

## The Spatial and Temporal Distribution Patterns of the Argentine Short-Finned Squid, *Illex argentinus*, Abundances in the Southwest Atlantic and the Effects of Environmental Influences

Chih-Shin Chen<sup>1,\*</sup>, Tai-Sheng Chiu<sup>2</sup>, and Wen-Bin Haung<sup>3</sup>

<sup>1</sup>Institute of Fishery Biology, College of Life Science, National Taiwan University, Taipei 106, Taiwan

<sup>2</sup>Institute of Zoology, College of Life Science, National Taiwan University, Taipei 106, Taiwan

<sup>3</sup>Institute of Biological Resources and Technology, National Hualien University of Education, Hualien 970, Taiwan

(Accepted January 24, 2006)

**Chih-Shin Chen, Tai-Sheng Chiu, and Wen-Bin Haung (2007)** The spatial and temporal distribution patterns of the Argentine short-finned squid, *Illex argentinus*, abundances in the Southwest Atlantic and the effects of environmental influences. *Zoological Studies* 46(1): 111-122. The spatial and temporal distribution patterns of the Argentine short-finned squid, *Illex argentinus*, abundances and relationships between the squid abundance and environmental variables in the Southwest Atlantic were analyzed using a geographical information system and statistical methods. The abundances of squid were estimated by standardizing commercial catch per unit effort (CPUE) data from the Taiwanese squid fishery during 1986-2003. *Illex argentinus* has a clear general annual migration pattern, which consistently occurred in different years. The monthly distribution patterns of sea surface temperature (SST) corresponded to the current systems in the Southwest Atlantic. Local squid abundances showed a negative correlation with SSTs during Mar.-Aug., although it was difficult to determine if this reflected any causal link. The Southern Oscillation Index (SOI) and SSTs on the southern and northern portions of the Patagonian Shelf were analyzed to investigate the teleconnection between them and a lag-effect on squid abundances. SSTs on both the southern and northern portions of the Patagonian shelf showed a link with the SOI, at respective lag times of 2 and 3 yr. No significant correlation was found between the SOI and squid abundances, or between SSTs of the southern portion of the Patagonian Shelf and squid abundances within the calculated range of the time lag (10 yr), while SSTs of the northern portion of the shelf were negatively correlated with squid abundances with a lag of 1 yr. Cold events on the northern portion of the Patagonian Shelf in the previous year could be a key factor for the high squid abundance in the current year. Whether or not there are high or low abundances, the distribution patterns of squid on the Patagonian Shelf are locally influenced by the presence of thermal fronts, which are themselves dependent upon the distribution and strength of the cold currents. <http://zoolstud.sinica.edu.tw/Journals/46.1/111.pdf>

**Key words:** *Illex argentinus*, Squid abundance, Environmental influence, SST, Southern Oscillation Index (SOI).

The Argentine short-finned squid, *Illex argentinus* (de Castellanos, 1960), is a neritic ommastrephid squid distributed along the Patagonian Shelf and slope in the Southwest Atlantic from 22° to 55° S (Hatanaka 1988, Haimovici et al. 1998). This species is one of the most important cephalopod fishery resources in the world, and is exploited by international fleets including those from Japan, Taiwan, Korea, Spain, and Russia. The annual production of *I. argenti-*

*nus* ranged 32,000-1,144,000 metric tons (t) during 1983-2002, with an annual average of 532,000 t, accounting for approximately 22.7% of the total cephalopod production in the world (Anon. 2004). Such a high potential for fishery exploitation has generated many studies on the population dynamics and abundance trends of *I. argentinus*, with the aim of sustainably managing this fishery (Brunetti et al. 1998, Haimovici et al. 1998).

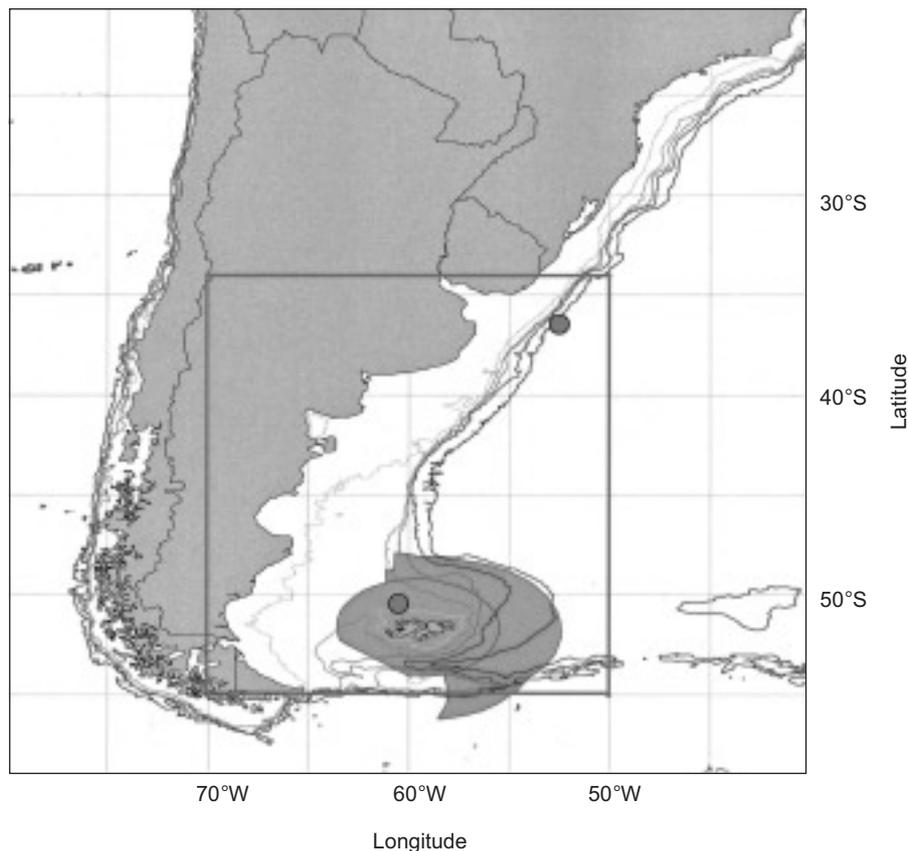
Using an empirical model involving environ-

\*To whom correspondence and reprint requests should be addressed. Tel: 886-2-33664549. Fax: 886-2-23639847. E-mail: ccshin@ntu.edu.tw

mental variables is an alternative approach to study stock dynamics of short-lived species such as squid (Rodhouse 2001, Agnew et al. 2002, Pierce and Boyle 2003). Waluda et al. (1999) showed that SSTs in the inferred hatching ground of *I. argentinus* during the hatching period were negatively correlated with the catch in the next fishing season from the waters around the Falkland Is. They also suggested a teleconnection of SST anomaly events between the Pacific and Atlantic Oceans, probably via the Antarctic Circumpolar Wave, which might provide a possible way to predict squid recruitment strength. Waluda et al. (2001a) defined 2 surface oceanographic conditions (the "frontal" waters, and "favorable" SST waters), and found that high abundances of *I. argentinus* were associated with a lower proportion of frontal waters or a higher proportion of favorable SST waters within the inferred hatching area in the previous year. During the period of fishery operations, *I. argentinus* was found to be associated with areas of thermal gradients, commonly seen

on the interface of the Falkland Current and Patagonian Shelf waters (Waluda et al. 2001b). However, an overall pattern of the spatial distribution of *I. argentinus* abundances and related environmental changes in the Southwest Atlantic is still lacking, mostly due to the scarce availability of large-scale fisheries or survey data.

The annual catch of *I. argentinus* by Taiwanese jiggers varied from 45,000 to 263,000 t during 1983-2003, with an annual average production of ~160,000 t, which accounted for ~30% of the total production of *I. argentinus* (Anon. 2004). The localities which Taiwanese jiggers covered in the past 2 decades included almost the entire distributional range of this species. In this study by applying fisheries data of Taiwanese jiggers to analyze the spatiotemporal patterns of the distribution of *I. argentinus* abundances in the Southwest Atlantic, we have attempted to (1) provide a more-detailed overall picture of intra- and inter-annual variations in squid distributions and abundances and (2) illustrate the sea surface temperature



**Fig. 1.** Study area (rectangle: 34°- 55°S, 50°- 70°W) in the Southwest Atlantic. The selected localities of sea surface temperature (SST) on the southern (50°30'S, 60°30'W) and northern portions of the Patagonian Shelf (36°30'S, 52°30'W) are also presented (circles).

(SST) influences on squid distributions and abundances in the Southwest Atlantic.

## MATERIALS AND METHODS

The catch data of *I. argentinus* in the Southwest Atlantic for Taiwanese squid jiggers were obtained from the Fisheries Agency, Council of Agriculture, Executive Yuan, R.O.C. Since 1986, Taiwanese far-sea squid jiggers are required to submit their logbooks to the fisheries administration after the end of the fishing season. The recorded items of this database include the date, locality (latitude, longitude), and catch in weight.

The region of 34°–55°S and 50°–70°W was selected as a range for the base map in this study (Fig. 1); this covers all locations of fishery operations and closely coincides with the distributional area of *I. argentinus* in the Southwest Atlantic. We compiled this squid catch database in a geographically referenced format using a statistical grid of 0.5° (0.5° longitude by 0.5° latitude), thus a 1680-grid database was constructed for each month (containing 42 grids of latitude, and 40 grids of longitude). The catch per unit effort (CPUE, t/vessel/d) of squid was standardized using a relative CPUE comparison method (Salthaug and Godø 2001). We used this adjusted CPUE as an index of squid abundances to illustrate the spatiotemporal patterns of population dynamics.

Reynolds SST data were downloaded from the National Center for Atmospheric Research (NCAR)'s US website (<http://dss.ucar.edu/datasets/ds277.0/>). The data are monthly average model results from remotely sensed data, survey temperature data, and the sea ice distribution, with a spatial resolution of 1° longitude x 1° latitude (Reynolds and Smith 1994).

Monthly SST time series from the locations, 36°30'S, 52°30'W and 50°30'S, 60°30'W, were respectively selected to represent the environmental conditions of the northern and southern portions of the Patagonian Shelf (denoted SST\_N and SST\_S). Data for the period 1982–2002 were used in this analysis. These SST values were averaged from the values of the surrounding 9 grids, and standardized using the mean and standard deviation.

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 is calculated as the difference in sea level air pressures 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 for the period from Jan. 1982 to Dec. 2003 were used in this analysis.

A geographical information system (GIS), based on the Environmental System Research Institute (ESRI) GIS software, ArcView®, was developed and used for the visual analysis. Fisheries and environmental data were imported from the Access database, and integrated in the GIS as shapefiles. Time-series maps of squid abundances against the background of SSTs for the same time period were created to visually analyze and depict spatial and temporal patterns of squid abundances, and changes in abundances relative to changes in SSTs.

Spatial correlations between squid abundances and SSTs were calculated using Spearman's rank correlation for the monthly grid dataset during 1986–2002. Different locations may experience different mechanisms of environmental change in the study area; this is true at least for the winter-spawning stock of *I. argentinus*, which has been proposed as hatching on the northern portion of the Patagonian Shelf and slope while feeding on the southern portion of the Patagonian Shelf (Brunetti et al. 1998). We separated the study area into 2 sub-areas with the division at latitude 45°S, for the different habitats experienced by different life stages of the squid.

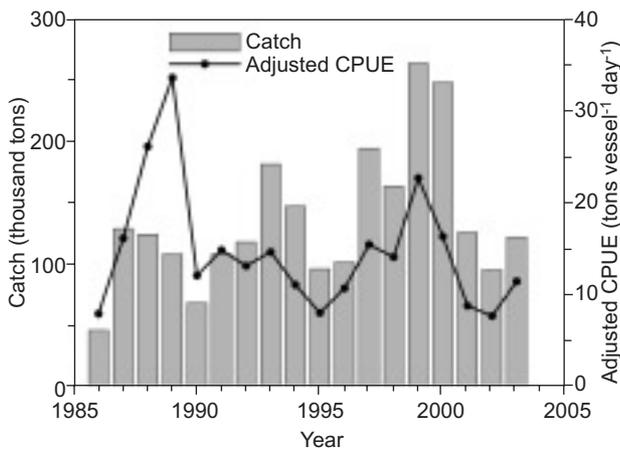
A time series analysis was applied to investigate the temporal autocorrelations of environmental variables (SOI, SST\_N, and SST\_S). Teleconnections between oceanographic events in the Pacific and Southwest Atlantic were examined. The oceanographic variability between the northern and southern portions of the Patagonian Shelf was analyzed. The lag-effects of the environmental variables on squid abundances (annual CPUE values) were examined.

## RESULTS

### Temporal and spatial patterns of squid abundances

The temporal trend of the catch and adjusted catch per unit effort (CPUE, t/vessel/d) of *I. argentinus* are shown in figure 2. The fishery was nearly totally mature for Taiwanese jiggers after 1988, as 132 jigging vessels were operating on

this fishing ground. Afterwards, the number of jigging vessels was ~100. The catch trend fluctuated with a cycle of ca. 4-5 yr before 1997, with peaks in 1987, 1993, and 1997. However, a historical high catch occurred in 1999, with ca. 263,000 t, followed by a decreasing trend to the present. The adjusted CPUE, which was calculated from standardized fishing efforts using the relative CPUE comparison method, showed an obvious increasing pattern during the 1980s, which may have been a result of the low proportion of retrieved logbooks during the early period of fisheries development. Squid abundances showed a decreasing



**Fig. 2.** Annual catch and adjusted catch per unit effort (CPUE, t/vessel/d) of *Illex argentinus* from the Taiwanese squid fishery during 1986-2003.

pattern in the early 1990s, and dropped to a low value of 8.0 t/vessel/d in 1995. After that, it increased to the highest value of 22.6 t/vessel/d in 1999, and decreased to the lowest value of 7.5 t/vessel/d in 2002.

The long-term monthly average CPUE and SST values are shown in figure 3. The long-term monthly average CPUE (1986-2003) values are presented in a grid format on a background of long-term monthly average SSTs (with isotherm intervals of 1°C). This illustrates the general spatial and temporal distribution patterns of *I. argentinus* abundances in the Southwest Atlantic. Squid occurred on the shelf and shelf break of 45°-47°S during Nov.-Jan. A southerly migration was detected during Feb.-Apr., while 1 concentrated area remained on the shelf break at 44°-47°S. Two concentrations of squid abundances were found during Mar.-May: one on the shelf and shelf break at 44°-47°S, and the other on the southern portion of the shelf at 52°-54°S. A northerly migration to the north of 40°S was detected in May, and the area of concentration on the southern portion of the shelf (52°-54°S) disappeared after July. No records were found in Oct. during the past 18 yr.

The monthly average CPUE values from 1986 to 2003 showed spatiotemporal variations in the distribution patterns of squid abundances during this period. We selected data from 1999 and 2001 to respectively represent years of high and low abundances (in terms of the CPUE). The season-

**Table 1.** Results of correlations ( $\rho$ ) between squid catch per unit effort (CPUE) and sea surface temperatures (SSTs), using Spearman's rank correlation method (a) for the entire area, (b) the area north of 45°S, and (c) the area south of 45°S. Single-month CPUE data from 1986 to 2002 for each cell (at a 0.5 x 0.5° spatial resolution) were used in the calculation.  $n$ , sample size. Only the months with a sample size of >20 were analyzed. Significant correlations ( $p < 0.05$ ) are indicated in boldface

		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Dec.
Entire area	$\rho$	-0.127	-0.063	<b>-0.175</b>	<b>-0.107</b>	<b>-0.173</b>	<b>-0.165</b>	<b>-0.309</b>	<b>-0.302</b>	-0.208
	$n$	188	395	736	810	829	453	182	109	50
	$p$	0.0827	0.2153	0.0000	0.0023	0.0000	0.0004	0.0000	0.0014	0.1474
North of 45°S	$\rho$	-0.314	-0.110	-0.142	<b>-0.225</b>	<b>-0.205</b>	-0.096	<b>-0.255</b>	<b>-0.304</b>	-
	$n$	33	47	64	99	239	201	157	106	6
	$p$	0.0753	0.4599	0.2641	0.0255	0.0014	0.1738	0.0013	0.0016	-
South of 45°S	$\rho$	-0.073	-0.051	<b>-0.176</b>	<b>-0.090</b>	<b>-0.154</b>	<b>-0.220</b>	<b>-0.759</b>	-	-0.276
	$n$	155	348	672	711	590	252	25	3	44
	$p$	0.3640	0.3435	0.0000	0.0165	0.0002	0.0004	0.0000	-	0.0697

al pattern of the distribution in these 2 yr differed from that of the long-term average pattern. A high abundance concentration was found on the shelf and shelf break at 45°- 47°S early in the fishery season (Jan.-Feb.) in 1999. Two obvious concentrations occurred on the shelf break at 45°- 47°S and 52°- 54°S during Mar.-May. A northerly migration of squid was found in June, while few records were located after July. However, squid abundances were low during the early fishery season of 2001. A high concentration was located on the shelf at 48°S and to the north and northeast of the Falkland Is. in Mar., and moved to the shelf at 52°- 54°S during Apr.-May. A minor concentration remained on the shelf break at 42°- 45°S during Mar.-June. A northerly migration was found on the shelf north to 40°S in June, while only coastal stocks were recorded after July.

#### Relationship between *Illex* squid abundances and SSTs

SST data displayed in the background of the spatiotemporal maps (Figs. 3-5) show that the pattern of oceanographic variations in the Southwest Atlantic was influenced by the current system. The warm water (as indicated by the 20°C isotherm) dominated to 37°S (south of the Rio de La Plata) during Dec.-Apr. The cold water (as indicated by the 10°C isotherm) intruded to the north of 37°S

during June-Oct. However, an obvious northerly intrusion of less-cold water (as indicated by the 15°C isotherm) on the shelf edge at 42°S was found in summer (Jan.-Mar.). The SST pattern in May showed less-cold water than the long-term condition in 1999, while a colder pattern was seen in 2001. High abundances of squid were located in the region of SSTs of between 10 and 15°C in summer, and in the region of 7-10°C in winter.

Spatial correlations between squid abundances and SSTs in the Southwest Atlantic were calculated using Spearman's rank correlation (Table 1). A negative correlation was found during Mar.-Aug. for the entire area, i.e., high squid abundances occurred in areas with lower SSTs. Populations of *I. argentinus* could be separated by meridional location (by latitude 45°S). The stock distributed to the south of 45°S was called the Bonaerensis-Northpatagonic Stock (BNPS) which spawns in winter (Brunetti et al. 1998) and comprises the majority of the *Illex* fishery (Rodhouse et al. 1995). Squid abundances to the south of 45°S were negatively correlated with SSTs during Mar.-July. However, to the north of 45°S, *Illex* abundances were negatively correlated with SSTs during Apr.-May and July-Aug.

The influence of surface oceanographic variability on squid abundances was examined using an SST series on the northern portion of the Patagonian Shelf during the previous spawning

**Table 2.** Results of temporal correlations ( $\rho$ ) between monthly squid catch per unit effort (CPUE) of the current year and sea surface temperatures in the northern portion (SST\_N) (at 36°30'S, 52°30'W) during the winter of the previous year from 1986 to 2002, using Spearman's rank correlation method. Significant correlations ( $p < 0.05$ ) are indicated in boldface

		Jan.	Feb.	Mar.	Apr.	May	June	July
SST_May	$\rho$	-0.3664	<b>-0.6223</b>	-0.1889	-0.3664	-0.4427	-0.2647	0.4615
	$n$	18	18	18	18	18	17	12
	$p$	0.1348	0.0058	0.4529	0.01348	0.0658	0.3045	0.1309
SST_Jun	$\rho$	-0.0691	<b>-0.5624</b>	-0.2755	-0.2962	-0.0423	-0.1275	-0.0350
	$n$	18	18	18	18	18	17	12
	$p$	0.7851	0.0151	0.2684	0.2327	0.8676	0.6259	0.9141
SST_Jul	$\rho$	0.4551	-0.0815	-0.1662	-0.0299	0.0712	-0.0221	0.0909
	$n$	18	18	18	18	18	17	12
	$p$	0.0577	0.7478	0.5099	0.9062	0.7789	0.9330	0.7787
SST_Aug	$\rho$	0.2962	-0.1558	-0.2094	-0.0774	0.1125	-0.0049	0.3217
	$n$	18	18	18	18	18	17	12
	$p$	0.2327	0.5369	0.4041	0.7602	0.6568	0.9851	0.3079

season (May-Aug.) of a fishery's operation. The location of SST\_N (at 36°30'S, 52°30'W) was selected from the inferred spawning ground of BNPS of *I. argentinus*. Temporal correlations between SST\_N during May-Aug. of the previous year and monthly squid abundances in the fishing season of the current year were calculated using Spearman's rank correlation (Table 2). Most of the correlations between SSTs in the previous May and June and squid abundances in the current fishing season were negative, although only 2 mo were statistically significant (SST\_May and squid in Feb. and SST\_Jun. and squid in Feb.).

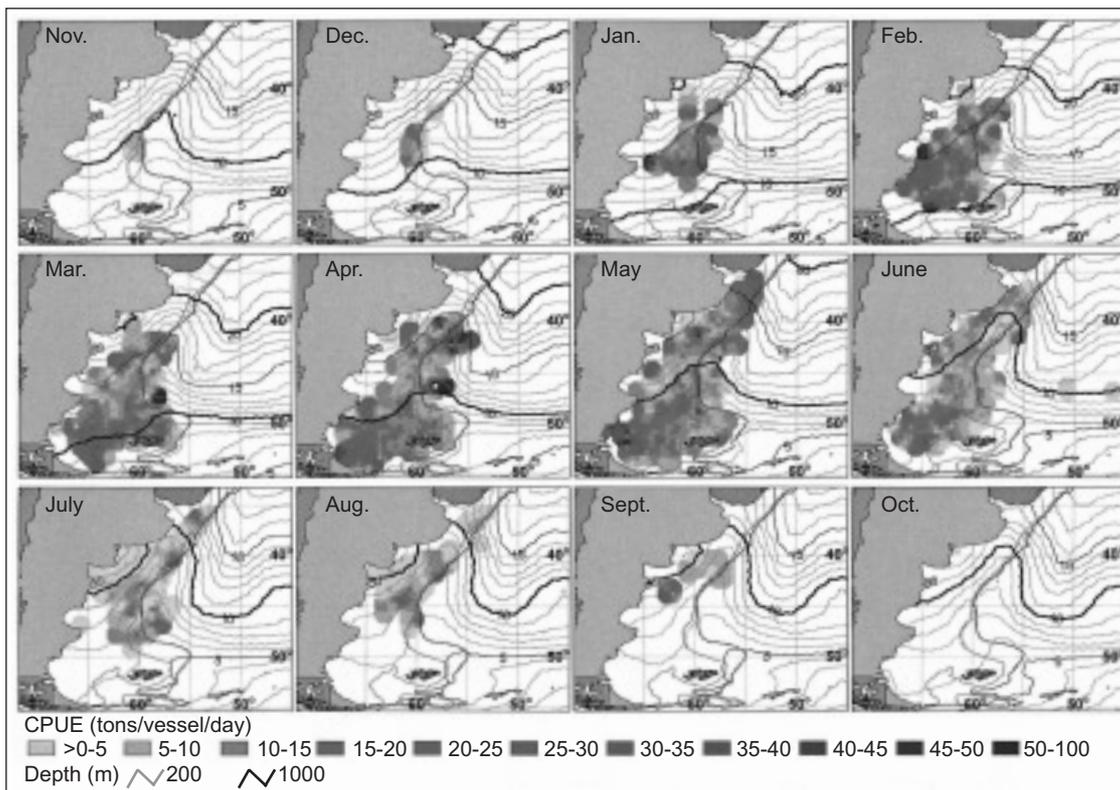
The time series of environmental variables, the Southern Oscillation Index (SOI), and SSTs on the southern and northern portions of the Patagonian Shelf (SST\_S and SST\_N) were examined to investigate the teleconnection of events between the Pacific and Southwest Atlantic and the lag-effect on squid abundances (Fig. 6). Sustained negative values of the SOI often indicate El Niño episodes, which occurred in 1992-1993 and 1997-1998 during the analysis period of

this study. The SST\_S series showed large fluctuations during the 1990s with 2 peaks in 1989 and 1993, and a dramatic decrease during 1999-2002. The SST\_N series showed an increasing pattern during 1988-1992, after which it decreased until 1997 then increased again until 2001.

The cross-correlation functions among environmental variables are shown in figure 7. Cross-correlations calculated between the SOI and SST\_S (Fig. 7, positive lag, SOI leading SST\_S, 0 to 60 mo) indicated a negative correlation at a lag of 22-32 mo (~2 yr) and a positive correlation at a lag of 51-54 mo (~4 yr). Correlations in the opposite direction (negative lag, SST\_S leading SOI, 0 to 60 mo) indicated positive correlations at lags of 11-12 and 15-16 mo (~1 yr) and a negative correlation at a lag of 51-54 mo (~4 yr).

Cross-correlations calculated between the SOI and SST\_N (Fig. 7, positive lag, SOI leading SST\_N, 0 to 60 mo) indicated positive correlations at lags of 36-41 and 45 mo (~3 and 3.5 yr). Correlations in the opposite direction (negative lag, SST\_N leading SOI, 0 to 60 mo) indicated nega-

Long-term average *Illex argentinus* abundance density (1986-2003) and SST (1982-2002)



**Fig. 3.** Long-term monthly average abundances of *Illex argentinus* (1986-2003) converted from a point format into a grid format and displayed in intervals of 0.5 t/vessel/d against a background of long-term monthly average sea surface temperatures (SSTs) (1982-2002), which were converted from point data into isotherms at intervals of 1°C.

tive correlations at lags of 10-11 and 14-15 mo (~1 yr) and positive correlations at lags of 46-48 and 52 mo (~4 yr).

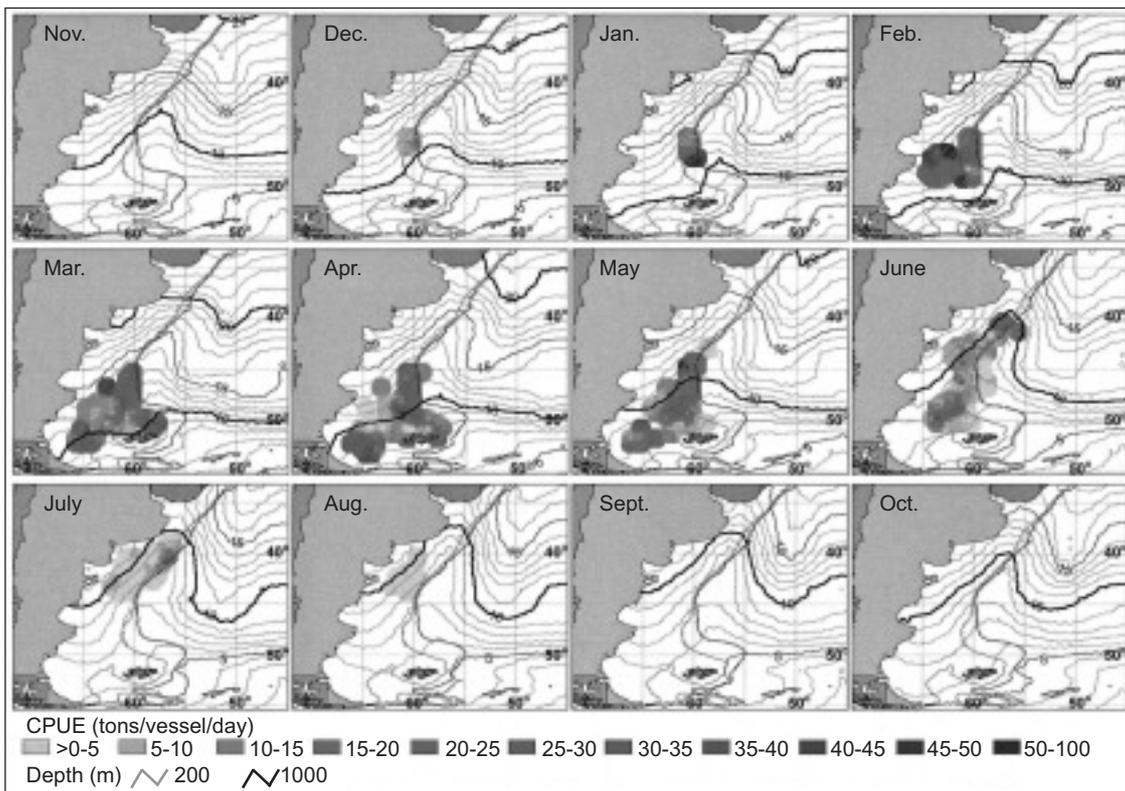
Cross-correlations calculated between SST\_S and SST\_N (Fig. 7, positive lag, SST\_S leading SST\_N, 0 to 60 mo) indicated positive correlations at lags of 18-26, 30, and 37-41 mo (~2 and 3 yr), while no significant correlation in the opposite direction (negative lag, SST\_N leading SST\_S, 0 to -60 mo) was found.

The cross-correlation functions of *Illex* abundances (as annual CPUE values) with environmental variables are shown in figure 8. No significant correlation was found between the SOI and squid abundances, or between SST\_S and squid abundances within the calculated range of the time lag (10 yr). Cross-correlations calculated between SST\_N and squid abundances (Fig. 8, positive lag, SST\_N leading squid, 0 to 10 yr) indicated a negative correlation at a lag of 1 yr.

## DISCUSSION

The distribution and migration patterns of *I. argentinus* in the Southwest Atlantic were proposed based on local surveys in previous studies (Brunetti et al. 1998, Arkhipkin 2000). However, an overall picture of spatiotemporal patterns of the distribution of *I. argentinus* from large-scale fisheries data is still lacking. In this study, we accessed long-term (1986-2003), large-scale (covering the entire distributional region of *I. argentinus*) fisheries data from Taiwanese squid jiggers to illustrate the spatiotemporal patterns of the distribution of *I. argentinus* in the Southwest Atlantic. The results suggest that a shift in squid abundances (CPUE) occurs in response to the migration patterns of winter-spawning stocks. The distribution of squid abundances may be influenced by local variations in SSTs, which result from the cold-warm circulation system. We determined that SSTs on the northern portion of the Patagonian Shelf can serve as a predictive proxy

*Illex argentinus* abundance density and SST (1999)



**Fig. 4.** Monthly abundances of *Illex argentinus* in 1999 converted from a point format into a grid format and displayed in intervals of 0.5 t/vessel/d against a background of sea surface temperatures (SSTs), which were converted from point data into isotherms at intervals of 1°C.

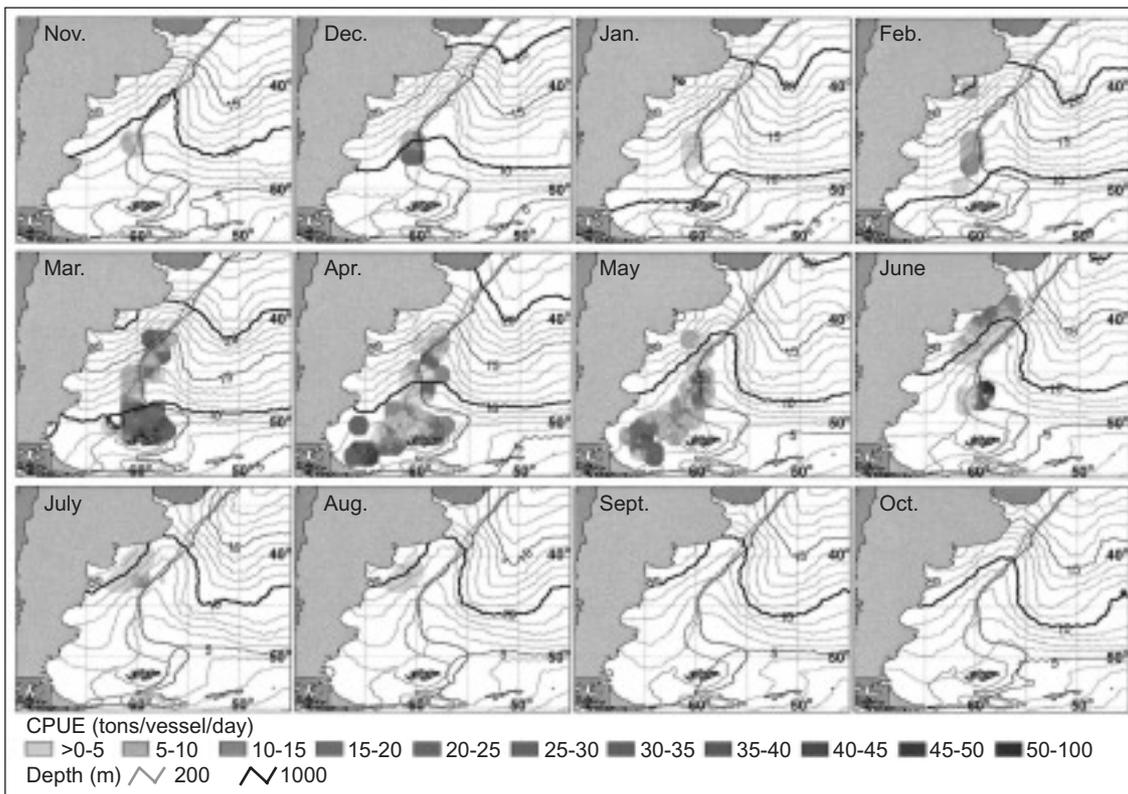
for variations in squid abundances with a lag effect of 1 yr.

There are 4 spawning cohorts of *I. argentinus* in the Southwest Atlantic (Brunetti et al. 1998). The *Illex* fishery in the Falkland Is. consists almost exclusively of winter spawners (Csirke 1987), which spawn in waters off southern Brazil, and migrate to the southern Patagonian Shelf for feeding. It can be assumed that the fishery targets a single stock to the south of 45°S (Basson et al. 1996). The winter cohort consists of the majority of the spawned squid in waters off southern Brazil, which then migrate to the southern Patagonian Shelf for feeding. The major catch of *I. argentinus* for Taiwanese jiggers is composed of the winter cohort (Chen et al. 2002). The winter cohort was further divided into 2 groups: a shelf group which matures at medium sizes and a slope group which matures at larger sizes (Arkhipkin 2000). These 2 groups of the winter cohort also undergo different pre-spawning migrations on the Patagonian Shelf and slope. In this study, the distribution patterns of long-term monthly average abundances of *I.*

*argentinus* in the Southwest Atlantic were consistent with migration patterns of the winter cohort (Fig. 3). The aggregations of squid abundances during Mar.-May may be a response to the 2 migratory routes of the winter cohort. One aggregation remains on the shelf and shelf edge at 44°-47°S, and moves northerly the following month, which corresponds to the shelf group. Another aggregation occurs on the southern shelf at 52°-54°S, and moves toward the slope regions the following month, which corresponds to the slope group (Fig. 3). These 2 groups were also obvious in 1999 (a high-abundance year; Fig. 4), while the shelf group was scarcer in 2001 (a low-abundance year; Fig. 5).

*Illex argentinus* is a short-lived ommastrephid species with a lifespan of about 1 yr (Rodhouse and Hatfield 1990). Abundance and recruitment dynamics of such a short-lived species are suspected of being vulnerable to environmental variability, which can result in apparently large fluctuations in annual catches (O'Dor 1993, Waluda et al. 1999, Sakurai et al. 2000, Anderson and

*Illex argentinus* abundance density and SST (2001)

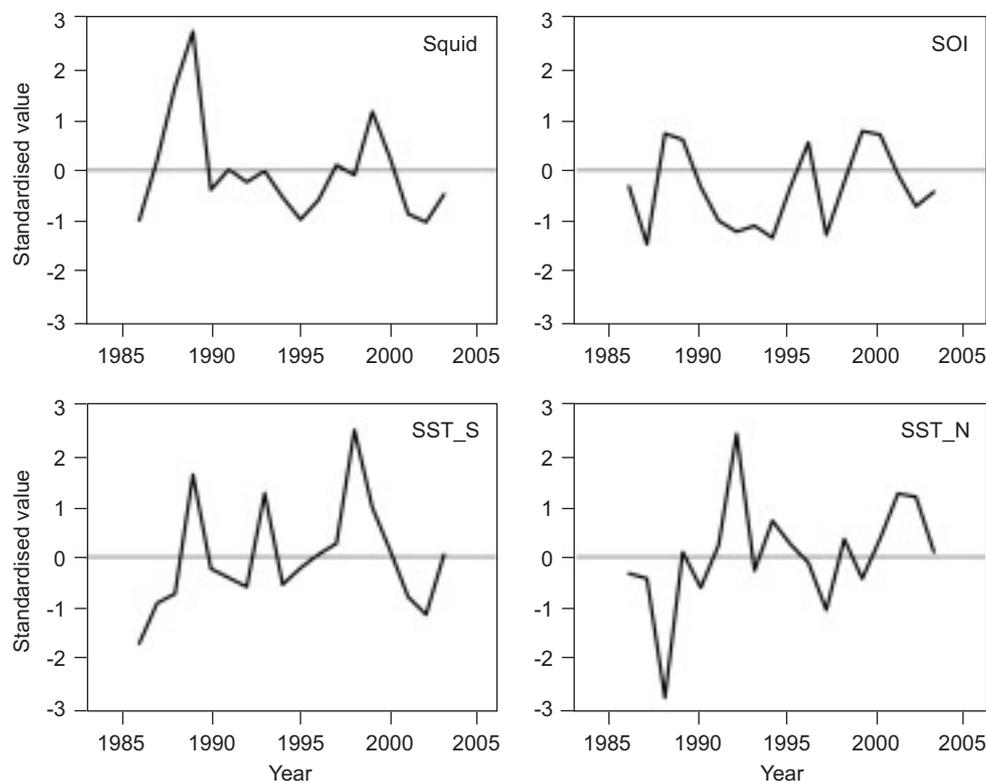


**Fig. 5.** Monthly abundances of *Illex argentinus* in 2001 converted from a point format into a grid format and displayed in intervals of 0.5 t/vessel/d against a background of sea surface temperatures (SSTs), which were converted from point data into isotherms at intervals of 1°C.

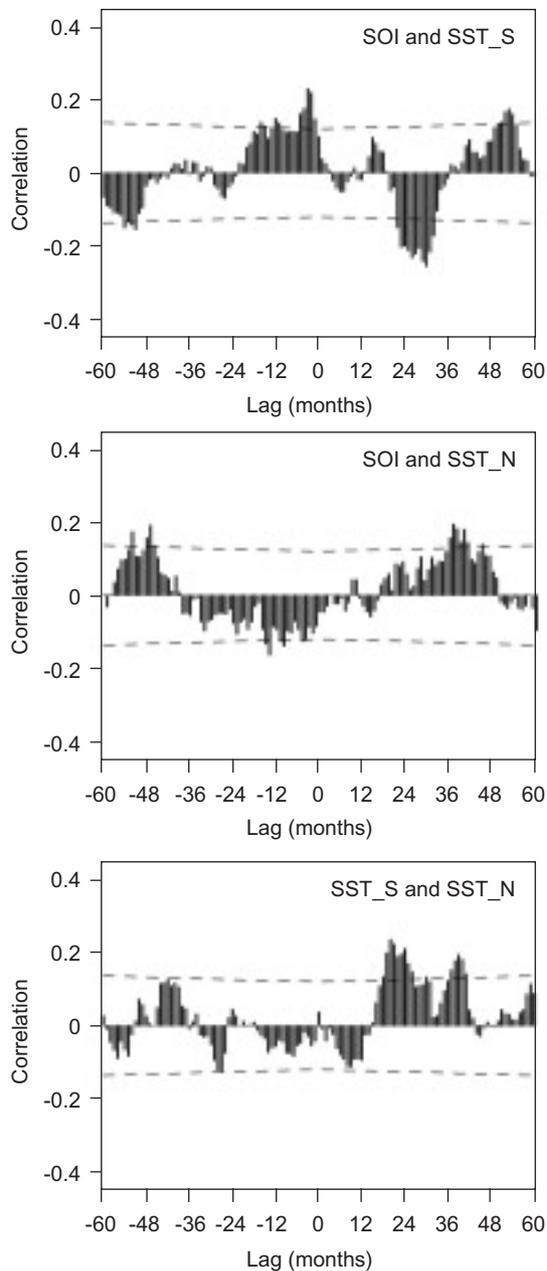
Rodhouse 2001). The oceanographic conditions on the Patagonian Shelf are dominated by the opposing flows of the Brazil and Falkland (Malvinas) Currents (Legeckis and Gordon 1982, Olson et al. 1988, Peterson and Whitworth III 1989, Peterson 1992). The Brazil Current flows polewards along the continental margin of South America as part of the western boundary current of the South Atlantic subtropical gyre (Olson et al. 1988). The Falkland Current, originating from the Antarctic Circumpolar Current, flows northward and splits into 2 branches: the eastern branch (Falkland Current) flows over the continental slope to the east of the Falkland Islands, and the western branch (Patagonian Current) flows northerly over the shelf. The confluence of the cold Falkland Current and the warm Brazil Current fluctuates between 38° and 46°S, and is accompanied by the intermittent formation of meanders and anticyclonic warm-core eddies (Legeckis and Gordon 1982, Olson et al. 1988). The mixing process of the cold and warm currents, and interactions with coastal waters generate high productivity in different areas and at different times which may correspond to the different life stages of *I. argentinus* (Ciotti et al. 1995, Willson and Rees

2000). High-productivity areas have been found on the shelf off southern Brazil in winter, which is associated with the northerly flowing coastal waters originating from runoff of the Rio de la Plata and the Patagonian Current (Ciotti et al. 1995). The shelf-break front which occurs between the waters of the shelf and the Falkland Current was found to have high phytoplankton biomass throughout spring and summer (Podestá 1990). Squid abundances appear to be associated with reduced frontal-water regions in hatching areas of the previous year, while tending to concentrate on thermal gradients in the fishing grounds around the Falkland Islands (Waluda et al. 2001a b). Squid abundances seem to be concentrated in areas of cold water along the boundary of the Brazil and Falkland Currents. The strength and spatial variations of the Falkland Current, which can be indicated by SST isotherms (Figs. 4, 5), may influence aggregations of squid during high- and low-abundance years.

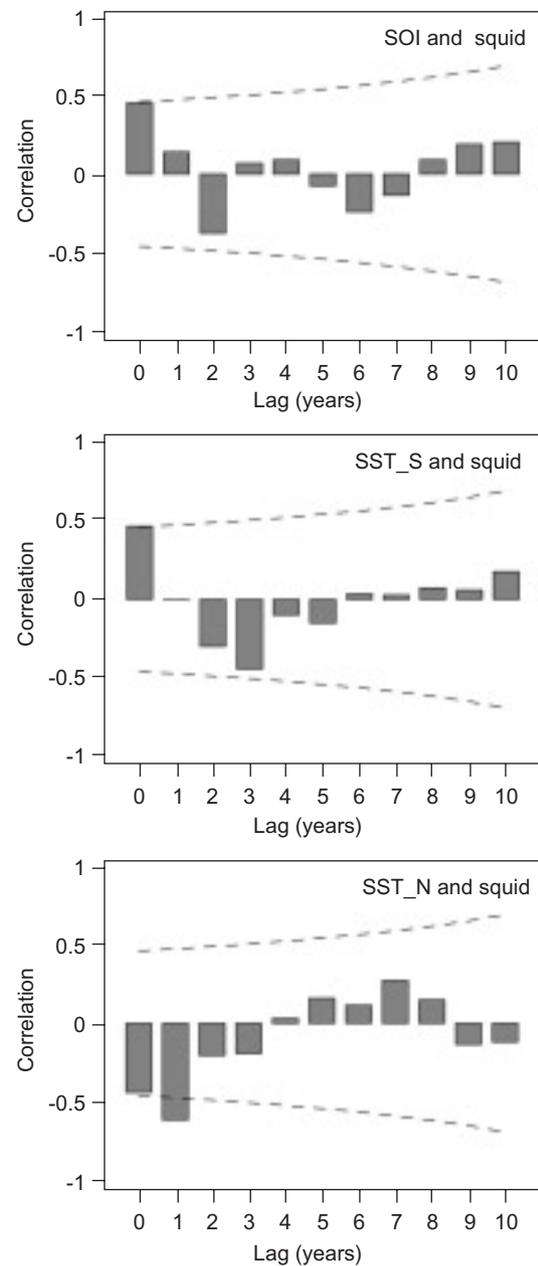
A negative correlation between squid abundances (for the entire area) and SSTs was found during Mar.-Aug. (Table 1). The migratory route of *I. argentinus* has been postulated as follows: the squid hatch in warm waters off the Patagonian



**Fig. 6.** Time series of squid abundances, the Southern Oscillation Index (SOI), and sea surface temperature anomalies of the southern (SST\_S) and northern portions of the Patagonian Shelf (SST\_N).



**Fig. 7.** Cross-correlation functions between monthly values of the Southern Oscillation Index (SOI), and sea surface temperature anomalies in the southern (SST\_S) and northern portions of the Patagonian Shelf (SST\_N). Dashed lines are 95% confidence intervals. A positive lag (0-60 mo) indicates that variable 1 (SOI, SST\_S) leads variable 2 (SST\_S, SST\_N), and a negative lag (0-60 mo) indicates that variable 2 leads variable 1. There was a positive correlation between the SOI and SST\_S at a lag of 51 mo, meaning that SOI led SST\_S by ~4 yr. There were positive correlations between the SOI and SST\_N at lags of 36 and 45 mo, meaning that SOI led SST\_N by ca. 3-3.5 yr. There were positive correlations between SST\_S and SST\_N at lags of 18-26 and 37-41 mo, meaning that SST\_S led SST\_N by ca. 2-3 yr.



**Fig. 8.** Cross-correlation functions of squid abundances with the Southern Oscillation Index (SOI), and sea surface temperature anomalies in the southern (SST\_S) and northern portions of the Patagonian Shelf (SST\_N). Dashed lines are 95% confidence intervals. Only the positive lag (0-10 yr), which indicates that environmental variables lead squid abundances, is shown.

Shelf and migrate onto the shelf for feeding. Strong cold waters along the confluence boundary (corresponding to lower SSTs) may result in a region of high productivity where squid aggregate for feeding. The effect of variations in the cold Falkland Current may play a more-important role in the aggregation of squid abundances than does the warm Brazil Current in the Southwest Atlantic. However, more information is necessary to understand the mechanism of the influences of cold and warm currents on aggregations of squid.

There are many studies which have analyzed the relationships between environmental variables and cephalopod abundances (Robin and Denis 1999, Waluda et al. 1999 2001a b, Sims et al. 2001, Pierce and Boyle 2003, Wang et al. 2003). SST values are considered to be convenient variables reflecting variability in surface oceanographic conditions. Waluda et al. (1999) found that SSTs in hatching areas of *I. argentinus* during the hatching period were negatively correlated with the catch of squid the following fishing season from the Falkland Islands (which only includes the slope group of the winter cohort). In this study, SSTs on the northern portion of the Patagonian Shelf showed a negative correlation with squid abundances (when the slope and shelf groups of the winter cohort were combined) at a lag of 1 yr, while no significance was found between the SOI and squid abundances, or between SSTs on the southern Shelf and squid abundances (Fig. 8). These results confirm that a cold SST event on the northern Patagonian Shelf during the hatching period can potentially increase subsequent squid abundances and recruitment success of both the slope and shelf groups of the winter cohort. SSTs can directly affect squid physiology, or may serve as a proxy for surface oceanographic conditions, in that they indicate appropriate habitats for squid recruitment during early life history stages.

The teleconnection of the SST anomaly between the Pacific and Atlantic Oceans was reported by Waluda et al. (1999), and it was suggested to provide a possible way to predict squid recruitment before actual fishery operations begin. In this study, we used the SOI to represent changes in oceanographic conditions in the Pacific. The link between events of the Pacific and Atlantic Oceans was similar to that of Waluda et al. (1999), i.e., SSTs of the southern and northern portions of the Patagonian Shelf were linked to the SOI at respective lags of 2 and 3 yr. However, the lag effect between the SOI and the northern Patagonian Shelf was shorter than that suggested

by Waluda et al. (1999) (of 5 yr). The variability of the Antarctic Circumpolar Wave (in terms of anomalies of wind stress, SSTs, sea level pressure, and sea-ice extent; White and Peterson 1996), with a cycle of 4-5 yr, has been proposed as the mechanism by which SST anomalies are transferred between the Pacific and Atlantic (Waluda et al. 1999). The shorter periodicity of the SST anomaly may result from the accompanying events of the frequently occurring SOI, an increasing pattern of SSTs on the northern Patagonian Shelf, and a decreasing pattern of SSTs on the southern Patagonian Shelf at the end of the 1990s (Fig. 6).

Interannual variability in the confluence zone of the Brazil and Falkland Currents has been shown to be important in influencing the recruitment success of *I. argentinus*. High squid abundances were found to be associated with reduced areas of frontal waters, or increased areas of favorable-SST waters (between 16 and 18°C) within the inferred hatching areas (32°- 39°S, 49°-61°W) in the preceding year (Waluda et al. 2001a). However, the concentration of squid abundances on the fishing grounds around the Falkland Is. during the fishery period was found to be associated with thermal gradients (Waluda et al. 2001b). In this study, we present the large-scale spatiotemporal distribution patterns of squid abundances in the Southwest Atlantic, and document differences in surface oceanographic conditions in high- and low-abundance years. A local thermal gradient on the feeding grounds may be crucial for aggregations of squid. The teleconnection between the Pacific and Atlantic Oceans confirms the results of Waluda et al. (1999), which imply the possibility of predicting recruitment strength of squid before the fishery begins, although different oceanographic variables were applied. More-detailed modeling of intra-annual variations in squid abundances including more environmental variables is necessary for further analyses.

**Acknowledgments:** We would like to thank Dr. J. Wang at the Univ. of Aberdeen (Aberdeen, Scotland) for assistance in processing Reynold's SST data from the NCAR and useful comments on the ArcView analysis process. We also thank Ms. K.Z. Chang for her help with database maintenance and the administrative process of this project. This study was partially supported by the Research Project "Stock Dynamics of Far-sea Squid Fishery in Taiwan", through a grant (93AS-9.1.2-FA-F1-01-02) from the Fisheries Agency,

Council of Agriculture, Executive Yuan, Taiwan. We would also like to thank 2 anonymous referees for their very useful comments on this manuscript.

## REFERENCES

- Agnew DJ, JR Beddington, SL Hill. 2002. The potential use of environmental information to manage squid stocks. *Can. J. Fish. Aquat. Sci.* **53**: 1851-1857.
- Anderson CIH, PG Rodhouse. 2001. Life cycles, oceanography and variability: ommastrephid squid in variable oceanography environments. *Fish. Res.* **54**: 133-143.
- Anonymous. 2004. FAO yearbook. Fishery statistics - capture production 2002. Vol. 94/1. Rome: Food and Agricultural Organization.
- Arkhipkin AI. 2000. Intrapopulation structure of winter-spawned Argentine shortfin squid, *Illex argentinus* (Cephalopoda, Ommastrephidae), during its feeding period over the Patagonian Shelf. *Fish. Bull. (US)* **98**: 1-13.
- Basson M, JR Beddington, JA Crombie, SJ Holden, LV Purchase, GA Tingley. 1996. Assessment and management techniques for migratory annual squid stocks: the *Illex argentinus* fishery in the Southwest Atlantic as an example. *Fish. Res.* **28**: 3-27.
- Brunetti N, M Ivanovic, G Rossi, B Elena, S Pineda. 1998. Fishery biology and life history of *Illex argentinus*. In T Okutani, ed. *Contributed Papers to International Symposium on Large Pelagic Squid*. Tokyo: Japan Marine Fishery Resources Research Center, pp. 217-232.
- Chen CS, MS Shiao, TS Chiu. 2002. Growth of Argentine shortfin squid, *Illex argentinus*, in the Southwest Atlantic during its post-recruitment migration. *ACTA Oceanogr. Taiwan.* **40**: 33-46.
- Ciotti AM, C Odebrecht, G Fillmann, OO Möller Jr. 1995. Freshwater outflow and subtropical convergence on phytoplankton biomass on the southern Brazilian continental shelf. *Cont. Shelf Res.* **15**: 1737-1756.
- Csirke J. 1987. The Patagonian fishery resources and the off-shore fisheries in the South-West Atlantic. FAO Fisheries Technical Paper no. 286. Rome: Food and Agricultural Organization.
- Haimovici M, NE Brunetti, PG Rodhouse, J Csirke, RH Leta. 1998. *Illex argentinus*. In PG Rodhouse, EG Dawe, RK O'Dor, eds. *Squid recruitment dynamics. The genus Illex as a model, the commercial Illex species and influence on variability*. FAO Fisheries Technical Paper no. 376. Rome: Food and Agricultural Organization, pp. 27-58.
- Hatanaka H. 1988. Feeding migration of short-finned squid *Illex argentinus* in the waters off Argentina. *Nippon Suisan Gakk.* **54**: 1343-1349.
- Legeckis MR, AL Gordon. 1982. Satellite observations of the Brazil and Falkland Currents, 1975 to 1976 and 1978. *Deep-Sea Res. Part A Oceanogr. Res. Pap.* **29**: 375-401.
- O'Dor RK. 1993. Big squid, big currents and big fisheries. In T Okutani, RK O'Dor, T Kubodera, eds. *Recent advances in cephalopod fisheries biology*. Tokyo: Tokai Univ. Press, pp. 385-396.
- Olson DB, GP Podest, RH Evans, OB Brown. 1988. Temporal variations in the separation of Brazil and Malvinas currents. *Deep-Sea Res. Part A Oceanogr. Res. Pap.* **35**: 1971-1990.
- Peterson RG. 1992. The boundary currents in the western Argentine Basin. *Deep-Sea Res. Part A Oceanogr. Res. Pap.* **39**: 623-644.
- Peterson RG, T Whitworth III. 1989. The sub-Antarctic and polar fronts in relation to deep-water masses through the southwestern Atlantic. *J. Geophys. Res.* **94**: 10817-10838.
- Pierce GJ, PR Boyle. 2003. Empirical modelling of interannual trends in abundance of squid (*Loligo forbesi*) in Scottish waters. *Fish. Res.* **59**: 305-326.
- Podest GP. 1990. Migratory pattern of the Argentine hake *Merluccius hubbsi* and oceanic processes in the southwestern Atlantic Ocean. *Fish. Bull. (US)* **88**: 167-177.
- Reynolds RJ, TM Smith. 1994. Improved global sea surface temperature analysis using optimum interpolation. *J. Clim.* **7**: 929-948.
- Robin JP, V Denis. 1999. Squid stock fluctuations and water temperature: temporal analysis of English Channel Loliginidae. *J. Appl. Ecol.* **36**: 101-110.
- Rodhouse PG. 2001. Managing and forecasting squid fisheries in variable environments. *Fish. Res.* **54**: 3-8.
- Rodhouse PG, J Barton, EMC Hatfield, C Symon. 1995. *Illex argentinus*: life cycle, population structure, and fishery. *ICES Mar. Sci. Symp.* **199**: 425-432.
- Rodhouse PG, EMC Hatfield. 1990. Dynamics of growth and maturation in the cephalopod *Illex argentinus* de Castellanos 1960 (Teuthoidea: Ommastrephidae). *Phil. Trans. R. Soc. London B* **329**: 229-241.
- Ropelewski CF, PD Jones. 1987. An extension of the Tahiti-Darwin Southern Oscillation Index. *Mon. Weather Rev.* **115**: 2161-2165.
- Sakurai Y, H Kiyofuji, S Saitoh, T Goto, Y Hiyama. 2000. Changes in inferred spawning areas of *Todarodes pacificus* (Cephalopoda: Ommastrephidae) due to changing environmental conditions. *ICES J. Mar. Sci.* **57**: 24-30.
- Salthaug A, OR Godø. 2001. Standardisation of commercial CPUE. *Fish. Res.* **49**: 271-281.
- Sims DW, MJ Genner, AJ Southward, SJ Hawkins. 2001. Timing of squid migration reflects the North Atlantic climate variability. *Proc. R. Soc. London B* **268**: 2607-2611.
- Waluda CM, PG Rodhouse, GP Podest, PN Trathan, GJ Pierce. 2001a. Surface oceanography of the inferred hatching grounds of *Illex argentinus* (Cephalopoda: Ommastrephidae) and influences on recruitment variability. *Mar. Biol.* **139**: 671-679.
- Waluda CM, PG Rodhouse, PN Trathan, GJ Pierce. 2001b. Remotely sensed mesoscale oceanography and the distribution of *Illex argentinus* in the South Atlantic. *Fish. Oceanogr.* **10**: 207-216.
- Waluda CM, PN Trathan, PG Rodhouse. 1999. Influence of oceanographic variability on recruitment in the *Illex argentinus* (Cephalopoda: Ommastrephidae) fishery in the South Atlantic. *Mar. Ecol. Prog. Ser.* **183**: 159-167.
- Wang J, GJ Pierce, PR Boyle, V Denis, JP Robin, JM Bellido. 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 J. Mar. Sci.* **60**: 1149-1158.
- White WB, RG Peterson. 1996. An Antarctic circumpolar wave in surface pressure wind temperature and sea-ice extent. *Nature* **380**: 699-702.
- Willson HR, NW Rees. 2000. Classification of mesoscale features in the Brazil-Falkland Current confluence zone. *Prog. Oceanogr.* **45**: 415-426.