within their inshore spawning grounds (30–60 km, one squid even 600 km). However, no movement was observed between the two spawning grounds separated by 25–30 km only in the southeastern part of Tasmania, Australia (Pecl et al., 2006). It means that during breeding season, an individual squid might move significantly within a habitat favourable for reproduction, but do not cross unfavourable areas from one breeding site to another.

Shelf squids of *Loligo* (and *Doryteuthis*) have longer migrations (up to several hundred kilometres) between their well-defined inshore spawning/nursery grounds and offshore feeding grounds. They also move substantial distances during foraging within their feeding grounds. European loliginids *L. vulgaris* and *L. forbesi* do not aggregate into dense migrating schools neither in their feeding nor in their spawning grounds, laying their eggs at wide range of depths between 10 and 300 m (Guerra and Rocha, 1994; Pierce et al., 1994). Other loliginids such as the southeast Pacific population of *D. gahi*, northeast Pacific *D. opalescens* and South African *L. reynaudii* disperse on their offshore feeding grounds but form dense spawning aggregations in their localized inshore spawning grounds (Sauer et al., 1992; Villegas, 2001; Vojkovich, 1998). The location of spawning sites depends on physical oceanographic dynamics with squids actively choosing areas on the shelf with bottom temperatures and dissolved oxygen concentrations, which are at optimal levels for egg development (Roberts, 2005). On the contrary, the southwest Atlantic population of *D. gahi* does not aggregate in shallow-water spawning grounds, but forms dense feeding schools offshore. The time of offshore migrations of *D. gahi* (thus its availability to predators and fishery) depends on water temperatures in their inshore spawning/nursery grounds.

Warmer temperatures induced earlier emigration, and colder temperatures delayed those emigrations. The variability in the extent and locations of *D. gahi* offshore migrations on the Falkland Shelf is determined by the location of their preferable offshore feeding habitat, the so-called transient zone that is a mixture between the shelf waters and the subantarctic superficial waters (Arkipkin et al., 2004).

As the juveniles move offshore, they start segregating by depth with females migrating deeper than males. The segregated feeding period lasts several months, with males predominating in shallower waters and females in deeper waters. After maturation, both sexes move to the inshore spawning grounds (kelp forests between 5 and 20 m depth) separately with males arriving earlier than females (Arkipkin and Middleton, 2002a).

Nektonic oegopsid squids of the families Ommastrephidae and Onychoteuthidae are highly migratory animals (Boyle and Rodhouse, 2005). The spatial structure of their ranges is usually complex with spawning, nursery and feeding grounds often located in different ecosystems (O'Dor and Coelho, 1993). Large species such as *I. argentinus*, *I. illecebrosus*, *T. pacificus* and *D. gigas* migrate thousands of kilometres between their feeding and spawning grounds during their short (usually) annual life cycle (Arkipkin, 1993; Froerman, 1986; Nigmatullin et al., 2001; O'Dor, 1983; Sakurai et al., 2002). These squids also transition vertically during diurnal migrations, rising to superficial epipelagic waters every night to feed and descending to deep mesopelagic and bathypelagic waters during daytime to rest (Hanlon and Messenger, 1996).

Nerito-oceanic squids *Illex* spp. use the waters of the polarward warm currents (Gulf Stream, Brazil Current) flowing along the continental slopes to transport their paralarvae and juveniles from the tropical/subtropical spawning grounds to temperate feeding grounds (O'Dor and Coelho, 1993). The abundance of their recruitment on the feeding grounds varies depending on the intensity, position of the stream and meandering of the current in a given year. Increased meandering of the Gulf Stream causes the enhanced shoreward transport of *I. illecebrosus* juveniles onto the shelf of Nova Scotia between 35°N and 45°N (Rowell et al., 1985). The intensity of the current determines how far downstream the juveniles of *I. illecebrosus* might be transported. In years of strong Gulf Stream intensity, the juveniles move as far as the Grand Banks to the east of Newfoundland (43–47°N); weakened Gulf Stream transport causes for recruitment to appear in Georges Bank and western part of the Nova Scotia shelf (35–42°N) (Dawe et al., 2000). Ambient temperature also determines the extent of feeding

migrations in the southwestern counterpart—*I. argentinus*. During warm years, squids penetrate almost to the southern edge of the Patagonian Shelf (54°S), whereas in cold years, they migrate only down to 45–46°S (Arkipkin, 2013). Water temperatures impacted not only the extent but also the migration routes of *T. pacificus* in the northwest Pacific. It has been shown that under a cool regime during the 1980s, migrations of *T. pacificus* were restricted to the Sea of Japan. When temperatures increased in 1989–1992, not only did biomass of the stock increased threefold, but also migration routes changed and included a new migration pattern in the Pacific side off Japan (Sakurai et al., 2002).

Several environmental factors like temperature regime shift and availability of preferred prey are believed to cause the dramatic change in the size of mature animals of the southeast Pacific Humboldt squid *D. Gigas* (Argüelles et al., 2008; Keyl et al., 2008, 2011). In the 1990s, most *D. gigas* populations consisted of small squids (<500 mm mantle length, ML) with the species range situated mainly in tropical and subtropical waters of the eastern Pacific between 30°N and 30°S. Since 2000, 2 years after the strong El Niño of 1997–1998, the average size of adult squids dramatically increased to 800–900 mm ML with simultaneous expansion of the species range to temperate and even subpolar waters of the Alaska 47°N in the north (Field et al., 2007; Zeidberg and Robison, 2007) and central Chile (43°S) in the south (Alarcón-Muñoz et al., 2008). Such an increase in adult squid size with simultaneous expansion of the species range has had important impacts on species abundance, diversity and community structure in the temperate and subpolar ecosystems of the eastern Pacific that are now under predation pressure of a large voracious predator that previously had been a less dominant member of the community.

3.3. Trophic ecology

Embryogenesis is probably the least vulnerable part of the cephalopod life cycle. Although egg masses of myopsid squids are laid on the bottom in large numbers and are easily available to potential predators, no major predation on eggs has been reported in spite of the fact that egg beds have been intensively explored by divers and ROVs in different oceans and at different latitudes. Some rare attempts of predation by benthic echinoderms and fish (Kato and Hardwick, 1975; Sauer and Smale, 1993) can probably be ignored and have little or no impact on survival of spawning products. However, eggs of some loliginids (primarily *D. opalescens*) collected in the wild might

be infested with capitellid polychaete worms (Fields, 1962; Boletzky and Dohle, 1967; Vidal et al., 2002). These worms cause the deterioration of the external egg envelope and expose the chorion of the eggs causing premature hatching and subsequent high mortality of paralarvae (Vidal et al., 2002). Zeidberg et al. (2011) found an exception to this pattern and observed that the disturbances by the worms slightly increased hatching rate, but did not provide data on paralarval survival (Vidal and Boletzky, 2004).

Among oegopsid pelagic egg masses, only those of *Thysanoteuthis rhombus* are commonly observed, and among numerous descriptions and photographs, there is no sign on possible predatory impact or mass mortality. Benthic octopod egg masses are generally well hidden from large predators in sheltered places and protected from small predators scavengers by a defensive female.

Feeding conditions are of crucial importance for cephalopod population dynamics from the early life stages in spite they still have some endogenous yolk reserves during first days after hatching while already hunting prey (Boletzky, 2003). Food availability can induce growth plasticity in paralarvae in very short time periods (Vidal et al., 2006).

Females of a sepiolid, *Euprymna tasmanica*, maintained in captivity on a low ration produced smaller egg clutches, consisting of smaller eggs and exhibiting higher embryo mortality rates than females fed *ad libitum* (Steer et al., 2004). Loliginid squid hatchlings living in better foraging conditions and at lower temperatures utilize yolk more slowly and so conserve their reserves longer (Vidal et al., 2002).

Cannibalism is an important element in the life cycle of many squids. It has been reported for many cephalopods in genera *Illex*, *Octopus*, *Sepia*, *Dosidicus*, *Onychoteuthis*, *Todarodes*, *Ommastrephes* and *Loligo* (Ibáñez and Keyl, 2010 and references within). In nature, cannibalism increases when prey availability decreases and larger squids are more cannibalistic than smaller. In captivity, it takes about 3 days of starvation for *I. illecebrosus* squid to induce cannibalism. Selective removal of smaller animals not only decreases stock size but also gives a false impression of faster somatic growth when size-frequency data are analysed (Arkipkin and Pérez, 1998; O'Dor and Dawe, 2013).

Generally, cannibalism is density-dependent and acts as a tool regulating population biomass within an optimum level. Years of high density of the schooling squid *I. illecebrosus* were associated with high rates of cannibalism in this species, though it is apparent that the shift to cannibalism does not merely reflect opportunity but is related to depletion of other suitable prey

types (Dawe, 1988). Because of density dependence, cannibalism also increases in artificial aggregations of ommastrephid squids in light fields of a fishing boat (Zuev et al., 1985). In octopuses *Enteroctopus megalocyathus* and *O. vulgaris*, a higher frequency of cannibalism has been reported in areas and periods where this species is more abundant (Ibáñez and Chong, 2008; Oosthuizen and Smale, 2003).

Easiness with which cephalopods switch to cannibalism might help populations survive episodes of low food availability. However, cephalopods generally have broad feeding spectra that are very flexible in both prey species composition and prey size, so food availability likely is not a very common problem. During their sudden explosion in number, squids normally have detrimental impact on potential food sources (Alarcón-Muñoz et al., 2008; Laptikhovsky et al., 2013) during a range of years rather than die out of starvation.

Another factor impairing well-being of cephalopods and making them more susceptible to predators and both biotic and abiotic stressors—and thus influencing cephalopod population variability—is parasite load. Cephalopods are hosts to a diverse assemblage of parasites and symbionts including potentially pathogenic organisms such as viruses, bacteria, fungi, protozoans, nematodes, monogeneans, digeneans, cestodes, acanthocephalans, polychaetes, hirudineans, crustaceans, copepods and isopods (Hochberg, 1983). Quantifying the incidence of diseases in cephalopod populations and impact on its dynamics may be difficult because diseased and dead animals (especially as they are soft-bodied) are likely to be rapidly removed by predators or scavengers (Pierce et al., 2010). Some parasites, such as the copepod family Pennellidae, might have such negative impact on squid condition that they cause important losses in commercially important stocks (Pascual and Guerra, 2001; Pascual et al., 1998, 2005, 2007).

Cephalopods, particularly schooling squids, are important prey of many large marine predators, sometimes the most important prey for species including pilot whales and sperm whales (Clarke, 1996; Piatkowski et al., 2001; Santos et al., 2001; Smale, 1996). Thus, annual cephalopod abundance might have a strong impact on populations of predators. However, predators, though possibly being the most important factor regulating squid population dynamics (together with fisheries), should probably not be counted as a major factor responsible for the fluctuation of populations in commercially exploited cephalopods. In the virtual absence of whaling, cetacean populations are probably stable over annual and possibly decadal timescales. There has been no documented case of top-down control, when changes in

predator abundance have been correlated with cephalopod prey abundance. However, when the predator is a cephalopod with highly fluctuating population biomass and distribution, top-down control has been observed. *I. argentinus* preying on *D. gahi* in Falkland Islands' waters have a negative impact on final cohort biomass. However, this inverse relation might be also (at least partially) explained by competition for the same food sources (Arkipkin and Middleton, 2002b).

3.4. Fisheries

Fishing pressure is an important source of variability in any of the commercially fished stocks. Direct (targeted) fishing as well as indirect (by-catch) fishing may overexploit and therefore deplete the stocks as has been reported for finfish fisheries worldwide (Pauly et al., 1998). Alternatively, some stocks may also increase in abundance if main predators have been fished out or the competitive pressure has been relieved by fishing out the main competitor and therefore vacating the econiche (Boyle and Rodhouse, 2005; Caddy and Rodhouse, 1998).

Among cephalopods, the chambered *Nautilus* spp. are characterized by low growth rates, relatively slow maturation and low fecundity, and they are especially vulnerable to overfishing. The growing market demands for their ornamental shells have resulted in up to 80% declines in reported catch per unit effort (CPUE) from 1980 to the present time in the Philippines, where the fishery became unsustainable (Dunstan et al., 2010). The current status of *Nautilus* populations in various areas of the tropical Indo-West Pacific is being estimated in order to include them on the list of Appendix-II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (De Angelis, 2012).

Other commercial species of octopods, cuttlefish and squids are short-living having high growth rates and high fecundity. Their populations have evolved to withstand substantial variations in abundance. Until the turn of the century, it seemed that only a few species of coleoid cephalopods had been locally overexploited, despite heavy fishing pressure on many stocks (Boyle and Rodhouse, 2005). More recently, annual world cephalopod catches reached 4.3 million t in 2007 but decreased to 3.6 million t in 2010, according to FAO statistics (FAO, 2011), having increased steadily from around 600,000 t in 1950 (Jereb and Roper, 2010).

Several collapses in squid fisheries (*I. illecebrosus* in the northwest Atlantic or *Todarodes sagittatus* in the northeast Atlantic) left unexplained what had been the main contributor of such a collapse—fishery or environmental

conditions or probably both. The fishery for the short-fin squid *I. illecebrosus* developed quickly in the second half of the 1970s, peaking at the annual catch of >100,000 t in 1979. After only 5–6 years of intense fishing, it collapsed in 1983 to <1000 t per year and has never recovered to its earlier size. One of the possible reasons of such a collapse was suggested to be sequential fishing pressure on various seasonal cohorts of the squids (first the most abundant winter-spawning cohort and then on the spring spawning cohort) that impacted the general population structure (O'Dor and Coelho, 1993). Changes in position of the main flow of the Gulf Stream relative to the shelf edge that happened in 1980s also contributed to the decrease in juvenile transport of the winter-spawning cohort to their common feeding grounds in temperate waters of Canada (Dawe et al., 2000). Similarly, overfishing of the winter-spawning cohort of *T. pacificus* caused the southern shift of the commercial fleet to fish off the autumn-spawning cohort; this dramatically changed the population composition of the species (Nakata, 1993). The autumn-spawning cohort may have acted as a reservoir that buffered the effect of fisheries until it was itself exploited.

Periodic intrusions of large quantities of the arrow squid *T. sagittatus* into the Norwegian Sea have resulted in being targeted by trawling fleets, with a maximum annual reported catch in Norwegian waters of ~18,000 t in 1982–83. However, possibly partially due to extensive exploitation, partially to changes in the environment, the commercial aggregations disappeared from that area after 1988 (FIGIS, 2011). A similar phenomenon has been reported for *L. forbesi* in the Rockall Bank area, (the United Kingdom, northeast Atlantic, 54–58°N, 12–17°W) (Pierce et al., 1994).

Fishing might also be sex-selective, removing the more active sex from their spawning grounds. In southern calamari *S. australis*, the commercial fishery alters the population structure on the spawning beds by removing the large males first and leaving relatively large numbers of small males and females. Sex-ratio studies on the same spawning grounds over several years suggested that progressively longer closures allowed time for more males to accumulate on the spawning beds, therefore maintaining the natural sex ratio during the spawning season (Hibberd and Pecl, 2007). Size selectivity in a jig fishery has been also recorded for *I. argentinus* in the southwest Atlantic. It was found that sizes of both sexes caught by jigging were 7 mm ML (males) and 12 mm ML (females) larger on average than those caught by the trawlers over the same time. Moreover, fishing method may also affect the proportions of mature squids in the population, that is, maturity-selective. The artificial lit area created by jigging vessels at night might cause

the differences in behavioural responses of immature and mature squids reacting to the lure. Proportions of mature squids caught by jiggers were greater than those caught by trawlers by 0.8% in males and 5.1% in females (Koronkiewicz, 1995). Fishing effort targeting inshore spawning aggregations of neritic species such as loliginid squids may cause population declines due to behavioural disruption or insufficient escapement of prespawning individuals (Hanlon, 1998; Iwata et al., 2010).



4. FORECASTING AND ASSESSMENT

Global fishery landings of cephalopods have increased over the past few decades, while fishery- or ecosystem-level assessments of many stocks have been undertaken infrequently or not at all (Anderson et al., 2011; Boyle and Rodhouse, 2005; Hunsicker et al., 2010; Payne et al., 2006). Rapid growth and a short lifespan render cephalopod fisheries difficult to assess and manage (Boyle and Rodhouse, 2005; Payne et al., 2006; Pierce and Guerra, 1994). Most cephalopod species targeted by fisheries are short-lived, usually with a 1-year life cycle and a semelparous life history strategy, with a single spawning soon followed by death (Boyle and Rodhouse, 2005). Individuals targeted in 1 year do not survive until the fishing season in the next year, meaning that even though the abundance in the current year may be relatively high, the stock size in the next year may decline greatly, due to high variability in abundance between generations. Boyle and Rodhouse (2005) noted that the effect of environmental variables on abundance of annual species at multiple scales is the main reason for difficulties in establishing reliable stock assessment and management procedures. While a greater understanding of environmental influences on recruitment is frequently recommended for improved management of squid fisheries (Agnew et al., 2005; Boyle and Rodhouse, 2005), knowledge of the relationships between squid distribution and environmental variables and the associated effects on squid availability to fisheries and assessment surveys also has the potential to improve fisheries management (Ish et al., 2004; Schön et al., 2002). An understanding of environmental effects on population dynamics and species distributions could be used to appropriately incorporate data into stock assessments to support cephalopod fisheries management. Environmental processes introduced into stock assessments generally include those that affect population dynamics in the form of recruitment, with only recent attention to spatially explicit effects on distribution and migration patterns (Keyl and Wolff, 2008). Extensive research

has been conducted on environmental effects on fish and cephalopod distributions (Fréon et al., 2005; Pierce et al., 2008; references therein). Studies of environmental effects on spatial and temporal distribution of marine species can inform stock assessment by defining stock structure at larger scales (Link et al., 2011) and identifying effects on availability to fisheries or assessment surveys (Brill and Lutcavage, 2001; Fréon and Misund, 1999; references therein). Approaches that incorporate environmental factors are identified in the following sections.

4.1. Stock identification and structure

For the purposes of fisheries management and stock assessment, populations or segments thereof are assumed to be a single unit stock within spatial boundaries in which the components of production (e.g. recruitment and mortality) are considered spatially homogenous (Cadrin et al., 2013). Cephalopod stock identification is complicated by taxonomic/systematic confusion along with variable abundance and distribution due to life history traits and environmental factors (Boyle and Boletzky, 1996). For management and assessment purposes, stock boundaries are often delineated based on territorial boundaries or the range of fisheries or resource assessment surveys rather than the distributional range of a species (Cadrin et al., 2013), and cephalopods are no exception. For example, the long-fin inshore squid *D. pealeii* is distributed in continental shelf and slope waters of the northwest Atlantic Ocean from Newfoundland to the Gulf of Venezuela but is considered a single unit stock within a much smaller area from Cape Hatteras north to Georges Bank, which encompasses most of the fishery and area routinely surveyed (NEFSC, 2011; Roper et al., 1984; Shaw et al., 2010). Since the comprehensive review by Boyle and Boletzky (1996), many advances have been made in tagging and genetic techniques useful for cephalopod stock identification and understanding stock structure (Semmens et al., 2007; Shaw et al., 2010), and a greater understanding has been attained regarding environmental effects on distribution and abundance (e.g. Pierce et al., 2008 and this chapter). While the remainder of this section is devoted to cephalopod stock assessment methods, it is important to recognize the importance of stock identification and the associated research as a prerequisite to assessment.

4.2. Stock assessment

For the sustainable fishery of cephalopods, most of which are considered to be annual species, it is important to determine the appropriate level of fishing

and the relationship between stock abundance and recruitment for each species (Boyle and Rodhouse, 2005; Caddy, 1983; Pierce and Guerra, 1994). Basically, stock assessment and forecasting for cephalopod species are methods widely used for fish stocks. However, estimating and forecasting cephalopod abundance using fishery-dependent data such as cohort analysis have had limited success because of their fast growth, maturing in less than 1 year and relatively short period of time for recruitment, although age-structured models are considered to be useful for forecasting stock size precisely (Boyle and Rodhouse, 2005; Caddy, 1983; Pierce and Guerra, 1994). Although some octopods live more than 3 or 4 years, it is considered to be difficult to apply age-structured models for octopods in the same manner as squids due to uncertainty in age estimation because their growth patterns and maturation process are highly variable and tend to be affected by environmental conditions and food availability. With relatively few exceptions to date (e.g. Royer et al., 2002), it has been most common to adapt simple population dynamics models for cephalopod stocks that do not require age composition data (Boyle and Rodhouse, 2005; Caddy, 1983; Pierce and Guerra, 1994). Generally, this requires assessment data (including catch statistics) and suitable models to forecast fisheries stocks, which are varied in the targets of what period should be forecast (e.g. stock size in the next week, next month and next year).

4.3. Assessment timescales/timing

Cephalopod stock assessment methods can be generally categorized based on the timing of their application relative to the fishing season: preseason, in-season and postseason (Boyle and Rodhouse, 2005; sensu Pierce and Guerra, 1994). Preseason assessment and forecasting usually use data obtained from experimental surveys on the individuals in the prerecruit stages. Preseason assessments are useful for forecasting stock size and proper management for cephalopod stocks of which life span is usually 1 year and all targets for fishing are composed of newly recruited individuals. In the *Illex* and *Doryteuthis* fisheries around the Falkland Islands, fishing effort is set based on the results of preseason assessments and previous experience of recruitment variability (Rodhouse, 2001). However, preseason assessments usually require special sampling gears to catch prerecruit stages, and it is difficult to obtain enough time to survey just before fishing seasons open. Preseason assessments are often conducted by using experimental methods like mid-water trawl nets to observe the abundance of cephalopods in the juvenile

stage (Brunetti and Ivanovic, 1992; Kawabata et al., 2006; Kidokoro et al., 2014) and plankton nets to be used for paralarval distribution surveys (Bower et al., 1999a; Goto, 2002; Murata, 1989; Yamamoto et al., 2007). Stock sizes are forecasted based on the suitable models (e.g. growth–survival model and correlation models) with the results of preseason assessment (e.g. juvenile abundance, paralarval and juvenile densities).

In-season assessment and forecasting methods generally use data on recruited individuals from commercial fisheries. In most cases, changes (usually declines) in stock abundance during a fishing season are monitored based on CPUE of commercial fisheries. Data are collected at high temporal resolution (daily) and abundance is modelled primarily with depletion models (see Section 4.4). In-season assessments include abundance estimates updated within a fishing season and compared to reference points to inform adaptive management measures such as fishery closures (Walters and Martell, 2004). Successful adaptive management systems depend upon the accumulation of experience regarding spatiotemporal patterns of abundance and impacts of regulatory measures (e.g. fishery openings) and are vulnerable to environmentally driven shifts in abundance or distribution (Walters and Martell, 2004). Most commercially important cephalopods (e.g. ommastrephid squids) are highly migratory species; therefore, in-season assessments are only used for a few special examples, such as the *Illex* fishery around the Falkland Islands (Arkhipkin et al., 2013; Basson et al., 1996; Rosenberg et al., 1990) and *T. pacificus* fisheries (Okutani, 1977). However, in-season assessments and knowledge about seasonal shifts in fishing grounds with migration patterns are useful for forecasting catches at individual fishing grounds, for example, in the Japanese *T. pacificus* fisheries (Kasahara, 1978; Kidokoro et al., 2010; Murata, 1989; Okutani, 1983). Postseason cephalopod stock assessments rely on data on former generations, generally using one or more of the methods described in the following section. It is also important to note that many cephalopod fisheries are assessed with multiple methods, conducted at some or all of the scales identified in the preceding text (e.g. Arkhipkin et al., 2013; Roa-Ureta and Arkhipkin, 2007).

4.4. Stock assessment methods

4.4.1 Surplus production models

The surplus production model, also referred to as a biomass dynamic model, is essentially the simplest stock assessment model. In theory, the surplus production model estimates the biomass of a resource for the year $y+1$ as the

biomass of the year γ plus the surplus production (an aggregated parameter of the recruitment and the growth) and minus the catch (Graham, 1935; Schaefer, 1954). However, the surplus production model presents a very simplified view of the population dynamic; age or spatial structure of the population is not considered. In addition, fitting a surplus production model is not easy, and the interpretation of the maximum sustainable yield can be difficult because the model assumes that the stock is at the equilibrium, a situation rarely encountered (Hilborn and Walters, 1992), and that has sometimes led to the overestimation of a stock. Finally, the surplus production model assumes that the recruitment is highly density-dependent, a situation rarely encountered in cephalopod species (Pierce and Guerra, 1994). Surplus production models have the advantage of quick application with very few data but give only mid- to long-term objectives in a stable environment, while cephalopod stocks are known to be highly variable resources and their abundance is generally linked to the environmental conditions (e.g. Pierce et al., 2008; Section 3).

Despite the aforementioned limitations, surplus production models have been adapted for cephalopod fisheries with some success. Some surplus production models have been developed to assess cephalopod stocks from the Saharan Bank, results of which indicated that octopus, squid and cuttlefish stocks in this area were overexploited (Bravo de Laguna, 1989; Sato and Hatanaka, 1983). More recently, a surplus production model with environmental effects was fitted to assess the *O. vulgaris* stock off Senegalese coast (Laurans et al., 2002). Results highlighted that the wind speed parallel to the shore that generates upwelling has a significant effect on the octopus abundance. A Fox surplus production model (Fox, 1970) was also fitted to assess the English Channel cuttlefish (*S. officinalis*) and the English Channel squid (*L. vulgaris* and *L. forbesii*, which are not distinguished by the fishermen) stocks in the framework of a bioeconomic modelling of the English Channel fishery (Ulrich et al., 2002). A surplus production model with quarterly time step was fitted, using fishery-dependent and fishery-independent abundance indexes, to assess *D. pealeii* (Cadrin and Hatfield, 1999). Recent assessments of *D. pealeii* have taken into account removals from the predation to define new reference points that are significantly different from those defined without accounting for predation (Moustahfid et al., 2009; NEFSC, 2011). Quetglas et al. (2013) studied combined effects of fishing and climate (using NAO effects) by fitting a surplus production model on several demersal species including *O. vulgaris*, *L. vulgaris* and *S. officinalis*.

4.4.2 Depletion method

The depletion method derived from [Leslie and Davis \(1939\)](#) and [De Lury \(1947\)](#) is the stock assessment methodology commonly used to assess cephalopod stocks, and it is considered as the least expensive methodology. In theory, this model estimates the consequences of the removal of individuals (natural or fishing mortality) on the population and determines the size of the population without fishing activity ([Hilborn and Walters, 1992](#)). The basic method ([Leslie and Davis, 1939](#)) uses the accumulated catch and the assumption of a closed population. Some variants use effort data and have been adapted to open populations with recruitment and natural mortality ([Rosenberg et al., 1990](#)). These methodologies are suitable to perform a real-time modelling of the data collected in a short period (in particular when exploitation does not exceed 1 year, they are favoured to assess cephalopod stocks; [Boyle and Rodhouse, 2005](#)). Its main limitation is the assumption of a population randomly distributed with a constant catchability, an important assumption rarely encountered in cephalopod stocks ([Pierce and Guerra, 1994](#)).

The depletion method has been applied to assess the Humboldt squid *D. gigas* stock in the Gulf of California ([Ehrhardt et al., 1983](#)). [Morales-Bojórquez et al. \(2001b\)](#) performed a stock assessment modelling three different fleets exploiting Humboldt squid in the same area and enabled the estimation of reference points. A modified standard Leslie–DeLury method (integrating a natural mortality parameter) was suggested to model the squid species exploited around the Falkland Islands with the proportional escape-migration as a management tool ([Beddington et al., 1990; Rosenberg et al., 1990](#)) and applied to *I. argentinus* ([Basson et al., 1996](#)). The modified standard Leslie–DeLury approach was then improved to assess the *D. gahi* stock by adding a migration parameter ([Agnew et al., 1998a](#)). This migration parameter was first introduced to improve the assessment of *D. pealeii* in the northwest Atlantic, which showed variations in abundance related to migration patterns ([Brodziak and Rosenberg, 1993](#)). Depletion estimates were then used to assess European squids *L. forbesii* and *L. vulgaris* ([Royer et al., 2002; Young et al., 2004](#)). A trial to assess the English Channel cuttlefish stock using the depletion method was carried out by [Dunn \(1999\)](#) using the UK fishery landings, which represents approximately a third of the total landings in the English Channel. Most recently, a state-space modelling framework was investigated for a DeLury depletion model applied to the *O. vulgaris* stock exploited off Morocco ([Robert et al., 2010](#)), and

[Roa-Ureta \(2012\)](#) extended the depletion approach to account for the several major in-season recruitment pulses occurring in the Falklands Islands *D. gahi* fishery.

4.4.3 Age-structured models

The virtual population analysis (VPA) is the most widespread method to assess long-lived finfish stocks in developed countries ([Hilborn and Walters, 1992](#)). In a VPA, the stock is considered to be composed of several annual cohorts. The number of individuals alive in each cohort is estimated by performing a back calculation from the last age class to the first one by adding the number of individuals lost to fishing and natural mortality during a year to the number of individuals at the end of the year to estimate the number of individuals at the beginning of the year. It is sometimes called cohort analysis because each cohort of the stock is analysed and followed separately from the other cohorts living at the same time in a given stock. In cephalopod stocks, as species have a short life cycle (generally 1 or 2 years), the VPA is generally implemented on a monthly basis and using microcohorts ([Jouffre et al., 2002; Royer et al., 2002, 2006; Thiaw et al., 2011](#)).

[Ehrhardt et al. \(1983\)](#) applied this methodology to assess the Humboldt squid *D. gigas* stock in the Gulf of California with microcohorts defined according to a polymodal decomposition of the length–frequency. VPA was also applied to the Senegalese *O. vulgaris* stock using age classes first defined using tagging methodology to estimate the growth rate ([Domain et al., 2000](#)) and then using landings split in 10 commercial categories in the fishery industry ([Jouffre et al., 2002; Thiaw et al., 2011](#)). VPA therefore enabled an estimation of the fishing closure effect on the exploitation of the stock ([Jouffre et al., 2002](#)), and the environmental and fishing effects on the cohorts were then established ([Thiaw et al., 2011](#)). VPA has also been used to assess stocks of the English Channel loliginid squids ([Royer et al., 2002](#)) and northwest Atlantic *D. pealeii* ([Cadrin and Hatfield, 1999](#)) indicating that exploitation levels of these resources were above the optimum at the time. In loliginid squids, length–frequency is not the most suitable tool to define monthly age classes but is used for practical reasons. Indeed, age determination based on statolith rings ([Challier et al., 2005b, 2006b](#)) is time-consuming and cannot be routinely implemented for a stock assessment trial. Further analysis suggested the introduction of interindividual growth variability into the cohort analysis ([Challier et al., 2006a](#)). VPA was also applied as a trial to the English Channel cuttlefish stock ([Royer et al., 2006](#)) to estimate fishing impact on the studied cohorts and interactions between fishing

fleets involved in the cuttlefish exploitation in the English Channel (mainly trawlers and trappers). As in the loliginid squid case, estimating age classes using statolith rings is feasible until the age of 240 days (Bettencourt and Guerra, 2001) but time-consuming and was mainly used to explore the recruitment period (Challier et al., 2002, 2005a). However, at ages greater than 240 days, no tool is currently able to estimate monthly age of the cuttlefish and length-frequency is the only suitable methodology. An age-based cohort analysis was developed to assess *I. illecebrosus* (Hendrickson and Hart, 2006), primarily to estimate natural mortality, particularly during the spawning season when this mortality increases greatly.

4.4.4 Two-stage models

When the data are not accurate enough to implement a VPA but are accurate enough to distinguish a recruitment period and a fully recruited phase (Collie and Sissenwine, 1983), the two-stage model can be considered as a solution and can give consistent results with a VPA fitted with unsuitable age data (Mesnil, 2003). The model has also the advantage to be able to be fitted using several time series (Roel and Butterworth, 2000) and can be implemented using indifferently numbers or biomass. In theory, the population is modelled from the recruited stage when abundance is estimated by adding the recruitment strength to the fully recruited individuals. According to Collie and Sissenwine (1983) and Mesnil (2003), the population dynamics can be modelled using the following equation:

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

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 in number of recruits at the beginning of the year t , C_t is the catch in number during the year t , M is the instantaneous natural mortality rate assumed to be equal for the different stages and τ is the fraction of the year when the catch is assumed to occur as a pulse. An alternative version of the model exists in biomass and uses an aggregated instantaneous growth and natural mortality parameter (Gras et al., 2014).

The two-stage model is often used to assess invertebrate stocks (Cadrin et al., 1999; Collie and Kruse, 1998; Conser, 1991; Conser and Idoine, 1992; Zheng et al., 1997). In cephalopod stocks, the first trial was made on the chokka squid (*L. reynaudii*) stock exploited since the 1980s (Roel and Butterworth, 2000) off South Africa. It was then updated by adding

process error using Bayesian methodology to the observation error (Glazer and Butterworth, 2006). The two-stage model was also fitted to assess the English Channel cuttlefish using four different abundance indexes coming from both fishery-dependant and fishery-independent data and enabled to highlight a correlation between the environmental conditions encountered during the early life stages and the recruitment strength that occurs at 1 year old (Gras et al., 2014). An application software was then developed to perform a routine assessment by the International Council for the Exploration of the Sea Working Group on Cephalopod Fisheries and Life History.

4.5. Forecasting methods and general/empirical models

Stock sizes can be forecasted based on the suitable models (e.g. growth–survival model and correlation models) with the results of preseason assessment conducted by using experimental methods like midwater trawl nets to observe the abundance of cephalopods in the juvenile phase (Brunetti and Ivanovic, 1992; Kawabata et al., 2006; Kidokoro et al., 2014) and plankton nets to be used for paralarval distribution surveys (Bower et al., 1999a; Goto, 2002; Murata, 1989; Yamamoto et al., 2007). For the Japanese *T. pacificus* fisheries, paralarval surveys have been conducted for over 40 years (Goto, 2002; Murata, 1989; Okutani and Watanabe, 1983). In the original plan, these surveys were conducted in order to forecast the stock size in the next year. However, the paralarval densities obtained in these surveys had weak power to predict the stock size in the next year while appearing highly related with the spawning stock size (escaped population number) in the former generation (Goto, 2002; Murata, 1989). These results meant that paralarval densities have almost the same power to forecast stock size in the next year as the forecasting methods based on spawner–recruitment relationships because survival rate in the prerecruit stages is highly variable. If cephalopod prerecruit abundance can be precisely estimated just before a fishing season opens, stock size can be estimated by the abundance of prerecruits using a simple model (e.g. proportional model). Surveys targeted for prerecruit abundance using midwater trawl nets have been conducted in the Japanese *T. pacificus* fisheries for a decade (Kidokoro et al., 2014). Midwater trawl surveys for the quantitative assessment of oceanic cephalopod populations are likely to provide serious underestimates of population density as well as biased size–frequency and species composition (Boyle and Rodhouse, 2005; Wormuth and Roper, 1983), resulting mainly from net avoidance. Therefore, the target of the midtrawl surveys for *T. pacificus* is

limited in the individuals ranging mainly 3–10 cm ML size class, which are not the stages with strong swimming power (Kidokoro et al., 2014). However, net avoidance rate remains unclear, so stock size is not quantified using data obtained in these surveys. Instead, stock size is shown as an index (e.g. average individuals/tow) obtained in these surveys. The relationship between the results of preseason assessment and stock size of recruits may not be proportional because these preseason assessments usually contain large observation errors. In the example of *T. pacificus* assessments, this relationship is fitted with a linear model with large intercept (Kidokoro et al., 2013). Although there are some problems and difficulties in forecasting methods based on preseason assessments, these methods have the advantage that they do not require historical data, which can be a useful feature for newly assessed cephalopod stocks.

Data from in-season assessments and knowledge about seasonal shifts in fishing grounds with migration patterns can be used to forecast catches on individual fishing grounds. In *T. pacificus* fisheries, detailed migration patterns have been examined for a long time because of the need to forecast catch condition at each fishing ground (Kasahara, 1978; Kidokoro et al., 2010; Murata, 1989; Okutani, 1983). Fishing grounds of *T. pacificus* shift seasonally according to migration routes (Figure 2.13). Therefore, forecasting methods for the catches at each fishing ground have been examined by the relationship among catches in each fishing ground and relationship between

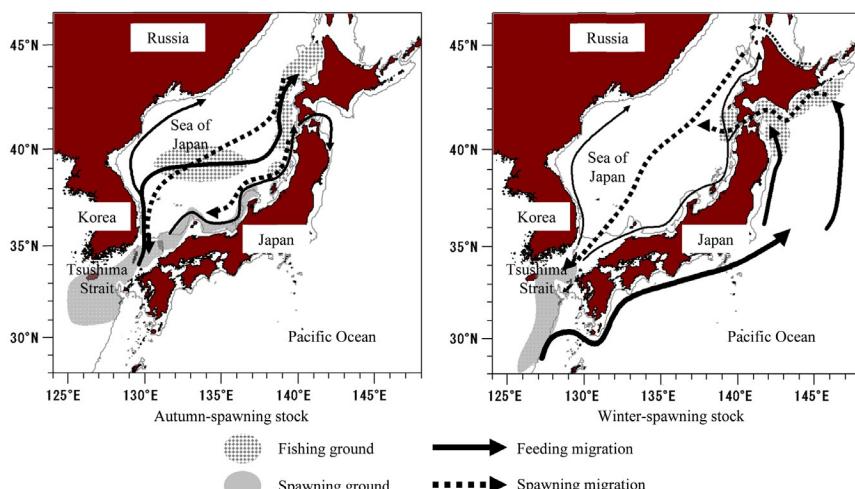


Figure 2.13 Schematic diagrams of the migration routes of *T. pacificus* autumn cohort and winter cohort. Modified from Kidokoro et al. (2010).

oceanographic conditions and CPUE (Kasahara, 1978). The site of fishing grounds of jigging fisheries and their oceanographic conditions are able to be monitored by the satellite images (Kiyofuji and Saitoh, 2004; Rodhouse et al., 2001), so it may be easy to understand the distribution area of squids, which is highly related with fishing grounds of squid jiggers. The ocean dynamics models (e.g. Regional Ocean Modeling System <http://www.myroms.org/>; Research Institute for Applied Mechanics Ocean Model <http://dreams-i.riam.kyushu-u.ac.jp/vwp/>) enable forecasts of oceanographic conditions at high resolution (mainly temperatures), which has become widely applied in fisheries. Based on these methods, shifts in fishing grounds can be forecasted in the next week or next month (Figure 2.14), with knowledge about the relationship of the distribution of cephalopods species to oceanographic conditions. Such forecasts of the distribution of fishing stocks (Figure 2.14) are considered to be useful for fishers to search fishing grounds at low cost.

Reliable spawner–recruitment relationships are quite important and useful for stock forecasting and management of cephalopod stocks. However, there is no clear relationship between spawning stock abundance and subsequent recruitment in cephalopod stocks (Basson et al., 1996; Pierce and Guerra, 1994; Uozumi, 1998). Annual variability in oceanographic conditions causes recruitment variability (e.g. Dawe et al., 2000; Waluda et al., 2001a), which leads spawner–recruitment relationships to be unreliable. In some cases, cephalopod spawner–recruitment relationships have been fitted into Ricker (1975) and Beverton and Holt (1957) models for forecasting recruitment in the next year (Agnew et al., 2000; Kidokoro, 2009). However, estimation parameters in these nonlinear models using spawner–recruitment data usually contain statistical problems that are mainly derived from observation errors in the explanatory variables (Walters and Martell, 2004). These problems lead to a tendency for stock size to be overestimated particularly in the case of low spawning stock size, which tends to mislead stock management strategies (Walters and Martell, 2004). State-space models that can be used to estimate both process and observation error may have promise for parameter estimation in stock dynamics models such as spawner–recruitment relationships (Bolker, 2008).

Empirical models based on oceanographic conditions data are often used to forecast recruitment strength for cephalopods, particularly for ommastrephid species. In the empirical models, recruitment strength is usually forecasted based on the oceanographic indexes that are often available as a long time series. Although these empirical models may be useful,

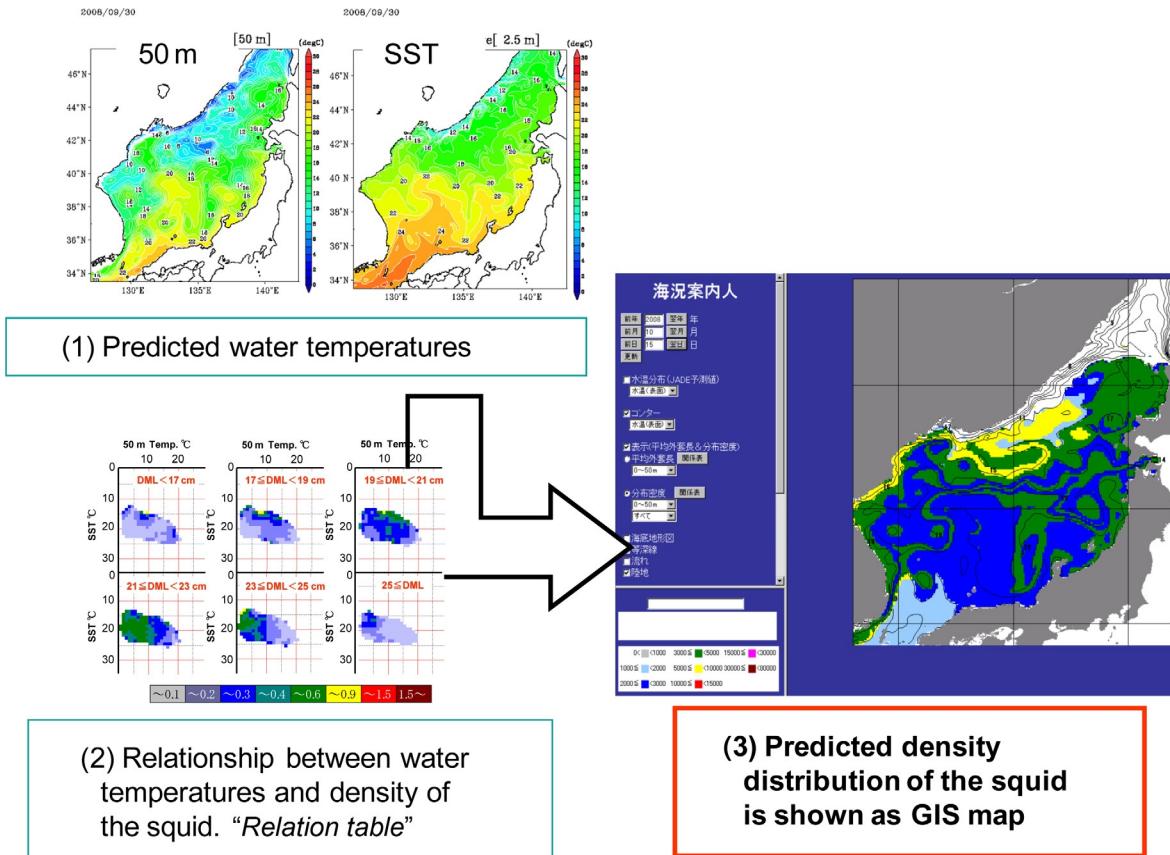


Figure 2.14 Forecasting system for distribution of *T. pacificus* in the Sea of Japan. In this system density distribution of *T. pacificus* (number of individuals/km²) are water temperatures of sea surface and 50 m deep which are forecasted based on data assimilation ocean dynamic model (<http://jade.dc.affrc.go.jp/jade/>). Density distribution of *T. pacificus* (number of individuals/km²) is able to be forecasted within the next month and can use freely through net work (<http://jsnfrf.fra.affrc.go.jp/shigen/kaikyo2/>).

mechanisms explaining how these oceanographic conditions influence recruitment variability are necessary for reliable forecasting. Recruitment strength for *D. gigas* is highly correlated with ENSO events. Commercial catches of *D. gigas* off Peru tend to be small in the year of El Niño when primary productivity tends to be low (Waluda and Rodhouse, 2006). These features are useful to apply forecasting methods for recruitment strength. Distribution ranges (Field et al., 2007) and body size (Keyl et al., 2011) varied largely during the recent 20 years along with recruitment variability in *D. gigas*, and it is important to determine how oceanographic conditions affect such changes.

Oceanographic conditions around spawning grounds are often identified as a contributing factor in stock size fluctuations of *Illex* species (O'Dor, 1998b; Waluda et al., 2001a) and *T. pacificus* (Okutani and Watanabe, 1983; Sakurai et al., 2000). Recruit success of *I. illecebrosus* is considered to be related to larval transport by the Gulf Stream (Dawe et al., 2000, 2007), which can be an indicator for forecasting recruitment strength. Stock size fluctuations of *T. pacificus* are hypothesized to be influenced by favourable conditions for spawning grounds inferred by the ideal water temperature as estimated with rearing experiments (Sakurai et al., 1996). This hypothesis was verified by comparison with the relationship between stock size and variations in oceanographic conditions and inferred spawning grounds (Rosa et al., 2011; Sakurai et al., 2000) and may be particularly useful for forecasting stock size at decadal or interdecadal timescales.

In the Japanese stock management procedure for *T. pacificus*, annual total allowable catch (TAC) is set based on an allowable biological catch (ABC), which is calculated from the fishing mortality (F_{lim}) and forecasted stock abundance in a target year. In this procedure, a spawner–recruitment relationship is used to forecast stock size in the target year, which is composed of new recruitment only. In the spawner–recruitment relationship for *T. pacificus*, proportional models were applied to forecast recruits and estimate a biological reference point (F_{med}) while avoiding overestimation derived from biases pointed out by Walters and Martell (2004). In a proportional model in which a density-dependent effect is ignored, estimates of stock size are going to be relatively high (sometimes unreliable) but are considered to be safer using parameters estimated from proportional models than using those from density-dependent models (Hiramatsu, 2010).

Decadal or interdecadal changes in environmental conditions are assumed to influence stock status and spawner–recruitment relationships of *T. pacificus* (Kidokoro, 2009; Kidokoro et al., 2013; Sakurai et al.,

2000; Yamashita and Kaga, 2013). Therefore, the parameters used in spawner–recruitment relationships are estimated from data collected since 1990 following an apparent regime shift (Hare and Mantua, 2000), but when the current regime changes, such parameters should be revised accordingly. Unfortunately, the exact mechanism with which changing environmental conditions influence the stock size of *T. pacificus* remains unclear, and it is difficult to predict when regime shifts might occur. However, the results of investigations show that spawning grounds (Goto, 2002), migration routes (Kidokoro et al., 2010; Nakata, 1993) and body size (Takayanagi, 1993) all show changes that coincide with changing stock size. These changes are assumed to be closely connected with changing environmental conditions (e.g. regime shift). Therefore, forecasts of oceanographic conditions that may be favourable or unfavourable for stock size based on changes in ecological traits may be easier to observe relative to estimation of stock size itself. It remains necessary to understand the mechanism with which these ecological changes affect stock size in order to allow better forecasts of future trends in stock size. However, caution must be exercised when deriving empirical stock–environment relationships in the absence of long time series (Solow, 2002).

In their in-depth review of cephalopod stock assessment methods, Pierce and Guerra (1994) noted the promise of time-series models incorporating environmental information and multispecies models incorporating trophic dynamics. Georgakarakos et al. (2006) applied autoregressive integrated moving average techniques, artificial neural networks and Bayesian dynamic models incorporating environmental factors to forecast squid landings in Greek waters. Using a static mass-balance model, Gaichas et al. (2010) demonstrated the utility of food web-derived predation information to inform stock assessments of incidentally caught squids for which predation mortality exceeds fishing mortality.

4.6. Fishery-dependent assessment data

Stock assessment methods incorporate several types of data, including abundance indexes and biological data (e.g. age, length and maturity), which can be collected from fisheries (fishery-dependent) or fishery-independent methods such as surveys (Hilborn and Walters, 1992). Many assessed cephalopod fisheries incorporate data from multiple sources. For example, the northwest Atlantic *D. pealeii* and *I. illecebrosus* fisheries are assessed using fishery-independent resource assessment trawl survey data, supplemented by a host of fishery-dependent data, including standardized landings per unit

effort (LPUE), size composition and discard data collected on board commercial fishing vessels (Johnson, 2011; NEFSC, 2011). Daily catch reports, fisheries observer data and electronic logbook data are all incorporated into assessments of *D. gahi* and *I. argentinus* off the Falkland Islands (Arkhipkin et al., 2013).

4.6.1 Landings/catch data

To fit a population dynamics or stock assessment model, a prerequisite is to collect suitable abundance indexes via fishery-independent surveys or by fishery-dependent catches. Fishery-independent surveys are generally designed to be standardized and data collected can be considered to be representative of trend in stock abundance (Hilborn and Walters, 1992), but fishery-independent data are generally available for a short period (or not at all in small-scale fisheries) and abundance indexes for the rest of the year are often derived from commercial fisheries (CPUE or LPUE). Effort data can be difficult to obtain for small-scale, diverse artisanal fisheries; data collected from sales at individual ports and auction sites can be used to generate CPUE indexes at a higher resolution than that possible with aggregated catch data (Lourenço and Pereira, 2006). In small-scale cephalopod fisheries, interviews can be a suitable method for collecting catch and effort data in the absence of the infrastructure noted in the preceding text (Young et al., 2006). However, in the absence of sufficient biological data collection, mis-identification of similar species with different life histories or sex-specific catchability such as that observed for some octopus species can confound the use of CPUE to derive abundance indexes (Leporati et al., 2009). Even in some relatively well-sampled cephalopod fisheries, for example, those targeting California market squid (*D. opalescens*) and *D. pealeii*, management measures (catch limits) are set based on historical landings data in the absence of a functional assessment model or when confidence in assessment models is low (NEFSC, 2011; Zeidberg et al., 2006).

4.6.2 Abundance index standardization

A challenge when using fishery-dependent data (CPUE) to derive abundance indexes is that fishing fleets are generally heterogeneous and fishing performance may vary with time. CPUE should therefore be standardized considering that resource catchability can vary according to spatiotemporal variables (such as fishing area, years and seasons) as well as vessel class variables (vessel length or engine power). The abundance index standardization was developed by Allen and Punsky (1984) for the Inter-American Tropical

Tuna Commission. [Hilborn and Walters \(1992\)](#) made a more general presentation of the methodology using a Gaussian error generalized linear model (GLM; [McCullagh and Nelder, 1989](#)) to statistically model the log-transformed CPUE using various explaining variables mentioned in the preceding text. However, this methodology is difficult to use when the data set is composed by numerous null values as is the case in multispecies fisheries such as trawl fisheries. In this case, a Delta-GLM enables modelling of resource presence/absence using a binomial error GLM and, at the same time, modelling of resource abundance using a Gaussian error GLM ([Acou et al., 2011](#); [Fletcher et al., 2005](#); [Gras et al., 2014](#); [Le Pape et al., 2003, 2007](#); [Rochette et al., 2010](#); [Stefansson, 1996](#); [Syrjala, 2000](#)). The explaining variables used in the Delta-GLM can be similar to those mentioned previously.

The GLM methodology was used to standardize CPUE for various species of octopods, *O. vulgaris* ([Diallo and Ortiz, 2002](#); [Erzini et al., 2005](#); [Tserpes and Peristeraki, 2002](#)), *O. pallidus* ([Leporati, 2008](#)), *E. cirrhosa* and *E. moschata* ([Belcari et al., 2002](#)). This methodology was also used to standardize loliginid CPUE ([Cao et al., 2011](#); [Glazer and Butterworth, 2002, 2006](#); [Roel and Butterworth, 2000](#); [Roel et al., 2000](#); [Royer et al., 2002](#); [Tserpes and Peristeraki, 2002](#)), and *Illex* CPUE ([Chen et al., 2007](#)). Finally, several studies performed the CPUE standardization for cuttlefish ([Erzini et al., 2005](#); [García-Rodríguez et al., 2006](#); [Royer et al., 2006](#); [Tserpes and Peristeraki, 2002](#)). In the NW Pacific Ocean, [Tian et al. \(2009a\)](#) found that using various spatial scales to aggregate *O. bartramii* CPUE influences the CPUE standardization. Moreover, [Tian et al. \(2009b\)](#) studied the influence of three groups of variables, spatial (longitude and latitude), temporal (year and month) and environmental (sea surface temperature, sea surface salinity and sea level height), concluding that month was the most important variable influencing CPUE. Standardization using the delta-GLM methodology has been used to standardize the English Channel cuttlefish LPUE derived from French and UK bottom trawl fisheries prior to fitting a two-stage biomass model ([Gras et al., 2014](#)). Increasingly, generalized additive models (GAMs; [Hastie and Tibshirani, 1986](#)) are being used to complement or supplement GLMs for abundance index standardization ([Venables and Dichmont, 2004](#)), including applications to cephalopods (e.g. [Tian et al., 2009b](#)).

4.7. Fishery-independent data

Fishery-independent data used in cephalopod stock assessments can be collected in a variety of ways, including paralarval surveys, trawl surveys, jigging surveys and acoustic surveys.

4.7.1 Paralarval surveys

Paralarval surveys have been carried out to reveal spawning and nursery grounds for certain species in relation to annual variation in the marine environment, to understand population dynamics and to develop stock-recruitment models for commercially important species (Ichii et al., 2011). The most precise method of collecting cephalopods for estimating distribution and abundance is by sampling paralarvae in their early life stage, because conventional estimation techniques such as trawling for mature adults have biases due to avoidance and escapement from net openings (Bower et al., 1999b; Vecchione, 1987). The density of cephalopod paralarvae is relatively higher and more easily sampled than adults.

A large variety of sampling gear has been used for capturing cephalopod paralarvae. Among them, the gear used for collecting plankton is used in many cases, such as a ring net (Bower, 1996; Bower et al., 1999b; Goto, 2002), a Nansen net (Baron, 2003) and a bongo net (González et al., 2005; Jorgensen, 2007). A neuston net that collects at the surface (rectangular midwater trawl; Hatfield and Rodhouse, 1994; Vidal et al., 2010b) used for sampling larger paralarvae or juveniles and multilayer samplers such as a MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System; Moreno et al., 2009) and BIOMOC (BIOlogical Multiple Opening/Closing; Diekmann et al., 2006) have also been applied to obtain paralarval samples.

There are three general categories of sampling gear deployment: horizontal tow, vertical tow and oblique tow. Horizontal tows are done when a vessel is moving at slow speed by attaching a weight to the net to ensure that the net is in a horizontal pattern. The length of the wire, vessel and winch speed are used to control the depth of the sampling gear. Vertical tows are usually used to study a particular layer and suitable to collect smaller paralarvae or eggs. Oblique tows combine features of both vertical tows and horizontal tows, which can sample from a desired depth layer between the surface and any depth (e.g. several metres off the bottom) while a vessel is running. It is done by slowly releasing the sampling gear from the surface to the given depth and then towing at that depth for a while before pulling the net towards the surface obliquely. A calibrated flowmeter is attached to the net mouth of sampling gear to measure the volume of water that passes through the net to quantify and standardize density. To confirm the accurate towing depth, a depth data logger or real-time depth sensor may be attached to the sampling gear.

Hatfield and Rodhouse (1994) used bongo net and RMT to determine the distribution and abundance of paralarvae of *D. gahi* around the Falkland

Islands, and the distribution on the coastal shelf was associated with water-column structure. [Bower \(1996\)](#) estimated ages and hatch dates of *O. bartramii* sampled by ring net near the Hawaiian Islands and inferred spawning sites from hatch dates by back calculating with physical data on the speed of ocean current. [Bower et al. \(1999b\)](#) sampled paralarvae of 58 cephalopod species using ring nets near the Hawaiian Islands and classified onshore and offshore distribution patterns of each species based on distance from the Island. [Goto \(2002\)](#) revealed that the extent and range of area of suitable habitat for spawning of *T. pacificus* was related to the adult stock size by analysing a long time series (1972–1999) of paralarval sampled by ring net.

[González et al. \(2005\)](#) found that the distribution and movement of *O. vulgaris* and *L. vulgaris* paralarvae collected in the western coast of the Iberian Peninsula followed the oceanographic circulation system associated with wind-driven seasonal upwelling. [Vidal et al. \(2010b\)](#) had shown that the patterns of distribution and density of *I. argentinus* paralarvae and small juveniles could be linked to oceanographic conditions (sharp pycnoclines) and high primary production in an upwelling area off southern Brazil.

It is critical to understand the biology and ecology of early life stages before routine quantitative sampling for paralarvae. The identification of paralarvae to species is essential. Morphological characteristics such as morphometrics and patterns of chromatophore distribution are usually useful for identifying species ([Baron, 2003; Jorgensen, 2007](#)). A molecular genetic method has also been employed for species-level identification of cephalopod paralarvae ([Gilly et al., 2006; Wakabayashi et al., 2006](#)).

It has also been reported that avoidance from the mouth of sampling gear in the survey of paralarvae may occur, as documented for adult and juvenile cephalopods ([Collins et al., 2002; Haimovici et al., 2002](#)). In order to collect more quantitative samples of paralarvae, larger openings of the net mouth and other modifications may be required, as well as an examination of the collection efficiency of each gear.

4.7.2 Trawl and jigging surveys

Assessing juvenile and adult stocks of cephalopods is a difficult task, and only a few assessments in the world have used fishery-independent data obtained by midwater or bottom trawl and jigging surveys. Nevertheless, long-term seasonal stratified random bottom trawl survey data have been used in the assessments of *I. illecebrosus* and *D. pealeii* in the continental shelf and slope waters of the northwest Atlantic Ocean ([Hendrickson, 2004; NEFSC, 2011](#)). [Pierce et al. \(1998\)](#) estimated distribution and abundance of

L. forbesii from length–frequency data collected during demersal trawling surveys in Scottish waters and denoted that abundance from the February survey was suitable for indicator of commercial catch rate in the autumn of the same year. Litz et al. (2011) used pelagic and midwater trawl nets to estimate the horizontal distribution and abundance of *D. gigas* in the northern California Current system and reveal the relationship between physical oceanographic features and spatial distribution of the squid and its predator or prey. As trawl surveys are usually used to sample juveniles or adults, net avoidance and catch efficiency of the used gear need to be considered. Cod-end mesh size of sampling gear may be an important factor in estimation of length–frequency and abundance; several studies have examined trawl cod-end selectivity for the target species (Fonseca et al., 2002; Hastie, 1996; Hendrickson, 2011; Ordines et al., 2006; Tosunoğlu et al., 2009).

The jigging method is a common way to catch squids and cuttlefish in a commercial fishery, but few studies using this method have been performed for the purpose of biomass estimation. One of the most important reasons for this is that colours and sizes of jigs and survey timing affect size selectivity and catch rate significantly because the jigging method employs a passive fishing gear exploiting the feeding behaviour of squids (Mercer and Bucy, 1983). Another problem with quantitative jigging surveys is the use of artificial lights to aggregate squid, so catch efficiency is affected by the spread and intensity of fishing light. Nonetheless, for the stock assessment of the Japanese common squid (*T. pacificus*), the results of a jigging survey (catch per time effort and number of jigging machines (CPUE)) and number of fishing machines) have been used for an abundance index (Kidokoro et al., 2013). Several studies of *D. gigas* in the Gulf of California have been conducted using jigging sampling for stock assessment (Nevárez-Martínez et al., 2000; Robinson et al., 2013). Nevárez-Martínez et al. (2000) estimated biomass of *D. gigas* by stratified random sampling and swept area by strata using jigging survey data, which covered a grid of stations.

4.7.3 Acoustic surveys

For several decades, significant advances have been made in acoustics as a direct stock assessment tool for marine species (Stanton, 2012). In particular, assessments of biomass using a quantitative echosounder have been widely used for various fish species (Koslow, 2009; Simmonds and MacLennan, 2005). The advantages of using acoustic methods over other traditional methods are the following: (1) nearly the whole vertical distribution can be

obtained quickly; (2) horizontal extent is continuous along a survey line; and (3) data resolution is high, that is, less than a metre vertically and tens of metres horizontally. Although several early studies of cephalopod stocks using acoustic methods were conducted (Shibata and Flores, 1972; Starr and Thorne, 1998; Suzuki et al., 1974), these surveys tended to be qualitative rather than quantitative. Focusing on the more quantitative aspects, Goss et al. (2001) conducted two-frequency acoustic surveys for *D. gahi* around the Falkland Islands. These surveys revealed the potential of separation of squids from fin-fish using dual-frequency acoustics, but the accurate biomass of this species was not estimated because the information about target strength, which is an essential parameter for the estimation of stock assessment using echo integration method, was not well enough understood. More recently, quantitative surveys for estimating cephalopod abundance have been conducted using acoustic equipment after obtaining reliable target strength measurements (Benoit-Bird et al., 2008; Kang et al., 2005; Kawabata, 2005; Mukai et al., 2000; Soule et al., 2010). Distribution and density of *T. pacificus* were estimated by acoustic survey using a quantitative echosounder off the Sanriku Coast of Japan in the western North Pacific Ocean and compared with a catch rate index of commercial fishery (Kawabata, 2005). These results showed that both density estimations almost agreed and demonstrated that direct abundance estimation of this species using the acoustic method is possible. A sequence of acoustic studies for estimating the biomass in spawning schools of *L. reynaudii* have been conducted over 20 years off the southeast coast of South Africa (Augustyn et al., 1993; Lipinski and Soule, 2007; Soule et al., 2010). These surveys have combined acoustic and trawl methods to obtain the abundance of inshore spawning aggregations and deeper offshore dispersed aggregations, respectively. A combination of both methods enables an estimate of the total abundance of mature squids during the spawning season. Acoustic surveys for estimating the distribution and abundance of *D. gigas* and the lightfish (*Vinciguerria lucetia*), which is one of the important prey for *D. gigas*, conducted in the Humboldt Current system off Peru indicated that spatial and temporal distribution and abundance between both species were similar (Rosas-Luis et al., 2011).

One of the most important tasks facing an acoustic assessment is species classification and identification of acoustically detected targets. The identification of acoustic targets on the echogram is typically inferred from sampling results that include species composition, length–frequency and other fundamental biological parameters. Other supplementary information such as detected depths in the water column, geographical location, survey timing

and knowledge of the species' habits is also essential and helped identify acoustic echo signals. For the acoustic approaches to noninvasive species identification, multifrequency acoustics have been used for not only fish–plankton separation (Kang et al., 2002; Swartzman, 1997) but also squid–fish separation (Goss et al., 2001). Recent advances in broadband acoustics, for example, dolphin mimetic sonar, may provide more accurate species identification and classification techniques (Imaizumi et al., 2008; Stanton et al., 2010), and broadband acoustic signal characteristics of live *D. pealeii* have already been estimated (Lee et al., 2012).

Extensions of traditional fisheries acoustics approaches are acoustic–optical platforms that combine traditional echosounders with cameras to allow simultaneous target detection, species identification, enumeration and target strength estimation (Miksis-Olds and Stokesbury, 2007; Sawada et al., 2004) and the application of high-frequency sonars, or “acoustic cameras”, that can detect and identify individual squid in darkness and turbidity (Belcher et al., 2001; Iida et al., 2006). The acoustic–optical platform employed by Miksis-Olds and Stokesbury (2007) has been used to quantify the abundance of *D. pealeii* captured in shallow-water fish traps with some success, particularly when squids were a high percentage of total catch.

4.8. Way forwards for forecasting and assessment

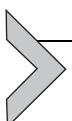
It is difficult to forecast stock size for most cephalopod stocks, often rendering management unreliable. In many cases, it may be most effective to combine forecasting, monitoring and revising estimated stock size using the methods of preseason, in-season and postseason assessments. For example, in the case of *T. pacificus* stock management, an original TAC is set based on the stock size forecasted from postseason assessment data (e.g. spawner–recruitment relationship), and preseason assessments are conducted just before fishing season opens to forecast stock size again. If the results of preseason assessments are quite different from the forecasted stock size, it will be revised. After the fishing season opens, if real-time monitored data are quite different from the forecasted stock size used to set TAC, then management measures can be adapted accordingly. Indicator-based approaches such as the “traffic light” approach employed by Ceriola et al. (2007) may also provide a dynamic means of generating timely information for fishery managers.

Many recent developments have been made in stock assessment models that incorporate environmental processes, including those that affect

population dynamics in the form of recruitment, and spatially explicit effects on distribution and migration patterns (Keyl and Wolff, 2008). As the body of research on environmental effects on cephalopod distribution and abundance grows, so too will the potential for application of such techniques. Similarly, as cephalopod stock identification techniques (e.g. tagging and genetics) improve (Semmens et al., 2007), the potential for application of the latest generations of spatially explicit stock assessment models (Cadrin and Secor, 2009; Goethel et al., 2011; Keyl and Wolff, 2008) will increase. Multispecies models or extensions of single-species models that incorporate trophic dynamics may improve assessments for some cephalopod species and are particularly timely with increasing emphasis on ecosystem-based approaches to fisheries management (e.g. Gaichas et al., 2010; Moustahfid et al., 2009).

Recent advances in data-poor stock assessment methods (Pilling et al., 2008; Starr et al., 2010) may have application for cephalopod species. Accounting for environmental effects on spatiotemporal distribution at multiple scales has implications for stock identification, survey design and interpretation of survey and landings data. For example, a revised understanding of stock structure based on an understanding of environmental effects on distribution has direct implications for assessment and management (e.g. *I. argentinus* off Patagonia; Crespi-Abril et al., 2013). At finer scales, a knowledge of habitat preference can provide data with which to design or interpret results of seasonal resource assessment trawl surveys such as those used to provide data to assess the *D. pealeii* stock in the western North Atlantic (Manderson et al., 2011). Environmental effects on cephalopod availability to surveys can be modelled as environmentally influenced variations in catchability (e.g. Fréon and Misund, 1999; Maunder and Watters, 2003), an important parameter in many stock assessment models that relates an index of abundance to population size (Arreguín-Sánchez, 1996; Hilborn and Walters, 1992; Wilberg et al., 2010). Adjustments can also be made to survey data before input to assessment models by incorporating data on environmental effects on distribution (e.g. Brodziak and Hendrickson, 1999). Environmentally induced distributional shifts render landings data difficult to interpret and create management challenges as new fisheries develop (e.g. *D. pealeii* off the northeast United States; Mills et al., 2013); this is particularly important for developing assessment and management strategies to address the effects of climate change (Link et al., 2011; Pinsky and Fogarty, 2012). Continued participation of fishing communities in data collection, stock assessment and management

is critical for the sustainability of cephalopod fisheries (Arkipkin et al., 2013; Johnson, 2011), particularly with respect to the performance of in-season monitoring and assessment (Walters and Martell, 2004). Advances in acoustic and optical survey techniques for benthic cephalopod egg masses (Young et al., 2011; Zeidberg et al., 2012) may have application as a fishery-independent index of future abundance of neritic species as well as a means of delineating important spawning habitat for protection.



5. MANAGEMENT AND GOVERNANCE

Globally, over half of all fish stocks are exploited. Of these, only 20% can be said to be moderately or underexploited, having the potential to expand (MRAG, 2010). Of those yielding less than their potential, 8% are depleted, 1% are recovering and 19% are overexploited (MRAG, 2010). According to MRAG (2010), the percentage of overexploited, depleted and recovering stocks has tripled since the 1970s. Worm et al. (2009) reported an 11% decline in total biomass across all ecosystems of regularly assessed stocks. Research survey data (targeted and nontargeted species) indicated a 32% decline in total biomass, a 56% decline in large demersal fish biomass (species ≥ 90 cm maximum length), 8% decline for medium-sized demersal fish (30–90 cm) and 1% decline for small demersal fish (≤ 30 cm), whereas invertebrates biomass increased by 23% and pelagic species by 143% (Worm et al., 2009). As mentioned by Worm et al. (2009), these increases are likely due to decreases in the predator population.

The depletion of many finfish species throughout the world over the last few decades has led to an increase in the commercial importance of cephalopods (Chen et al., 2008; Pierce et al., 2010; Young et al., 2004). Cephalopods seem to be one of the remaining marine resources, in some areas, that still experience an increase in landings (Boyle and Rodhouse, 2005). This has led to both the exclusive target of cephalopods using a variety of gear types and the increased targeting of cephalopods by fisheries traditionally targeting finfish. For example, the Indian trawl fleet started targeting cephalopods along the west coast of India during certain seasons (Meiyappan et al., 2000), while the Tasmanian arrow squid, *N. gouldi*, fishery expanded rapidly between November 1999 and February 2000, requiring the immediate closure of state waters to the majority of large-scale automatic jig operators (Willcox et al., 2001). In the coastal waters of Africa, there has been an expansion of the foreign trawl fishery and a high

international demand for octopus, resulting in overfishing in some instances ([Sauer et al., 2011](#)). However, the development of local pot fisheries and adequate management based on economic analysis are being developed in some cases ([Oosthuizen, 2004; Raberinary and Peabody, 2011](#)). Since 2003, industrial fishing using longlines of pots targeting *O. vulgaris* and *O. insularis* has developed in southern and northeastern Brazil ([Barahona et al., 2010](#); [VASCONCELLOS et al., in press](#)), and large-scale international fisheries for jumbo flying squid (*D. gigas*), Argentine short-fin squid (*I. argentinus*) and neon flying squid (*O. bartramii*) have also developed beyond the 200 miles territorial limit with a concomitant lack of management.

5.1. General management challenges

The increase in exploitation of cephalopods has resulted in a number of management challenges, with managers faced with not only the unique aspects of cephalopod biology but a large selection of management strategies and tools available for teleost stocks, including EAF, integrated coastal zone management, marine protected areas (MPA), balanced harvesting and various input and output control tools. In deciding on appropriate management strategies and measures, a broad understanding of the current management frameworks available is essential.

Several management regimes exist for cephalopod fisheries, ranging from co-management regimes to rights-based management. A rights-based (access rights and withdrawal rights) approach is now broadly accepted as the most successful form of management for marine stocks, with a number of options applicable to cephalopods. As summarized by [Charles \(2009\)](#), access rights include both territorial use rights for fisheries (TURFs) where rights are assigned to individuals and/or groups to fish in certain locations, generally, although not necessarily, based on long-standing tradition, and limited entry access rights where governments issue a limited number of licences to fish. Withdrawal rights include quantitative input or effort rights. Effort-based use rights are where each fisher has the right to use a specified amount of gear or fish for a certain time period. In some instances, all fishers may have equal quantitative rights within a fishery or the rights may vary dependent on location, boat size or other criteria. Quantitative output rights or harvest quotas require the subdivision of TAC into quotas allocated to sectors of the fishery, individual fishers or communities. Harvest rights can also be allocated as trip limits, while quotas can be further subdivided into individual transferable quotas (ITQs) or individual nontransferable quotas (INTQs).

Co-management systems are also popular, particularly in developing countries. In co-management regimes, resource users, government agencies and, sometimes, other stakeholders are responsible for the management of a specific area or set of resources (Gutiérrez et al., 2011; IUCN, 1996). There are many advantages to involving fishers in the management of their activity. Co-management arrangements have the capacity to increase fishers' responsibility and accountability, decrease their scepticism towards management, increase fishers' likelihood of compliance with management policies and decisions and facilitate common understanding and establishing trust between fishers, government bodies and scientists (Coffey, 2005; Guidetti and Claudet, 2010; Jentoft and Kristoffersen, 1989; Jentoft and McCay, 1995; Mikalsen and Jentoft, 2001; Pita et al., 2010). However, true co-management is rare and, in practice, fishers often still have little or no say in management decisions (Mikalsen and Jentoft, 2008). Examples of both rights-based and comanaged cephalopod fisheries are given under Section 5.3, which addresses current management initiatives.

5.2. Limitations to management of cephalopod fisheries

While management measures for finfish can be said to be fairly well advanced, managers responsible for cephalopod fisheries face a number of significant challenges. Cochrane and Garcia (2009) provided a useful set of general guidelines for fishery managers, which are applicable to cephalopods, while Pierce and Guerra (1994) provided a list of the requirements for the successful assessment and management of cephalopod fisheries (see also Section 4). Certainly, a key challenge to successful management is the fact that all species are short-lived, often necessitating in-season assessment and real-time management of cephalopod populations (Pierce and Guerra, 1994). Further complicating management is the understanding of the role of cephalopods in exploited communities and ecosystems, particularly with respect to trophic interactions (Pierce and Guerra, 1994), and the fact that many species may have expanding numbers due to a decline of key predators and therefore thrive in disturbed environments.

Broadly, fisheries management can be divided into three general aims: sustaining the fish stock, sustaining the fishery and sustaining fishery-related employment (Pilling et al., 2008). While the determination of the distribution and boundaries of cephalopod stocks can be said to be a fundamental requirement for fisheries management, the identification of these is often not possible, and many species undertake fairly extensive migrations and

have an expanding home range in years of good recruitment. A lack of species discrimination in official statistics, which often lump together species with very distinct distribution ranges and population dynamics (Cavaleiro, 2006), further complicates any attempt to determine stock boundaries. Complicating management is also the fact that many fisheries straddle political boundaries, requiring intergovernmental bodies (Pope, 2009), often not geared towards making rapid decisions around a short-lived resource (e.g. *D. gigas* in the eastern central Pacific, which is exploited in the Peru, Mexico and Chile Exclusive Economic Zone (EEZ).

Almost all management requires good long-term data on catch and effort and key biological information. This is a challenge to many cephalopod fisheries, particularly where cephalopods are caught as by-catch. The collection of appropriate fisheries statistical data by countries involved in cephalopod fisheries often lags that for finfish (Pierce and Guerra, 1994). Total nominal catches, fishing effort and CPUE and biological data are required for both simple and complex assessments of cephalopod stocks (Pierce et al., 2010).

As described in the previous section on assessment and forecasting, stock assessments can be categorized as preseason, in-season or postseason, with preseason assessments used to estimate stock biomass at the start of the fishing season, in-season assessment using incomplete CPUE data to adjust fishing level activity throughout the fishing season and postseason assessment using complete CPUE data sets to establish management goals for the following fishing season. For example, DeLury depletion methods of assessment have been the approach of choice in squid fisheries around the Falkland Islands (e.g. Agnew et al., 1998a; Beddington et al., 1990; Rosenberg et al., 1990), combined with limited entry access rights and quantitative output rights/harvest quotas. With modifications, this has been successfully used for a number of years. Production models (requiring only catch and effort data) have been applied with some success to cephalopod fisheries in the Saharan Bank (Bravo de Laguna, 1989), and modifications of this methodology, including additions for the influence of environmental factors, culminated in the implementation of a management plan in 2006 (Binet, 2012). Relatively accurate estimates of within-season stock size are essential for cephalopod fisheries managed by way of limiting catch (Young et al., 2004); however, the cost of such an undertaking is often prohibitive and not a realistic management option. However, as stated by Cochrane (2002), fisheries managed by way of effort require slightly lower precision as removal rates generated by fishing effort levels can be judged over a series of years rather than on a year-by-year basis.

As for all fishing resources, a comprehensive knowledge of cephalopod species life cycles, particularly with respect to the distribution of spawning sites and early life stages, can be essential when implementing management measures such as gear restrictions and spatial or temporal closures/restrictions. Gear restrictions and closed areas and/or seasons have been used to limit the harvest of specific life stages (e.g. the South African *L. reynaudii* fishery closed season during the peak spawning period), protect genetic reservoirs, protect habitat that is critical for the sustainability of a harvested resource, restrain excess fleet capacity and optimize the value of the catch, by limiting by-catch and protecting attributes of the ecosystem that are critical for its preservation ([Cochrane, 2002](#)).

Interactions with other fisheries operating in an area, as well as biological and fisheries information for mixed fisheries and/or by-catch species, further complicate management. Not only cephalopod fisheries using unselective fishing gear, as well as those fisheries where cephalopods form one component of a mixed fishery, need to consider operational interactions with other fisheries, but also management measures taken for one component of the fishery may conflict with measures taken for other components ([Meiyappan et al., 1993](#)). In the case of the western North Atlantic fishery for *D. pealeii*, by-catch of finfish in small-mesh trawls has led to management measures such as minimum mesh sizes and fishery closures when by-catch limits are exceeded ([Mid-Atlantic Fishery Management Council, 2011](#)).

A global problem in the management of fish stocks is the lack of information on the economic and social dimensions of fisheries with key information for managers often lacking. This is particularly important for both existing and new cephalopod fisheries, where stocks may go through a boom and bust period, and an understanding of the social and economic implications is essential when allocating access rights. For example, cephalopods are important fishery resources for several EU countries such as Spain, Portugal, Italy, Greece, France and the United Kingdom ([Pierce et al., 2010](#)). According to [FAO \(2004\)](#), the European market is the most important market in the world for this resource, and most imports go to the south of Europe. Spain and Italy, for instance, are major importers of cephalopods ([Pierce et al., 2010](#)). Small-scale, directed coastal fisheries for cephalopods have increased dramatically in Europe, particularly in southern European countries where cephalopods are traditionally consumed. The huge increase in landings over the last few decades is basically due to the replacement of traditional relatively inefficient fishing gears (e.g. clay pots and trammel nets)

by more efficient gears, including modernized traditional gears and newly introduced gears such as plastic pots and fyke nets (Borges, 2001; Lefkaditou et al., 2002; Pierce et al., 2010; Young et al., 2006). Inshore local small-scale fishing fleets targeting squid, cuttlefish and octopus in Portugal, Spain, Italy and Greece are of considerable socioeconomic importance in terms of providing employment and income in coastal fishing communities (Pierce, 1999; Pierce et al., 2010; Shaw, 1994).

In Portugal, the economic importance of cephalopods is relatively high, and there is an increasing economic dependence of small-scale fisheries on cephalopods. In Italy, most landings of cephalopods come from bottom trawlers, but a substantial fraction still depends on small-scale and mixed fisheries. Both activities employ an important number of local fishers in many small coastal communities along the Italian coast. Cuttlefish (*S. officinalis*) is one of the most significant marine resources in Lower Normandy, France (Pierce et al., 2010). In the United Kingdom, the most important commercial cephalopod is the cuttlefish, and most catches of this species are from the English Channel. The cuttlefish fishery is based on a combination of trawling and artisanal fishing, the latter exclusively directed at cuttlefish. There is also increased targeting of squid (*L. forbesii*) by small-scale inshore trawlers in the Moray Firth (east coast of Scotland, the United Kingdom) (Young et al., 2006). For instance, the small inshore trawler fleet in Burghead (a small fishing community in the Moray Firth) can make up to 50% of their annual revenue targeting squids for 3–4 months of the year.

Therefore, the effect of management measures, such as effort or catch limitations and spatial or temporal closed seasons, on social and economic objectives needs to be considered. Also important is the effect of management measures on the opportunity window to fish short-lived and fast-growing species. Such measures can have large implications on catchability and therefore reduce profitability by reducing the available biomass production. Measures, often seen as used to secure the biological objectives of a fisheries management plan, must also secure the socioeconomic objectives. Pomeroy and Fitzsimmons (1998) mentioned that both social information and economic information can aid fishery managers by giving them a better understanding of how management measures will be received and affected by individuals involved.

Illegal, unreported and unregulated (IUU) fishing activities have become a global problem. They not only do have far-reaching economic and social impacts (DfID, 2007) but also are harmful to global fish stocks and undermine the effectiveness of management measures adopted regionally,

nationally and internationally (Agnew et al., 2009; Berg and Davies, 2002; Schmidt, 2004). IUU has been estimated to account for annual catches of 11–26 million t of fish worth US \$10–20 billion (Agnew et al., 2009). Addressing the global extent of illegal fishing, Agnew et al. (2009) calculated illegal and unreported cephalopod catch to be in the region of 25% of reported catch (lower and upper bounds of ~12.5% and ~38.5%, respectively). IUU is particularly difficult to control on the high seas as the only authority able to prosecute a vessel for illegal activities is the vessels own flag state. High seas squid fishing activity has resulted in a number of issues such as unreported catches from high seas waters, the use of illegal gear and the poaching of resources in adjacent EEZ waters (MRAG, 2005). In a review of the impacts of IUU, MRAG (2005) summarized IUU squid fishing activity on the high seas. The southwest Atlantic Ocean high seas fishery for *I. argentinus* has been estimated to catch 50–100,000 t per year. The operation of this fleet, composed of jigging vessels and trawlers from numerous countries, just outside the Argentine and Falkland Islands' EEZ has led to poaching within EEZ waters. Chinese vessels have been reported to use illegal driftnets to target neon flying squid *O. bartramii* in the Pacific Ocean. Off Peru and northern Chile, licensed Japanese and Korean vessels target jumbo flying squid *D. gigas*, mainly within the Peruvian EEZ. Combined, an annual catch of 45,000 t has been recorded. China, a recent entrant into this fishery, has been estimated to catch around 40,000 t from adjacent high seas waters alone. In total, annual high seas IUU squid landings have been estimated to have a value of US \$108 million.

Most catches from small-scale octopus and squid fisheries in developing countries go unreported, in part because they are consumed locally and in part because keeping track of artisanal landings is difficult and expensive due to the large number of vessels involved and the geographically widespread nature of their activities.

Localized or regional IUU activity can have equally harmful results. Often, the lucrative nature of short-term gains overrides long-term interests in maintaining the sustainability of the resource (Hauck and Sweijd, 1999). IUU activity reduces the incentives to comply with rules, particularly for legal fishers (Schmidt, 2004). An example of an extreme case of IUU activity (poaching) would be the South African abalone fishery. Not only were management initiatives unsuccessful due to the high financial returns of illegal fishing, but also criminal syndicates developed, fuelling exploitation and providing the means to export the product (Hauck and Sweijd, 1999). The commercial South African abalone fishery has since been closed.

Therefore, apart from scientific, economic and social information, compliance with conservation-based measures is also essential to the proper management of fishery resources (Berg and Davies, 2002). Fishery monitoring, control and surveillance (MCS) contributes to good fisheries management by ensuring that appropriate controls are set, monitored and complied with (Berg and Davies, 2002). MCS involves both a preventative approach, encouraging voluntary compliance through understanding and support of management strategies by communities/fishers, and a deterrent/enforcement approach that ensures the compliance by fishers who resist the management regime to the detriment of both the fishery and the economic returns to fellow fishers (Flewelling, 2001). No one MCS solution exists for all fisheries but instead should be developed for either a specific fishery or a group of interacting fisheries based upon, among other factors, available and cost-effective resources, the desired and expected level of compliance, the value of the fishery and the state of the stock (Flewelling, 2001). Flewelling (2001) stressed every MCS system requires regular assessment to determine success in achieving strategic targets in the most cost-effective and efficient manner and to ascertain its effectiveness on compliance over time.

5.3. Examples of current management of cephalopod fisheries worldwide

While not exhaustive, Tables 2.3 and 2.4 give a synthesis of current management initiatives for cephalopod fisheries, highlighting some of the differences in approaches. For example, cephalopod fisheries in Europe are excluded from quota regulations under the Common Fisheries Policy (CFP). Pierce et al. (2010) came to the conclusion that this is likely a good thing, since the management arrangements that have evolved in the various small-scale fisheries across the EU effectively operate under a precautionary principle, apparently successfully regulating exploitation, despite the unknown size of stock. Plus, most management arrangements in place are tailored at the local level; fishers participate in the management of their activity; and, in some cases, co-management arrangements are in place (Pierce et al., 2010). European management regimes for cephalopod fisheries are done through input and output controls. Input controls consist mostly of setting limits to the characteristics of the gear and the number of licences and output controls by limiting the size and weight of the specimens landed (Pierce et al., 2010). Southern European countries appear to be the ones that more actively manage their cephalopod fisheries, possibly a reflection of the

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						
<i>Sepia officinalis</i>	Greece, Aegean and Ionian Seas		Trammel nets			Pierce et al. (2010)
Octopus						
<i>Enteroctopus megalocyathus</i>	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)	IIstituto de Fomento Pesquero (2010), Castilla (2010)
<i>Enteroctopus megalocyathus</i>	Patagonian Gulfs and Shelf, SW Atlantic	Targeted	Scuba diving and gaffs	No management		Ortiz et al. (2011)
<i>Octopus insularis</i>	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)
<i>Octopus insularis</i>	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)

<i>Octopus insularis</i>	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)
<i>Octopus maya</i> (and <i>O. vulgaris</i>)	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)
<i>Octopus mimus</i>	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)
<i>Octopus tehuelchus</i>	Nuevo and San Jose Northern Patagonian Gulfs, SW Atlantic	Targeted	Fishing with gaffs during low tide	No fisheries management but access restricted by MPA		Narvarre et al. (2007)

Continued

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
<i>Octopus vulgaris</i>	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)
<i>Octopus vulgaris</i>	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)
<i>Octopus vulgaris</i>	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)
<i>Octopus vulgaris</i>	Portugal	Targeted	Pots and traps		MLS (main measure, 750 g), technical measures regulating gear	Pereira (1999)

Squid					
<i>Dosidicus gigas</i>	Eastern Pacific Mexico EEZ and Gulf of California	Targeted	Hand jigging	Sonora (Mexico): effort control	Morales-Bojórquez et al. (2001b)
<i>Loligo reynaudi</i>	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)
<i>Todarodes pacificus</i>	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 2.4 Current management initiatives for industrial cephalopod fisheries

Species	Location/country	Targeted/ by-catch	Gear type	Management regime	Management measures	References
Cuttlefish						
<i>Sepia officinalis</i>	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)
Octopus						
<i>Octopus insularis</i>	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)
<i>Octopus vulgaris</i>	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)

<i>Octopus vulgaris</i>	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	
<i>Octopus vulgaris</i>	Greece	Targeted	Traps and fyke nets	Technical measures (number of pots/traps per vessel), time restrictions, MLS, closure period	Pierce et al. (2010)	
<i>Octopus vulgaris</i>	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						
<i>Berryteuthis magister</i>	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)	
<i>Doryteuthis opalescens</i>	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)
<i>Doryteuthis pealeii</i>	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
<i>Illex argentinus</i>	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)
<i>Illex argentinus</i>	Southwest Atlantic FICZ of Falkland (Malvinas) Islands	Targeted, by-catch	Jigging machine and squid fishing light, bottom trawl catch		<i>Illex</i> licences. Real-time control (until the cumulative catch reaching 40% escapement). Restricted entry, closures	Arkhipkin et al. (2013)
<i>Illex illecebrosus</i>	United States	Targeted	Small-mesh trawl		TAC, ABC and DAH, depending on area	Mid-Atlantic Fishery Management Council (2011)
<i>Loligo forbesi</i>	Scotland, the United Kingdom	By-catch (whitefish directed trawl fishery)	Trawl	None	None	Hastie et al. (2009)
<i>Doryteuthis gahi</i>	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), “ <i>Loligo box</i> ”: grounds reserved for <i>D. gahi</i> fishing, i.e. finfish trawlers prohibited (coastal habitat is <i>de facto</i> MPA), individual transferable quotas	Hatfield and des Clers (1998), Arkhipkin et al. (2013)

<i>Loligo vulgaris</i>	Portugal			MLS	Pierce et al. (2010)
<i>Nototodarus gouldi</i>	Tasmania and Australia	Targeted	Automatic squid jigging gear, trawl	Rights-based	Limited entry licensing for all fisheries, TAE (Southern Squid Jig Fishery only)
<i>Nototodarus sloanii</i>	New Zealand: southern islands only	Targeted	Trawl	TACC	Chilvers (2008)
<i>Nototodarus sloanii</i> and <i>N. gouldi</i>	Southern New Zealand	Targeted	Jigging machine and squid fishing light	TACC	Chilvers (2008)
<i>Nototodarus sloanii</i> and <i>N. gouldi</i>	Southern New Zealand	Targeted	Trawl	Squid TACC. Since 2001, sea lion exclusion devices	Chilvers (2008)
<i>Uroteuthis duvaucelii</i>	India	By-catch but targeted seasonally	Trawl	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.

long history of the exploitation of these resources and of the local importance of the species. These countries are the ones with the greatest internal consumption of the resources and those in which the relative economic and/or social value of the fisheries is the greatest. For instance, in Portugal and Spain, the minimum landing weight for the common octopus is 750 g, and in Greece, it is 500 g (Pierce et al., 2010). In some parts of Spain (e.g. Galicia, northwest Spain and the Gulf of Cádiz, all in the Atlantic), the minimum landing weight for common octopus was increased to 1 kg in 2008 (Pierce et al., 2010). Examples of cephalopod fisheries management through co-management systems include the Asturian octopus artisanal fishery (Spain), cuttlefish in Lower Normandy (France) and the small-scale octopus fishery in northern Chile.

In contrast to the aforementioned European examples, cephalopod fisheries in Africa are often largely unmanaged, exceptions being a hand jig fishery for *L. reynaudi* in South Africa and some octopus fisheries. For *L. reynaudi*, management is by way of effort limitation. Effort has been capped at a level that secures the greatest catch in the long term without exposing the resource to the threat of reductions to levels at which recruitment success is compromised or catch rates become economically unviable (Anon, 2010), with limits on the number of fishers, a closed season and closed areas for fishing. Artisanal fishing for octopus is an important subsistence and economic activity practised by local coastal communities in the western Indian Ocean, particularly in Tanzania, Mozambique, Madagascar and Kenya (Guard, 2009; Otieno, 2011). Initially caught for local and inland consumption, export to European and Far Eastern markets has led to a rise in demand (Guard, 2009). An interesting community-based approach to managing octopus fisheries has recently been introduced in the south of Madagascar with pilot no-take zones introduced to demonstrate the tangible fisheries benefits of protecting one of the region's most economically important marine resources and to increase the involvement of local communities in marine resource management (Epps, 2007). The pilot no-take zone was successful and resulted in an increase of catches as well as an increase in the price paid by commercial buyers after the closure. This success increased the interest of the Andavadoaka community and adjacent fishing communities in Madagascar in developing additional no-take zones. A similar exercise has recently taken place in Rodrigues (Epps, 2007).

Tables 2.3 and 2.4 highlight the lack of routine assessment for cephalopods with few countries collecting detailed data on cephalopod fisheries, suggesting the introduction of a precautionary approach to management

in many cases. In 1996, following a 1995 Technical Consultation on the Precautionary Approach to Capture Fisheries in Sweden, the FAO published a set of guidelines on the precautionary approach to capture fisheries and species introductions (FAO, 1996). These guidelines, as summarized by Punt (2006), include the following principles:

- A level of precaution commensurate to risk should be applied at all times to all fisheries.
- Potentially irreversible changes should be avoided (to maintain options for future generations).
- Undesirable outcomes should be anticipated and measures be taken to reduce their likelihood.
- Corrective measures should be applied immediately and be effective within an acceptable time.
- Precautionary limits should be placed on fishing capacity on highly uncertain resources.
- All fishing activities should be subject to prior authorization and periodic review.
- The burden of proof should be appropriately (realistically) placed.
- Standards of proof commensurate with the potential risk to the resource should be established.
- The approach should be formalized in a comprehensive legal and institutional framework.

Specific guidelines for applying the precautionary approach to artisanal fisheries and new or developing fisheries were also addressed (FAO, 1996). For artisanal fisheries, guidelines suggest limiting risks to resources and the environment with the use of closed areas, delegating certain management decisions to the community (co-management), limiting the influence of industrial fishing on resources harvested by the community and investigating the influence of social and economic factors on fishing pressure.

Precautionary principles that would apply to data-poor and unmanaged fisheries include (1) controlling access to the fishery; (2) conservatively capping fishing capacity and mortality rate by limiting effort or TAC until data analysis to justify increases can be carried out; (3) avoiding new investment in the fishery by temporarily licensing vessels from another fishery and allowing flexibility to phase out vessels if necessary; (4) closed areas to limit risks to the resource; (5) establishing precautionary, preliminary biological limit reference points; (6) encouraging responsible fishing through co-management or tenure of fishing rights; (7) encouraging the

development of fisheries that are economically viable without long-term subsidies; (8) establishing a data collection and reporting system; (9) starting research programmes on the stock and fisheries; and (10) setting up experimental situations to generate information on the resources.

In the past, management approaches have been based on target reference points (TRPs), the specific values of indicators for catch, biomass and fishing mortality regarded as optimal (Caddy, 2004). However, it has been shown that once a TRP is overshot, the stock becomes vulnerable to overfishing (Caddy, 1998). Caddy and Mahon (1995) put forwards the concept of limit reference points (LRPs) (which has been recommended following the United Nations Conference on Environment and Development; Caddy, 2004) as one way of defining the limits to exploitation of a stock and so implementing a more precautionary approach. Integral to this approach is prenegotiating responses to unfavourable events and implementing these responses when a fishery approaches an LRP (Caddy, 1998). As noted by Caddy (1998), almost all RPs currently in use are based on the availability of age-structured data and on information on stock and recruitment accumulated over a significant period of time. Defining reference points for data-poor fisheries, such as the majority of cephalopod fisheries, could be somewhat difficult. Caddy (1998) however had proposed a number of ways LRP can be used in the management of data-poor fisheries. For example, it may be possible to set a single LRP that corresponds to serious but not catastrophic conditions and then pick a TRP based on estimates of variance and probability of overshoot. See Caddy (1998) for a full review on application in data-poor fisheries and Caddy (2004) for the potential application of RPs to invertebrate fisheries specifically.

However, in undeveloped or developing countries, in which many small-scale octopus fisheries occur, obtaining adequate data for fisheries management is only a small part of the problem. The lack of adequate institutions; management organizations; monitoring, control and surveillance (MCS) bodies; and enforcement prevents the efficient management of resources.

Factors contributing to the unsustainability and overexploitation of small-scale octopus, and other invertebrate, fisheries in Latin America have been explored by Narvarte et al. (2007). Unsustainability of these fisheries is explained as follows:

- The irregularity in recruitment of target species produces difficulties in long-term planning (complexity and lack of knowledge concerning biological/ecological processes).

- There are numerous incentives for entering the fishery, investments required are low, and there is a common belief held in the community that the fishery could mitigate all unemployment problems when reduction or collapse occurs in other economic activities.
- Violations of norms and regulations (evident in illegal captures of banned species, violation of established catch quotas, use of unpermitted methods, etc.) and the high prices obtained for the resources in closed seasons lead to irresponsible behaviour (e.g. clandestine harvesting) by some individuals.
- Lack of organization among fishers and lack of understanding of harvesting rights for the resources.
- Poverty and lack of satisfaction of basic living requirements in the coastal collector segment, especially related to those engaged in collecting octopus. One problem is the abandonment of fishing as an activity to pursue other nonfishing-related employment. When the trade is abandoned at an early age, it is difficult to recover abilities required for fishing.
- Conflicts with other activities (e.g. growth of tourism affects the natural habitat of the octopus).
- Lack of organization and a collective strategy by fishers in marketing their catches, which produces competition among them, thus lowering prices. This in turn puts pressure on increasing the catches to maintain incomes.
- Lack of initiatives for fishers to develop value-added products at the site of production. Although infrastructures exist for processing catches, catches are commercialized whole, at places far from their origin.
- Institutional difficulties to rapidly and efficiently respond to requests for information and technical assistance.

These points raised by [Narvarre et al. \(2007\)](#) also apply to other regions. For instance, cephalopod fisheries in Argentina, Brazil, Chile and Mexico have some data on landings, are subject to nominal rules and have some information on the biology of the resources, yet rules are seldom enforced and fishers usually violate the norms.

5.4. The use of Marine Protected Areas as a general conservation tool

MPAs may provide refugia for a variety of species including cephalopods, and they have occasionally been used as management tools (sometimes experimentally) for cephalopod fisheries (e.g. in Portugal and Spain).

In general, MPAs set up in areas of previous small-scale fisheries continue to allow small-scale exploitation of a variety of species including cephalopods, which is a special form of spatial planning. In Portugal legislation regulates cephalopod catches by recreational fishers within specific MPAs. The MPA “Parque Natural do Sudoeste Alentejano e Costa Vicentina” in the southwest coastal area of Portugal, for instance, limits octopus catches to two octopuses per fisher per day, while the number of entry licences is also restricted (legal diploma “Portaria” 115-A/2011). In northeastern Brazil, most small-scale octopus fisheries can function within MPAs, but legislation on MPAs is more strict and enforced more efficiently than fisheries legislation, which results in easier and more efficient implementation of catch limitations. In South Africa, no-take MPAs are used as a management tool for *L. reynaudi* (Sauer, 1995).

5.5. Recreational fishery data

Recreational fisheries for cephalopods do exist in countries with a traditional consumption of cephalopods, but they are often not well documented. As a long-standing recreational tradition, people hunt for octopus on the shore by employing dedicated gear to catch the animals from rocky tide pool areas or in shallow infratidal areas accessible during low tides. By luring them out of shelter with bait, octopuses become accessible to any spearing or hooking device, of which the “Bicheiro” has been described already in the nineteenth century by [Baldaque da Silva \(1891\)](#). Octopuses are also caught by recreational fishers from boats or other floating platforms by means of jiglike devices, which are essentially baited rods terminated by a number of hooks designed to penetrate the muscle of the attracted animal by means of a sudden jerking movement. Squids are caught with hand-held jigs in a number of countries. Cuttlefish are recreationally caught by means of snorkelling and spearing, throughout much of the distributional range of each species. Where legislation exists, it often sets an overall limit on daily allowable catches, regardless of species: for example, in Portugal, Ordinance n°14 of 23 January 2014, Article 12, n°1, states that recreational fishery catches cannot exceed the daily limit of 10kg per person for all species combined, excepting the possibility of one larger-than-the-limit specimen of fish or cephalopod; and n°2 further states that if fish or cephalopods are not included in the catches, the limit is lowered to 2 kg per person. Where legislation exists, it often sets an overall limit on numbers, regardless of species.

5.6. The way forwards: Balancing the many objectives of management

We suggest that in order to address the complexities discussed in this chapter, we should be exploring an ecosystem approach to cephalopod fisheries (EACF) ([FAO, 2003](#)) defined as “An ecosystem approach to fisheries strives to balance diverse societal objectives, by taking into account the knowledge and uncertainties about biotic, abiotic and human components of ecosystems and their interactions and applying an integrated approach to fisheries within ecologically meaningful boundaries”. A set of general practical guidelines exists and a start is now being made in a number of countries in implementing EAF, including South Africa, Mauritius, Seychelles, Tanzania, Kenya, Madagascar and Uganda.

The goals of EAF are “to balance diverse societal objectives, by taking into account the knowledge and uncertainties about biotic, abiotic, and human components of ecosystems and their interactions and applying an integrated approach to fisheries within ecologically meaningful boundaries” ([FAO, 2003](#)). The approach thus intends to foster the use of existing management frameworks, improving their implementation and reinforcing their ecological relevance, and will contribute significantly to achieving sustainable development ([Garcia, 2003](#)).

However, implementation and effectiveness will undoubtedly benefit from reducing important uncertainties, and further research is needed for this purpose including better understanding of ecosystem structure and function and how fisheries affect them; integrating social, economic and ecological considerations into decision making; improving the management measures available to implement EAF; understanding the management process better; and improving monitoring and assessments ([Garcia and Cochrane, 2005](#)).

Fisheries production and yield are constrained by a number of factors that can be classified as biological, ecological and environmental, technological, social and cultural and economic considerations ([Cochrane, 2002](#)). Fisheries for cephalopods are often multispecific, which means that it is nearly impossible to manage them on a single-species basis. However, nearly all fisheries management to date is focused on biological reference points for single species. This means that measures taken to ensure the sustainable yield of a species completely ignore the remaining assemblage. Yet, it is a well-established fact that many fisheries will include destructive gear impacts on the sea floor, unwanted by-catch and eventually ecosystem effects such as changes in species richness and composition and relative species abundance.

We recognize the sometimes conflicting objectives and management aiming to maximize fisheries production often make it impossible to have a large abundance of both cephalopods and finfish (perhaps due mostly to predatory interactions). Management is often aimed at optimizing species assemblage abundance, either from a purely economical perspective (i.e. maximizing the abundance of the economically most-valuable species) or from a biodiversity (or species richness) perspective (i.e. maintaining the undisturbed species balance). More complex adaptive management systems are currently being explored, of which the responsive fisheries management system being developed through the EU-funded EcoFishMan project (www.ecofishman.com) is a good example.

Despite the increasing social and economic importance of cephalopod fisheries in Europe, very little information exists on the human dimensions of these fisheries. As identified by [Pierce et al. \(2010\)](#) on a major review of cephalopods fisheries in Europe, there is an urgent need for a detailed analysis of the economic and social importance of these fisheries locally as well as at the national levels, including bioeconomic studies of the fleets targeting cephalopods, and the evaluation of possible socioeconomic implications of alternative management strategies at the local level.

Small-scale and artisanal fisheries face different challenges. [Guard \(2003, 2009\)](#) had listed potential management actions that can be applied to artisanal octopus fisheries. They are as follows:

- Initiation of a stock assessment programme and continued catch monitoring
- Introduction of rotational or “pulsed” fishing regimes
- Collaborative agreements for restriction of fishing outside of spring tide periods
- Temporary reef closures and reduced fishing effort during brooding periods
- Introduction of size limits
- Collaborative licence scheme for octopus fishermen and the formation of community stewardship groups
- Introduction of recommended maximum sustainable yields and associated effort for each octopus fishery
- Dissemination of results and community awareness raising

Fishers input (through co-management) should always be utilized when developing management strategies. Fishers can contribute information regarding the stock structure (in terms of migrations patterns, spawning grounds and juvenile habitat), schooling behaviour, habitat preference, gear

selectivity and effort changes as a result of new regulations (Johnson, 2011; Johnson and van Densen, 2007). Another positive outcome of co-management is the potential for cooperative research or research conducted in partnership with industry (Arkipkin et al., 2013; Johnson, 2011; Johnson and van Densen, 2007).

Several approaches have promise for by-catch reduction in cephalopod fisheries, for example, finfish by-catch and the associated regulations in the United States. *D. pealeii* small-mesh trawl fishery has spurred experimentation with gear modifications to reduce by-catch (Bayse et al., 2014; Glass et al., 1999; Hendrickson, 2011) and research on environmental factors driving species co-occurrence (Lange and Waring, 1992; Manderson et al., 2011), as well as exploration of the potential utility of by-catch avoidance strategies (e.g. Bethoney et al., 2013).

There is a need for more effective monitoring, control and surveillance (MCS) while recognizing that there is no unique MCS solution for all fishery situations, nor inherently right or wrong approaches to the implementation of MCS systems (Berg and Davies, 2002). Large-scale cephalopod fisheries, especially international industrial squid fisheries, generally target straddling stocks or species occurring both within the exclusive economic zone and in areas beyond and adjacent to the zone. *I. argentinus*, *D. gigas*, *T. pacificus* and *O. bartramii* stocks are under proper management and regulation by each country or bilateral exploiting these resources and are well monitored, controlled and kept under surveillance. In contrast, however, those stocks caught on the high seas are generally under no control or management due to the lack of international regulation or no establishment of regional fisheries management organizations (RFMOs). Cooperation between RFMOs or multi-national agreements are essential, especially for neon flying squid *O. bartramii*, jumbo flying squid *D. gigas*, Japanese common squid *T. pacificus* and Argentine short-fin squid *I. argentinus* fisheries operating in country EEZs and open seas. Small-scale cephalopod fisheries target species generally more local and nonmigratory and stocks are smaller. The lack of effective monitoring, control and surveillance and basic statistical information hampers effective management and should be addressed, including an understanding of migrant fishers. In many cases, policy/legislation is not adequate.



6. CONCLUSIONS

The understanding of cephalopod population dynamics is largely based on coastal and shelf species that are exploited by fisheries, but these

may not represent the large populations of oceanic and deepwater species. The exploited species often have complex and variable cohort and micro-cohort structures within the population, which may vary annually in terms of life cycle parameters, migration and abundance. There is a risk that this complexity can obfuscate interpretation of population dynamics, especially when only short-term data sets are available. Population variability is linked to the environment, but trophic relationships, a dominant theme in theoretical ecology, are poorly understood over the whole life cycle in cephalopod populations and receive little attention in research on population variability. In most cases, neither environmental impacts nor trophic relationships are explicitly included in stock assessment models. Intrinsic elements and trophic relationships are probably no less important than environment in shaping cephalopod life cycles, population dynamics and recruitment, but their incorporation into workable management strategies is more difficult than incorporating environmental effects because of the mathematical and statistical challenges involved and high biological variability, which may in fact contain a strong environmental signal.

The effects of environmental parameters on cephalopod population variability will operate on different timescales. Fisheries management in the short term is concerned with interannual variability. In the long-term ecologists, fishery managers and policy makers are concerned with the effects of global climate change. Although much attention focuses on warming, other aspects of measured and predicted change include ocean acidification, changes in oxygen tension, salinity and macro- and mesoscale oceanography. All of these will drive changes to whole ecosystems, which will impact on particular species groups including cephalopods.

Cephalopod populations could be good indicators of short-term environmental variability, if we could only understand fully what they are telling us, but their response to short term variability means they are poor indicators of long-term change because the long-term signal is masked by the annual noise. Nevertheless, cephalopods could be long-term winners under global climate change because they are ecological opportunists and have plastic population dynamics. Also, because they are short-lived and can reproduce fast, they may be able to evolve more rapidly under high selection pressure relative to many fish competitors and predators.

A range of assessment methods is used in different cephalopod fisheries, depending on the characteristics of the species concerned, the particular fishery and the resources available to managers. Given the importance of

forecasting in fisheries for short-lived species, there is a strong argument for combining appropriate stock assessment methods with environmental predictions based initially on empirical relationships between environmental variability and stock variability. In the longer term, as mechanisms explaining these relationships become better understood, this approach will become more robust. With current state of knowledge, the use of pre-fishing season assessments is strongly recommended. Empirical relationships between stock and environment, especially when they are based on short time series, should be used with caution as they may be revealed to have been illusory in the light of data collected over a longer period.

Given the current levels of uncertainty in even the best-managed fisheries, a precautionary approach is nearly always indicated. Ecosystem-based management of cephalopod fisheries should become the norm. Generally, this involves ensuring that harvesting does not decrease the size of any population below that which is required for stable recruitment over time, that ecological relationships are maintained between harvested populations and those populations that depend on them or are otherwise related to them and that the risk of causing irreversible changes to the ecosystem is prevented or minimized. The ecosystem approach to fisheries also implies consideration of the socioeconomic dimensions of fisheries. Cephalopod fisheries, in common with fisheries for other groups of organisms, will benefit in most cases from the introduction of participatory approaches to management, which engage all stakeholders from fishers to managers, scientists and policy makers. Where this approach has been adopted collaboration has increased understanding on all sides resulting in better regulations and better compliance and hence greater likelihood of long-term sustainability.

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