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SQUID INTERSPECIFIC COMPETITION: POSSIBLE IMPACT OF *ILLEX ARGENTINUS* ON *LOLIGO GAHI* RECRUITMENT IN THE SOUTHWEST ATLANTIC

by

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Abstract

Fishery statistics for two abundant Southwest Atlantic squid, *Illex argentinus* (Ommastrephidae) and *Loligo gahi* (Loliginidae), in Falkland waters between 1987 and 1999 were analysed. Despite fisheries regulation producing reasonably consistent fishing effort, the total catch and CPUE of both squid varied considerably from year to year. The areas of concentration of the two species are usually separated, with *I. argentinus* most abundant to the north-west of the Islands in February-May and *L. gahi* to the south-east in February-May (first season) and August-October (second season). However, in some years, *I. argentinus* do intrude in great numbers into nursery or feeding areas of *L. gahi* in April-May possibly affecting, either directly (via predation) or indirectly (by competition for food) the abundance and recruitment of the second cohort of *L. gahi*. Catches and CPUE of *I. argentinus* in the first half of the season (February-March) did not correlate with those of *L. gahi* in February-May. In contrast, catches and CPUE of *I. argentinus* in the second half of the season (April-May) are negatively correlated with those of *L. gahi* in April-May and August-October of the same year. Possible reasons for such negative correlations in abundance of the two squid species, and their implications for fisheries management, are discussed.

Keywords: squid, fishery, *Illex argentinus, Loligo gahi,* Southwest Atlantic.

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Introduction

The Falkland Islands Interim Conservation and Management Zone and Outer Conservation Zone (FICZ and FOCZ) support two main squid fisheries in the Southwest Atlantic targeting the ommastrephid squid *Illex argentinus* and loliginid squid *Loligo gahi*. The total annual catch within the FICZ/FOCZ exceeded 300,000 tonnes in 1999 (FIG, 2000). The catch of each species has varied from year to year, ranging from 64,000 to 266,000 tonnes (mean 130,000 tonnes) for *I. argentinus* and from 26,000 to 98,000 tonnes (mean 61,000 tonnes) for *L. gahi* in 1990-1999 (FIG, 2000). The reasons for these variations in catch (and, presumably, in abundance of squid) are largely unknown.

Illex argentinus is the most important squid fishery resource of the Southwest Atlantic. During the first half of the year it is fished in the FICZ/FOCZ and Argentine Exclusive Economic Zone, as well as in international waters of 45-47°S. The south Patagonian and Falkland shelves are used as feeding grounds by the two most abundant winter-spawning groups of *I. argentinus*: the boanerensis north Patagonian stock (BNPS) and the south Patagonian stock (SPS) (Brunetti, 1988). Squid of both groups migrate to this area from their nursery grounds (the continental slope of northern Argentina and Uruguay) in February, feed during the austral summer and autumn and emigrate to their spawning grounds in May-June (Hatanaka, 1988; Haimovici *et al.*, 1998). In both the FICZ/FOCZ and Argentine EEZ, *I. argentinus* is fished mainly by Asian jigging vessels (Csirke, 1987). Two main waves of abundance are usually observed in the *I. argentinus* fishery on the southern Patagonian shelf (Arkhipkin, 2000). The first wave appears in February in the north-west of the FICZ/FOCZ and feeds mainly in that region. By the start of April squid of this wave are concentrated on the shelf break in the north-east of the zones before their northward migration, causing a significant peak in catches. The second wave starts to move from the Argentine EEZ to the western part of the FICZ in the second half of April. Squid of this wave migrate across the zone from the south-west to north-east, and again concentrate on the shelf break north of 50°30’S, resulting in the second peak of catches in the beginning of May. Aggregations of *I. argentinus* remain in the zones until the middle of June (FIG, 2000).

Loligo gahi is another important squid fishery resource within the FICZ (Patterson, 1988). Juvenile *L. gahi* move from the inner shelf to the outer shelf and shelf break of the Falkland Islands, feed and grow there as immature and maturing adults and, upon maturation, return to shallow waters to spawn (Hatfield and Rodhouse, 1994). It is assumed that there are at least two cohorts of *L. gahi* with different spawning periods (autumn and spring) and growth rates (Agnew *et al.*, 1998a). This squid is targeted by a trawl fleet primarily during its feeding period within the '*Loligo* box', the region located to the south-east of the Falkland Islands. The whole fishing season is split into two parts (February-May and August-October). During the first season both cohorts (with a predominance of the autumn spawners) are fished, whereas during the second season only the second cohort is exploited (Hatfield and des Clers, 1998).

Until now little has been known about the interactions between the two squid species. Both are opportunistic predators eating all possible pelagic prey, primarily abundant amphipod and euphausiid crustaceans (Guerra *et al.*, 1991; Brunetti *et al.*, 1998). With its slimmer body and smaller size (mean mantle length, ML, of adults is 140-160 mm) *L. gahi* is a more likely potential prey for the larger and more robust (320-390 mm adult ML) *I. argentinus*, than the reverse. On the Patagonian shelf *L. gahi* has been reported in the diet of *I. argentinus* (10-15% frequency of occurrence) during the austral summer and autumn (Ivanovic and Brunetti, 1994).

In the Falkland Islands Fisheries Department, fisheries catch and effort data has been gathered on a daily basis since the beginning of the licensed fishery in 1986 (FIG, 2000). This series offers the potential to make real progress in understanding fishery dynamics and interactions. In this paper we examine the relationship between abundance of the major squid species *I. argentinus* and *L. gahi*. Our aim is to better understand the factors that affect recruitment to the Falkland squid fisheries and so improve stock assessment and prediction capabilities and guide management for continued conservation of the stocks.

Materials & Methods

The overall distribution of *Illex argentinus* and *Loligo gahi* in the Falkland Island's fishery zones was compared by considering the total catch reported in the period 1987 to 1999 inclusive (Figure 1). All licensed vessels in the Falkland's zones submit daily catch reports identifying midday and midnight position on a 0.5° longitude by 0.25° latitude grid system. The majority of the *I. argentinus* catch is taken by jigging vessels so midnight position was used to assign their daily catch to a particular grid square, whereas *L. gahi* is fished by trawlers and midday position was used in this case.

For the separation of catch by wave of abundance, fishing season, or area, and for the calculation of catch per unit effort (CPUE), we considered only those vessels licensed to target *I. argentinus* or *L. gahi*. Data for the licensed fishery from 1989 to 1999 was included. All catches of *I. argentinus* during February and March were considered to be from the first wave of abundance (wave 1 = BNPS; Brunetti, 1988) and all catches from May and June were assigned to the second wave (wave 2 = SPS; Brunetti, 1988; Arkhipkin, 1993, 2000). In April catches south of 49.5°S and west of 60.25°W (Figure 2) were assigned to wave 2 while catches north and east of this area were assigned to wave 1. This division is supported by length-frequency and maturity data. In the case of *L. gahi* the fishery operates in two seasons. The first season runs from 1 February to 31 May, and the second season from 1 August to 31 October. *L. gahi* licenses allow fishing to the south and east of the Falkland Islands. This area was split into two sub-regions: north and south of 52° S (Figure 3). The fishery for *I. argentinus* takes place in a single season, currently running from 15 February to 15 June. The fishery season for either species may be ended earlier than the normal season closing date if within-season stock assessments indicate the stock has reached a minimum escapement threshold.

Calculation of CPUE for *I. argentinus* was restricted to the licensed jigging fleet, which takes the majority of the annual catch (95.4% in 1999; FIG, 2000). Effort was calculated as jig line hours (vessels report the number of lines used and time spent jigging daily), and CPUE expressed as kg line-hour^{-1}. The licensed fishery for *L. gahi* is restricted to trawlers (which report daily trawling time) and CPUE was calculated as metric tonnes (MT) hr^{-1}. The median CPUE (where CPUE was calculated daily for each licensed vessel fishing) in a given period was used as a general measure of abundance (usually referred to simply as CPUE in the remainder of this paper). This was chosen in preference to the standard stock estimates (calculated by depletion methods) as these currently consider only total stock *for I. argentinus* (Basson, *et al*. 1996) and total first/second season stock for *L. gahi* (Agnew, *et al*. 1998a) and so do not allow an easy separation of the estimated stock size by area (for *L. gahi*) or by wave of abundance (for *I. argentinus*).

To further illustrate the annual patterns in abundance for the various groups the annual deviation in CPUE from the long term mean CPUE of the group over the period 1989-1999 was calculated. To allow comparison between stocks this deviation was expressed as a proportion of the long term mean.

The relationship between CPUE for the two waves of *I. argentinus* and CPUE for *L. gahi* in each region and season was investigated by calculating Spearman's rank correlation between the data sets. All statistical calculations were carried out using the R statistical package, v 1.1.0 (Ihaka and Gentleman, 1996). Median CPUE was also calculated on a monthly basis for each stock and comparisons between months also made using Spearman's rank correlation.

Results

Distribution

Generally the distributions of *I. argentinus* and *L. gahi* within the FICZ/FOCZ are quite similar. Both squid are encountered almost everywhere around the Islands with the exception of the southern part of the Zones (mainly Burdwood Bank). In the east, however, *I. argentinus* tend to occur further offshore than *L. gahi*. Unlike *L. gahi*, *I. argentinus* do not appear in the shallow nearshore waters (<50 m depths) of the Falklands. However the dispersal of both squid is very different. The densest aggregations (and, correspondingly, catches) of *I. argentinus* are noted in the north-western and north-eastern parts of the Zones, whereas *L. gahi* is most abundant in the southern and eastern parts of the FICZ/FOCZ (the '*Loligo* box') (Figure 1). Thus the bulk of the populations of *I. argentinus* and *L. gahi* are separated spatially on the Falkland shelf.

The dispersal of *I. argentinus* and *L. gahi* varies in years of high and low abundance, to a greater extent in *I. argentinus* than *L. gahi*. For example, in a year of low *I. argentinus* abundance (1994) the first wave was observed basically along the northern perimeter of the FICZ, never approaching the vicinity of the Islands. The second wave was abundant only along the north-western periphery of the FICZ (Figure 2a, c). In a year of high abundance (1999) the dispersal of both waves was much wider. Squid of wave 1 were also abundant in the central northern part of the Zone, even approaching the shallow waters to the north and north-east of the Islands. Squid of wave 2 penetrated in great numbers down to 52°S in the western part of the FICZ and also into the shallow waters to the north of the Falklands (Figure 2b, d).

The annual variation in dispersal of *L. gahi* is not as evident as that of *I. argentinus* because the *Loligo*-licensed trawlers are allowed to fish only in a certain region of the FICZ (the "*Loligo* box"; Hatfield and Des Clers, 1998). In a year of high abundance (1994) the distribution of *L. gahi* was somewhat wider during both seasons than in a year of low abundance (1999) (Figure 3).

Illex argentinus *fishery statistics*

The total catch of both waves of *I. argentinus* by jigging vessels varied over the last decade. In 1989-1992, the catches were at a high level, ranging from 50 to 120 thousand tonnes. In 1993, there was a decline in the total catch of wave 1 with a corresponding increase in catch of wave 2. In 1994-1996 the catches were quite low, especially those of wave 2. Catches increased again at the end of the decade with the highest total catch occurring in 1999 when wave 1 catch exceeded all previous levels (Figure 4a). CPUE of the jigging fleet showed similar variability over the whole period, and was usually higher for wave 1 than wave 2 (Figure 4a). Total jigging effort was highest in 1989 and 1991-1993. From 1994 it stabilised at a level of around four million jig line hours for wave 2, but remained more variable for wave 1, dropping to two million jig line hours in 1998. The *I. argentinus* season duration was 91 days in 1990-1993 and was increased to 100-120 days in 1994-1999 (Figure 4b).

Daily *I. argentinus* CPUE showed different trends throughout the fishing season in different years. In 1992, a year of intermediate abundance, daily CPUE was high in the first half of the fishing season (February-March) but decreased markedly during the second half of the season (April-May). In 1999, a year of high abundance, CPUE were high for longer (February-May), decreasing only in June (Figure 5).

Loligo gahi *fishery statistics*

Statistics for both seasons of the *L. gahi* fishery are shown in Figure 6. During the first season, the total catch was greatest in 1989 in the southern area (105,000 tonnes), declining thereafter until 1993. Another peak in catch from this area occurred in 1995. First season catch in the northern area was continuously low with the exception of 1996 when it reached 17,000 tonnes. During the second season the total catch was greatest in the northern area in 1995 (24,000 tonnes) and in southern area in 1994 (20,000 tonnes) (Figure 6a).

The CPUE time series showed basically the same pattern throughout the decade as the corresponding catch series. The highest CPUE was recorded in the southern area for the first season in 1995 (5.6 t/hr) and for the second season in 1992 (2.0 t/hr) (Figure 6b). However, although season 1 catch was always higher in the south, CPUE in the northern area exceeded that in the southern area in some years. Low annual catches in the northern area, even when median CPUE is high, may result from variability in catches in the northern area. In 1999 it appeared that fishing vessels preferred to have high catches in the northern region for several days then, as soon as CPUE dropped, moved to the southern region where median CPUE was lower but catch was more stable.

The duration of both fishing seasons was practically constant throughout the decade except 1997, when the second season was closed earlier (Figure 6c). Trends in daily CPUEs in *L. gahi* fishery in years of high (1992) and low (1999) abundance are shown in Figure 5.

Correlation between I. argentinus *and* L. gahi *abundance*

To illustrate potential relationships in the abundance of different groupings of the two squid species, the proportional deviation from the long term mean of median CPUE (Table 1) for each grouping was constructed over the period from 1989 to 1999 (Figure 7). Of all the groupings of *L. gahi*, only the southern area in the second season demonstrated a consistent inverse pattern in CPUE relative to the two *I. argentinus* groupings (Figure 7d). This *L. gahi* grouping was the only one that showed a negative correlation with *I. argentinus* abundance (wave 2) that was significant at the 5% level (Figure 8).

An analysis of monthly median CPUE for both waves of *I. argentinus* and for both regions of *L. gahi* fishery also shows significant negative correlation between abundances of the two species. In the northern area a strong negative correlation was observed between abundance of *I. argentinus* in April (both waves) and *L. gahi* abundance in April ($p<0.05$) and in August-September ($p<0.1$) of the same year. The May abundance of the *I. argentinus* wave 2 correlates negatively with the *L. gahi* abundance in the following August-September (Table 2).

In the southern area, the April abundances of *I. argentinus* correlated negatively with the following May, August and September abundances of *L. gahi*. Median CPUE of the *I. argentinus* wave 2 in May in has a negative correlation with that of *L. gahi* in May and August (Table 3).

Examination of the relationship between the second season *L. gahi* CPUE in the south and wave 2 *I. argentinus* CPUE (Figure 8) suggests that there is a threshold level of wave 2 *I. argentinus* abundance at approximately 9 kg line-hr^{-1}. When this threshold is exceeded the second season CPUE for *L. gahi* in the southern area is invariably low (Figure 8, Figure 9). It is clear that there is a distinction in second season *L. gahi* CPUE in the south between years where *I. argentinus* wave 2 abundance exceeded this threshold and years where it did not.

Once this effect of the second wave *I. argentinus* abundance is taken into account the remaining variation in median CPUE is suggestive of a traditional stock-recruit relationship with highest recruitment resulting from the intermediate population sizes in the previous year (Figure 9). Fitting the Ricker stock-recruit curve separately to years where the wave two *I. argentinus* abundance exceeded the threshold median CPUE of 9 kg line-hr^{-1}, and years where it did not, did not yield very satisfactory fits. A generalised linear model (GLM) was therefore constructed for the second season CPUE of *L. gahi* in the southern area based on two factors. One factor indicated whether the median CPUE of wave 2 *I. argentinus* in the current year exceeded the threshold level of 9 kg line-hr^{-1}, while the other factor had three levels indicating the CPUE of the second season *L. gahi* in the southern area in the preceding year. This was allocated 3 levels: less than 0.55 tonnes hr^{-1}, between 0.55 and 1.2 tonnes hr^{-1}, and greater than 1.2 tonnes hr^{-1}. A gamma error distribution with log link function was used in the model fitting. The model fit is summarised in Table 4 and compared with the realised time series in Figure 10. The model accounts for 75% of the null deviance (Table 4).

Discussion

There could be several reasons for the strong negative correlations in the abundance of some groups of *I. argentinus* and *L. gahi* on the Falkland Shelf. *L. gahi* is the coldest water dwelling loliginid species spending its entire ontogenesis, and reaching its highest abundance, in waters associated with the Falkland Current which derives from the Antarctic Circumpolar Current (Hatfield and Des Clers, 1998). In contrast, *I. argentinus* is a temperate species associated mainly with waters of the Patagonian Shelf (Haimovici *et al*., 1998). It has recently been shown that fluctuations in abundance of both squid depend on environmental conditions in their spawning grounds. Catches of *I. argentinus* within the FICZ/FOCZ were negatively correlated with the sea surface temperature during the peak of their spawning in July of the previous year (Waluda *et al.*, 1999). Agnew *et al.* (in prep.) have demonstrated that lower sea-surface temperatures in October precede higher recruitment of the second cohort of *L. gahi* the following April. Thus, assuming that SST is a proxy for the environmental conditions determining the abundance of squid populations in the Southwest Atlantic, and taking into account their annual life cycle (Arkhipkin, 1990; Hatfield, 1991), one could expect a higher abundance of colder water species (in this case, *L. gahi*) and a lower abundance of warmer water species (such as *I. argentinus*) in a colder year, and *vice versa.* Generally, our data do not support this assumption: the correlation between total catch of the two species, as well as overall CPUE in the same year, is low and non-significant.

However, by splitting both squid species into their natural cohorts (or waves of abundance) (Agnew *et al.*, 1998b; Arkhipkin, 2000), and by analysing both catch and CPUE separately for each period and month, evidence of a relationship between the species emerges. There are some groupings of *I. argentinus* and *L. gahi* with strong negative correlation and there are others that are uncorrelated. As noted earlier, both squid are voracious predators. *L. gahi*, however, is abundant only around the Falkland Islands. This is far from the supposed *I. argentinus* spawning and nursery grounds (the southern Brazilian and northern Argentinian continental slopes; Haimovici *et al.*, 1998) and, therefore, predatory impact of *L. gahi* on *I. argentinus* recruitment may be neglected. The opposite situation is observed with *I. argentinus.* This squid migrates to the Falkland shelf seasonally (austral summer and autumn). On arrival the migrating *I. argentinus* are already much larger (> 220-240 mm ML), and have higher growth rates, than the local *L. gahi* (100-130 mm ML) (Rodhouse and Hatfield, 1990; Hatfield and Rodhouse, 1994).

Possible impact of I. argentinus *on* L. gahi

I. argentinus may affect *L. gahi* populations either indirectly (by competing for planktonic crustacean prey) or directly (by feeding on adult squid of the first cohort and/or small juveniles of the second cohort of *L. gahi*). It seems that competition for food resources is the less important relationship between the two squid, as the abundance of the first wave of *I. argentinus* does not correlate with that of the first season of *L. gahi* in February-March. However, *I. argentinus* of second wave do intrude into areas of *L. gahi* aggregations (to the west and north of the

Islands) in April-May. There are indications that during this period *I. argentinus* quickly switch from a crustacean to a squid diet, as their stomachs have been found full of *L. gahi* (unpublished FIFD scientific observer data). In the northern region fishing grounds for both squid species are very close (northwest of East Falkland) and an immediate impact of the second wave (and end of the first wave) of *I. argentinus* on *L. gahi* abundance is pronounced in April. Our method of dividing the April *I. argentinus* catches between the two waves is somewhat arbitrary. Although it is broadly in line with the biological patterns observed, it does not take account of inter-annual variation in the size and maturity characteristics that distinguish the two waves. This may well be responsible for the fact that the correlation between *L. gahi* abundance and *I. argentinus* abundance in April are similar for both waves.

In the southern region the fishing grounds for the two species are further apart (west of the Islands for *I. argentinus* and south for *L. gahi*). It is not surprising, therefore, that significant negative correlations were observed between April abundance of *I. argentinus* and May abundance of *L. gahi*: it should take some time (several weeks) for the slowly migrating *L. gahi* to reach their main feeding grounds (south of the Islands) from nursery grounds located west of West Falkland (our data). However the correlation between second wave *I. argentinus* and southern region *L. gahi* abundances in May also suggests some direct interaction closer to the fishing grounds. The strong negative correlation between abundance of *I. argentinus* in April-May and *L. gahi* in the following August-September suggests that large *I. argentinus* of the second wave may be feeding on small juveniles and immatures of the second cohort of *L. gahi*, which starts recruiting to the fishery in April-May (Agnew *et al.*, 1998b). It is notable that the *I. argentinus* abundance in April-May seems to have a threshold level below which *I. argentinus* do not appear to affect *L. gahi* abundance. However, when this threshold abundance is exceeded, there is invariably depletion of those *L. gahi* groups which are unfortunate enough to coincide with pre-spawning migratory schools of *I. argentinus* (Arkhipkin, 1993).

Despite its wide distribution in the shelf waters of the Southwest Atlantic and Southeast Pacific (Roper *et al.*, 1984), *L. gahi* is very abundant only in a rather small region located to the south-east of the Falkland Islands which seems to be an ecological ‘refuge’ for this species. But even in this refuge squid of the second cohort of *L. gahi* are vulnerable seasonally to predation by *I. argentinus* as it migrates in great numbers to feed in shallow waters around the Falkland Islands. It is notable that, in some years, dense aggregations of *L. gahi* are encountered on the Patagonian shelf break as far north as 45-47°S in September-October, i.e. during the almost complete absence of *I. argentinus* in that area. As soon as *I. argentinus* migrate into the region of 45-47°S in December, the abundance of *L. gahi* sharply declines (Chesheva, 1990). In other parts of its distribution *L. gahi* is never abundant, possibly as a result of predation pressure by more powerful and larger co-habitant ommastrephid squids, *I. argentinus* in the Southwest Atlantic and *Dosidicus gigas* in the Southeast Pacific.

Implications for fishery management

Squid fishery management and stock assessment have proved to be difficult tasks due to the high variation in squid abundance from year to year, a complicated population structure, and short life cycle (Rosenberg *et al.*, 1990). Management in the Falkland's zones is currently based largely on in-season assessments using methods based on Leslie-DeLury depletion analyses, which are generally reliable only after the peak of catches and even then not in all years (Basson *et al.*, 1996; Agnew *et al.*, 1998). This fact motivates the search for additional models for squid stock assessment and prediction that can contribute to the management of the fishery. It was recently found that models using a stock-recruit relationship and sea-surface temperatures on the spawning ground during spawning of a given cohort fitted the data more successfully than common stock-recruit models (Waluda *et al.*, 1999, Agnew *et al.*, in prep). The simple GLM constructed in the present study illustrates the potential of incorporating another important parameter (predator abundance) in predicting likely abundance of squid (i.e. the second cohort of *L. gahi*) before the season opens. The model fitted is, of course, very simplistic. The presence of only three factor levels for preceding year CPUE, and a single factor for *I. argentinus* abundance in the current year rather limits the possible predicted values. Nevertheless, the model successfully captures the pattern in median CPUE from year to year. With the small number of data points it is perhaps not surprising that the fitted values for the factors representing preceding year CPUE are not significantly different from zero, or indeed that the model can account for a rather large proportion of the null deviance. However, predicting forthcoming squid recruitment using factors such as predator abundance and environmental data is a very useful step forward for fisheries management. It offers the potential of refining the licensed effort based on likely abundance, with the aim of meeting conservation targets while reducing the likelihood of early fishery closures, and associated disruption to the fishery, should in-season assessments reveal that recruitment has been low.

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Table 1. Long term mean of median CPUE for each grouping of squid over the period 1989 to 1999 in the FICZ/FOCZ.

Species	*Region*	*Grouping*	*Mean*
Illex argentinus		wave 1	15.7 kg line-hr^{-1}
Illex argentinus		wave 2	8.7 kg line-hr^{-1}
Loligo gahi	northern region	season 1	1.46 t hr^{-1}
Loligo gahi	northern region	season 2	0.78 t hr^{-1}
Loligo gahi	southern region	season 1	2.20 t hr^{-1}
Loligo gahi	southern region	season 2	0.85 t hr^{-1}

Table 2. Spearman's rank correlation (and, in parenthesis, probability that correlation is non-zero) between monthly median CPUE for *Loligo gahi* in the northern area and *Illex argentinus* monthly median CPUE in the current year. Bold type highlights correlations that are significant at the 5% level, while italics indicate significance at the 10% level.

	Illex argentinus wave 1			*Illex argentinus* wave 2		
	Feb	Mar	Apr	Apr	May	Jun
Feb	0.400 (0.750)					
Mar	0.143 (0.803)	-0.282 (0.402)				
Apr	0.314 (0.564)	-0.291 (0.386)	**-0.682 (0.025)**	**-0.692 (0.023)**		
May	0.714 (0.136)	0.036 (0.924)	-0.309 (0.356)	-0.301 (0.371)	-0.309 (0.356)	
Aug	0.200 (0.714)	-0.196 (0.558)	*-0.597 (0.056)*	*-0.589 (0.061)*	*-0.556 (0.082)*	-0.600 (0.350)
Sep	0.257 (0.658)	-0.209 (0.539)	*-0.591 (0.061)*	*-0.574 (0.071)*	**-0.700 (0.021)**	*-0.900 (0.083)*
Oct	-0.200 (0.783)	0.067 (0.838)	-0.080 (0.838)	-0.049 (0.892)	-0.006 (1.000)	0.400 (0.750)

Table 3. Spearman's rank correlation (and, in parenthesis, probability that correlation is non-zero) between monthly median CPUE for *Loligo gahi* in the southern area and *Illex argentinus* monthly median CPUE in the current year. See Table 2 for details.

	Illex argentinus wave 1			*Illex argentinus* wave 2		
	Feb	Mar	Apr	Apr	May	Jun
Feb	0.257 (0.658)					
Mar	0.200 (0.714)	-0.055 (0.881)				
Apr	0.086 (0.919)	-0.355 (0.286)	-0.473 (0.146)	-0.478 (0.137)		
May	0.086 (0.919)	-0.309 (0.356)	**-0.655 (0.034)**	**-0.620 (0.048)**	**-0.791 (0.006)**	
Aug	0.429 (0.419)	-0.209 (0.539)	*-0.564 (0.076)*	-0.524 (0.100)	*-0.600 (0.056)*	-0.300 (0.683)
Sep	0.200 (0.714)	-0.456 (0.163)	**-0.629 (0.044)**	**-0.614 (0.048)**	-0.497 (0.121)	-0.500 (0.450)
Oct	-0.359 (0.517)	-0.280 (0.427)	-0.353 (0.313)	-0.317 (0.368)	-0.164 (0.657)	-0.316 (0.750)

Table 4. Summary of the parameters and fit of the GLM for median CPUE of *L. gahi* in the second season south of 52°S. In the coefficients x1 represents the median CPUE in the preceding year and x2 represents the median CPUE of the second wave of *I. argentinus* in the current year. Fitting was carried out using treatment contrasts, so values are relative to the case where CPUE in the preceding season was < 0.55 tonnes hr^{-1} and the *I. argentinus* threshold was not exceeded.

Coefficients:	*Estimate*	*Std. Error*	*t value*	*Pr(>|t|)*
(Intercept)	-0.211	0.217	-0.972	0.3686
0.55<=x1<=1.2	0.516	0.273	1.890	0.1077
x1>1.2	-0.030	0.325	-0.093	0.9288
x2 > 9	-0.788	0.217	-3.633	0.0109

Deviance Residuals:				
Min	*1Q*	*Median*	*3Q*	*Max*
-0.4235	-0.1636	-0.0007	0.1104	0.4379

Fitting statistics:		
Dispersion parameter for Gamma family taken to be 0.0940		
Null deviance:	2.29047 on 9	degrees of freedom
Residual deviance:	0.55644 on 6	degrees of freedom
AIC: 4.5769		

Figure captions

Figure 1. Total catch (metric tonnes) by reporting grid (see text) in Falkland Island fishery zones in the period 1987-1999 of (a) *Illex argentinus* and (b) *Loligo gahi*.

Figure 2. Total catch of *Illex argentinus* by licensed jiggers reporting grid square in 1994 (left column) and 1999 (right column). The top row shows the catch assigned to the first wave, and the bottom row the catch assigned to the second wave. The heavier lines denote the area used to separate the catch by wave in April.

Figure 3. Total licensed catch of *Loligo gahi* by reporting grid square in 1994 (left column) and 1999 (right column). The top row of shows the catch during the first season and the bottom row the second season. The heavy line shows the separation between the northern and southern fishery areas.

Figure 4. Time series of (a) total catch and median CPUE, and (b) total effort and season duration for vessels licensed to target *Illex argentinus* in the Falkland Islands' fishery zones from 1989 to 1999.

Figure 5. Daily CPUE for *Illex argentinus* (left column) and the second season of *Loligo gahi* south of 52° S (right column) in 1992 and 1999. Daily CPUE is calculated for each licensed vessel which is fishing, and each day's CPUE values are presented as a boxplot (McGill, *et al.* 1978) to illustrate both the variability and central tendency of the daily data.

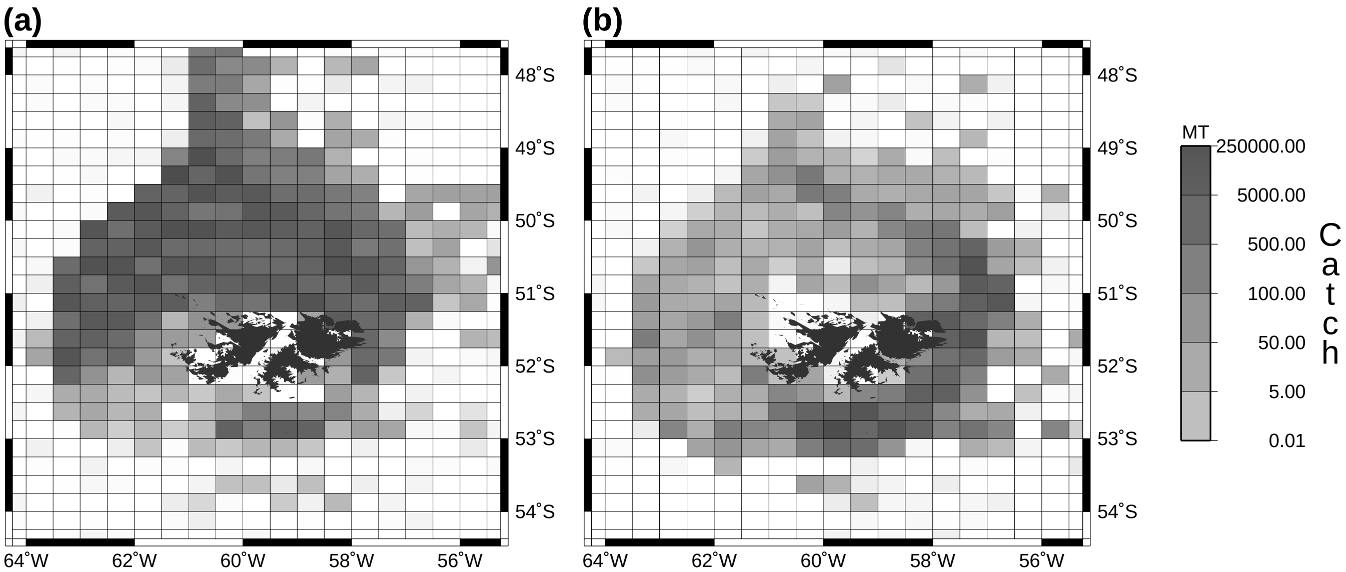
Figure 6. Time series of (a) total catch, (b) median CPUE, and (c) total effort and season duration for vessels licensed to target *Loligo gahi* in the Falkland Island's fishery zones from 1989 to 1999. Separate time series are presented for the two seasons in the northern and southern areas.

Figure 7. Deviations in *L. gahi* CPUE from the long term mean group value over the period 1989-1999 expressed as a proportion of the long term mean (a) first season north of 52°; (b) first season south of 52° S; (c) second season north of 52° S; (d) second season south of 52° S. In each case the deviation from the long term mean group CPUE is also shown for *I. argentinus* waves one and two.

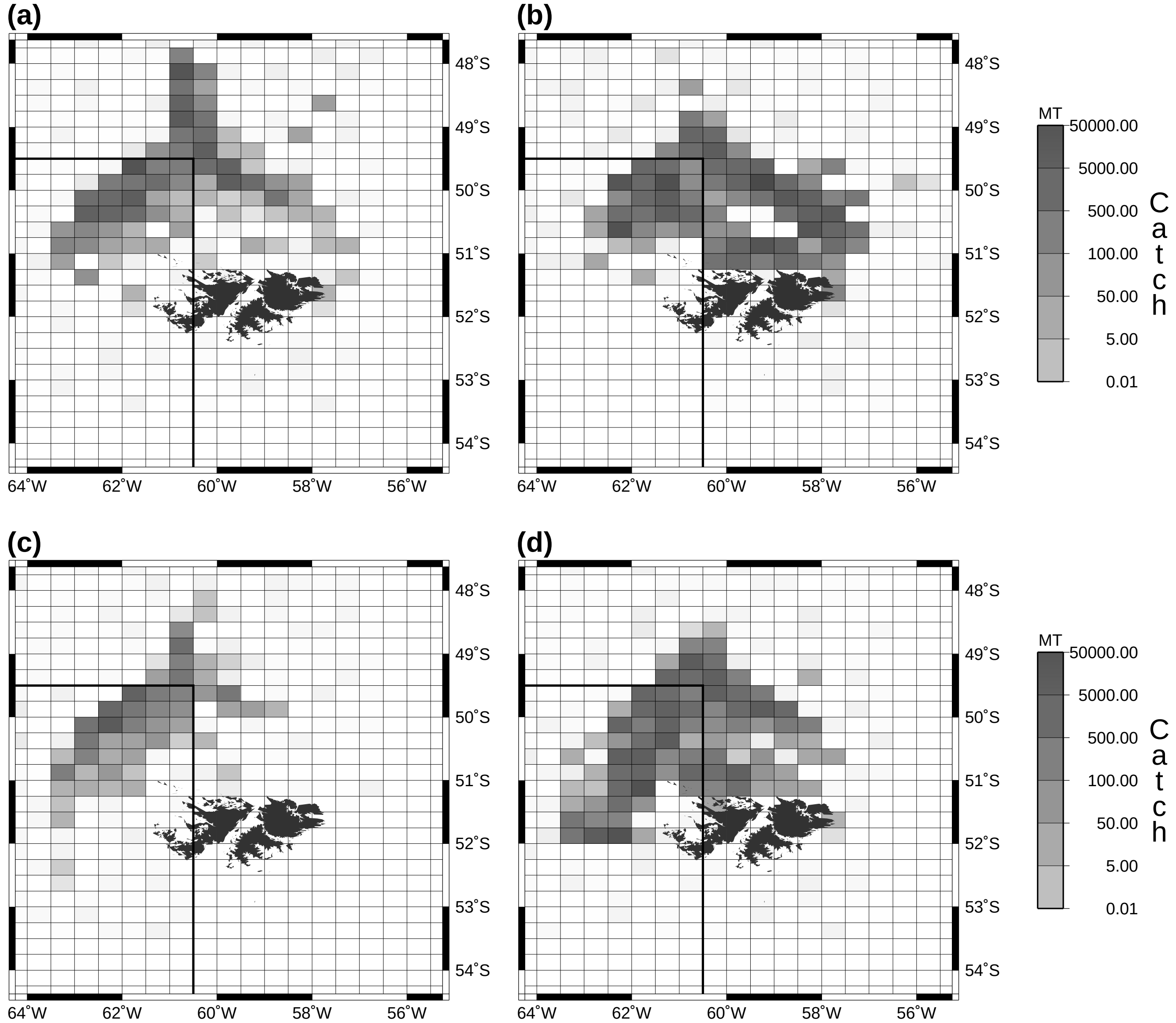
Figure 8. Relationship between median CPUE for the two waves of *I. argentinus* and median CPUE for each season of *L. gahi* in the northern and southern fishery areas.

Figure 9. Relationship between median CPUE in the current year and that in the previous year for *L. gahi* in the second season south of 52°S. Circles mark those points where the median CPUE of second wave *1. argentinus* in the current year was less than 9 kg line-hr^{-1}, stars mark those points where this threshold was exceeded. The dashed vertical lines illustrate the division of median CPUE in the preceding season into the three factor levels used in the GLM (see text).

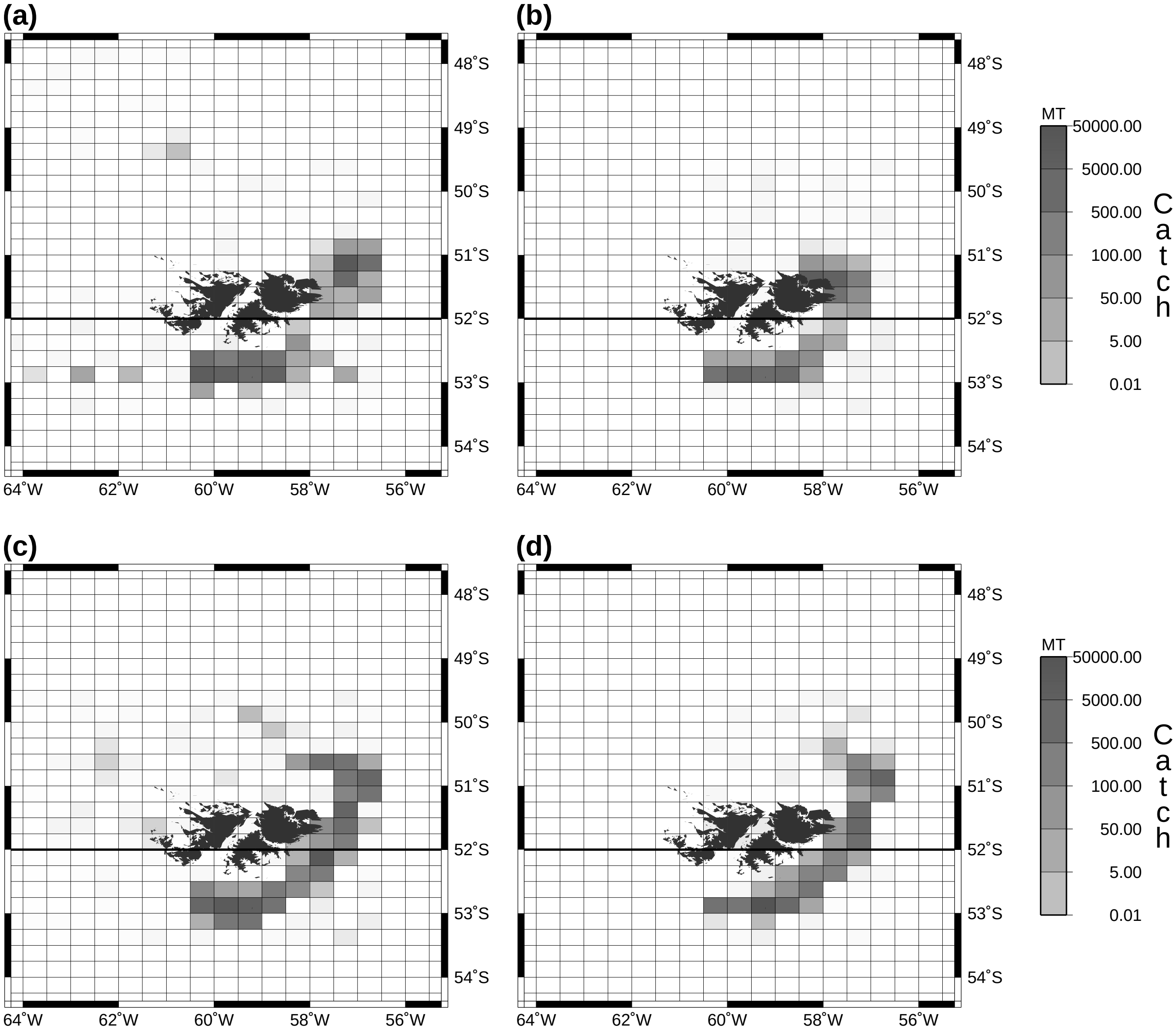
Figure 10. Circles and solid lines: realised time series for median CPUE of second season *L. gahi* in the southern area compared with (crosses and dashed lines) output of the GLM with three factor levels for preceding year *L. gahi* CPUE and a factor indicating whether the threshold abundance of wave 2 *I. argentinus* was exceeded in the current year.



Arkhipkin & Middleton, Figure 1



Arkhipkin & Middleton, Figure 2



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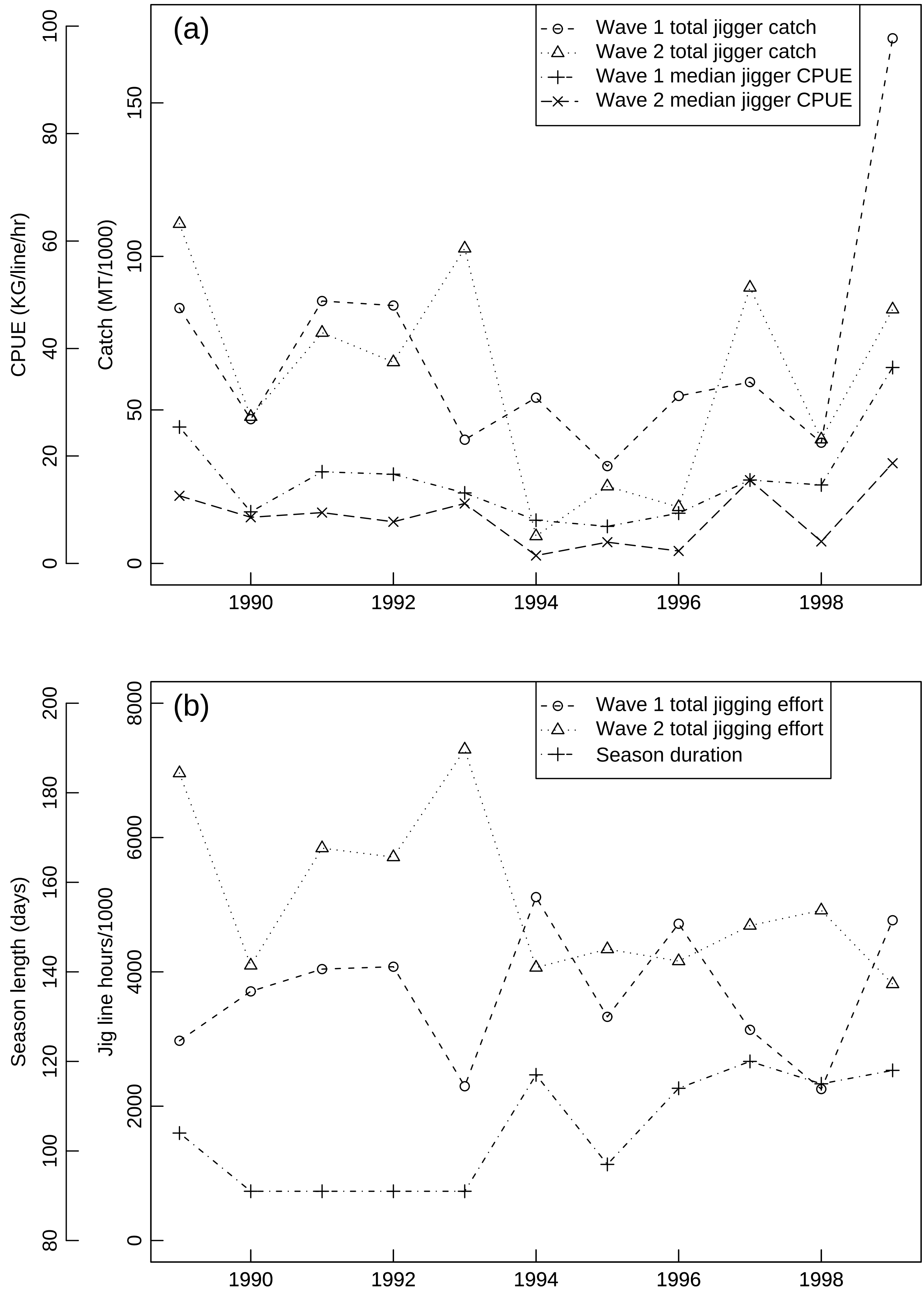

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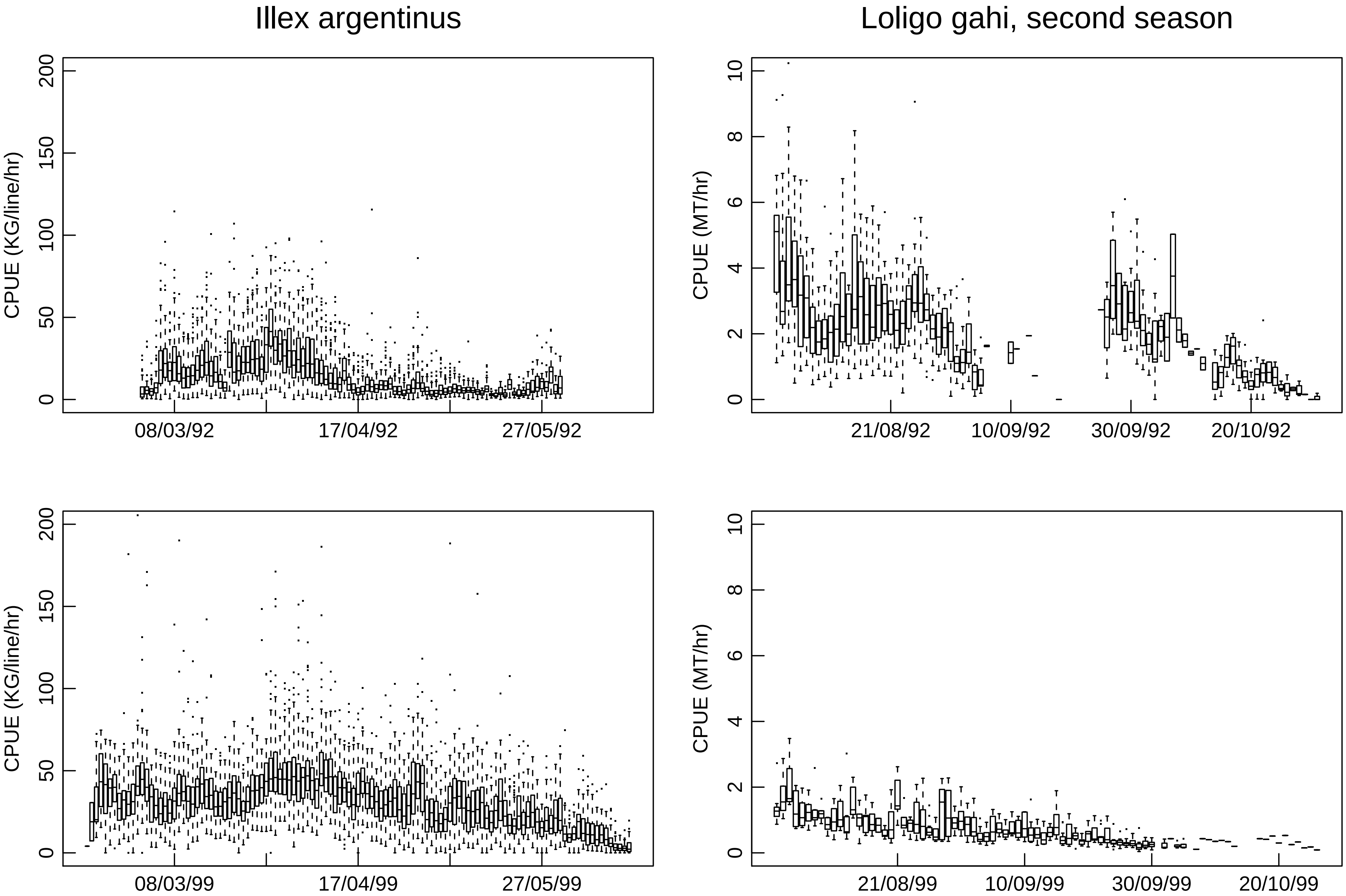

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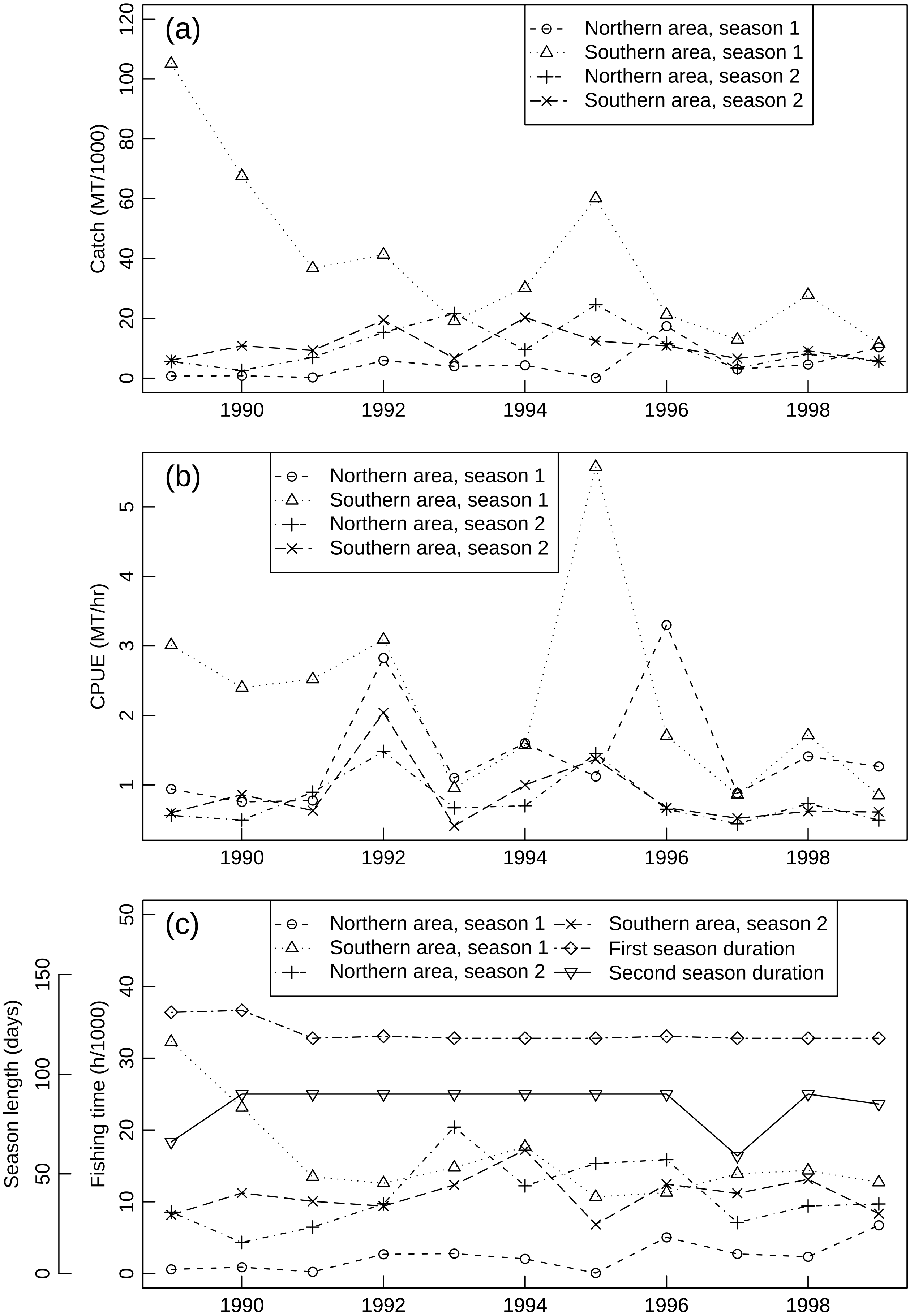

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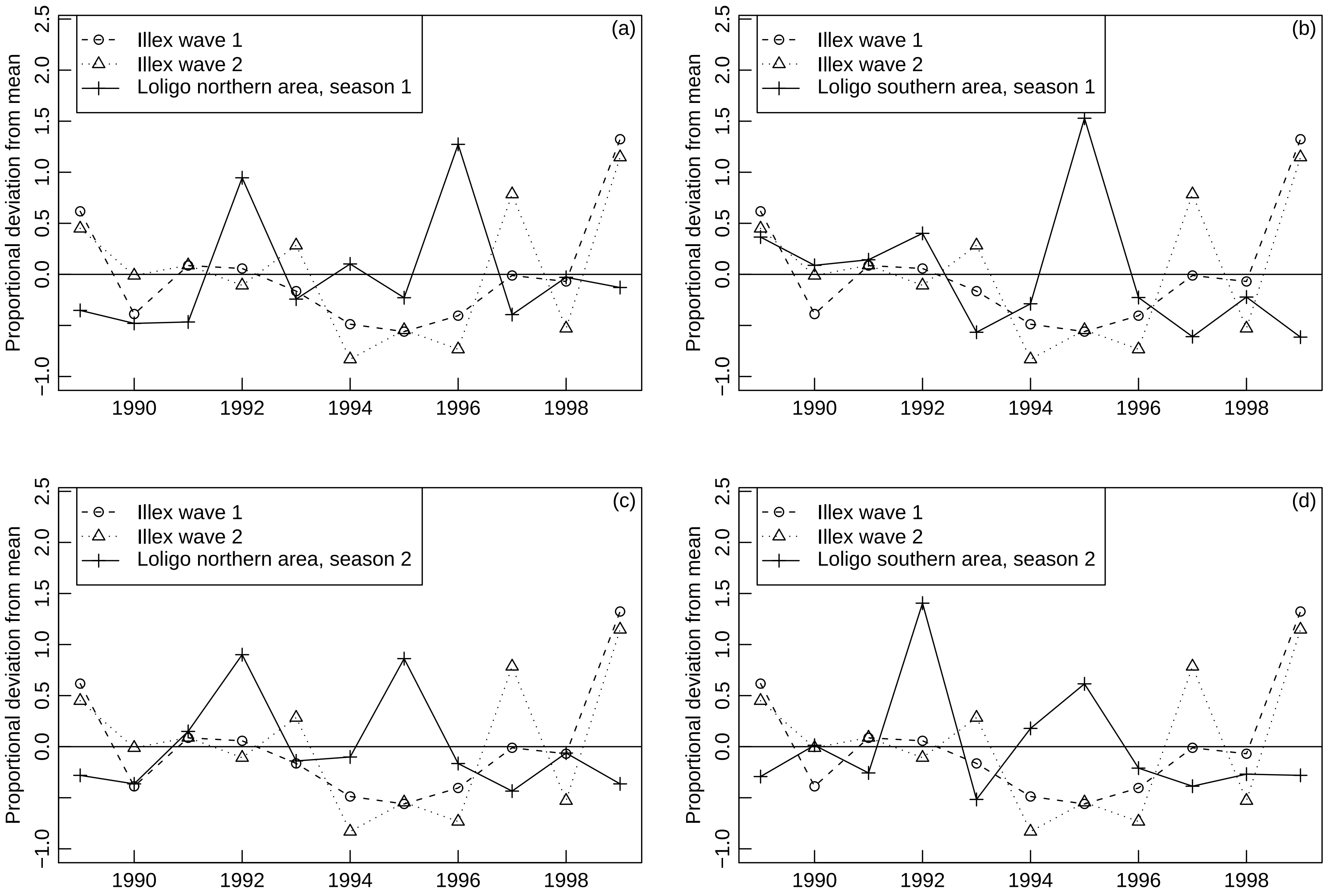

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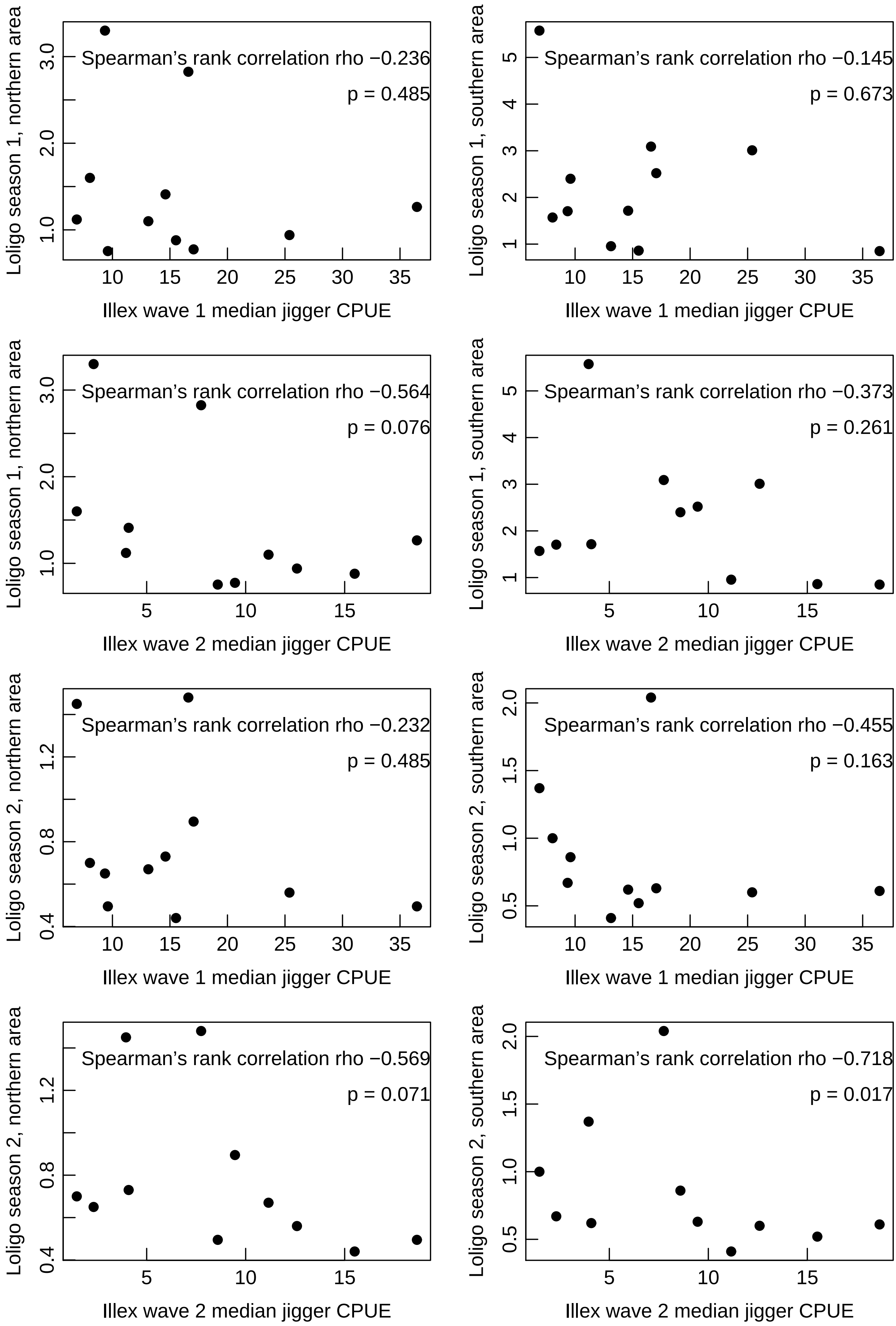

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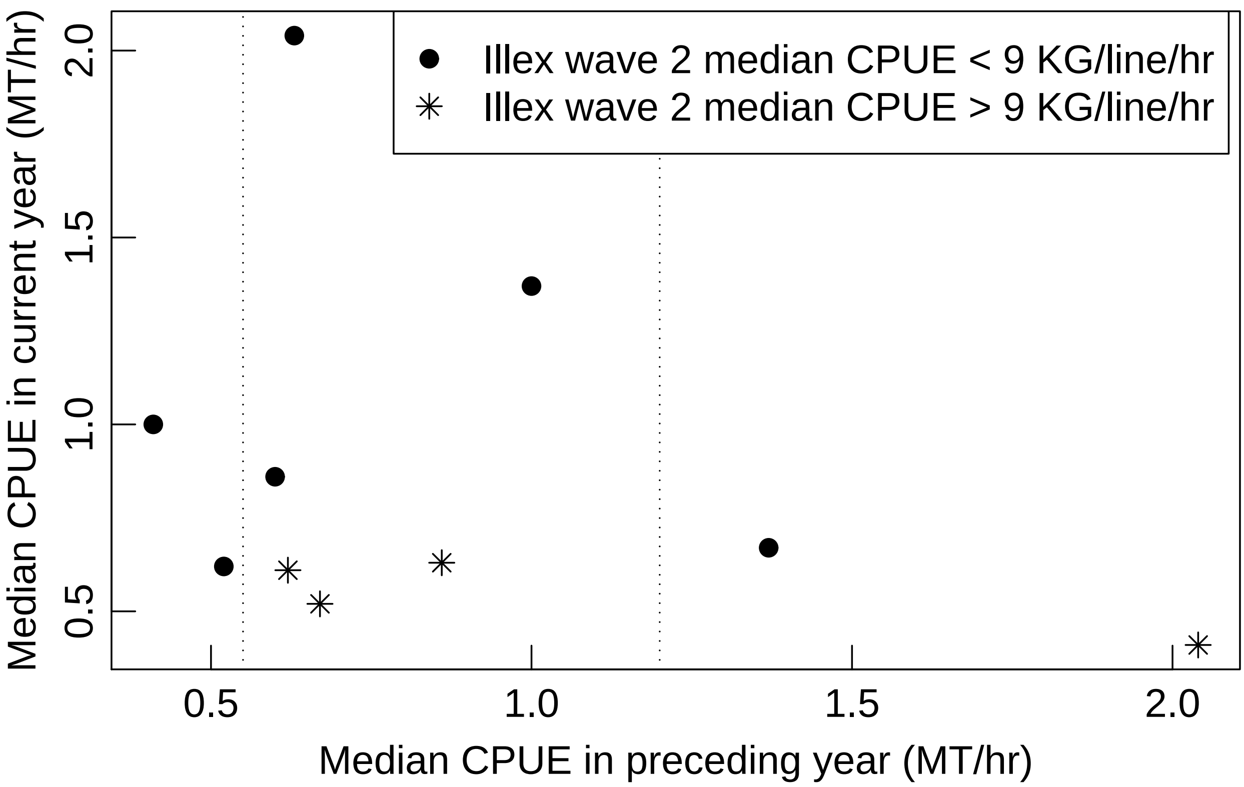

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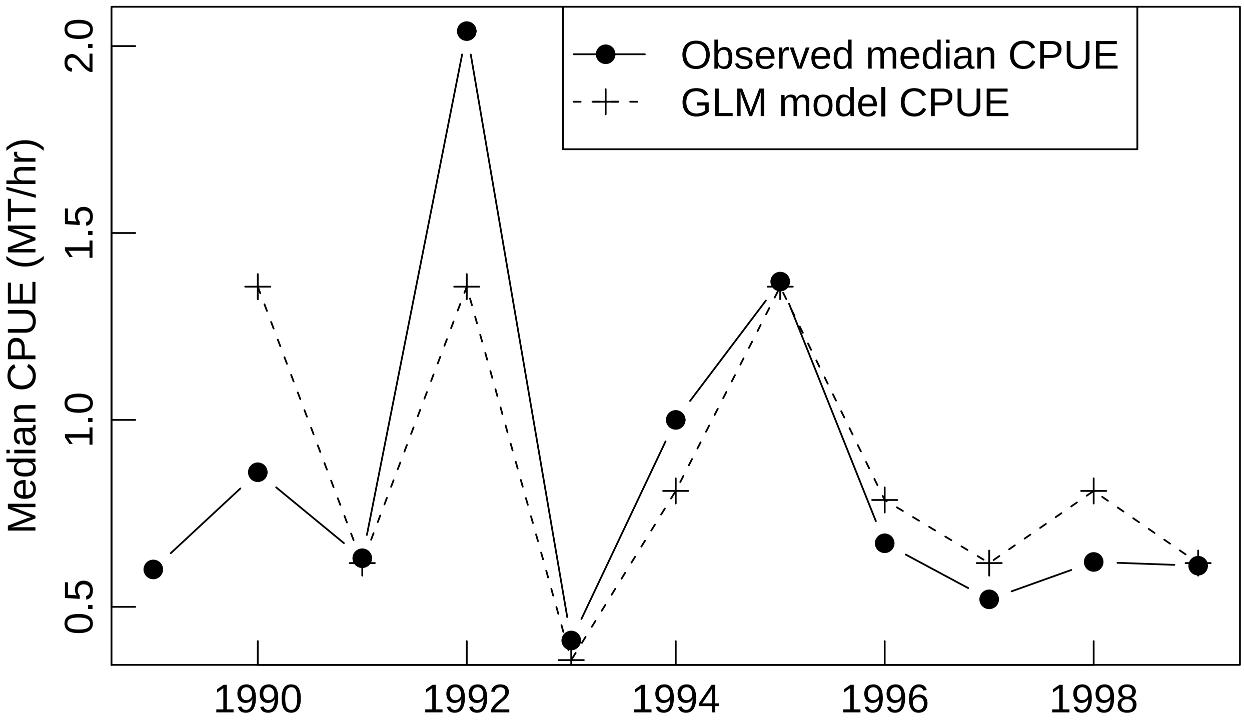

Arkhipkin & Middleton, Figure 10