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Research Article

Biological patterns of the Argentine shortfin squid *Illex argentinus* in the slope trawl fishery off Brazil

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ABSTRACT. Commercial exploitation of the Argentine shortfin squid (*Illex argentinus*) was virtually non-existent in Brazilian waters until 2000 when foreign trawlers initiated their operations on slope grounds as part of a government-induced chartering program. Since then, the species has been included among the targets of a developing slope trawl fishing off southeastern and southern Brazil. Biological samples were collected from commercial catches of 25 national and seven foreign (chartered) trawlers between 23°-33°S and 170-740 m depth. These samples represent two periods of the commercial exploitation of *Illex argentinus* in Brazil: 2001-2003, when both chartered and national trawlers operated simultaneously, and 2006-2007, when only national vessels continued to exploit *I. argentinus* along with other slope stocks. Catches contained immature and maturing squid throughout the year, as well as at least two distinct, fully mature, spawning groups: one composed of small-sized males and females present year-round on the shelf-break/ upper slope (< 400 m), and the other consisting of large squid present only in austral winter-spring in southern (26°-29°S) and deep fishing grounds (400-700 m). The latter group has sustained the large winter catches reported since 2000 and the large sizes and concentrations of the specimens sparked the interest of the fishing industry as a potential target of the slope fishery. The reproductive attributes and temporal/ spatial distribution patterns of winter spawners support the hypothesis that relates this group to migrating concentrations of a north Patagonian shelf stock. If confirmed, the present data would underscore the need to consider multinational shared stock management strategies in the SW Atlantic.

Keywords: ommastrephid squid, *Illex argentinus*, slope trawl fishery, southern Brazil.

Patrones biológicos del calamar argentino *Illex argentinus* en la pesquería de arrastre en el talud continental de Brasil

RESUMEN. La explotación comercial del calamar argentino (*Illex argentinus*) no existía en aguas brasileñas hasta el año 2000, cuando buques extranjeros iniciaron sus operaciones en el talud como parte de un programa gubernamental de arrendamiento. Desde entonces la especie forma parte de un conjunto de recursos que han motivado el desarrollo de una pesquería de arrastre en el talud del sur y sureste de Brasil. Se colectaron muestras biológicas de las capturas comerciales de 25 buques arrastreros nacionales y siete extranjeros entre los paralelos 23°-33°S y en profundidades de 170 a 740 m. Estas muestras representaron dos periodos de la explotación comercial de *I. argentinus* en Brasil: 2001-2003, cuando buques nacionales y extranjeros operaron simultáneamente, y 2006-2007 cuando sólo buques nacionales permanecieron explotando el calamar argentino en conjunto con otros recursos del talud. Las capturas estuvieron constituidas por calamares inmaduros y en-maduración a lo largo de todo el año, así como al menos dos grupos distintos de individuos maduros y desovantes: un grupo constituido por machos y hembras de pequeño tamaño que están presentes en todas las estaciones del año en el borde de la plataforma continental y talud superior (< 400 m), y otro grupo, constituido por calamares de gran tamaño, presente solamente durante el invierno-primavera australes en áreas sureñas (26°-29°S) y profundidad (400-700 m). Este grupo ha sostenido las grandes capturas invernales reportadas desde 2000 y, dado su largo tamaño y concentración, ha justificado el interés de la industria pesquera como un potencial recurso para la pesca en el talud. Características reproductivas y patrones de distribución temporales/ espaciales de los desovantes de invierno corroboran la hipótesis que les relaciona a concentraciones migratorias de stock del norte de la plataforma Patagónica. Si se confirma esta hipótesis, estos datos resaltan la importancia de considerar estrategias de manejo dirigidas a stocks compartidos en el Atlántico SW.

Palabras clave: calamares omastréfidos, *Illex argentinus*, pesquería de arrastre de talud, sur de Brasil.

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INTRODUCTION

Squids have long represented important bycatch components of the multispecific trawl fishery off Brazil (Costa & Haimovici, 1990; Perez & Pezzuto, 1998). On the continental shelf, loliginids have further become seasonal targets of both hand jigging and trawl fisheries, as they are densely concentrated in space and time (Perez, 2000; Martins & Perez, 2007). In recent years, however, commercial landings of the ommastrephid Argentine shortfin squid *Illex argentinus* (Castellanos, 1960) have been recorded in the southeastern and southern sectors of the Brazilian coast and have placed this squid among the main cephalopod resources exploited in the country (Perez *et al*., 2009a).

The species is distributed in the SW Atlantic from Rio de Janeiro (23°S) to southern Argentina (54°S) sustaining, on the Patagonian shelf and around the Falkland (Malvinas) Islands, one of the largest cephalopod fisheries in the world (Boyle & Rodhouse, 2005). Off Brazil, several fishing surveys conducted since the 1970s have revealed important concentrations of paralarvae, juveniles, and spawning individuals, particularly in the shelf break and slope waters of the southern coast (south of 25°S) (Haimovici & Andriguetto Fo, 1986; Haimovici & Perez, 1991; Haimovici *et al*., 1995, 2007, 2008). In this area, the species has also been often found in stomach contents of large predators, and it is regarded as one of the key components of both pelagic and demersal trophic chains (Santos & Haimovici, 2000; Gasalla *et al.*, 2007).

Commercial exploitation of the Argentine shortfin squid was virtually non-existent in Brazilian waters until 2000, when foreign-chartered trawlers initiated their operations on the slope grounds south of 20°S (Perez *et al*., 2003, 2009b). In that year, the Portuguese trawler "Joana" landed approximately 48 ton of this species caught during one fishing trip between 26-29°S and 235-401 m isobaths (Perez *et al*., 2003). In 2002, the South-Korean trawler "In Sung 207" exploited the same area in winter (June-September) catching, on average, 199 kg of *I. argentinus* per trawling hour. After four fishing trips, this vessel landed a total of 1,400 ton, the largest catch ever recorded in Brazilian waters (Perez *et al*., 2009b). In total, landings of *I. argentinus* that year reached 2,601 ton, nearly twice the amount recorded for other squids (mostly loliginids). These catches, however, decreased to 100-400 ton in the following years, as chartered trawlers either abandoned Brazilian waters or moved to deeper areas (> 700 m). Since then, national trawlers have included *I. argentinus* among the targets of a developing "upper slope" (250-500 m) trawl fishery (Perez & Pezzuto, 2006; Perez *et al*., 2009a).

Preliminary assessments of this fishery have considered *I. argentinus* to be a seasonal resource with a fishing potential that has not been objectively defined but that is generally considered to be highly variable and unpredictable (Haimovici *et al*., 2006). The main questions regarding the biological aspects of *I. argentinus* commercial exploitation off Brazil, however, revolve around its complex population structure and potential connections with migrating stocks exploited off Uruguay and Argentina (Perez *et al.*, 2003; Haimovici *et al*., 2006). As most ommastrephid squids, *I. argentinus* is a short-lived species (~1 year) that matures late in life and dies after a single and terminal spawning event (Haimovici *et al.*, 1998). Because generations do not overlap in time, population resilience is highly dependent on recruitment and, consequently, annual abundances typically exhibit wide oscillations, as do commercial catches (Boyle & Rodhouse, 2005). Associated with this extreme life history pattern, ommastrephids tend to combine extended spawning seasons, long reproductive migrations, and the passive transport of offspring by surface geostrophic currents to produce both seasonal and geographic population units (stocks); this complex structure is regarded as an evolutionary strategy to minimize the risks of semelparity (O'Dor, 1998).

In the SW Atlantic, at least four stocks were distinguished from general size-at-maturity patterns: summer spawning stock (SSS), south Patagonian stock (SPS), Bonaerensis north Patagonian stock (BNS), and southern Brazil stock (SBS) (Brunetti, 1988; Haimovici *et al*., 1998). The latter group included the main concentrations of spawning squid found in winter months on the slope off southern Brazil (Haimovici & Perez, 1990; Santos & Haimovici, 1997). Growing biological evidence (*i.e.* maturation patterns, trophic relationships, the occurrence of certain parasites, statolith morphometrics), however, suggests that these squid are in fact BNS members that migrate north to spawn in Brazilian waters (Santos & Haimovici, 1997; Schwarz & Perez, 2007). Although local spawning was also observed occuring off Brazil throughout the year, winter spawning was potentially linked to recruitment off the northern Patagonian shelf through paralarval transport by the Falkland (Malvinas) – Brazil Current system (Haimovici *et al*., 1995). In this context, this study analyzes biological attributes of commercial catches of the Argentine shortfin squid off southern Brazil as a descriptive approach to assess both the population structure subject to the seasonal exploitation regime and the hypothesis of a shared stock scenario.

MATERIAL AND METHODS

Biological samples of the Argentine shortfin squid were obtained from commercial catches of 25 national and seven foreign (chartered) trawlers all derived from operations in the southeastern and southern sectors of the Brazilian coast (Fig. 1) between 23°-33°S and 170-740 m depth. Samples represent two periods of the species' commercial exploitation in Brazil: 2001-2003, when both chartered and national slope trawlers operated simultaneously, and 2006-2007, when only national vessels continued to exploit *I. argentinus* along with other slope stocks (Table 1) (Perez & Pezzuto, 2006; Perez *et al.*, 2009b).

Onboard observers collected samples from chartered trawlers for all fishing trips conducted principally between September 2001 and April 2003. After each positive trawl, a sample was taken from the catch

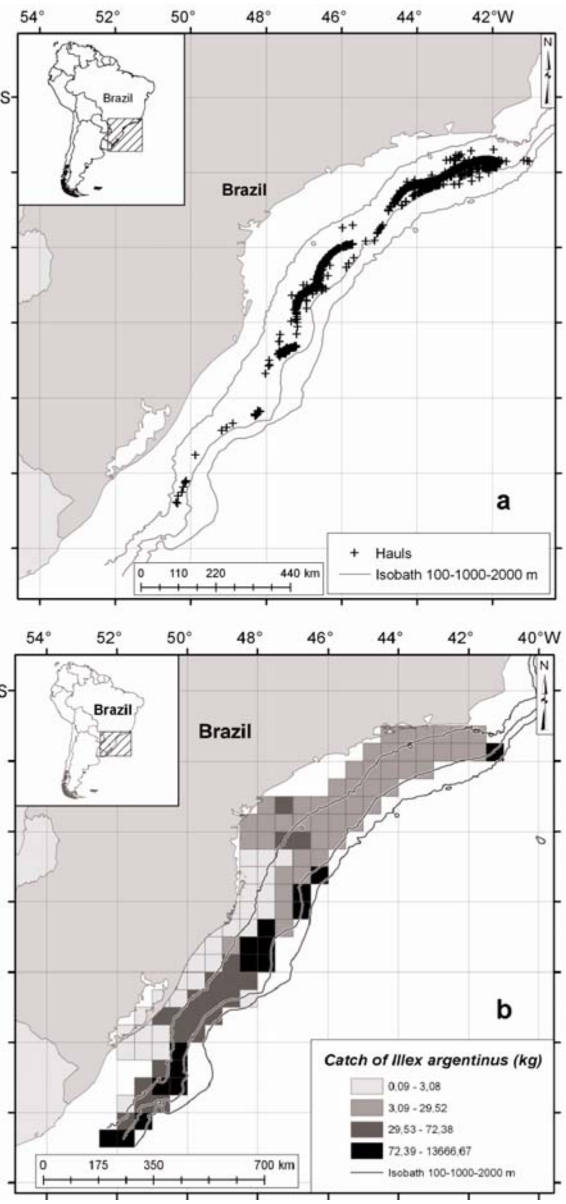

Figure 1. Spatial distribution of Argentine shortfin squid *Illex argentinus* catches off southeastern and southern Brazil. a) chartered trawlers (2001-2003), b) national trawlers (2006-2007). Latitude and longitude were decimal transformed.

Figura 1. Distribución espacial de las capturas del calamar argentino *Illex argentinus* en el sureste y sur de Brasil. a) arrastreros arrendados (2001-2003), b) arrastreros nacionales (2006-2007). Latitudes y longitudes fueron transformadas en valores decimales.

and deep-frozen for posterior analysis in the laboratory ashore. Each sample had detailed information on trawl position (lat-long), date, time, and fishing effort (trawling hours). Samples from national trawlers were collected from landings at the harbors of Santa Ca-

Table 1. Summary of data for the Argentine shortfin squid *Illex argentinus* obtained from chartered and national trawlers operating off Brazil between 2001 and 2007. N: number of individuals; Min-Max: smallest and largest mantle length (ML) and total wet body weight (BW).

Tabla 1. Resumen de datos de calamar argentino *Illex argentinus* obtenidos en las operaciones de pesca de arrastreros arrendados y nacionales en Brasil entre 2001 y 2007. N: número de individuos, Min-Max: valores máximos y mínimos de la longitud del manto (ML) y peso total húmedo (BW).

	Males			Females		
		ML (mm)	BW (g)		ML (mm)	BW (g)
Trimester	N	Min-Max	Min – Max	N	Min – Max	Min – Max
Chartered						
Jan-Mar/2001		-	-	-	-	-
Apr-Jun/2001		-	-	-	-	-
Jul-Sep/2001	32	78 – 195	14 – 240	24	91 – 332	18 – 455
Oct-Dec/2001	966	110 – 278	23 – 425	506	105 – 336	33 – 655
Jan-Mar/2002	395	115 – 221	25 – 295	262	98 – 254	18 – 320
Apr-Jun/2002	466	115 – 239	26 – 345	524	104 – 299	23 – 560
Jul-Sep/2002	153	119 – 316	27 – 570	307	114 – 346	26 – 775
Oct-Dec/2002	4	221 – 275	260 – 420	7	280 – 325	228 – 670
Jan-Mar/2003	73	105 – 191	29 – 188	60	143 – 234	52 – 260
Apr-Jun/2003	131	123 – 200	40 – 192	130	130 – 250	43 – 400
Apr-Jun/2006		-	-		-	-
Jul-Sep/2006	7	229 – 259	195 – 325	1	250	162
Total	2227	78 – 316	14 – 570	1821	91 – 346	18 – 775
National						
Jan-Mar/2001	4	154 – 174	76 – 121	6	155 – 185	79 – 145
Apr-Jun/2001	136	129 – 245	30 – 253	213	115 – 395	32 – 580
Jul-Sep/2001	12	190 – 261	163 – 405	16	195 – 315	90 – 655
Oct-Dec/2001	36	135 – 166	38 – 148	89	124 – 204	39 – 255
Jan-Mar/2002	81	114 – 254	30 – 309	125	117 – 262	31 – 375
Apr-Jun/2002	86	100 – 250	30 – 335	88	130 – 376	44 – 605
Jul-Sep/2002	95	110 – 340	31 – 450	86	118 – 350	25 – 830
Oct-Dec/2002	5	220 – 262	211 – 249	8	252 – 367	196 – 580
Jan-Mar/2003		-	-		-	-
Apr-Jun/2003	27	159 – 225	100 – 315	16	190 – 290	180 – 645
Apr-Jun/2006	24	130 – 210	49 – 162	51	117 – 305	68 – 700
Jul-Sep/2006	43	110 – 289	128 – 470	45	166 – 351	57 – 860
Oct-Dec/2006	73	111 – 249	28 – 390	77	132 – 344	35 - 870
Jan-Mar/2007						
Apr-Jun/2007	75	145 -246	50 -299	122	135 - 338	37 -740
Jul-Sep/2007	46	160 - 289	116 - 505	54	223 - 353	184 -910
Oct-Dec/2007						
Total	743	100 – 340	28 - 505	996	115 - 395	25 - 910
TOTAL	2970	78 – 340	14 - 570	2817	91 - 395	18 - 910

tarina state (southern Brazil) as part of a daily fishery sampling program (Perez *et al*., 1998). From each landed catch, approximately 20 kg of squid were measured for their dorsal mantle length (ML) to the nearest centimeter, and a length stratified subsample was taken to the laboratory. These subsamples could not be related to individual trawls conducted during each fishing trip, but represented the entire fishing area covered by it. Information on the fishing area, effort (mean trawl duration, number of trawls per day, trip duration in days), and total catch were obtained during interviews with skippers at the time of the landings.

In the laboratory, the ML and the total body weight (BW) were recorded to the nearest millimeter and gram, respectively. After dissecting the mantle, males and females were differentiated and maturity stages were assigned according to the macroscopic scale proposed by Brunetti (1990). This scale defined seven and eight maturity stages for males and females, respectively, including: immature (stages I and II), in maturation (stage III), early maturity (stage IV), advanced maturity (stage V), spawning (stage VI for males and stages VI and VII for females), and spent (stage VII for males and stage VIII for females).

In females, the ovary and accessory organs (oviduct + nidamental glands + oviducal gland) were weighed (OW and AOW, respectively), the nidamental gland length was measured (*NGL*), and the gills were checked for the presence of spermatophores as signs of mating. In males, the testis and accessory organs (spermatophoric complex + Needhan's sac + penis) were weighed (TW and AOW, respectively), the testis length was measured (*TL*), and the Needhans's sac was examined for the presence of spermatophores. All weights were taken to the nearest 0.1 g and measurements to 0.1 mm.

Maturation in males and females was expressed numerically by three indices:

a) the Gonadosomatic index defined for males (GSI_M) and females (GSI_F) as:

$$GSI_M = \frac{TW + AOW}{(BW - (TW + AOW))} 100$$
$$GSI_F = \frac{OW + AOW}{(BW - (OW + AOW))} 100 \quad (1)$$

b) the Hayashi index (*HI*) defined for males (HI_M) and females (HI_F) as

$$HI_M = \frac{AOW}{TW + AOW}, \qquad HI_F = \frac{AOW}{OW + AOW} \quad (2)$$

c) the Testis (*TI*) - Nidamental Gland (NGI) indices defined as

$$TI = \frac{TL}{ML}, \qquad NGI = \frac{NGL}{ML} \quad (3)$$

A data bank was produced in which each squid was described by its origin (sample, landing date), sex, size (ML, BW), and reproductive characteristics (maturity stage, OW, TW, AOW, GSI, HI, TI/ NGI).

Size-at-maturity was assessed from the cumulative ML frequency distribution of mature and spawning males and females (stages > IV). This distribution was linearized by the probit transformation of cumulative ML frequencies and a straight line was then fitted to the transformed frequency *vs*. ML class relationship using the least-squares method. Precise ML at different percentiles were then estimated by substituting the probit values in the estimated linear equation (*i.e.* probit 5 corresponds to 50% percentile):

$$ML_m = \frac{pf - c}{d} \quad (4)$$

where *pf* is the probit transformed ML cumulative frequency and *c* and *d* are the intercept and the slope of the fitted line, respectively.

Population differentiation among squid caught by commercial trawlers was explored through a multivariate Principal Component Analysis (PCA) applied separately for males and females. Variables included in this analysis involved size and reproductive attributes (BW, GSI, HI, TI/ NGI), day-of-the-year (DYR), decimal latitude (LAT), decimal longitude (LONG), and depth (DEPTH). A correlation matrix was calculated for the variables (previously standardized as a proportion of their mean) and new axes (factors) were extracted in the direction of greatest variance. These factors were linear combinations of the original variables and used to interpret the potential existence of biologically similar groups of squids and their occurrence in space and time.

RESULTS

Size structure of catches

Males and females caught during slope trawl fishing exhibited a bi-modal ML frequency distribution (Fig. 2). Males ranged from 78 to 340 mm ML, exhibiting one pronounced mode centered around 160 mm ML and a secondary mode between 220 and 240 mm ML. Females were generally larger, ranging from 91 to 395 mm ML. A main modal group was formed around 180 mm ML and a less pronounced one between 280-320 mm ML (Fig. 2, Table 1). The overall size structures remained practically unchanged as the catches by the chartered and national trawlers in 2001-2007 were examined separately, although larger females were found in the former (Fig. 2).

During the early exploitation period (2001-2003), the size structure of the chartered fleet catches varied with the season, latitude, and depth of commercial operations (Figs. 3 and 4). Large males (ML > 200 mm) dominated catches obtained in winter (July-September) south of 28°S, between 350-540 m depth (Fig. 3). During the rest of the year, catches were generally unimodal, concentrating on individuals between 100-250 mm ML that originated north of 28°S and on the upper slope (< 400 m depth). In females, the patterns observed were virtually the same (Fig. 4), with an uniform group of individuals (100-250 mm ML long) dominating the catches throughout the year, except for winter months when a distinct group of large females was caught in southern (south of 28°S) and deeper (> 350 m) areas.

Slope trawling between 2006-2007, as conducted by the national fleet, concentrated on the larger fractions of both males and females (Fig. 5). These fractions were generally obtained in areas south of 29°S (Fig. 1), inshore of the 400 m isobath, and in autumn (April-June) and winter (July-September) months.

Maturation and maturity stages

Males and females in all maturity stages were present in the slope trawling catches off southeastern and southern Brazil (Table 2). The spawning stage (stage VI) was the most frequently identified maturity condition in both sexes and nearly 50% off all individuals caught were at least in an early maturity stage (stage IV and higher). This overall maturity stage composition was observed in 2001-2003 but shifted towards a complete dominance of spawning (and spent) squid after 2003, as the national trawlers that continued to exploit the Argentine shortfin squid tended to catch and land larger males and females (Fig. 6).

Catches included immature males and females as small as 78 and 91 mm ML, respectively. Spawning males (stage VI) and females (stage VII) attained the largest sizes (Table 2). Squids of both sexes enlarged homogenously as maturation progressed. At an advanced maturity-spawning condition (stages V, VI, and VII), however, two distinct size groups were found (Fig. 7). The first group was dominant in the samples and was composed of males and females ranging from 140-180 mm ML and 160-240 mm ML, respectively. The second group was less abundant but included larger individuals (males > 200 mm ML;

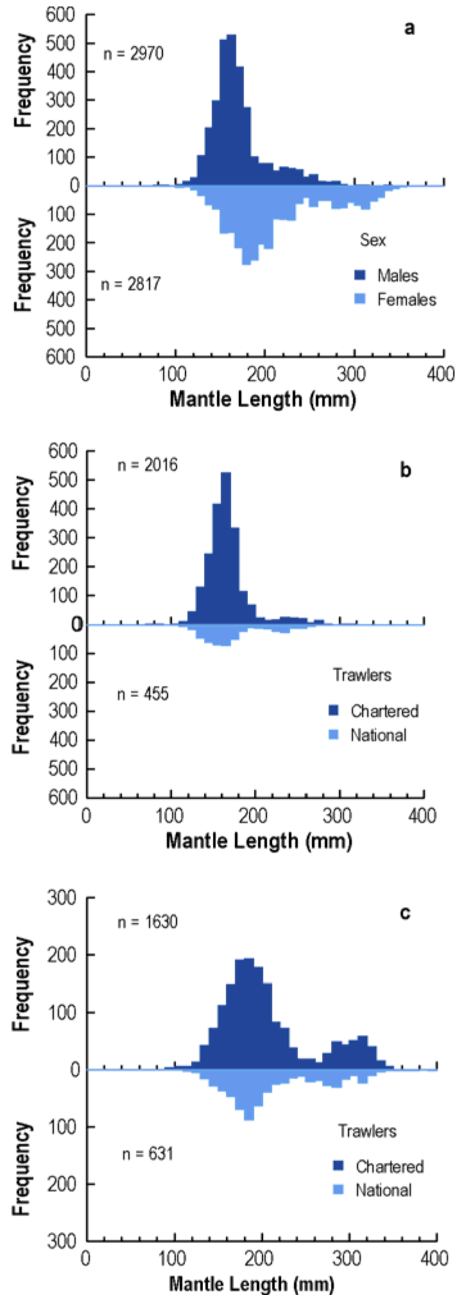

Figure 2. Mantle length frequency distributions (in mm) of males and females of the Argentine shortfin squid *Illex argentinus* caught by commercial trawlers off Brazilian coast between 2001 and 2007. a) total catches, b) male catches obtained by chartered *vs.* national trawlers, c) female catches obtained by chartered *vs.* national trawlers.

Figura 2. Distribución de tallas (largo de manto ML en mm) de machos y hembras del calamar argentino *Illex argentinus* capturados por arrastreros comerciales en la costa de Brasil entre 2001 y 2007. a) capturas totales, b) capturas de machos obtenidas por arrastreros arrendados y nacionales, c) capturas de hembras obtenidas por arrastreros arrendados y nacionales.

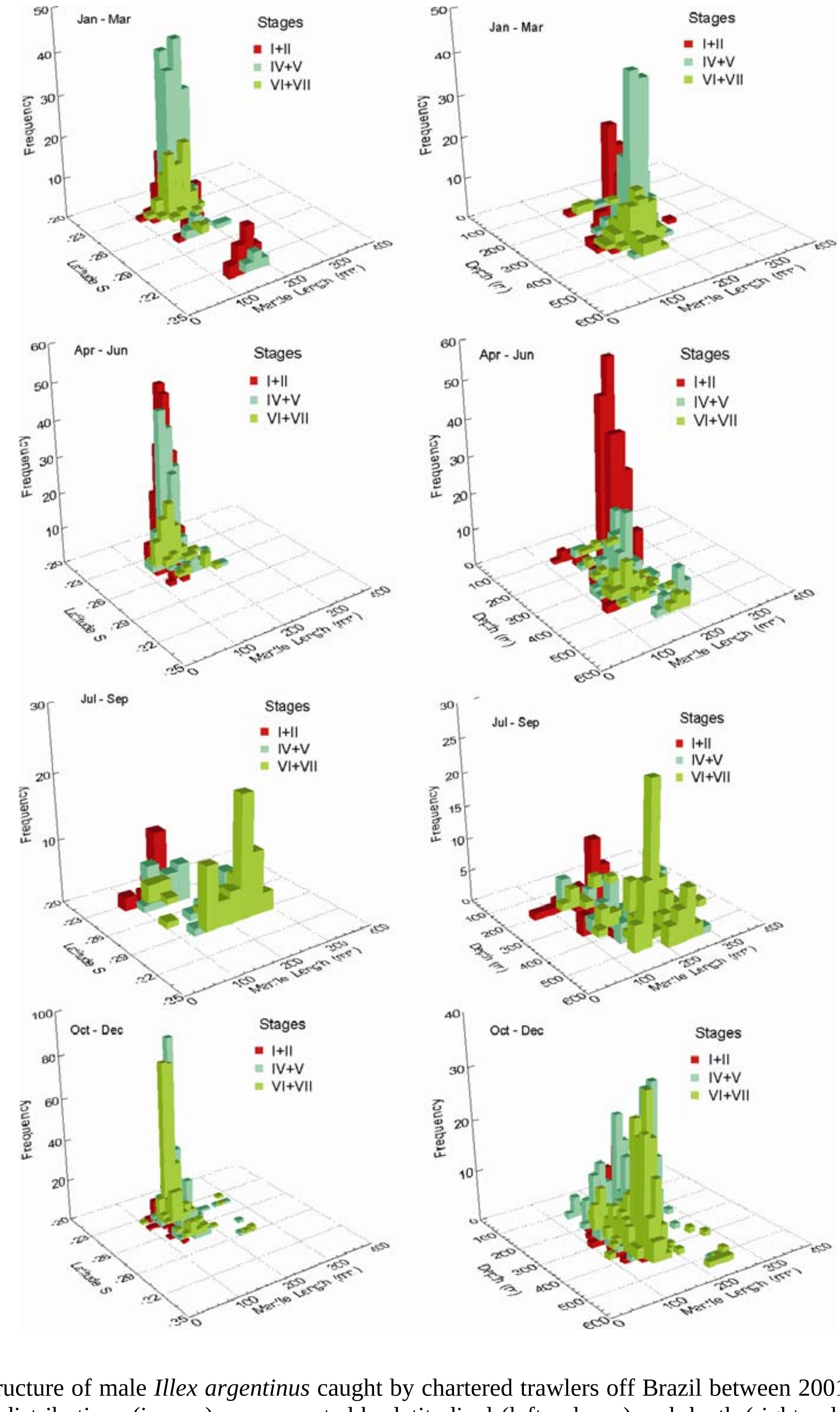

Figure 3. Size structure of male *Illex argentinus* caught by chartered trawlers off Brazil between 2001 and 2003. Mantle length frequency distributions (in mm) are presented by latitudinal (left column) and depth (right column) strata. Colors differentiate maturity stages according to the Brunetti (1990) macroscopic scale.

Figura 3. Estructura de tallas de machos del calamar argentino *Illex argentinus* capturados por arrastreros arrendados en Brasil entre 2001 y 2003. Las distribuciones de frecuencia de tallas (largo de manto ML en mm) están presentadas por estratos latitudinales (columna de la izquierda) y estratos batimétricos (columna de la derecha). Los colores diferencian los estadios de maduración sexual según la escala macroscópica de Brunetti (1990).

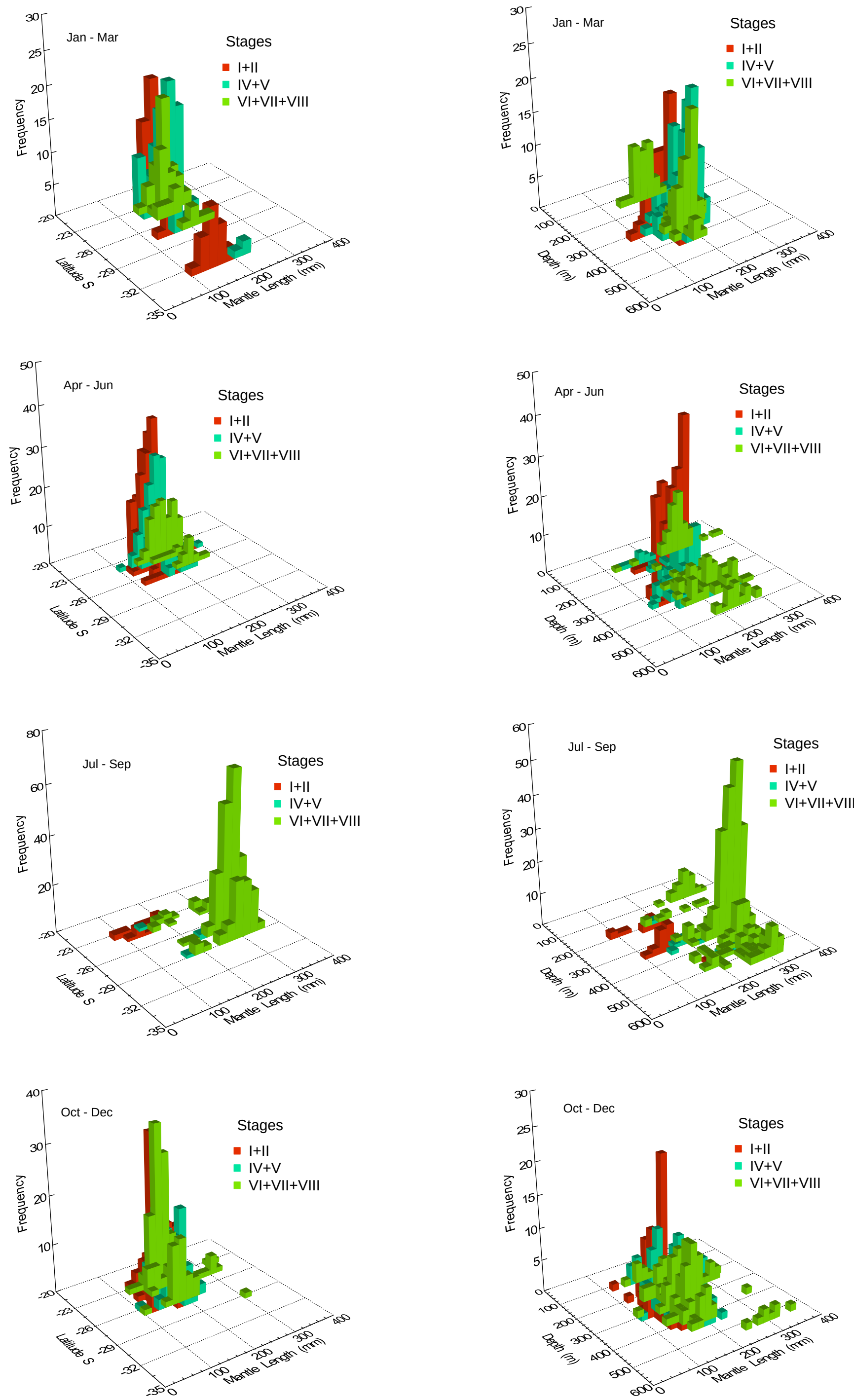

Figure 4. Size structure of female *Illex argentinus* caught by chartered trawlers off Brazil between 2001 and 2003. Mantle length frequency distributions (in mm) are presented by latitudinal (left column) and depth (right column) strata. Colors differentiate maturity stages according to the Brunetti (1990) macroscopic scale.

Figura 4. Estructura de tallas de hembras del calamar argentino *Illex argentinus* capturadas por arrastreros arrendados en Brasil entre 2001 y 2003. Las distribuciones de frecuencia de tallas (largo de manto ML en mm) están presentadas por estratos latitudinales (columna de la izquierda) y estratos batimétricos (columna de la derecha). Los colores diferencian los estadios de maduración sexual según la escala macroscópica de Brunetti (1990).

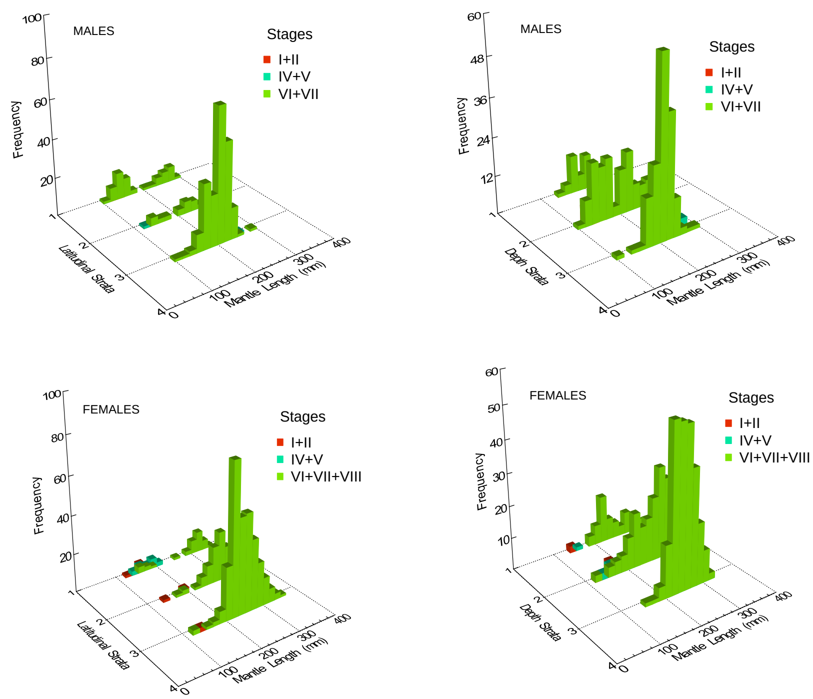

Figure 5. Size structure of *Illex argentinus* caught by national trawlers off Brazil between 2006 and 2007. Mantle length frequency distributions (in mm) are presented for males and females by latitudinal (left column) and depth (right column) strata. Colors differentiate maturity stages according to the Brunetti (1990) macroscopic scale.

Figura 5. Estructura de tallas del calamar argentino *Illex argentinus* capturados por arrastreros nacionales en Brasil entre 2006 y 2007. Las distribuciones de frecuencia de tallas (largo de manto ML en mm) de machos y hembras están presentadas por estratos latitudinales (columna de la izquierda) y estratos batimétricos (columna de la derecha). Los colores diferencian los estadios de maduración sexual según la escala macroscópica de Brunetti (1990).

females > 260 mm ML). Male size-at-maturity was estimated to be 163.3 mm ML and 211.8 mm ML for the smaller and larger modal groups, respectively (Fig. 8). In females, size-at-maturity was estimated to be 201.3 mm ML for the smaller modal group and 292.3 mm ML for the larger one.

The overall maturity condition of the squid in the catches oscillated in space and time (Fig. 9). The GSI variability in males and females indicated that gonads and accessory organs tended to be relatively larger in the second half of the year in both central and northern latitudinal strata. In the southern areas, however, they enlarged earlier, reaching a maximum in autumn. A similar pattern was also revealed by the Hayashi index, which expresses the advanced maturity condition when values are low (Table 2, Fig. 9).

Sex ratio and mating activity

Overall catches during the 2001-2003 period were slightly but significantly biased towards males (male/female ratio = 1.1; $p = 0.001$) (Table 3). Season, latitudinal, and depth strata, however, significantly affected this general pattern, particularly as females tended to outnumber males in winter months, both in shallow areas (< 250 m) and along the central latitudinal stratum (Table 3). A contrasting scenario characterized the 2006-2007 samples: females dominated all spatial and temporal situations except in the northern areas (Table 3).

Spermatophore production and storage increased in stage IV males and peaked in fully mature males (stage V) (Table 2). Mating activity was evidenced in the subsequent maturity stages by a sharp decrease in the presence of spermatophores in the Needhan's sac. Similarly, mated females (evidenced by the presence of spermatophores inside the mantle) were generally scarce in the catches obtained between 2001-2003 period (not mated/ mated female ratio = 1.8) (Table 4) except in winter months and > 400 m depths between 25°-29°S, where the opposite pattern was observed. On the other hand, mated females largely dominated landings in 2006-2007 (Table 4).

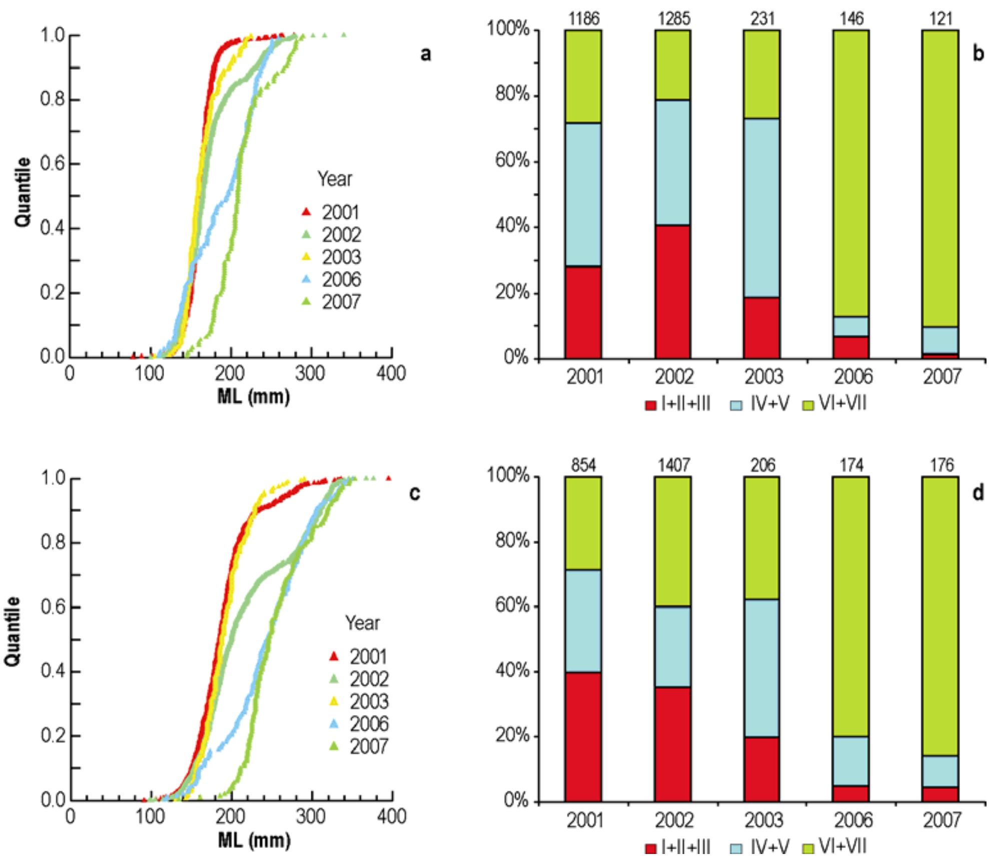

Figure 6. Annual distribution of mantle length (ML in mm) (right column) and maturity stages (left column) of the Argentine squid *Illex argentinus* in commercial catches off Brazil. a and b, males; c and d, females. Size distributions are represented by cumulative frequencies.

Figura 6. Distribución anual de tallas (largo de manto ML en mm) (columna de la derecha) y estadios de maduración sexual (columna de la izquierda) del calamar argentino *Illex argentinus* en capturas comerciales en Brasil. a y b, machos; c y d, hembras. Las distribuciones de tallas están representadas por las frecuencias cumulativas.

Stock differentiation

The association among squids caught by trawlers between 2001-2003 was analyzed from the scores produced by the first three PCA extracted factors (axes) that, together, explained 63% and 72% of the total variance in males and females (Table 5). In males, factor 1 was defined mainly by geographical variables (lat, long) and squid size (BW) (higher positive and negative weights, respectively). Consequently, in the graphic representation (Fig. 10), large mature males caught at southwesterly sites should be plotted on the left hemiplane, whereas small mature squid caught at northeasterly sites should appear in the right hemiplane. Depth and maturity condition, as expressed by the Hayashi Index (HI), were particularly important in factor 2 (Table 5); males caught in deep areas with enlarged accessory reproductive organs (i.e. Needham's sac loaded with spermatophores) should be plotted on the left hemiplane and small mature males caught in shallower areas on the right one (Fig. 10). Factor 3 was highly influenced by seasonality, being mostly defined by the day-of-the-year (DYR) (Table 5); squid caught in spring and summer should be plotted in the extremes of the upper and lower hemiplanes, respectively, whereas autumn-winter squids should appear near the center of the axis (Fig. 10). A similar spatial scenario resulted from the three factors obtained with female variables except that factor 2 was also highly influenced by maturity indices (GSI and NGI) and high loads for the depth (DEPTH) variable were placed in factor 3 (Table 5).

In the spatial representation of both males and females, a large group of squid corresponded to small mature animals caught throughout the year in shallower areas of the northeastern slope. In contrast, a smaller group of both sexes, detached from the former

Table 2. Summary of the maturity conditions of the Argentine shortfin squid *Illex argentinus* in commercial trawl catches off Brazil between 2001 and 2007. Examined males and females were pooled by maturity stages (after Brunetti, 1990) and the relative and cumulative frequencies of each stage were calculated and expressed in percentages (% and Cum.% respectively). The largest (Max) and smallest (Min) mantle length of squid in each maturity stage are indicated. Males with no, few, and many spermatophores (spermat.) in the Needhan's sac and females with and without spermatophores at the base of the gills were also quantified for each maturity stage.

Tabla 2. Resumen de las condiciones de madurez sexual de calamar argentino *Illex argentinus* en capturas comerciales de la pesca de arrastre en Brasil entre 2001 y 2007. Los machos y hembras examinados fueron agrupados por estadios de madurez (según Brunetti, 1990). Para cada estadio se calcularon las frecuencias relativas y acumuladas expresadas en valores porcentuales (% y Cum.% respectivamente). Para cada estadio de madurez sexual se indica la longitud máxima (Max) y mínima (Min) del manto. También se contaron para cada estadio de madurez los machos con ninguno, pocos o muchos espermatóforos (spermat.) en la bolsa de Needhan y las hembras con y sin espermatóforos en las bases de las branquias.

		Maturity stages								
		Immature+Maturing			Mature		Spawning+Spent			
		I	II	III	IV	V	VI	VII	VIII	Total
Males	N	108	286	517	621	535	728	174	-	2969
	%	3.6	9.6	17.4	20.9	18.0	24.5	5.9	-	
	Cum.%	3.6	13.3	30.7	51.6	69.6	94.1	100.0	-	
ML	Max	199	218	254	260	316	340	302		340
	Min	78	100	102	111	122	110	131		78
GSI	Mean	1.02	1.93	3.56	4.86	5.58	5.09	4.27		
	(SE)	(0.11)	(0.10)	(0.10)	(0.12)	(0.07)	(0.08)	(0.31)		
HI	Mean	0.60	0.65	0.72	0.64	0.46	0.51	0.43		
	(SE)	(0.02)	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.02)		
No spermat.	N	109	286	517	0	2	1	1	-	916
	%	11.9	31.2	56.4	0.0	0.2	0.1	0.1	-	
	Cum. %	11.9	43.1	99.6	99.6	99.8	99.9	100.0	-	
Few spermat.	N	0	0	0	625	3	791	189	-	1608
	%	0.0	0.0	0.0	38.9	0.2	49.2	11.8	-	
	Cum. %	0.0	0.0	0.0	38.9	39.1	88.2	100.0	-	
Many spermat.	N	0	0	0	0	540	0	0	-	540
	%	0.0	0.0	0.0	0.0	100.0	0.0	0.0	-	
	Cum. %	0.0	0.0	0.0	0.0	100.0	100.0	100.0	-	
Females	N	183	365	344	366	383	643	399	134	2817
	%	6.5	13.0	12.2	13.0	13.6	22.8	14.2	4.8	
	Cum. %	6.5	19.5	31.7	44.7	58.3	81.1	95.2	100.0	
ML	Max	205	213	277	299	334	351	395	367	395
	Min	91	115	124	104	105	242	262	120	91
GSI	Mean	2.4	2.6	3.7	13.6	25.2	25.1	19.5	16.0	
	(CE)	(0.7)	(0.3)	(0.2)	(0.4)	(0.8)	(0.4)	(0.5)	(0.9)	
HI	Mean	0.51	0.48	0.48	0.46	0.38	0.30	0.27	0.20	
	(CE)	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.00)	(0.01)	(0.02)	
Mated	N	183	368	347	370	383	0	0	1	1652
	%	11.1	22.3	21.0	22.4	23.2	0.0	0.0	0.1	
	Cum. %	11.1	33.4	54.4	76.8	99.9	99.9	99.9	100.0	
Non-mated	N	0	0	1	1	2	665	529	157	1354
	%	0.0	0.0	0.1	0.1	0.1	49.1	39.1	11.6	
	Cum. %	0.0	0.0	0.1	0.1	0.3	49.4	88.5	100.1	

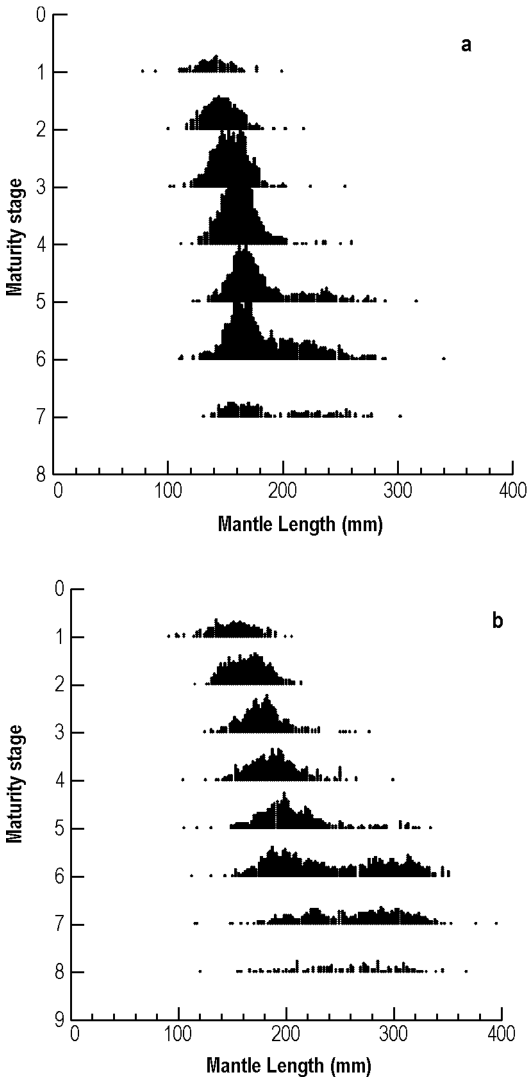

Figure 7. Size distribution (mantle length in mm) of the Argentine squid *Illex argentinus* caught by commercial trawlers off Brazil between 2001-2007 according to sexual maturity stages (defined following Brunnetti, 1990). a) males, b) females.

Figura 7. Distribución de tallas (largo de manto ML en mm) del calamar argentino *Illex argentinus* capturado por arrastreros comerciales en Brasil entre 2001-2007 según estadio de maduración sexual (definidos según Brunetti, 1990). a) machos, b) hembras.

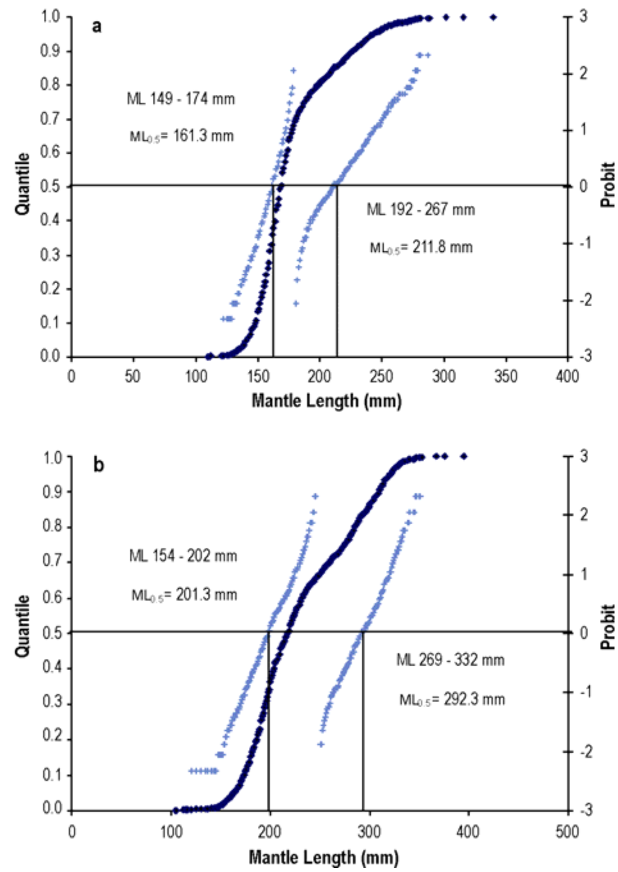

Figure 8. Mantle length (ML) cumulative frequency distribution of mature males (a) and females (b) Argentine squid *Illex argentinus* caught by commercial trawlers off Brazil between 2001 and 2007 (dark blue symbols). ML-at-maturity of two modal classes are indicated for both sexes as calculated after the probit transformation of frequencies (light blue symbols).

Figura 8. Distribución acumulada de tallas (largo de manto ML en mm) de machos (a) y hembras (b) sexualmente maduras del calamar argentino *Illex argentinus* capturado por arrastreros comerciales en Brasil entre 2001 y 2007 (puntos azules oscuros). ML del inicio de la maduración sexual de las dos clases modales están indicados para los dos sexos según estimados por la transformación *probit* de frecuencias (puntos azules claros).

group, was composed of large mature animals caught in deep southwestern areas during a restricted period in the middle of the year (winter) (Fig. 10).

DISCUSSION

Interpreting the biological patterns of *I. argentinus* from commercial catches off Brazil requires the initial consideration that these patterns may combine the mixed effects of three critical sources: (a) existing biologically distinct population units that may exhibit particular spatial/ temporal distribution patterns, (b) non-random spatial/ temporal fishing strategies that may or may not include squid as a principal target, and (c) on board discards (at least for the national trawl fleet). The two latter sources of bias limit our capacity to comprehensively address the entire population diversity of the species in Brazilian waters. On the other hand, it is possible to conclude, by confronting bio-

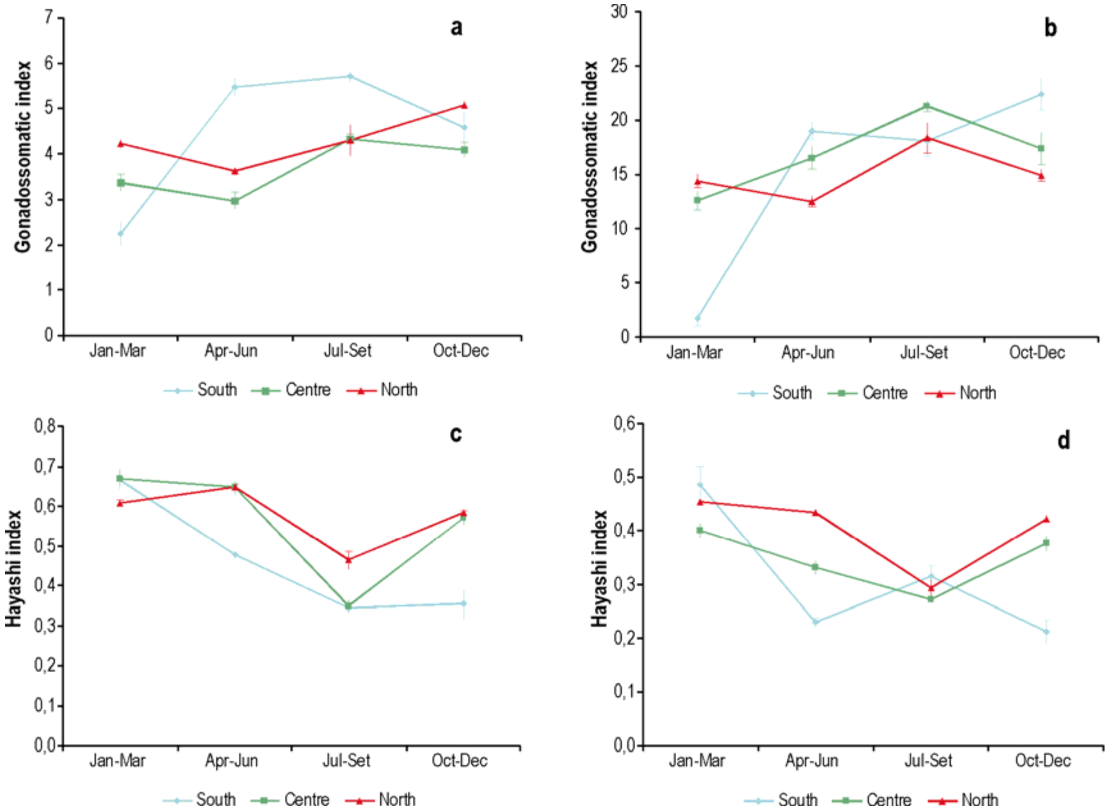

Figure 9. Seasonal and latitudinal variability of maturity indices of the Argentine shortfin squid *Illex argentinus* caught by commercial trawlers off Brazil between 2001 and 2003. Symbols represent median values and vertical bars represent standard errors. a and c, males; b and d, females.

Figura 9. Variabilidad temporal y latitudinal dos los índices de madurez sexual del calamar argentino *Illex argentinus* capturado por arrastreros comerciales en Brasil entre 2001 y 2003. Símbolos representan valores medianos y líneas verticales representan error estándar. a y c, machos; b y d, hembras.

logical patterns of the catches with synoptic descriptions of the *Illex* population structure as produced by preceding trawl surveys (Haimovici & Perez, 1990, 1991; Santos & Haimovici, 1997), that different spawning groups can be identified in the commercial catches and, more importantly, that the availability/vulnerability of these groups and their specific biological features may have influenced the trawl fishing patterns on the slope off southern Brazil (Perez & Pezzuto, 2006; Perez *et al*., 2009b).

Samples of commercial catches obtained between 2001-2003 contained immature and maturing squid throughout the year, as well as at least two distinguishable fully mature-spawning groups. The first group, composed of small-sized males and females, was present during all seasons on the shelf-break/upper slope (< 400 m). In winter-spring, however, a distinctive group of large squid dominated the catches in southern (south of 28°S) and deep fishing grounds (400-700 m). Both groups had been previously identified in trawl surveys off southern Brazil, the latter being specifically referred to as the southern Brazil stock (SBS) (Haimovici *et al*., 1998). In the present study, this group was shown to sustain the exceptionally large catches obtained by the chartered trawler "In Sung 270" in September 2001 and also the winter catches produced by national trawlers, mostly from 2003 onwards (Perez & Pezzuto, 2006; Perez *et al*., 2009b). Unlike the upper slope concentrations of small squid, it seems evident that these large individuals, seasonally available in dense concentrations on the lower slope, attracted the attention of the fishing industry and became valued targets of the developing multispecies deep-water trawl fishery off southern Brazil (Perez & Pezzuto, 2006; Perez *et al*., 2009b). A relevant issue regarding this pattern, however, has been the fact that SBS squid could actually be connected to the Patagonian shelf stocks through spaw-

Table 3. Sex ratio of the Argentine shortfin squid *Illex argentinus* in commercial trawl catches off Brazil in two periods: 2001-2003 and 2006-2007. M/F: male/ female ratio, p: probability (Π^2). Values in bold correspond to probabilities obtained by contingency table analysis to compare the effects of trimesters, depth, and latitudinal strata on the sex-ratio.

Table 3. Proporción de sexos del calamar argentino *Illex argentinus* en capturas de la pesca comercial de arrastre en Brasil en dos periodos: 2001-2003 y 2006-2007. M/F: fracción número de machos / número de hembras; p: probabilidad (Π^2). Valores en negrita corresponden a probabilidades resultantes del análisis de la tabla de contingencia para comparar los efectos de trimestres, estratos batimétricos y estratos latitudinales sobre la proporción sexual.

	2001-2003				2006-2007			
Trimester	Males	Females	M/F	p	Males	Females	M/F	p
Jan-Mar	553	453	1.2	0.002	0	0	-	-
Apr-Jun	846	971	0.9	0.003	164	308	0.5	< 0.001
Jul-Sep	292	433	0.7	< 0.001	126	155	0.8	0.084
Oct-Dec	1011	610	1.7	< 0.001	73	77	0.9	0.74
p				**< 0.001**				**0.002**
Depth strata								
< 250 m	224	313	0.7	< 0.001	46	60	0.8	
250 - 400	1992	1822	1.1	0.006	145	214	0.7	
> 400 m	450	288	1.6	< 0.001	172	266	0.6	
p				**< 0.001**				**0.736**
Latitudinal strata								
North	2015	1537	1.3	< 0.001	77	57	1.4	0.137
Centre	483	741	0.7	< 0.001	25	101	0.2	< 0.001
South	144	78	1.8	< 0.001	226	338	0.7	< 0.001
p				**< 0.001**				**< 0.001**
Total	2702	2467	1.1	0.001	363	540	0.7	0.002

ning migrations and paralarval transport, as described for other ommastrephid species elsewhere (Hatanaka *et al.*, 1985). If confirmed, this hypothesis would directly characterize a shared stock scenario with important implications for management in Argentina, Uruguay, and Brazil (Haimovici *et al*., 2007).

Population connections between *I. argentinus* occurring in the SW Atlantic were formerly addressed by Brunetti (1988), who defined three major stocks occurring off the coast of Argentina and Uruguay (SSS, SPS, and BNS) and concluded that squid distributed along southern Brazil were an extension of the northernmost stock (BNS). Because partly spawned or spent squid were never observed in BNS catches, the spawning location remained uncertain but was speculated to occur between July and September somewhere offshore, north of 38°S, under the Falkland (Malvinas) or Brazil Currents. Santos & Haimovici (1997) analyzed reproductive patterns of the previously considered SBS members and also concluded that these squid were, in fact, members of BNS, but proposed alternatively that southern Brazil was their major winter-spring spawning ground. Taking into consideration records of elevated concentrations of *I. argentinus* paralarvae under the core of the Brazil Current (Haimovici *et al*., 1995) and other evidence derived from trophic relations, parasites, and body proportions (Santos, 1992), Santos & Haimovici (1997) further postulated that maturing BNS squid would migrate in early winter from northern Argentina to southern Brazil slope waters, where spawning would take place under the warm Brazil Current. During spring-summer, as the Subtropical Convergence retracted, egg masses and paralarvae would be transported southwards, allowing recruitment to occur on the southern feeding grounds off northern Argentina (Haimovici *et al*., 1998). Whereas this hypothesis still requires corroboration through high-resolution me-

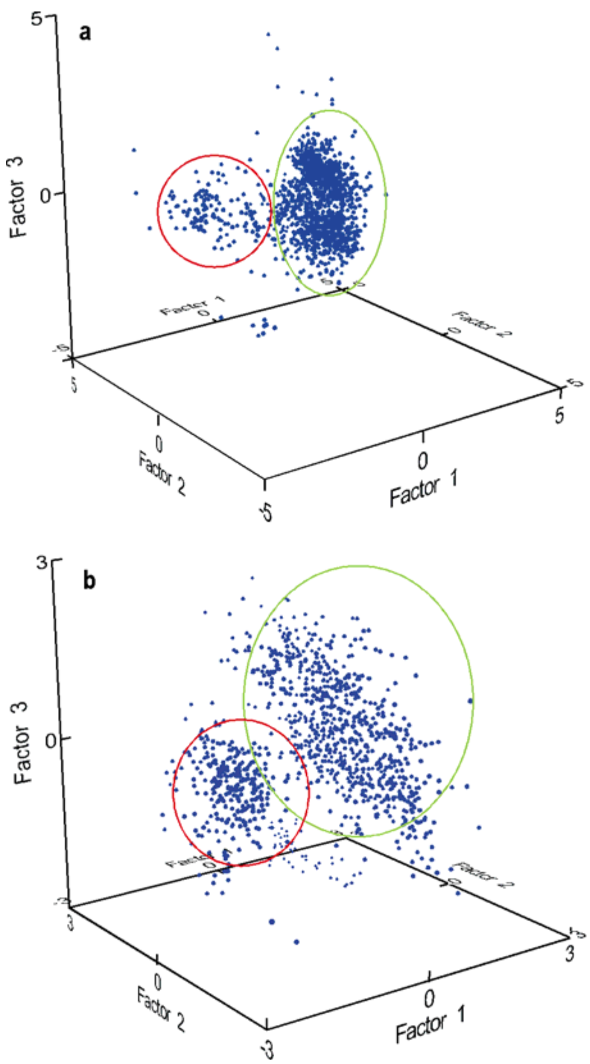

Figure 10. Spatial representation of males (a) and females (b) of the Argentine shortfin squid *Illex argentinus* caught by commercial trawlers off Brazil between 2001 and 2003 according to the values generated by the first three factors obtained with Principal Component Analysis. The green line indicates small-sized mature squid caught all year round on the upper slope. The red line indicates large-sized mature squid caught in winter at depths over 400 m.

Figura 10. Representación espacial de machos (a) y hembras (b) de calamar argentino *Illex argentinus* capturado por arrastreros comerciales en Brasil entre 2001 y 2003 según los valores generados por los tres primeros factores obtenidos con el Análisis de Componentes Principales. La línea verde indica el grupo de calamares sexualmente maduros de pequeño tamaño capturado a lo largo del año en el talud superior. La línea roja indica el grupo de calamares sexualmente maduros de mayor tamaño capturado en los meses de invierno a profundidades mayores de 400 m.

thods such as tagging experiments or genetic markers, the biological data from commercial catches off southern Brazil may provide further indirect evidence in its support.

Initially, the sizes of mature squid present in winter catches off Brazil resembled those reported for members of both BNS and SBS, although precise comparisons were not possible because the different studies included different maturity stages for estimating size-at-maturity. Nonetheless, mantle lengths of males and females of these groups were noticeably larger than those estimated for a presumably "local" upper -slope stock, suggesting that these squid were, in fact, biologically distinct (Table 6). Schwarz & Perez (2007) analyzed the morphology and morphometry of statoliths extracted from squid caught by commercial trawlers off Brazil and reached similar conclusions.

Secondly, the majority of the squid present in the winter catches off Brazil were mated females in a spawning-spent condition, indicating that fishing was concentrated on a spawning event that could be related to a) the spawning seasons proposed for BNS and SBS and b) the spawning grounds proposed for the latter, namely the slope area between 27°S and 34°S (Brunetti, 1988; Santos & Haimovici, 1997) (Table 6). Within these grounds, commercial catches further revealed that large spawning squid concentrated in high densities during the day on the deep slope (400-700 m). This pattern was also observed by both fishing and acoustic surveys conducted between 2001 and 2002, which further associated spawning squid concentrations with temperature ranges between 7° and 13°C (Madureira *et al*., 2005; Haimovici *et al*., 2008). The deep, cold environment off southern Brazil is generally associated with the influence of South Atlantic Central Water (SACW), which flows southwards over the slope as a deep layer of the Brazil Current (Castro *et al*., 2006). Temperature and salinity within this water mass range from 6-20°C and 34.6-36.0, respectively, characterizing a considerably colder, less saline environment than that of the overlaying Tropical Water, which is also transported, although superficially, by the Brazil Current. Considering that (a) spawning squid from the Patagonian shelf may require an optimal thermal environment ranging from 4° to 13°C (Brunetti *et al*., 1998) and (b) that pre-reproductive BNS members at the Argentine-Uruguayan Common Fishing Zone (34º00'- 39º30'S) were shown to concentrate in subantarctic waters between 4-10ºC (Bazzino *et al*., 2005), it seems reasonable that a spawning migration towards Brazilian waters (Santos & Haimovici, 1997) would take place in association with deep water masses such as SACW. A final element in support of a connection between Bra-

Table 4. Evidence of mating in female Argentine shortfin squid *Illex argentinus* caught in commercial trawl catches off Brazil in two periods: 2001-2003 and 2006-2007. N/M: not mated/mated female fraction, p-values correspond to probabilities obtained by contingency table Π^2 analysis to compare the effects of trimesters, depth, and latitudinal strata on the mated condition of females.

Tabla 4. Evidencias de cópula en hembras de calamar argentino *Illex argentinus* capturado por la pesca comercial de arrastre en Brasil en dos periodos: 2001-2003 y 2006-2007. N/M: fracción no-copuladas/copuladas. P: probabilidades resultantes del análisis Π^2 para comparar los efectos de trimestres, estratos batimétricos y estratos latitudinales sobre la actividad de cópula de las hembras.

	2001-2003			2006-2007		
	Not-mated	Mated	N/M	Not-mated	Mated	N/M
Trimester						
Jan-Mar	339	114	3.0			
Apr-Jun	752	219	3.4	20	288	0.1
Jul-Sep	67	366	0.2	26	128	0.2
Oct-Dec	423	187	2.3	25	52	0.5
p		<0.001			<0.001	
Depth Strata						
< 250 m	150	163	0.9	6	54	0.1
250 - 400	1281	541	2.4	39	175	0.2
> 400 m	107	181	0.6	26	239	0.1
p		<0.001			0.019	
Latitudinal strata						
North	1201	336	3.6	23	34	0.7
Centre	262	479	0.5	9	92	0.1
South	47	31	1.5	38	299	0.1
p		<0.001			<0.001	
Total	1581	886	1.8	71	468	0.2
p		<0.001			<0.001	

zilian and Patagonian squid stocks can be drawn from the combination of the commercial value of "big squid", the opportunistic behavior of the trawl fishery, and the general evolutionary population strategies of ommastrephid squids (O'Dor, 1992). These squids normally exhibit complex population structures in association with geostrophic currents, protracted spawning, and latitudinal migrations as a strategy to spread – over space and time – the risks of their short, semelparous life cycle (O'Dor, 1998). Because cold, nutrient-enriched temperate waters tend to delay maturity and enhance survivorship of juvenile squid, stocks whose offspring drift, carried by geostrophic currents, to these waters attain larger sizes, are more abundant, and sustain larger fisheries (e.g. *I. illecenbrosus*, O'Dor & Coelho, 1993; Perez & O'Dor, 1998). Although these squid need to perform long migrations, their large body size favors swimming long distances (O'Dor, 1988). In contrast, those stocks that remain in food-poorer, warmer, tropical and subtropical waters tend to grow fast but also to mature early at smaller sizes (O'Dor & Coelho, 1993). In a less productive environment, these squids are also less abundant and sustain significantly lower annual landings.

By experiencing their early life in a highly productive and cold environment such as the Patagonian Shelf, BNS squid would tend to be abundant (actually sustaining large catches in the northern Patagonian Shelf) and to mature late in life at large sizes, fit for a ~2,000-km-long winter spawning migration towards Brazilian waters. Because these are cold-water squid, they would tend to reach the deep layers of the slope as they approach southern Brazil, concentrating within the 300-400-m-high SACW layer (Madureira *et al*., 2005; Castro *et al*., 2006) and, hence, becoming vulnerable to the slope trawling in winter and early-spring. Off southern Brazil during this period of the year, winter spawners should be markedly distinct from the "local" spawners, both by their larger body

Table 5. Principal Component Analysis employed to differentiate Argentine shortfin squid *Illex argentinus* stocks within the catches obtained by commercial trawlers off Brazil between 2001 and 2003. Variables included were: day-of-the-year (DYR), decimal latitude (LAT), decimal longitude (LONG), depth (DEPTH), body wet weight (BW), gonadosomatic index (GSI), Hayashi index (HI), Nidamental gland/ Testis Index. The linear coefficients of the variables (loadings) in the first three factors rotated by the PCA are indicated for males and females. The eigenvalues and the variance explained by each factor are indicated in the last three rows.

Tabla 5. Análisis de Componentes Principales aplicada en la diferenciación de los stocks de calamar argentino *Illex argentinus* en las capturas de arrastreros comerciales en Brasil entre 2001 y 2003. Las variables incluidas fueron: día-del-año (DYR), latitud decimal (LAT), longitud decimal (LONG), profundidad (DEPTH), peso húmedo del cuerpo (BW), índice gonadosomático (GSI), índice de Hayashi (HI), índice de la glándula nidamental/ testículo. Los coeficientes lineales de las variables (pesos) en los tres primeros factores rotacionados por el PCA se indican para machos y hembras. Los valores propios y la varianza explicada por cada factor se indican en las últimas tres líneas.

Component	Males Factor			Females Factor		
	1	2	3	1	2	3
DYR	-0.105	-0.051	0.846	-0.379	0.043	0.662
LAT	0.929	0.157	0.090	0.952	0.031	0.084
LONG	0.896	0.306	0.102	0.940	0.117	-0.008
DEPTH	-0.006	0.694	-0.163	0.105	0.445	-0.686
BW	-0.699	0.358	-0.020	-0.737	0.059	-0.282
GSI	0.149	0.310	0.453	0.027	0.873	0.114
HI	0.425	-0.683	-0.213	0.363	-0.685	0.014
NGI / TI	0.185	0.392	-0.427	0.128	0.766	0.263
Eigenvalue	2.403	1.447	1.195	2.639	2.037	1.079
Variance explained (%)	30.035	18.087	14.933	32.983	25.461	13.483
Cum. variance explained (%)	30.035	48.122	63.055	32.983	58.444	71.927

Table 6. Summary of characteristics of two stocks of the Argentine shortfin squid *Illex argentinus* in waters of the northern Patagonian shelf (BNS) and southern Brazil (SBS) in comparison with spawning groups differentiated in the commercial trawl catches off southern Brazil between 2001 and 2007. Sizes at maturity refer to modal mantle lengths of males and females in different maturity stages (between parentheses) as defined by Brunetti (1990).

Tabla 6. Resumen de las características de dos stocks de calamar argentino *Illex argentinus* en el norte de la plataforma patagónica (BNS) y el sur de Brasil (SBS) en comparación con los grupos desovantes diferenciados en las capturas comerciales de pesca de arrastre en el sur de Brasil entre 2001 y 2007. La talla de madurez sexual corresponde a la longitud modal del manto de machos y hembras en diferentes estadios de madurez (entre paréntesis) definidos por Brunetti (1990).

	Proposed stocks		Commercial catches off Brazil	
	Bonaerensis-north patagonic (BNS)[1]	Southern Brazil (SBS)[2]	Large spawners[3]	Small spawners[3]
Spawning Grounds	Slope, north of 38°S, under the Falkland/ Malvinas Current or Brazil Current	Slope, between 27°S and 34°S under the Brazil Current	Between 26° and 29°S, 360-520 m depth	North of 28°S, shallower than 360 m depth
Spawning season	July – September	July – November	July - September	All year-round
Modal size at maturity (ML)	Males: ~200 mm Females: ~240 mm (Stages IV+V)	Males: ~250 mm Females: ~300 mm (Stages > V)	Males: 212 mm Females: 292 mm (Stages > IV)	Males: 161 mm Females: 201 mm (Stages > IV)

[1]Brunetti *et al.* (1991), [2]Santos & Haimovici (1997), [3]This study.

size and their deeper bathymetric distribution, attracting the attention first of the highly efficient and exploratory foreign chartered trawlers (Perez *et al*., 2009b) and later the more conservative but overcapitalized national trawl fleet (Perez & Pezzuto, 2006). In 2002, trawler skippers persistently tried to convince fishing biologists involved with this study that their large catches off Brazil were, in fact, a different squid species due to their obviously different body proportions and suggested that it be given a new name as a marketing strategy (Perez *pers. observ*.). Albeit anecdotal, this fact highlights the effect of the diversity of this species population (and particular biological attributes) on the observed exploitation patterns in the SW Atlantic, reinforcing the need to consider multinational, shared stock management strategies in the region. Other shellfish and finfish resources exploited in the deep waters off southern Brazil (*e.g.* deep-water crabs, hake, and others) seem to justify the same strategies (Perez *et al*., 2009a).

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REFERENCES

Bazzino, G., R.A. Quiñones & W. Norbis. 2005. Environmental associations of shortfin squid *Illex argentinus* (Cephalopoda: Ommastrephidae) in the northern Patagonian Shelf. Fish. Res., 76: 401-416.

Boyle, P.R. & P. Rodhouse. 2005. Cephalopods. Ecology and fisheries. Blackwell Publishing, Oxford, 451 pp.

Brunetti, N.E. 1988. Contribución al conocimiento biológico-pesquero del calamar argentino (Cephalopda, Ommastrephidae, *Illex argentinus*). Tesis doctoral, Universidad Nacional de La Plata, Buenos Aires, 135 pp.

Brunetti, N.E. 1990. Escala para la identificación de estadios de madurez sexual del calamar (*Illex argentinus*). Frente Marítimo, 7: 45-52.

Brunetti, N.E., M.L. Ivanovic & B. Elena. 1998. Calamares omastréfidos (Cephalopoda: Ommastrephidae). In: E. Boschi (ed.). El mar argentino y sus recursos pesqueros, Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, 2: 37-68.

Brunetti, N.E., M.L. Ivanovic, E. Louge & H.E. Christiansen. 1991. Reproductive biology and fecundity of two stocks of the squid (*Illex argentinus*). Frente Marítimo, 8: 73-84.

Castro Fo., J.A. Lorenzzetti, I.C.A. Silveira & L.B. Miranda. 2006. Estrutura termohalina e circulação na região entre o Cabo de São Tomé (RJ) e o Chuí (RS). In: C.L.D.B. Rossi-Wongtschowski & L.S-P. Madureira. (eds.). O ambiente oceanográfico da plataforma continental e do talude na região sudeste-sul do Brasil, São Paulo, EDUSP - Editora da Universidade de São Paulo, pp. 11-120.

Costa, P.A.S. & M. Haimovici. 1990. A pesca de lulas e polvos no litoral do Rio de Janeiro. Ciência & Cultura, 42(12): 1124-1130.

Gasalla, M. de los A., G. Velasco, C.L.D.B. Rossi-Wongstchowski, M. Haimovici & L.S-P. Madureira. 2007. Modelo de equilíbrio de biomassa do ecossistema marinho da região Sudeste-Sul do Brasil entre 100-1000 m de profundidade. Série Documentos REVIZEE, Score Sul. Instituto Oceanográfico, Universidade de São Paulo, São Paulo, 56 pp.

Haimovici, M. & J.M. Andriguetto Fo. 1986. Cefalópodes costeiros capturados na pesca de arrasto do litoral sul do Brasil. Arq. Biol. Tecnol., 29(3): 473-495.

Haimovici, M. & J.A.A. Perez. 1990. Distribución y maduración sexual del calamar argentino, *Illex argentinus* (Castellanos, 1960) (Cephalopoda: Ommastrephidae), en el sur de Brasil. Sci. Mar., 54: 179-1895.

Haimovici, M. & J.A.A Perez. 1991. Abundância e distribuição de cefalópodes em cruzeiros de prospecção pesqueira demersal na plataforma externa e talude continental do sul do Brasil. Atlântica, Rio Grande, 13(1): 189-200.

Haimovici, M., E.G. Vidal & J.A.A. Perez. 1995. Larvae of *Illex argentinus* from five surveys on continental shelf of southern Brazil. ICES Mar. Sci. Symp., 199: 414-424.

Haimovici, M., N.E. Brunetti, P.G. Rodhouse, J. Csirke & R.H. Leta. 1998. Chapter 3. *Illex argentinus*. In: P.G. Rodhouse, E.G. Dawe & R.K. O'Dor (eds.). Squid recruitment dynamics. The genus *Illex* as a model. The commercial *Illex* species. Influences on variability. FAO Fish. Tech. Pap., 376: 27-58.

Haimovici, M., J.A.A. Perez & R.A. Santos. 2006. Diagnóstico do estoque e orientações para o ordenamento da pesca de *Illex argentinus* (Castellanos, 1960). In: C.L.D.B. Rossi-Wongtshchowski, A.O. Ávila-da-Silva & M.C. Cergole (eds.). Análise das principais pescarias comerciais da região sudeste-sul do Brasil: dinâmica populacional das espécies em explotação. II. Série Documentos REVIZEE, Score Sul. Instituto

Oceanográfio, Universidade de São Paulo, São Paulo, pp. 19-27.

Haimovici. M., A.O. Ávila da Silva, L.W. de Miranda & S. Klippel. 2007. Prospecções na região sudeste-sul. In: M. Haimovici (ed.). A prospecção pesqueira e abundância de estoques marinhos no Brasil nas décadas de 1960 a 1990. Levantamento de dados e avaliação crítica. Ministério do Meio Ambiente. Secretaria de Mudanças Climáticas e Qualidade Ambiental. Programa REVIZEE: Levantamento de Dados Pretéritos, Brasília, pp. 35-74.

Haimovici, M., C.L.D.B. Rossi-Wongstchowski, R.A. Bernardes, L.G. Fisher, C.M. Vooren, R.A. dos Santos, A.R. Rodrigues & S. dos Santos. 2008. Prospecção pesqueira de espécies com rede de arrasto-de-fundo na região sudeste-sul do Brasil. Série Documentos REVIZEE, Score Sul. Instituto Oceanográfico, Universidade de São Paulo, São Paulo, 183 pp.

Hatanaka, H., S. Kawahara, Y. Uozumi & S. Kasahara. 1985. Comparison of life cycles of five ommastrephid squids fished by Japan: *Todarodes pacificus*, *Illex illecebrosus*, *Illex argentinus*, *Nototodarus sloani sloani*, and *Nototodarus sloani gouldi* (Mollusca: Cephalopoda). NAFO Sci. Council Studies, 9: 59-68.

Madureira, L.S-P., R.G.P. Habiaga, A.C. Duvoisin, D. Eliseire Jr., C.F. Soares, S.C. Weigert, C.S. Ferreira & P.A. Saldo. 2005. Identificação de registros acústicos do calamar argentino *Illex argentinus* (Castellanos, 1960) no talude da região sudeste-sul do Brasil. Série Documentos REVIZEE, Score Sul. Instituto Oceanográfico, Universidade de São Paulo, São Paulo, 32 pp.

Martins, R.S. & J.A.A. Perez. 2007. The ecology of loliginid squid in shallow waters around Santa Catarina Island, southern Brazil. Bull. Mar. Sci., 80(1): 125-146.

O'Dor, R.K. 1988. Energetic limits on squid distributions. Malacologia, 29(1): 113-119.

O'Dor, R.K. 1992. Big squid in big currents. S. Afr. J. mar. Sci., 12: 225-235.

O'Dor, R.K. 1998. Chapter 11. Squid life-history strategies. In: P.G. Rodhouse, E.G. Dawe & R.K. O'Dor (eds.). Squid recruitment dynamics. The genus *Illex* as a model. The commercial *Illex* species. Influences on variability. FAO Fish. Tech. Pap., 376: 233-250.

O'Dor, R.K. & M.L. Coelho. 1993. Big squid, big currents and big fisheries. In: T. Okutani, R.K. O'Dor & T. Kubodera (eds.). Recent advances in cephalopod fisheries biology, Tokay University Press, Tokyo, pp. 385-396.

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Perez, J.A.A. 2000. Biomass dynamics of the squid *Loligo plei* and the development of a small-scale seasonal fishery off southern Brazil. Bull. Mar. Sci., 71(2): 633-651.

Perez, J.A.A. & R.K. O'Dor. 1998. The impact of environmental gradients on the early life inshore migration of the short-finned squid *Illex illecebrosus*. S. Afr. J. mar. Sci., 20: 294-303.

Perez, J.A.A. & P.R. Pezzuto. 1998. Valuable shellfish species in the by-catch of shrimp fishery in southern Brazil: spatial and temporal patterns. J. Shell. Res., 17: 303-309.

Perez, J.A.A. & P.R. Pezzuto. 2006. A pesca de arrasto de talude do Sudeste e Sul do Brasil: tendências da frota nacional entre 2001 e 2003. Bolm. Inst. Pesca, São Paulo, 32: 127-150.

Perez, J.A.A., R. Wahrlich & P.R. Pezzuto. 2009b. Chartered trawling on the slope off Brazilian coast. Mar. Fish. Rev., 71(2): 24-36.

Perez, J.A.A., P.R. Pezzuto, R. Wahrlich & A.L.S. Soares. 2009a. Deep-water fisheries in Brazil: history, status and perspectives. Lat. Am. J. Aquat. Res., 37(3): 513-541.

Perez, J.A.A., S.H.B. Lucato, H.A. de Andrade, P.R. Pezzuto & M. Rodrigues-Ribeiro. 1998. Programa de amostragem da pesca industrial desenvolvido para o porto de Itajaí, SC. Not. Téc. FACIMAR, 2: 93-108.

Perez, J. A.A., R. Wahrlich, P.R. Pezzuto, P.R. Schwingel, F.R.A.Lopes & M. Rodrigues-Ribeiro. 2003. Deep-sea fishery off southern Brazil: recent trends of the Brazilian fishing industry. J. Northw. Atl. Fish. Sci., 31: 1-18.

Santos, R.A. 1992. Relações tróficas do calamar argentino *Illex argentinus* (Castellanos, 1960) (Teuthoidea: Ommastrephidae) no sul do Brasil. MSc. Thesis. Fundação Universidade Federal do Rio Grande, Rio Grande, 83 pp.

Santos, R.A. & M. Haimovici. 1997. Reproductive biology of winter-spring spawners of *Illex argentinus* (Cephalopoda: Ommastrephidae) off southern Brazil. Sci. Mar., 61(1): 53-64.

Santos, R.A. & M. Haimovici. 2000. The Argentine shortfin squid *Illex argentinus* (Cephalopoda: Ommastrephidae) in the food webs off southern Brazil. Sarsia, 85: 49-60.

Schwarz, R. & J.A.A. Perez. 2007. Diferenciação populacional do calamar argentino (*Illex argentinus*) (Cephalopoda: Teuthida) no sul do Brasil através da morfologia e morfometria do estatólito. Braz. J. Aquat. Sci. Technol., 11(1): 1-12.