Abundance trends of two neon flying squid (*Ommastrephes bartramii*) stocks in the North Pacific

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Two stocks of neon flying squid (*Ommastrephes bartramii*) have been identified in the North Pacific, with differing life-history traits and geographic distributions, one in the Northeast Pacific and the other in the Northwest Pacific, each with seasonal cohorts. Both stocks are targeted by commercial fishing fleets from China, Japan, and Taiwan. The variability in abundance for each stock has been studied independently, but a comparable analysis between the two stocks is lacking. The abundance trends for the two stocks were examined using catch data from the Taiwanese squid fishery between 1986 and 2006. A time-series of monthly catch per unit effort and three explanatory variables, sea surface temperature in the presumed hatching grounds, the Southern Oscillation Index, and the number of vessels, were analysed using dynamic factor analysis to quantify squid abundance. The optimal model contained one common trend and all three explanatory variables. The Northwest Pacific and Northeast Pacific stocks exhibited opposing trends in abundance, and the results suggest that large-scale environmental factors, rather than regional factors, are more critical in influencing the abundance of oceanic squid species.

Keywords: abundance, dynamic factor analysis, North Pacific, *Ommastrephes bartramii*, squid fishery.

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Introduction

The neon flying squid, *Ommastrephes bartramii*, also known as the red flying squid, is an oceanic species distributed worldwide in subtropical and temperate waters (Roper *et al.*, 1984). In the North Pacific, it has been commercially exploited by Japanese fishers since 1974, when catches of the Japanese common squid *Todarodes pacificus* were in drastic decline (Araya, 1983; Murata, 1990). The Taiwanese fishing fleet began harvesting neon flying squid in 1977, initially by jigging, but in 1980 using large driftnets imported from Japan. Because of the low cost and great efficiency of this means of fishing, the driftnet became the main fishing gear used by the squid fishery on the North Pacific high seas during the 1980s (Yeh and Tung, 1993). However, owing to controversy over large-scale driftnet harvesting and its inherent problems of incidental catch and non-selective nature of harvesting, driftnetting was deemed unsustainable and a threat to marine resources and the ecosystem as a whole. After a moratorium on driftnet fishing was put into effect at the end of 1992, neon flying squid in the North Pacific were harvested thereafter by jig, starting in 1993.

China started its fishery for neon flying squid in 1994, and the fishery developed rapidly, the escalating catch accounting for >90% of the total production of neon flying squid (Chen *et al.*, 2007b). The annual driftnet catch of neon flying squid was estimated to be 248 000–378 000 t between 1985 and 1990 (Gong *et al.*, 1993; Yatsu *et al.*, 1993; Yeh and Tung, 1993), but the annual jig catch was just 100 000–200 000 t between 1994 and 2004 (Chen *et al.*, 2007b).

The North Pacific population of neon flying squid consists of two seasonal cohorts, an autumn cohort hatching from September to February and a winter–spring cohort hatching from January to August (Yatsu *et al.*, 1997). Age determination by statolith microstructure suggests that both cohorts have a 1-year lifespan (Yatsu *et al.*, 1997; Chen and Chiu, 2003). The autumn cohort grows to a relatively large size (mantle length, ML, ≥35 cm) in June–September on the feeding grounds. The large size of the autumn cohort has been attributed to the faster growth rate in the early stages of life when the squid develop in an environment of higher water temperature (Chen and Chiu, 2003), or when they are spawned in an environment richer in nutrients (Ichii *et al.*, 2004, 2009). Nearly all the larger squid of the autumn cohort found on the feeding grounds are female, which could suggest size-segregated migration patterns for squid populations, wherein the sexes are of different size (males attain maturity and stay in the subtropical regions whereas females migrate towards Subarctic regions; Ichii *et al.*, 2009). The feeding grounds of the autumn cohort are just east of 170°E (the NE stock of Chen and Chiu, 2003).

The autumn cohort was once the main target of the driftnet fishery. In contrast, the winter–spring cohort is currently the main target for the jig fishery. The winter–spring cohort is generally smaller (ML <35 cm) in the period June–September. The feeding grounds of the winter–spring cohort are distributed right across the North Pacific. The neon flying squid caught west of 170°E are considered to be a part of the winter–spring cohort (the NW stock of Chen and Chiu, 2003).

The abundance and distribution of cephalopod stocks are influenced by changes in environmental conditions (Robin and Denis, 1999; Waluda *et al.*, 1999, 2001a, b; Dawe *et al.*, 2000; Sakurai *et al.*, 2000; Anderson and Rodhouse, 2001; Wang *et al.*, 2003; Waluda and Rodhouse, 2006; Chen *et al.*, 2007a, b). This may be attributed to their short lifespan, which consequently creates greater sensitivity and rapid response to variations in the environment (Boyle and Rodhouse, 2005; Pierce *et al.*, 2008).

The variability in *O. bartramii* abundance and the potential factors affecting it have been fairly well studied. The abundance of the autumn cohort has been influenced by driftnet fishing mortality and sea surface temperature (SST) at the prerecruitment stage (Yatsu *et al.*, 2000). The abundance of the winter–spring cohort, on the other hand, has been explained by ocean-climate variability of large-scale events (*El Niño/La Niña*) and regional-scale events such as SST on the spawning grounds (Chen *et al.*, 2007b), or by the proportion of areas with favourable SST, a factor which explained ~60% of the variability in squid abundance between 1995 and 2004 (Cao *et al.*, 2009). However, the interannual variability in abundance between the two cohorts is seldom compared at the same time.

Dynamic factor analysis (DFA) is a dimension-reduction technique for analysing time-series data. It can be applied to relatively short periods of time (15–25 years), with non-stationary (not constant or persistent) time-series, and can identify the common patterns with explanatory variables included (Zuur *et al.*, 2003a). DFA has been applied in the fields of hydrology (Muñoz-Carpena *et al.*, 2005; Ritter and Muñoz-Carpena, 2006) and phenology (Gordo and Sanz, 2005). Zuur *et al.* (2003b) first applied DFA to fisheries data in exploring landings trends of *Nephrops* in European waters. Recently, it has been applied to identify landings trends in the fisheries of southern Portugal and to explore possible environmental variables (Erzini, 2005), the latent temporal patterns in Mauritanian trawl survey data and the influence of relevant environmental factors (Erzini *et al.*, 2005), and the abundance trends of *Loligo* spp. in the Northeast Atlantic (Zuur and Pierce, 2004; Chen *et al.*, 2006). The results of these studies demonstrate that DFA is an adequate and reliable technique for analysing fisheries time-series data, which sometimes suffers from relatively short time-series and are hampered by their non-stationary nature.

Addressing the variability of stock abundance and the potential contributing factors is essential in proposing effective management measures for squid fisheries, which are always characterized by wide annual fluctuations in production. Here, DFA was applied to identify the latent abundance trends for the two stocks (cohorts) of neon flying squid in the North Pacific, using catch data from the Taiwanese squid fishery between 1986 and 2006. Possible influences of the environment and fisheries were explored in the DFA model to explain the variability in neon squid stock abundance.

Material and methods

Squid data

The data used are from the squid fishery database maintained at the Fisheries Agency, Council of Agriculture of Executive Yuan, Republic of China (Taiwan). The data records consist of fishing dates, locations, and catches of squid (by weight) over the period 1986–2006. The catch data were compiled in a geographic reference format with a unit statistical grid of 0.5° (0.5° longitude by 0.5° latitude). Catch per unit effort (cpue) was calculated as the weight of squid caught per vessel per day (i.e. t vessel-day^{-1}). The Taiwanese squid fleet consists of vessels of similar size (700–800 grt), manned with similar numbers of fishers (30–40), and equipped with similar jigging machines (40–60 sets) and lamp power (300–400 kW). Fishing operations are conducted at night from about 18.00 to 06.00. There is no bycatch in the fishery because of the selectivity of the jig as a fishing gear. Hence, because the fishing power of vessels in the fleet was fairly homogenous, cpue can be used as a reasonable index of squid abundance.

During the study period, there were two types of fishing gear used by the Taiwanese squid fleet: a driftnet during the period 1986–1992 and jigs from the start of 1993. There were no periods when both fishing methods were employed, but to construct a single time-series from the data, conversions factors between the two gears were required. During the early stage of the Taiwanese squid fishery (1982–1983), both fishing methods were employed on the fishing grounds, and sometimes two vessels operated quite close to each other, and it was reasonable to assume that they were fishing a resource of similar abundance. Data collected during that period therefore gave us an opportunity to compare the fishing efficiency of the two types of fishing gear. The conversion factors were calculated from comparative data collected from vessels operating in the same fishing rectangles of 0.5° within the broader region 34–46°N 145–175°E. The median of all possible comparisons (ratios of the two vessels' cpue) was used as a conversion factor (Chen and Chiu, 2009). The conversion factors (driftnet to jig) ranged from 0.59 to 2.78 in 1982 and from 0.62 to 1.65 in 1983 (Figure 1), and the average annual values over the 2 years were used to convert driftnet cpue to an equivalent jig cpue.

The two seasonal cohorts (autumn and winter–spring) of *O. bartramii* can be identified from their distribution on the feeding grounds (Yatsu *et al.*, 1998). Squid caught east of 170°E (the NE stock) comprise the autumn cohort, and those caught west of 170°E (the NW stock) comprise the winter–spring cohort (Yatsu *et al.*, 1998; Chen and Chiu, 2003). The terms NE stock and NW stock are used hereafter to represent the squid caught in different geographic regions, and also to correspond to the two seasonal cohorts.

The original monthly series of squid cpue showed large interannual fluctuations, so the data were log-transformed to reduce the effect of extreme values. The monthly squid cpue series was standardized by subtracting the long-term (1986–2006) monthly mean and dividing by the standard deviation. Each series was centred to zero and unit-less. Eight monthly time-series were

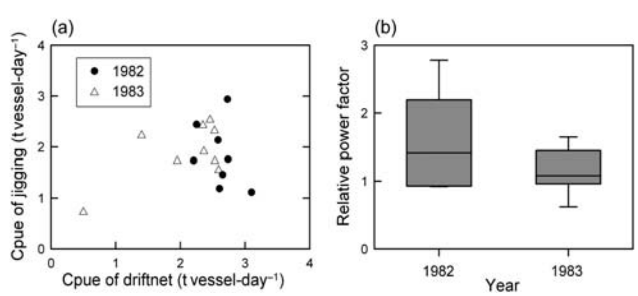

Figure 1. (a) Cpue values by 0.5° latitude and longitude blocks of driftnet and jigging vessels in the western North Pacific (34–46°N 145–175°E) in 1982 and 1983, and (b) the calculated relative power factors (driftnet/jigs).

used in the study, three for the NE stock (from June, July, and August), and five for the NW stock (from July to November).

Environmental data

The presumed spawning grounds for the two stocks of *O. bartramii* are located in the area 20–30°N 130–170°W, and 20–30°N 130–170°E, based on hatching dates, presumed migratory routes, and collection sites of paralarvae (Young and Hirota, 1990; Hayase, 1995; Bower, 1996). Monthly SST data were obtained from the website for the Joint WMO/IOC Technical Commission for Oceanography and Marine Meteorology Products Bulletin Data Products (http://iridl.ldeo.columbia.edu/sources/.igoss/.data_products.html). The spatial resolution is 1° latitude and longitude. SST data for the period 1985–2006 were used in the analysis. Monthly SST values were averaged for all regions (the presumed spawning grounds), and standardized by the long-term (1985–2006) monthly mean and standard deviation (denoted as SST_E and SST_W for the NE and NW stocks, respectively). Average monthly SST ranged from 21.5 to 25.2°C and from 22.7 to 28.8°C for SST_E and SST_W, respectively. Peak hatching months for the NE and NW stocks are October and November, respectively (Chen and Chiu, 2003). Therefore, SST_E in October and SST_W in November were selected to represent the SST conditions during the hatching period.

Monthly Southern Oscillation Index (SOI) data were obtained from the Climate Research Unit, University of East Anglia, UK (http://www.cru.uea.ac.uk/). The SOI anomaly was calculated as the difference in sea level air pressure between Tahiti in the central Pacific (17°37′S 149°27′W) and Darwin, Australia (12°25’S 130°51’W), using the method of Ropelewski and Jones (1987). Data from January 1986 to December 2007 were used in the analysis.

Dynamic factor analysis

DFA is a multivariate time-series analytical technique used to identify underlying common trends in a set of time-series. The DFA model can be written as

$$y_t = A \times z_t + B \times x_t + e_t, \tag{1}$$

where y_t is a matrix containing the value of the N time-series at time t, z_t a matrix containing the values of the M common trends at time t, A the factor loadings (an $N \times M$ matrix), x_t a matrix containing values for the explanatory variables, B represents the regression parameters for each explanatory variable, and e_t the noise components. Detailed information on the DFA model can be found in Zuur *et al.* (2003a).

The model assumes that $e_t \sim N(0, \mathbf{R})$, where $\mathbf{R}$ is the error covariance matrix. The magnitude and sign of the factor loadings (A) determines how these trends are related to the original time-series data. The regression parameters (B) and their standard errors indicate the influence of the explanatory variables on the time-series. Two options exist for modelling $\mathbf{R}$, using a diagonal or a symmetric non-diagonal matrix. The elements of a symmetric non-diagonal matrix represent the information that cannot be explained by the common trends and explanatory variables.

A series of models was tested, including combinations with and without explanatory variables, and a diagonal or symmetric non-diagonal error covariance matrix (Table 1). The Akaike information criterion (AIC) was used for model selection (Zuur *et al.*, 2003a, b). It judges the degree of fit (maximum likelihood) and the number of parameters (number of trends, explanatory variables, and the structure of matrix $\mathbf{R}$) that should be used. Here, the DFA model with the smallest AIC value was taken to be the optimal model. DFA was performed using the software package Brodgar version 2.5.7 (Highland Statistics Ltd, http://www.brodgar.com).

Relationships between common trends in squid abundance and environmental variables identified using the DFA model were further explored to determine whether there were time-lag effects, using a combination of simple- and cross-correlation analyses. Spearman's correlation coefficient was calculated between monthly SST series and estimated common trends. For SOI series, because of the difficulty in interpreting monthly series, cross correlations between common trends and SOI were calculated to detect time-lag effects yearly.

Results

The transformed and standardized monthly squid cpue series were characterized by considerable interannual variability (Figure 2), and there were differences between months for both stocks. For comparable data in July and August, the temporal patterns of the NE and NW stocks were similar in some years (1989–1992),

Table 1. Values of the AIC for DFA models with 1–3 common trends and 0–3 explanatory variables.

Model	Number of trends (*M*)				
	Diagonal matrix			Symmetric non-diagonal matrix	
Explanatory variable(s)	1	2	3	1	2
M common trends + noise	426.767	425.643	437.639	414.138	426.022
M common trends + explained var(s) + noise					
SST_E	433.883	435.193		420.227	428.876
SST_W	431.937	431.498	443.803	425.433	435.391
SOI	425.683	433.608		404.449	419.831
Number of vessels	414.865	425.116		407.598	416.345
SST_E + SOI	431.503	434.409		403.820	413.671
SST_E + number of vessels	424.208	434.434		414.931	421.751
SOI + number of vessels	414.916	428.916		392.992	402.577
SST_E + SOI + number of vessels	423.036	422.047	427.619	**384.359**	397.484

The lowest AIC value of the model is shown emboldened.

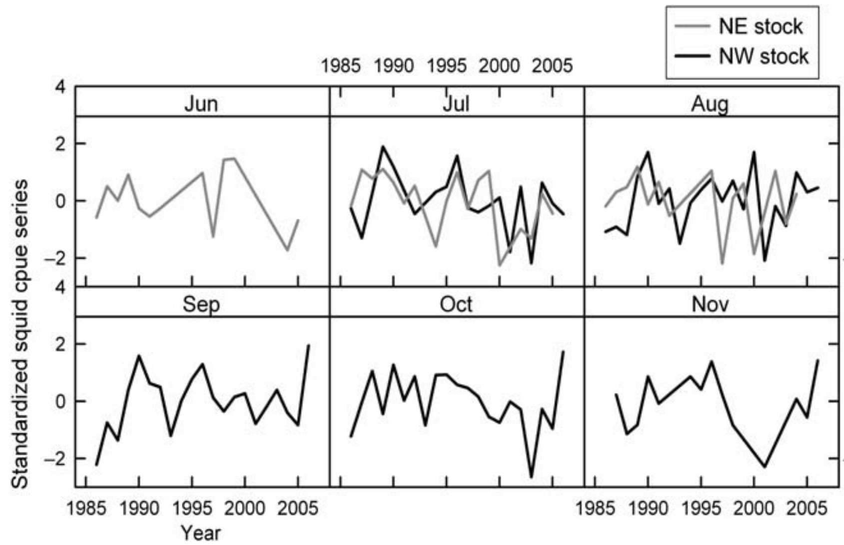

Figure 2. Standardized monthly cpue series for the NE (grey line) and NW (black line) stocks of *O. bartramii* in the North Pacific from the Taiwanese squid fishery.

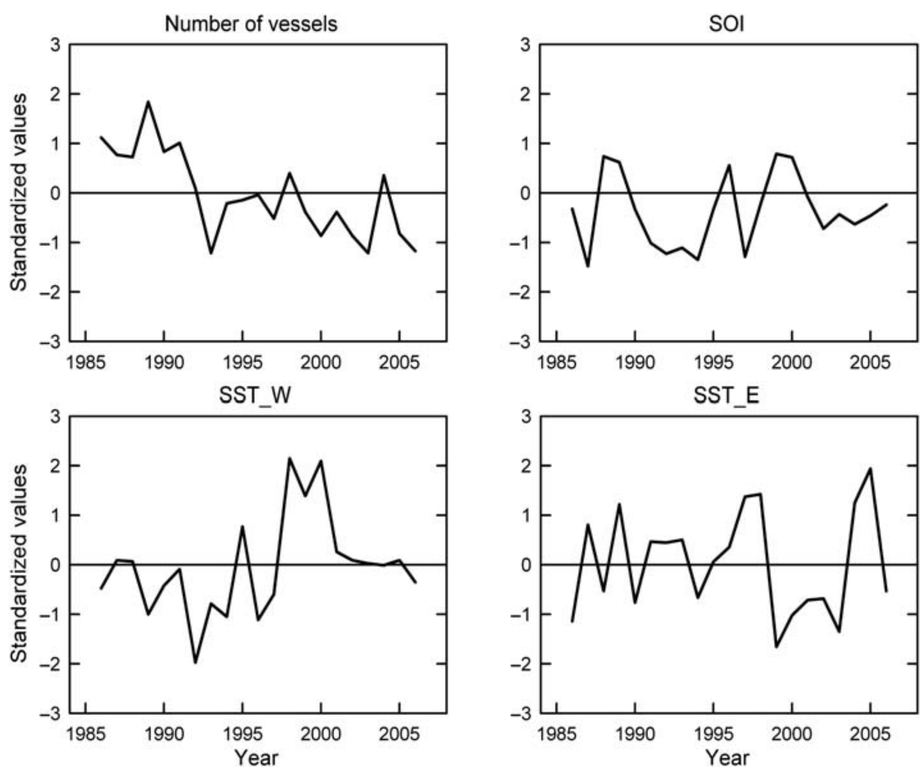

Figure 3. The explanatory variables used in the model. The standardized time-series of number of vessels, the SOI, and SST in the eastern (20–30°N 170–130°W, SST_E in October) and western (20–30°N 130–170°E, SST_W in November) North Pacific.

but different in others (1993–1995 in July, and 1997 and 2000 in August).

The number of vessels decreased dramatically during 1992 and 1993 when the fishing gear shifted from driftnet to jig (Figure 3). Negative SOI values are a response to *El Niño* events, significant correlations of which occurred in 1987, 1992–1994, and 1997 (Figure 3). The SST_W and SST_E series showed different patterns. The SST_W series showed a decrease from 1986 to 1992, increased during 1990–2000, then stabilized thereafter. The SST_E series was stable during the 1990s, followed by low temperatures during 1999–2003, an increase in 2005, then stable (Figure 3).

The model that included both SST series (SST_W and SST_E) was less satisfactory than the model containing either of the SST series in isolation. In addition, SST_W showed co-linearity with SST_E and SOI, which suggested that a model containing both

SST series is unstable. Therefore, only SST_E was selected for models including more than two explanatory variables. In general, models based on a symmetric non-diagonal covariance matrix gave better fits (lower AIC values) than those based on a diagonal covariance matrix (Table 1). The optimal model for only one explanatory variable was that using SOI (1 common trend, AIC = 404.449; 2 common trends, AIC = 419.831) and based on a symmetric non-diagonal covariance matrix (Table 1). The optimal model, evaluated by the smallest AIC values, was the one with a single common trend and three explanatory variables under a symmetric non-diagonal covariance matrix (1 common trend, AIC = 384.359; 2 common trends, AIC = 397.484).

The pattern of the first common trend in the two-trend model is similar to that of the one-trend model, which suggested that the temporal pattern in the first common trend is essential for the time-series (Figure 4). The common trend shows an increase from 1986 to 1992, a slight decline during 1992 and 1993, a dramatic decrease from 1995 to 1998, and an increase again in 1998 and thereafter. The canonical correlations between the original squid abundance series and the estimated trend demonstrate that the common trend correlates positively with the monthly series of NW stock abundance (w_jul, w_aug, w_sep, w_oct, and w_nov), but negatively with the monthly series of NE stock abundance (e_jun and e_jul; Figure 4). The common trend therefore characterizes the general fluctuation pattern of NW stock abundance in the North Pacific.

Usually, the fits between the values observed and the fitted curves for the models were reasonable (Figure 5). In general, the data for the NW stock fitted better than those of the NE stock. The normality test for the residual distribution (data not shown) suggested that the differences between estimated and observed data did not deviate significantly from normality at a 5% level of significance (Kolmogorov–Smirnov test statistic = 0.1055–0.1502, Lilliefors $p = 0.1608–0.8659$), which indicates a good fit for the estimated model.

There were no significant relationships between SST and the monthly series of squid abundance (Table 2; note that a t-value

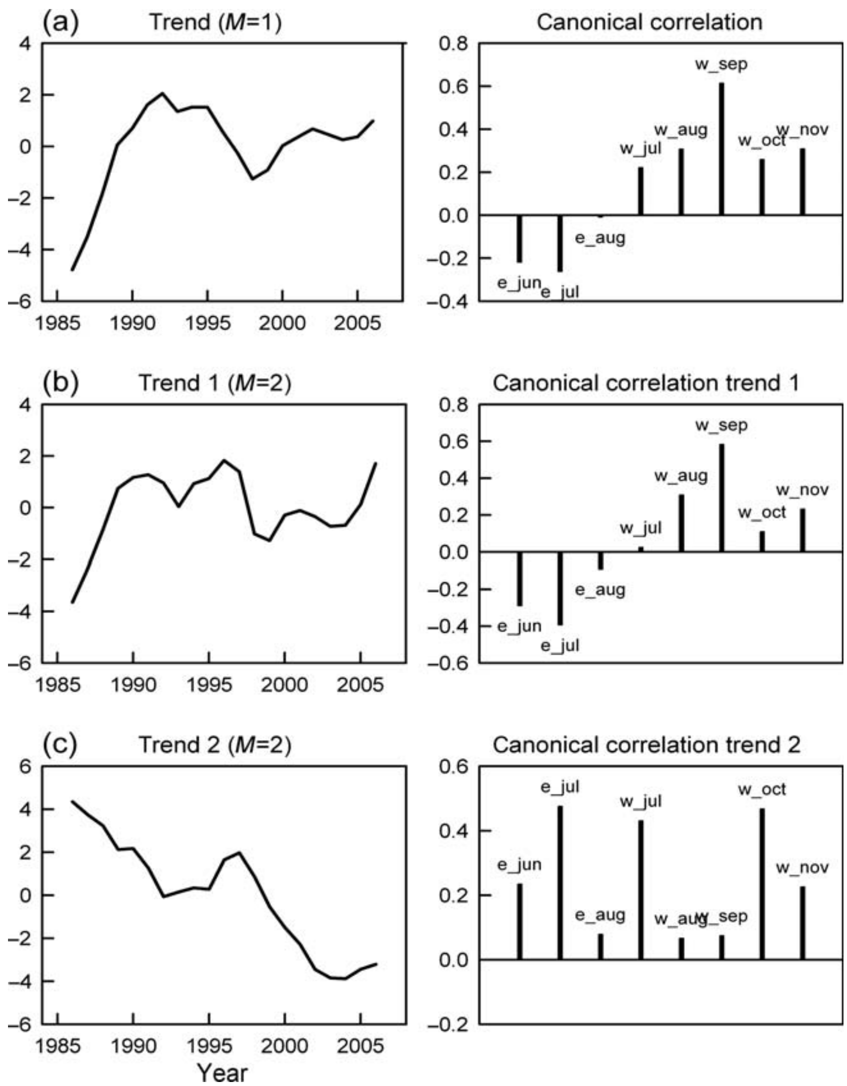

Figure 4. (a) Common trend (left) and canonical correlation (right) for the optimal DFA model with three explanatory variables. (b) Common trend 1 (left) and canonical correlation (right), and (c) common trend 2 (left) and canonical correlation (right) for the two-trend model with three explanatory variables. Series labels are as in Table 2. Correlations less than −0.5 or >0.5 are significant ($p < 0.05$).

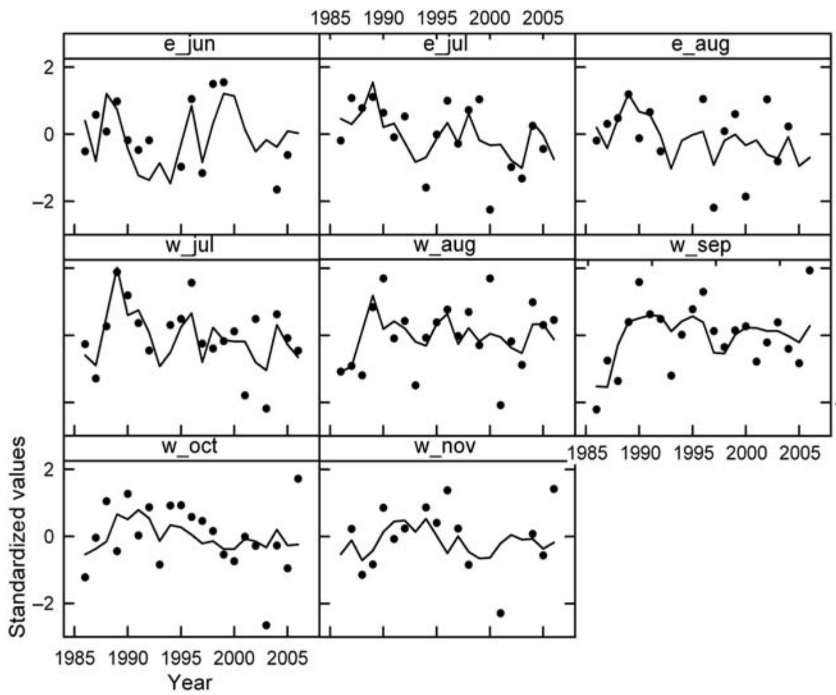

Figure 5. Fitted values (lines) and standardized observed values (dots) for the cpue series of the NE and NW stocks of *O. bartramii*. The labels for each graph are as in Table 2.

Table 2. Estimated regression parameters and *t*-values for the explanatory variables (SST, SOI, and number of vessels) in the optimal DFA model.

Squid series	SST_E		SOI		Number of vessels	
	Estimate	*t*-value	Estimate	*t*-value	Estimate	*t*-value
e_jun	0.103	0.351	**1.094**	**2.688**	−0.186	−0.520
e_jul	0.239	1.285	0.350	1.359	**0.511**	**2.311**
e_aug	−0.144	−0.747	0.225	0.859	**0.690**	**2.930**
w_jul	0.163	0.947	**0.588**	**2.482**	**0.695**	**3.184**
w_aug	0.246	1.222	0.460	1.645	0.226	0.935
w_sep	−0.106	−0.539	0.222	0.815	0.152	0.592
w_oct	−0.021	-0.098	−0.065	−0.219	0.392	1.532
w_nov	−0.100	−0.424	−0.432	−1.321	0.144	0.514

Significant values are shown emboldened.
e_month denotes the monthly abundance series for the NE stock of *O. bartramii* from June to August, and w_month the monthly abundance series for the NW stock from July to November.

Table 3. Spearman's correlation coefficient (*r*) between common trends of squid abundance and monthly SST.

Variables	*n*	Trend and SST_W		Trend and SST_E	
		Spearman *r*	*p*-value	Spearman *r*	*p*-value
SST_Jan	21	−0.112	0.628	0.037	0.873
SST_Feb	21	0.014	0.953	−0.297	0.191
SST_Mar	21	−0.029	0.900	−0.319	0.159
SST_Apr	21	-0.108	0.640	0.151	0.513
SST_May	21	0.018	0.940	0.082	0.722
SST_Jun	21	0.064	0.782	−0.051	0.825
SST_Jul	21	0.185	0.422	−0.068	0.769
SST_Aug	21	0.045	0.847	−0.095	0.681
SST_Sep	21	−0.150	0.516	−0.128	0.580
SST_Oct	21	−0.205	0.374	0.002	0.993
SST_Nov	21	−0.234	0.306	0.086	0.710
SST_Dec	21	−0.415	0.061	0.003	0.989

n is the sample size.

of ~2.0 is significant at a 5% significance level). The SOI series was positively related to the NE stock in June and to the NW stock in July. The series for number of vessels was positively related to the NE stock for July and August and to the NW stock for July (Table 2).

The common trend of squid abundance was compared against monthly SST series (SST_W and SST_E) to examine possible lag SST effects on squid abundance. However, there were no significant correlations between the common trend and monthly SST series (Table 3). Cross correlation calculated between SOI and the common trend indicates a negative correlation at a lag of 2 years (Figure 6; positive lag, SST leading squid trend). No significant correlations were found between SST_E and the common trend of squid abundance (Figure 6).

The estimated common trend of squid abundance was compared with the published data for the abundance of *O. bartramii* from Japan (Bower and Ichii, 2005) and China (Chen *et al.*, 2007b). Although there was no significant correlation between these squid abundance series (Spearman's correlation coefficients = −0.346 to 0.373, $p = 0.155–0.974$), some temporal patterns were similar (Figure 7), there was a slight decrease during 1992 and 1993 (common trend and the winter–spring cohort from Japan), an apparent decrease during 1995 and 1996, and 1997 and 1998 (common trend and the winter–spring cohort from Japan), and an increase after 2001 (common trend and the winter–spring cohort from China).

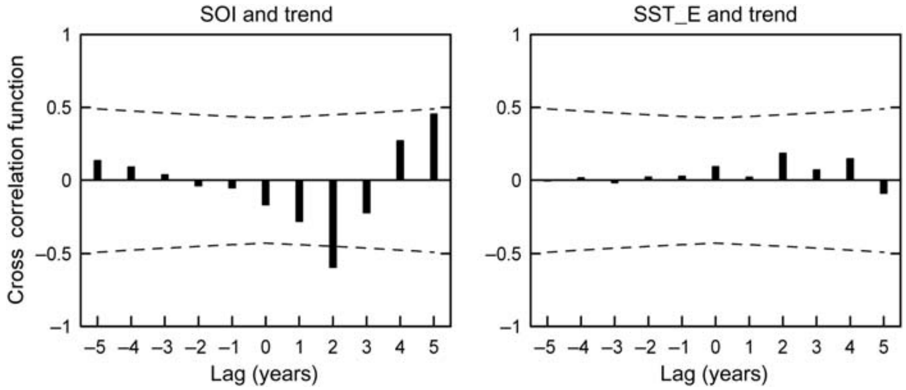

Figure 6. Cross correlation functions between common trends of squid abundance and environmental variables: SST in the eastern North Pacific (20–30°N 130–170°W, SST_E) and the SOI series. A positive lag (0–5 years) indicates the environmental variable leading the squid abundance trend, and a negative lag (0 to −5 years) the squid abundance trend leading the environmental variable. Dashed lines are 95% confidence intervals.

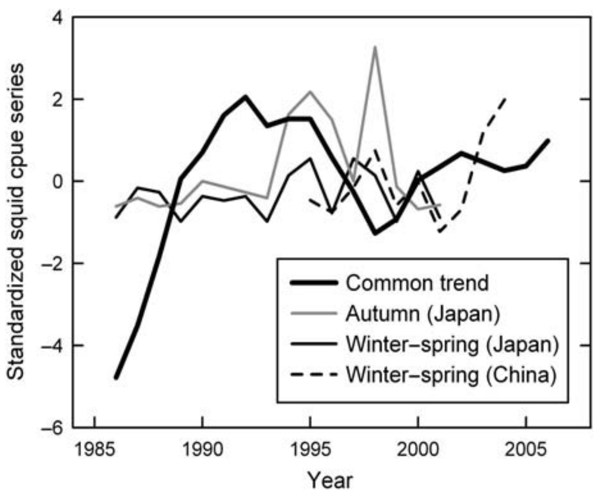

Figure 7. Temporal variations of abundance for *O. bartramii* stocks in the North Pacific (common trend, this study; Japan data, extracted from Bower and Ichii, 2005; China data, extracted from Chen *et al.*, 2007b). Squid abundance was standardized using the mean and the standard deviation.

Discussion

Two stocks (cohorts) of *O. bartramii* have been identified in the North Pacific (Yatsu *et al.*, 1997; Chen and Chiu, 2003). The variability in abundance of each of these stocks has been suggested to be related to changes in environmental and fisheries variables (Yatsu *et al.*, 2000; Chen *et al.*, 2007b; Cao *et al.*, 2009), but comparable analyses between the two stock have yet to be published. I applied DFA to analyse catch data from the Taiwanese squid fishery over a period of 21 years to identify trends in abundance trends of both *O. bartramii* stocks in the North Pacific and the potential influences of environmental and fisheries factors. The estimated common trend of squid abundance suggested that the two stocks showed contrasting temporal patterns over the past two decades. SST, the SOI, and the number of vessels were included as explanatory variables in the optimal DFA model. The SOI and the number of vessels were positively related to squid abundance in June and July, and in July and August, respectively. The SOI showed a lag effect on the common trend of squid abundance.

Although normality of time-series data is not essential for DFA modelling, it is beneficial to model performance (Zuur *et al.*, 2003b). The wide fluctuations in annual production of squid stocks are generally attributed to the species' short life and hence their vulnerability to changes in environmental conditions (Rodhouse, 2001; Boyle and Rodhouse, 2005). In this study, the monthly series of squid abundance were log-transformed to reduce the influence of extreme values. A normality test of residuals suggested a good fit in the DFA models, particularly for the abundance series of the NW stock, which apparently has a longer series of datapoints.

The estimated common trend in the optimal DFA model characterizes the fluctuating abundance patterns of the NW stock of *O. bartramii* in the North Pacific (Figure 4), which increased during the years 1986–1992, decreased sharply from 1995 to 1998, then increased again after 1998, a pattern in contrast to that of the NE stock. The resource was harvested by driftnet from 1980 to 1992, when it was the NE stock targeted mainly. As stated above, the annual catch of *O. bartramii* by driftnet fisheries was an estimated 248 000–378 000 t during the years 1985–1990 (Gong *et al.*, 1993; Yatsu *et al.*, 1993; Yeh and Tung, 1993), and based on Japanese driftnet fishery data, the autumn cohort (NE stock) was estimated to have produced 330 000–380 000 t annually during the years 1982–1992 (Ichii *et al.*, 2006). Based on this assessment, Ichii *et al.* (2006) suggested that large-scale driftnetting could be considered to be sustainable. However, a low cpue for the autumn cohort (the NE stock) was evident during the period of intensive commercial driftnetting (1980–1992) using research driftnet data from 1979 to 1998 (Yatsu *et al.*, 2000). The common trend in the DFA model of this study suggests a decreasing trend in the NE stock during the driftnetting period (1986–1992), opposite to the increasing trend in the NW stock for the same period. This suggests that the fishing operation may have played a large role in the abundance variations of the NE stock during the period of driftnet fishing.

Some common temporal patterns of *O. bartramii* abundance are clear between estimated common trend and published abundance data from Japan and China (Figure 7). A moratorium was imposed on high seas large-scale driftnet fishing at the end of 1992. Thereafter, *O. bartramii* in the North Pacific was harvested by jig, starting from 1993, when the NW stock was targeted. The transition in fishing gear (from driftnet to jigs) and corresponding fishing targets (from the NE stock to the NW stock) of the *O. bartramii* fisheries may have resulted in heterogeneous effects on the abundance for the two stocks. The cpue of the autumn cohort (NE stock) increased after 1992 (Yatsu *et al.*, 2000), but no studies on abundance of the NW stock were conducted during the period of fishing gear transition. The common trend of this study has indicated a slight decrease in abundance of the NW stock as driftnet fishing was phased out (1992–1994). The same temporal pattern is clear in the cpue variation of the winter–spring cohort (the NW stock) from Japanese driftnet research data (Figure 7).

China's squid fishery started jigging for *O. bartramii* in 1994. With a fleet of >400 jigging boats, China's annual catch has accounted for >90% of the total catch of the species in the North Pacific since 1996 (Chen *et al.*, 2008b). The annual catch of *O. bartramii* in the North Pacific by jig fisheries was 100 000–200 000 t during the years 1994–2004 (Chen *et al.*, 2007b). The initial population sizes were estimated to be between 199 and 704 million individuals (assuming natural mortality of 0.03–0.10) during the period 2000–2005, and the annual maximum allowable catch ranged from 80 000 to 100 000 t (Chen *et al.*, 2008a). The NW stock decreased sharply between 1995 and 1998, and a similar pattern was evident from Japanese data, which show a decrease in the winter–spring cohort in 1995 and 1996, and from 1997 to 1999 (Bower and Ichii, 2005; Figure 7). The rapid development of the Chinese squid fishery in the North Pacific may therefore have had a substantial effect on the NW stock.

The estimated regression parameters and *t*-values in the DFA model indicated that the NE stock in July and August and the NW stock in July are positively related to the number of vessels involved in harvesting (Table 2). The Taiwanese squid fleet usually heads to the eastern North Pacific (east of 170°E) at the beginning of the fishing season (May and June), and hence exploits the NE stock of *O. bartramii*. In the middle of the fishing season (July and August), the vessels move to the western North Pacific (west of 170°E), so are pursuing the NW stock. Meanwhile, some of the vessels may switch their fishing gear and head off to harvest Pacific saury (*Cololabis saira*), if squid yield is low from the outset. The positive relationship between squid abundance and the number of vessels involved in harvesting seems to suggest that the number of fishing vessels harvesting squid depends annually on the squid abundance at the start of each fishing season. However, further detailed fishery data are needed to address this interaction with initial squid abundance in a rigorous manner.

The effects of environmental variability on the abundance and distribution of cephalopod stocks have been evident not only on a regional scale (e.g. SST in spawning and feeding grounds), but also on a larger scale, such as those of *El Niño* and *La Niña* events (e.g. Waluda *et al.*, 1999; Yatsu *et al.*, 2000; Chen *et al.*, 2007b). Large-scale environmental indices can sometimes explain natural processes better than local ecological factors, because they usually reflect the combination of effects in environmental variability and their substantially impact on ecological processes (Hallett *et al.*, 2004). In this work, the estimated regression parameters of SST (SST_E in October) in the DFA model showed no significant relationship with squid abundance, whereas the SOI was positively related to the NE stock in June and to the NW stock in July. This may imply that composite effects of environmental conditions, rather than local environmental factors, are more critical in determining the fluctuating abundance of oceanic squid species such as *O. bartramii* in the North Pacific. The SOI also negatively lagged by 2 years the common trend of squid abundance. The negative SOI values are related to *El Niño* events that would lead to an increase in abundance of the NW stock (winter–spring cohort) by decreasing SST on the spawning grounds (Chen *et al.*, 2007b), or by increasing the proportion of areas with favourable SST (Cao *et al.*, 2009). However, the potential effects of the SOI on squid abundance, and specifically its variability, need to be examined explicitly when long-term, wide-scale data on squid abundance become available.

Currently, no organization is invested with a legal mandate for dealing with the conservation and management issues involving *O. bartramii* in the North Pacific. However, the variability in abundance of the two stocks assessed here suggests that multiple approaches to fisheries management should be considered. Although there have been a number of studies on population structure and abundance variability of the species from Japan (Yatsu *et al.*, 1997; Ichii *et al.*, 2006, 2009), Taiwan (Chen and Chiu, 1999, 2003), and China (Chen *et al.*, 2007b, 2008b; Cao *et al.*, 2009; Fan *et al.*, 2009; Tian *et al.*, 2009), these studies may provide only part of the information on the stock dynamics of *O. bartramii* in the North Pacific. For rapidly developing fisheries, it is necessary to gather and analyse data under a regional fisheries management organization or within the international community. This is essential not only for developing greater understanding of the population ecology of *O. bartramii*, but also for ensuring the sustainable development of its fisheries.

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References

Anderson, C. I. H., and Rodhouse, P. G. 2001. Life cycles, oceanography and variability: ommastrephid squid in variable oceanographic environment. Fisheries Research, 54: 133–143.

Araya, H. 1983. Fishery, biology and stock assessment of *Ommastrephes bartrami* in the North Pacific Ocean. Memoirs of the National Museum of Victoria, 44: 269–283.

Bower, J. R. 1996. Estimated paralarval drift and inferred hatching sites for *Ommastrephes bartramii* (Cephalopoda: Ommastrephidae) near the Hawaiian Archipelago. Fishery Bulletin US, 94: 398–411.

Bower, J. R., and Ichii, T. 2005. The red flying squid (*Ommastrephes bartramii*): a review of recent research and the fishery in Japan. Fisheries Research, 76: 39–55.

Boyle, P. R., and Rodhouse, P. G. 2005. Cephalopods: Ecology and Fisheries. Blackwell Science, Oxford. 451 pp.

Cao, J., Chen, X., and Chen, Y. 2009. Influence of surface oceanographic variability on abundance of the western winter–spring cohort of neon flying squid *Ommastrephes bartramii* in the NW Pacific Ocean. Marine Ecology Progress Series, 381: 119–127.

Chen, C-S., and Chiu, T-S. 1999. Abundance and spatial variation of *Ommastrephes bartramii* (Mollusca: Cephalopoda) in the eastern North Pacific observed from an exploratory survey. Acta Zoologica Taiwanica, 10: 135–144.

Chen, C-S., and Chiu, T-S. 2003. Variations of life history parameters in two geographical groups of the neon flying squid, *Ommastrephes bartramii*, from the North Pacific. Fisheries Research, 63: 349–366.

Chen, C-S., and Chiu, T-S. 2009. Standardising the CPUE for the *Illex argentinus* fishery in the Southwest Atlantic. Fisheries Science, 75: 265–272.

Chen, C-S., Chiu, T-S., and Huang, W-B. 2007a. The spatial and temporal distribution patterns of the Argentine short-finned squid, *Illex argentinus*, abundance in the Southwest Atlantic and the effects of environmental influences. Zoological Studies, 46: 111–122.

Chen, C-S., Pierce, G. J., Wang, J., Robin, J-P., Poulard, J. C., Pereira, J., Zuur, A. F., *et al.* 2006. The apparent disappearance of *Loligo forbesi* from the south of its range in the 1990s: trends in *Loligo* spp. abundance in the northeast Atlantic and possible environmental influence. Fisheries Research, 78: 44–54.

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

Chen, X., Liu, B., and Chen, Y. 2008b. A review of the development of Chinese distant-water squid jigging fisheries. Fisheries Research, 89: 211–221.

Chen, X., Zhao, X., and Chen, Y. 2007b. Influence of *El Niño/La Niña* on the western winter–spring cohort of neon flying squid (*Ommastrephes bartramii*) in the northwestern Pacific Ocean. ICES Journal of Marine Science, 64: 1152–1160.

Dawe, E. G., Colbourne, E. B., and Drinkwater, K. F. 2000. Environmental effects on recruitment of short-finned squid (*Illex illecebrosus*). ICES Journal of Marine Science, 57: 1002–1013.

Erzini, K. 2005. Trends in NE Atlantic landings (southern Portugal): identifying the relative importance of fisheries and environmental variables. Fisheries Oceanography, 14: 195–209.

Erzini, K., Inejih, C. A. O., and Stobberup, K. A. 2005. An application of two techniques for the analysis of short, multivariate non-stationary time-series of Mauritanian trawl survey data. ICES Journal of Marine Science, 62: 353–359.

Fan, W., Wu, Y., and Cui, X. 2009. The study on fishing ground of neon flying squid, *Ommastrephes bartramii*, and ocean environment based on remote sensing data in the Northwest Pacific Ocean. Chinese Journal of Oceanology and Limnology, 27: 408–414.

Gong, Y., Kim, Y. S., and Hwang, S. J. 1993. Outline of the Korean squid driftnet fishery in the North Pacific. Bulletin of the International North Pacific Fisheries Commission, 53: 45–69.

Gordo, O., and Sanz, J. J. 2005. Phenology and climate change: a long-term study in a Mediterranean locality. Oecologia, 146: 484–495.

Hallett, T. B., Coulson, T., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M., and Grenfell, B. T. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. Nature, 430: 71–75.

Hayase, S. 1995. Distribution of spawning grounds of flying squid, *Ommastrephes bartramii*, in the North Pacific Ocean. Japan Agricultural Research Quarterly, 29: 65–72.

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

Ichii, T., Mahapatra, K., Sakai, M., Inagake, D., and Okada, Y. 2004. Differing body size between the autumn and winter–spring cohorts of neon flying squid (*Ommastrephes bartramii*) related to the oceanographic regime in the North Pacific: a hypothesis. Fisheries Oceanography, 13: 295–309.

Ichii, T., Mahapatra, K., Sakai, M., and Okada, Y. 2009. Life history of the neon flying squid: effect of the oceanographic regime in the North Pacific Ocean. Marine Ecology Progress Series, 378: 1–11.

Muñoz-Carpena, R., Ritter, A., and Li, Y. C. 2005. Dynamic factor analysis of groundwater quality trends in an agricultural area adjacent to Everglades National Park. Journal of Contamination Hydrology, 80: 49–70.

Murata, M. 1990. Oceanic resources of squids. Marine Behaviour and Physiology, 18: 19–71.

Pierce, G. J., Valavanis, V. D., Guerra, A., Jereb, P., Orsi-Relini, L., Bellido, J. M., Katara, I., *et al.* 2008. A review of cephalopod–environment interactions in European Seas. Hydrobiologia, 612: 49–70.

Ritter, A., and Muñoz-Carpena, R. 2006. Dynamic factor modelling of ground and surface water levels in an agricultural area adjacent to Everglades National Park. Journal of Hydrology, 317: 340–354.

Robin, J-P., and Denis, V. 1999. Squid stock fluctuations and water temperature: temporal analysis of English Channel Loliginidae. Journal of Applied Ecology, 36: 101–110.

Rodhouse, P. G. 2001. Managing and forecasting squid fisheries in variable environments. Fisheries Research, 54: 3–8.

Ropelewski, C. F., and Jones, P. D. 1987. An extension of the Tahiti–Darwin Southern Oscillation Index. Monthly Weather Review, 115: 2161–2165.

Roper, C. F. E., Sweeney, M. J., and Nauen, C. E. 1984. FAO species catalogue: an annotated and illustrated catalogue of species of interest to fisheries. 3. Cephalopods of the world. FAO Fisheries Synopsis, 125. 277 pp.

Sakurai, Y., Kiyofuji, H., Saitoh, S., Goto, T., and Hiyama, Y. 2000. Changes in inferred spawning areas of *Todarodes pacificus* (Cephalopoda: Ommastrephidae) due to changing environmental conditions. ICES Journal of Marine Science, 57: 24–30.

Tian, S., Chen, X., Chen, Y., Xu, L., and Dai, X. 2009. Evaluating habitat suitability indices derived from CPUE and fishing effort data for *Ommastrephes bartramii* in the northwestern Pacific Ocean. Fisheries Research, 95: 181–188.

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

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

Waluda, C. M., Rodhouse, P. G., Trathan, P. N., and Pierce, G. J. 2001b. Remotely sensed mesoscale oceanography and the distribution of *Illex argentinus* in the South Atlantic. Fisheries Oceanography, 10: 207–216.

Waluda, C. M., Trathan, P. N., and Rodhouse, P. G. 1999. Influence of oceanographic variability on recruitment in the *Illex argentinus* (Cephalopoda: Ommastrephidae) fishery in the South Atlantic. Marine Ecology Progress Series, 183: 159–167.

Wang, J., Pierce, G. J., Boyle, P. R., Dennis, V., Robin, J-P., and Bellido, M. 2003. Spatial and temporal patterns of cuttlefish (*Sepia officinalis*) abundance and environmental influences—a case study using trawl fishery data in French Atlantic coastal, English Channel, and adjacent waters. ICES Journal of Marine Science, 60: 1149–1158.

Yatsu, A., Hiramatsu, H., and Hayase, S. 1993. Outline of the Japanese squid driftnet fishery with notes on the by-catch. Bulletin of the International North Pacific Fisheries Commission, 53: 5–24.

Yatsu, A., Midorikawa, S., Shimada, T., and Uozumi, Y. 1997. Age and growth of the neon flying squid, *Ommastrephes bartrami*, in the North Pacific Ocean. Fisheries Research, 29: 257–270.

Yatsu, A., Tanaka, H., and Mori, J. 1998. Population structure of the neon flying squid, *Ommastrephes bartramii*, in the North Pacific. *In* International Symposium on Large Pelagic Squids, pp. 31–48. Ed. by T. Okutani. Japan Marine Fishery Resources Research Center, Tokyo.

Yatsu, A., Watanabe, T., Mori, J., Nagasawa, K., Ishida, Y., Meguro, T., Kamei, Y., *et al.* 2000. Interannual variability in stock abundance of the neon flying squid, *Ommastrephes bartramii*, in the North Pacific Ocean during 1979–1998: impact of driftnet fishing and oceanographic conditions. Fisheries Oceanography, 9: 163–170.

Yeh, S-Y., and Tung, I-S. 1993. Review of Taiwanese pelagic squid fisheries in the North Pacific. Bulletin of the International North Pacific Fisheries Commission, 53: 71–76.

Young, R. E., and Hirota, J. 1990. Description of *Ommastrephes bartramii* (Cephalopoda: Ommastrephidae) paralarvae with evidence for spawning in Hawaiian waters. Pacific Science, 44: 71–80.

Zuur, A. F., Fryer, R. J., Jolliffe, I. T., Dekker, R., and Beukema, J. J. 2003a. Estimating common trends in multivariate time series using dynamic factor analysis. Environmetrics, 14: 665–685.

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

Zuur, A. F., Tuck, I. D., and Bailey, N. 2003b. Dynamic factor analysis to estimate common trends in fisheries time series. Canadian Journal of Fisheries and Aquatic Sciences, 60: 542–552.

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