Modelling environmental influences on squid life history, distribution, and abundance

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Following Caddy and Gulland's (1983) classification, squid populations can be described as displaying irregular or spasmodic abundance fluctuations, as opposed to steady or cyclical patterns. Squid are short-lived, fast growing marine animals, thought to be especially sensitive to environmental influences (Coelho, 1985). Because generations are essentially non-overlapping, modelling of population dynamics reduces to predicting recruitment success (Caddy, 1983; Pierce and Guerra, 1994). Environmental signals are expected to have a strong effect on spawning and hatching success and on growth and survival of early life stages. Since squid are increasingly important fishery resources in many parts of the world, much recent research has focused on understanding their distribution and abundance, to provide the basis for efficient and sustainable utilisation of these resources. The recent high abundance of jumbo squid *Dosidicus gigas* in the eastern Pacific Ocean raises questions as to why abundance and range have increased, the ecological consequences and whether or for how long its current status will persist. The aim of this brief review is to synthesise approaches to modelling the spatiotemporal patterns in squid life history, distribution, abundance and fisheries, and to identify relevant research questions in relation to *D. gigas*.

In principle, models of spatio-temporal variation can be fitted to data on fishery catches and squid distribution, abundance and life history parameters. Critical stages of the life cycle include spawning, hatching, early growth, recruitment to the fishery and movements to the spawning grounds. In many squid, the paralarval (post-hatching) period tends to be the least well known. Because there is no buffering effect of older age classes, environmental effects on the extant generation are a particularly important feature of population dynamics, which has led to a focus on empirical rather than mechanistic models of abundance. In particular, we need to understand the relationship between spawning stock size and subsequent recruitment and pre-spawning mortality of recruits.

Data on squid may arise from fisheries, surveys, predators, tagging or direct observation: all have associated limitations and biases. Relevant considerations include availability, coverage, resolution (in time and space), accuracy and precision. Relevant environmental factors include large scale phenomena such as the *El Niño*-Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO), current systems, fixed physical phenomena such as seabed depth and substrate, oceanographic parameters such as sea surface temperature (SST) and salinity (SSS), meso-scale ocean surface (and sub-surface) features and daily, lunar and seasonal cycles. The selection of relevant variables is normally a compromise between biological relevance and data availability. The most readily available oceanographic data tend to be related to surface characteristics measured by satellite-based instruments, but it is also important to consider the vertical dimension. Developments in remote sensing, geographic information systems (GIS) and statistical modelling have all facilitated current modelling applications.

Empirical modelling is not without its critics: by focusing on the data rather than the underlying mechanisms it encourages data-driven rather than hypothesis-driven research. However, these are also advantages: hypotheses can be generated about the mechanisms and functional forms of relationships. As with all models, adequate testing of predictions is needed to eliminate spurious (coincidental) relationships: as noted by Solow (2002), time-series correlations often disappear once longer series become available, and similar caveats apply to spatial models.

Several generic issues apply to time-series and spatial modelling: these include model selection, model fitting, testing predictions, decisions about scale, incorporating environmental effects that are displaced in space and/or time (time-lags and teleconnections), autocorrelation, seasonal patterns and unexplained trends, interactions between variables, identification of data distributions, variance structure and linearity of relationships.

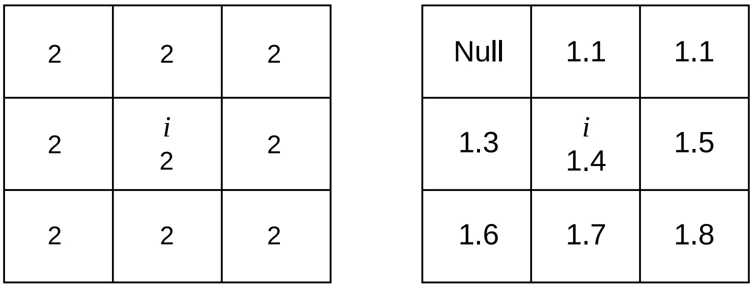
Time series can be modelled using regression, generalised linear or additive models (GLM or GAM), but such models may be invalidated by temporal auto-correlation, i.e. non-independence of adjacent values of the response variable, which can inflate apparent statistical significance by up to 400% (Zuur *et al.,* 2007). In short-lived species, the link between abundance or life history parameter values in successive generations (years) may be weak or non-existent. In the former case, inserting a term for the previous year's value as an extra explanatory variable into the model may adequately account for autocorrelation. Whether this is an issue can be confirmed by testing the model residuals for temporal autocorrelation. Otherwise, solutions include Generalised Additive Mixed Modelling (GAMM), Seasonal and Trend decomposition using Loess (STL), Autoregressive Integrated Moving Average Models (ARIMA) or Dynamic Factor Analysis (DFA, a multivariate extension of STL). On a cautionary note here, the autocorrelation, moving average, seasonal and trend terms in such models capture variation without explaining it. Environmental parameters may however, be included. Time-lagged relationships with environmental variables can also be detected using cross-correlation analysis; some authors recommend so-called "pre-whitening" (de-trending) of series prior to analysis. However, common trends thus removed may indicate a genuine causal link. Links between *Illex argentinus* abundance and ENSO events, with a 5-year time-lag were detected by Waluda *et al*. (1999).

ARIMA and DFA models of temporal trends in *Loligo forbesi* abundance have been published, and demonstrate effects of SST and the NAO index on abundance (Pierce and Boyle, 2003; Zuur and Pierce, 2004). However, these models tend to have low predictive power and, given the weak temporal structure of the squid time-series, approaches using regression, GAMs or regression trees, may be equally useful (e.g. Bellido *et al*., 2001; Waluda *et al*., 2001). Sims *et al*. (2001) used polynomial regression to demonstrate a link between timing of migration and the NAO index in *L. forbesi*. Pierce *et al*. (2005) used GAMs to extract interannual variation in size at maturity in *L. forbesi*, and then used correlation analysis to demonstrate that this residual variation could be related to the NAO index.

Spatial modelling has been greatly facilitated by GIS (Pierce *et al*., 2002). Routines have been developed to identify meso-scale ocean surface features from variability or discontinuities in temperature (Valavanis *et al*., 2005; Wang *et al*., 2007, see Figure 1), as well as from variability in temperature and chlorophyll anomalies (Valavanis *et al*., 2004a). It is also possible to incorporate temporal variation into such models, although to date, there has been little work modelling distribution in the vertical dimension. Data from tagging have allowed description of squid movements underwater, in relation to oceanographic data, and such data would be amenable to fitting models.

Essential habitat and migration corridor models may be constructed using an entirely GIS-based process, incorporating fishery and environmental data constrained by life history data on species' "preferred" living environmental conditions (Valavanis *et al*., 2002; Valavanis *et al*., 2004b). GAMs have been used to describe distribution patterns in both *L. forbesi* and *I. argentnus*, while regression trees have also been applied to data on *L. forbesi*, revealing relationships with temperature, salinity and depth (Pierce *et al*., 1998; Bellido *et al*., 2001; Sacau *et al*., 2005). Moreno *et al*. (in press) used GAMs to separate seasonal, annual and temperature effects on growth rates in *L. vulgaris*. The latter effects represent spatial variation in growth rates.

Where presence records are available (e.g. from predator samples or tags) but there are no absence records, presence only modelling techniques such as ENFA (Hirzel *et al*., 2000) may be applied. There are no current applications to data on squid.

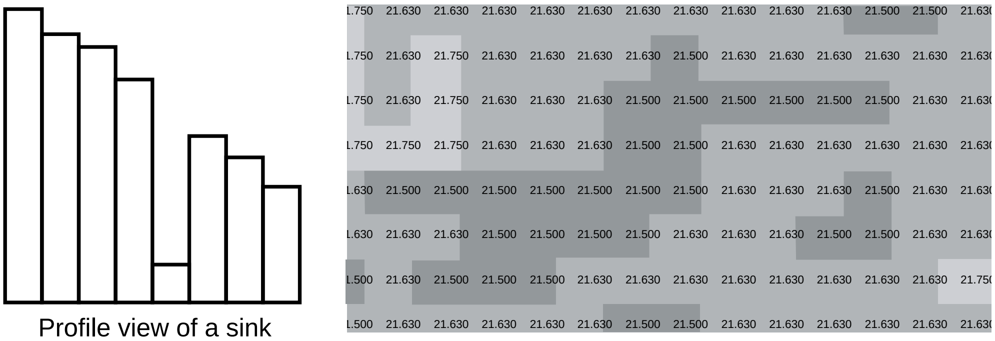


2	2	2
2	i 2	2
2	2	2

a) Local SST relative variability
$RV_i = 1/9 = 0.111$

Null	1.1	1.1
1.3	i 1.4	1.5
1.6	1.7	1.8

b) Local SST relative variability
$RV_i = 7/8 = 0.875$



Profile view of a sink

1.750	21.630	21.630	21.630	21.630	21.630	21.630	21.630	21.630	21.630	21.630	21.500	21.500	21.63
1.750	21.630	21.750	21.630	21.630	21.630	21.630	21.500	21.630	21.630	21.630	21.630	21.630	21.63
1.750	21.630	21.750	21.630	21.630	21.630	21.500	21.500	21.500	21.500	21.500	21.500	21.630	21.63
1.750	21.750	21.750	21.630	21.630	21.630	21.500	21.500	21.630	21.630	21.630	21.630	21.630	21.63
1.630	21.500	21.500	21.500	21.500	21.500	21.500	21.500	21.630	21.630	21.630	21.500	21.630	21.63
1.630	21.630	21.630	21.500	21.500	21.500	21.500	21.630	21.630	21.630	21.500	21.500	21.630	21.63
1.500	21.630	21.500	21.500	21.500	21.630	21.630	21.630	21.630	21.630	21.630	21.630	21.630	21.75
1.500	21.630	21.630	21.630	21.630	21.630	21.500	21.500	21.630	21.630	21.630	21.630	21.630	21.63

Figure 1. Use of AVHRR SST data to identify meso-scale ocean surface features. Right: calculating relative variability in SST (Wang *et al*., 2007). Below: identifying SST (and Chla) "sinks" (Valavanis *et al*., 2005).

As with time-series models, autocorrelation in spatial data is an important issue. Model residuals can be checked for spatial autocorrelation, and if none exists, spatial autocorrelation may be ignored. However, ideally, spatial autocorrelation should be included in the model (Pinheiro and Bates, 2000; Wood, 2004; Zuur *et al*., 2007) and this is possible using the software package R, among others. Latitude and/or longitude may be included in models as explanatory variables, although if these effects interact, results will be difficult to interpret. In any case, spatial trends revealed in this way are essentially unexplained trends.

Many of the published models of environmental variation in squid relate to demersal species, in which temperature, salinity and large-scale phenomena (e.g. NAO) have been shown to influence distribution, abundance and life history parameters. While the role of mesoscale ocean surface features was not analysed in these studies, generally because the relevant data were not available, recent analysis has shown that local variability in SST (presumed to be related to fronts) affects hake distribution in the south west Atlantic (Wang *et al*., 2007).

Pelagic squid such as *D. gigas* tend to occur more remotely from land and are less well known than demersal squid. Less dependent on the substrate, they produce many more eggs, with the eggs being pelagic rather than attached to the seabed, hence strongly dependent on currents for dispersal. They tend to be highly migratory and might be expected to show stronger associations with meso-scale ocean surface features and have more variable abundance patterns.

Useful goals for environmental modelling in *D. gigas* would include improved understanding of egg and paralarval distribution, recruitment success and limits to distribution. Tagging data should facilitate 4-dimensional (in space and time) modelling of individual movement patterns. Useful parallels could be drawn from comparative studies on European ommastrephid species such as *Todarodes sagittatus*.

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