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Population dynamics of the squids *Dosidicus gigas* (Oegopsida: Ommastrephidae) and *Doryteuthis gahi* (Myopsida: Loliginidae) in northern Peru

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ARTICLE INFO

ABSTRACT

Pelagic squids of continental shelf ecosystems mostly include oceanic and migratory species of the family Ommastrephidae and neritic species of the family Loliginidae. These two families have contrasting life history strategies; ommastrephids spawn in the open ocean and are thought to have a high dispersal potential, while loliginids spawn on the bottom and are likely to have a low dispersal potential. Consequently, these squid species should display different patterns in their population dynamics, which can be inferred through commercial catches. To study the population dynamics of the Ommastrephidae and the Loliginidae families, monthly time series catches of *Dosidicus gigas* and *Doryteuthis gahi* were used. These artisanal fishery catches were made in northern Peru from 1999 to 2010. They were standardized to construct autocorrelation functions so that the relationship between catch dynamics and short-term environmental change (thermal anomalies of sea surface temperature were used as a proxy) could be studied. The results revealed that increases in catches of *D. gigas* and *D. gahi* are not related to thermal anomalies, but rather a pattern of drastic fluctuations in *D. gahi* catch sizes are seen. In, both species, temporal relationships indicate that the annual growth rate and changes in abundance can modelled as a function of the catch density observed in previous years. We propose that these population differences result from the contrasting life history strategies and differential habitat use of these two squid species.

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1. Introduction

Extending along the west coast of South America from Southern Chile (ca. 42°S) to the Galapagos Islands near Ecuador (Thiel et al., 2007), the Humboldt Current System (HCS) is the most productive marine ecosystem on Earth. Oceanographically this area is characterized by several features that increase primary productivity in this region. These features include local coastal upwelling and a predominant northward flow of sub-Antarctic waters (Montecino et al., 2005; Thiel et al., 2007). Large-scale climate phenomena produce strong fluctuations in temperature and productivity in oceanic and neritic ecosystems that supply the abundant fishery grounds off Chile and Peru (Montecino et al., 2005; Thiel et al., 2007). An example of this is the El Niño Southern Oscillation (ENSO), which drastically alters coastal upwelling and consequently primary productivity. In this scenario, cephalopods, fish, and other invertebrate populations have experienced dramatic inter-annual fluctuations in abundance principally due to environmental variation (Keyl et al., 2008; Rosa et al., 2013). Moreover, the migration pattern, population size, and geographic distribution of many marine organisms, and particularly cephalopods, are particularly susceptible to changes in oceanographic conditions (Boyle and Boletzky, 1996; Anderson and Rodhouse, 2001; Dawe et al., 2007; Semmens et al., 2007).

Globally, the pelagic squid fauna of most continental shelf ecosystems is dominated by species of the families Ommastrephidae (Suborder Oegopsina) and Loliginidae (Suborder Myopsina) (Dawe et al., 2007). These squids are common in many ecosystems;
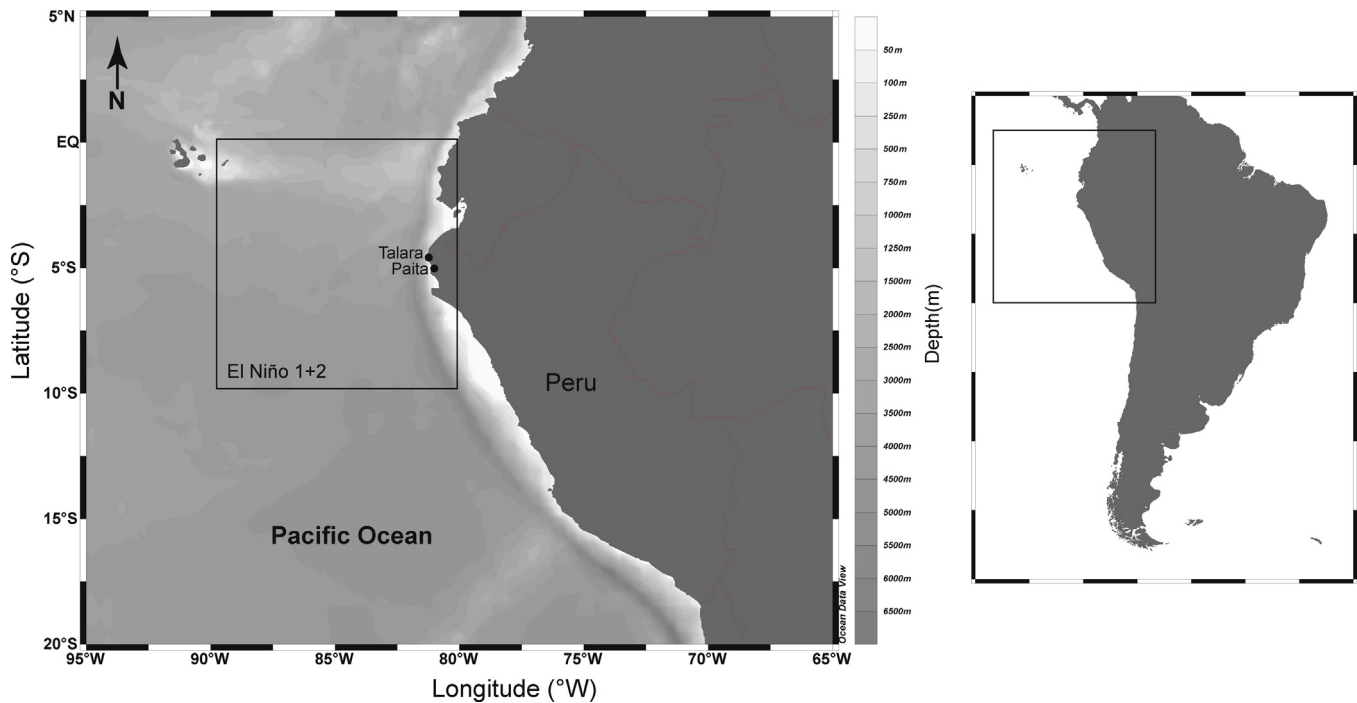

Fig. 1. Map showing the fishing zone where *Dosidicus gigas* and *Doryteuthis gahi* were captured by artisanal fleets in northern Peru.

however, ommastrephids are typically oceanic and more migratory than the neritic loliginids (Boyle and Rodhouse, 2005; Dawe et al., 2007). In the HCS, these two groups are represented by *Dosidicus gigas* (d'Orbigny, 1835) and *Doryteuthis gahi* (d'Orbigny, 1835). *D. gigas* is a species that inhabits both oceanic and neritic waters from the surface to 1200 m in the Pacific Ocean (Nigmatullin et al., 2001; Keyl et al., 2008) while *D. gahi* is a neritic species that inhabits surface waters down to 600 m (Jereb and Roper, 2010). According to fisheries data both in Chile and Peru (Cardoso, 1991; Rocha and Vega, 2003), these are the most abundant squids in the HCS. In addition to their differing habitats, the life history strategies of these two squids are also in contrast. While *D. gigas* has been shown to have multiple spawning events near the surface (Rocha et al., 2001; Nigmatullin et al., 2001; Staaf et al., 2008), *D. gahi* is a terminal spawner that lays its eggs attached to the sea bottom (Cardoso et al., 1998, 2005). The benthic spawning of loliginids is a key difference between them and ommastrephids and it is this benthic spawning that can lead to lower a dispersal ability of loliginids (O'Dor and Webber, 1991). These differences in reproductive strategies have meaningful implications for genetic diversity and spatial structure of these squid species (Ibáñez and Poulin, 2014).

In the last 15 years, fisheries statistics of these species both in Chile and Peru have shown some consistent patterns in squid landings. This has been explained by the increase of squid population biomass in response to varying environmental conditions occurring at different time scales in the HCS. Despite poor abundance data of squid populations, some authors have postulated that environmental conditions, especially relatively short-term events such as El Niño and La Niña, play an important role in determining the abundance of *D. gigas* and *D. gahi* (Villegas, 2001; Anderson and Rodhouse, 2001; Rocha and Vega, 2003; Waluda and Rodhouse, 2006). Specifically, an increase in sea surface temperature (i.e., El Niño) was postulated to have a negative effect on squid catches while a decrease in sea surface temperature (i.e., La Niña) has been found to have a positive effect (Villegas, 2001; Rodhouse, 2001; Anderson and Rodhouse, 2001; Taipe et al., 2001; Rocha and Vega, 2003; Waluda et al., 2006; Waluda and Rodhouse, 2006). However, the results and conclusions of these studies could be questioned

since the authors did not address the theory of population dynamics properly. As such, these studies should be reviewed in order to address possible reasons and mechanisms for the observations presented. Nevertheless, their hypotheses are consistent with the observed landing time series of the 1990s; the high volume of landings of *D. gigas* in Peru and Chile observed in 1992 declined and disappeared during the 1997–98 El Niño event (Rocha and Vega, 2003). The last decade showed a sharp increase of landings after 2000 such that in 2005, 296, 953 t were recorded; this coincided with a longer-lasting cooling of the Eastern Pacific. However, the landings also show seasonal synchronous periodicity (Zúñiga et al., 2008) in line with seasonal patterns of size structure (Chong et al., 2005; Ibáñez and Cubillos, 2007). This phenomenon is not addressed by the studies described above. The pattern of size structure of *D. gahi* is different from that of *D. gigas* as the landing fluctuations are less drastic and more consistent. Interestingly in the North Atlantic, asynchronous population fluctuations of an ommastrephid and a loliginid species were observed in relation to thermal anomalies caused by the North Atlantic Oscillation (NAO) (Dawe et al., 2007). It has been suggested that climate-related events (e.g., ENSO, NAO) could cause changes in population distributions (horizontal and vertical) rather than changes in population size (Semmens et al., 2007). Changes in the geographical range of migratory patterns of squids have been described as "invasions" or "population expansions" in both hemispheres of the Pacific Ocean (Field et al., 2007; Zeidberg and Robison, 2007; Keyl et al., 2008 Keyl et al., 2008).

Thus, the contrasting life history strategies of *D. gigas* and *D. gahi* populations in the HCS should influence the population dynamics of these squids. Here, we test the hypothesis that the observed intra-annual variation in biomass of *D. gigas* and *D. gahi* in the HCS is the result of population dynamics influenced by density-dependent factors and climate effects.

2. Materials and methods

Statistical data of monthly Catch Per Unit Effort (CPUE) from the IMARPE database were compiled for the study period

Table 1
Results of Generalized Additive Models (GAM) applied to catch fluctuations of *D. gigas* and *D. gahi* as function of year and season in northern Peru.

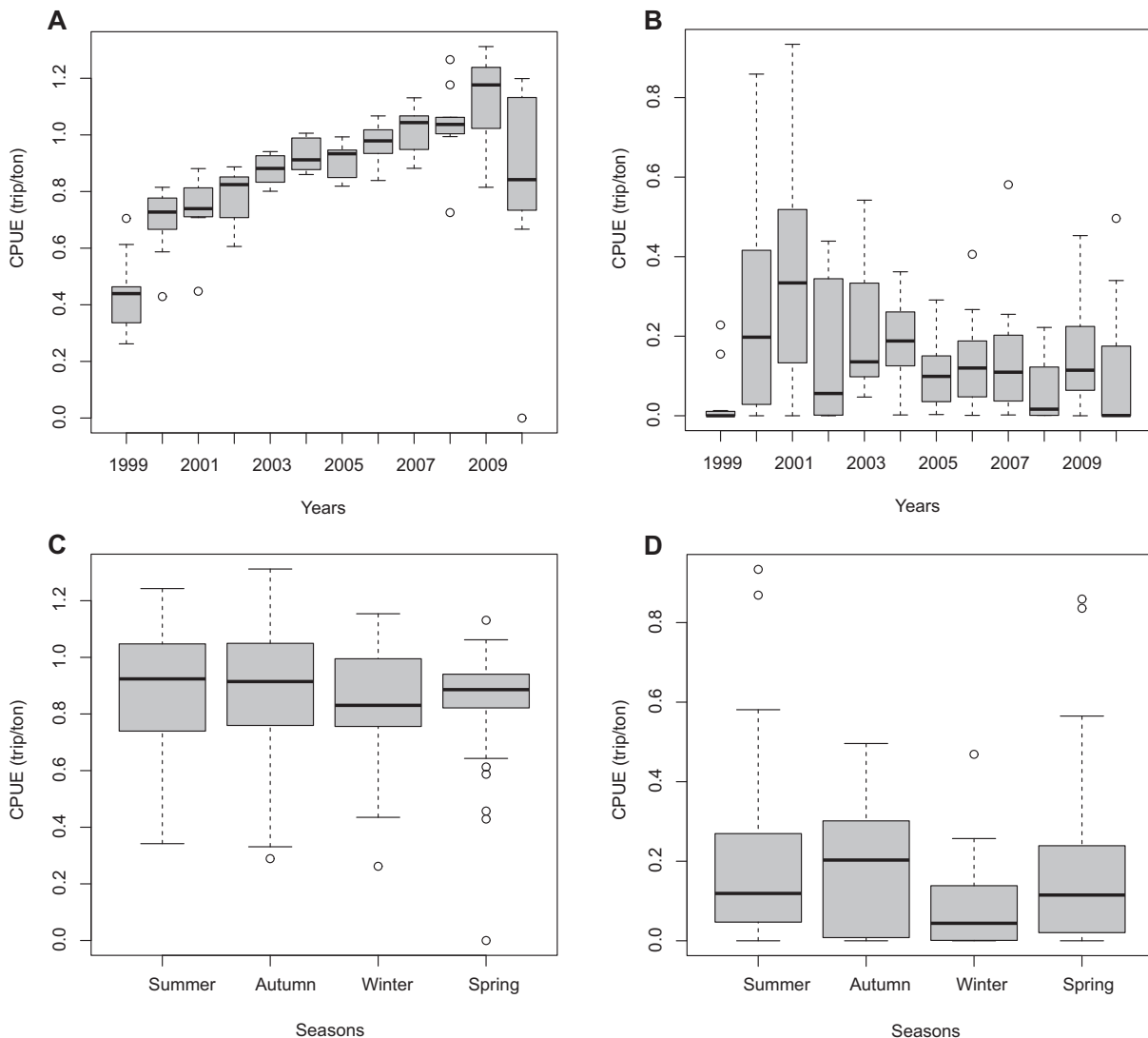|		Estimate	S.E.	*t*-Value	*P*
Dosidicus gigas	Intercept	−3058.38	5089.60	−0.601	0.549
	Year	1.530	2.538	0.603	0.548
	Season	−0.195	0.653	−0.299	0.756
Doryteuthis gahi	Intercept	−715.13	2495.86	−0.287	0.775
	Year	0.357	1.245	0.287	0.774
	Season	0.032	0.321	0.098	0.922

(January 1999 to December 2010). The catch data used were collected by an artisanal fleet focused on fishing *D. gigas* and *D. gahi* squids in northern Peru (5–6°S). The CPUE were estimated as tonnes/trip from two locations in Northern Peru (Talara and Piura) (Fig. 1). We used thermal anomalies of sea surface temperature (hereafter SSTA) from the maritime region known as El NIÑO1 + 2 as a proxy for environmental variation (http://www.esrl.noaa.gov/psd/data/climateindices/list/for info) (Fig. 1).

To assess the relationship of the CPUE data to the time series and thermal anomaly data (SSTA from El NIÑO1 + 2), we used a Generalized Additive Model (GAM) imploying a Quasi-Poisson distribution and a link log function which is robust against zero values and cor-

rects the asymmetry of the distribution. Specifically the model is as follows: CPUE = α + s(time) + s(SSTA El Niño1 + 2) + Year + Season, ~Quasi-Poisson, where CPUE corresponds to the catch data, α is the model intercept, *s* is a smoothing tensor, *time* represents the time series from January 1999 to December 2010 (1–144 months) and *SSTA* corresponds to the sea surface anomalies at El Niño 1 + 2. This analysis was done for both squid species.

We performed a time series diagnosis using an autocorrelation function (ACF) with log-CPUE. The CPUE data were standardized by a log transformation. This transformation was used because the population size through time depends linearly on time (Lima, 2006). The ACF allowed us to determine if the time series was stationary. Then, we used a partial autocorrelation function (PACF) to calculate the order of the time series; this allowed us to determine whether endogenous or exogenous factors rule the dynamics of the population (Berryman, 1999).

Finally, we estimated the realized per capita population growth rate. This metric represents the processes of individual survival and reproduction that drives population dynamics. The R-function (Berryman, 1999) is defined as follow: $Rt = \log(X_t) - \log(X_{t-1})$, where X_t is the CPUE annual data. We compared first order (N_{t-1}) and second order (N_{t-2}) dynamics using Ordinary Least Squares (OLS) comparing the coefficient of determination (r^2), *F*- and

Fig. 2. Squid catches by the artisanal fleet in northern Peru as a function of time in years (A and B) and seasons (C and D) for *Dosidicus gigas* and *Doryteuthis gahi*, respectively.

Table 2
Results of Generalized Additive Models (GAM) applied to catch fluctuations of *D. gigas* and *D. gahi* as a function of time and thermal variation in northern Peru.

		Coefficient (edf)	F-Value	P
Dosidicus gigas	s (Time)	8.23	8.581	<0.001
	s (SSTA NIÑO1 + 2)	1.00	0.061	0.805
	Explained deviance (%)	71.0		
	r^2 Adjusted	0.686		
	GCV	4.683		
Doryteuthis gahi	s (Time)	8.38	4.765	<0.001
	s (SSTA NIÑO1 + 2)	1.38	1.689	0.671
	Explained deviance (%)	30.0		
	r^2 Adjusted	0.237		
	GCV	1.129		

Table 3
Goodness of fit of the instantaneous population growth rates of the standardized time series of *D. gigas* and *D. gahi* squids in northern Peru.

		F	r^2	P	AIC
Dosidicus gigas	N_{t-1}	11.083	0.552	0.008	16.368
	N_{t-2}	1.098	0.121	0.325	19.257
Doryteuthis gahi	N_{t-1}	8.893	0.497	0.015	16.585
	N_{t-2}	0.437	0.052	0.526	17.760

P-values. Additionally, we computed the Akaike's Information Criterion (AIC; Akaike, 1974) to select the best model where the lowest values of the AIC imply the best fit. The number of parameters was adjusted when making this computation. The GAM analyses were performed using the "mgcv" package, and other analyses were performed using the "stats" package. All statistical analyses were implemented in R (R Development Core Team, 2011).
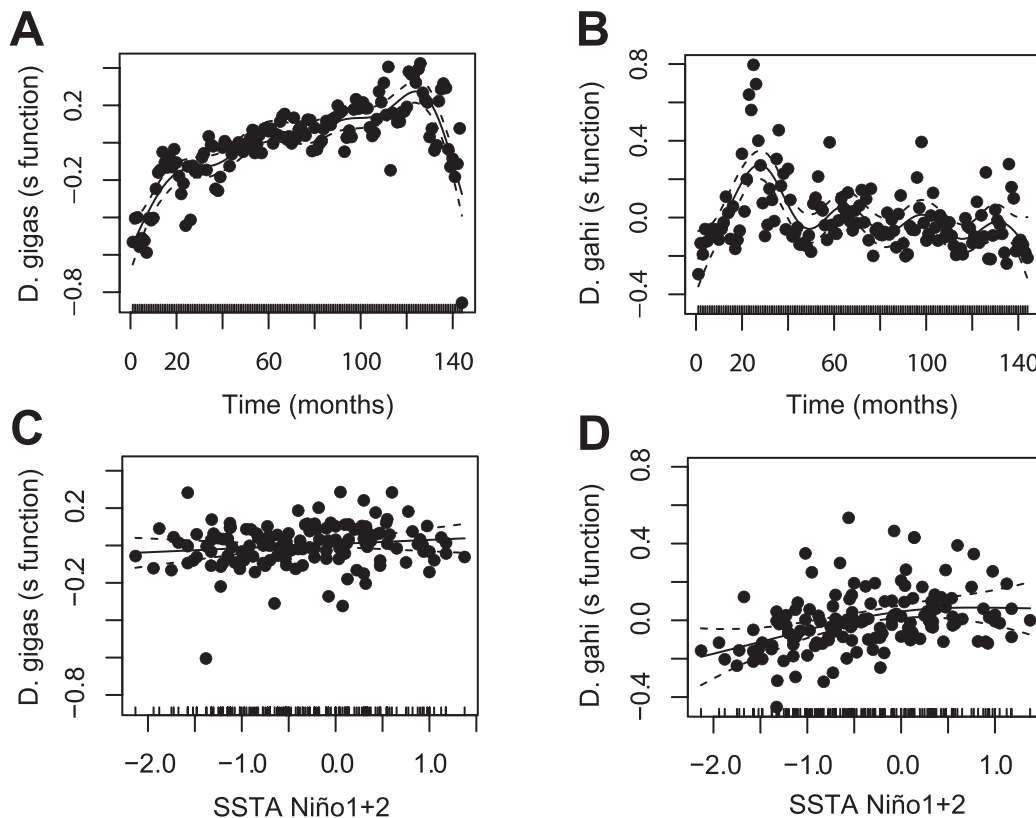
3. Results

The time series of the squid landings showed a very different temporal response for the two squid species. For *D. gigas,* the time series shows sustained growth over time with low periodicity (Fig. 2A). In contrast, the time series of *D. gahi* shows variable landings with strong periodicity, decreasing to zero in some periods and with marked peaks in spring and summer (Fig. 2B). For both species, the CPUE was not significantly different between years and seasons (Table 1, Fig. 2C and D). The GAM of standardized landings of *D. gigas* sh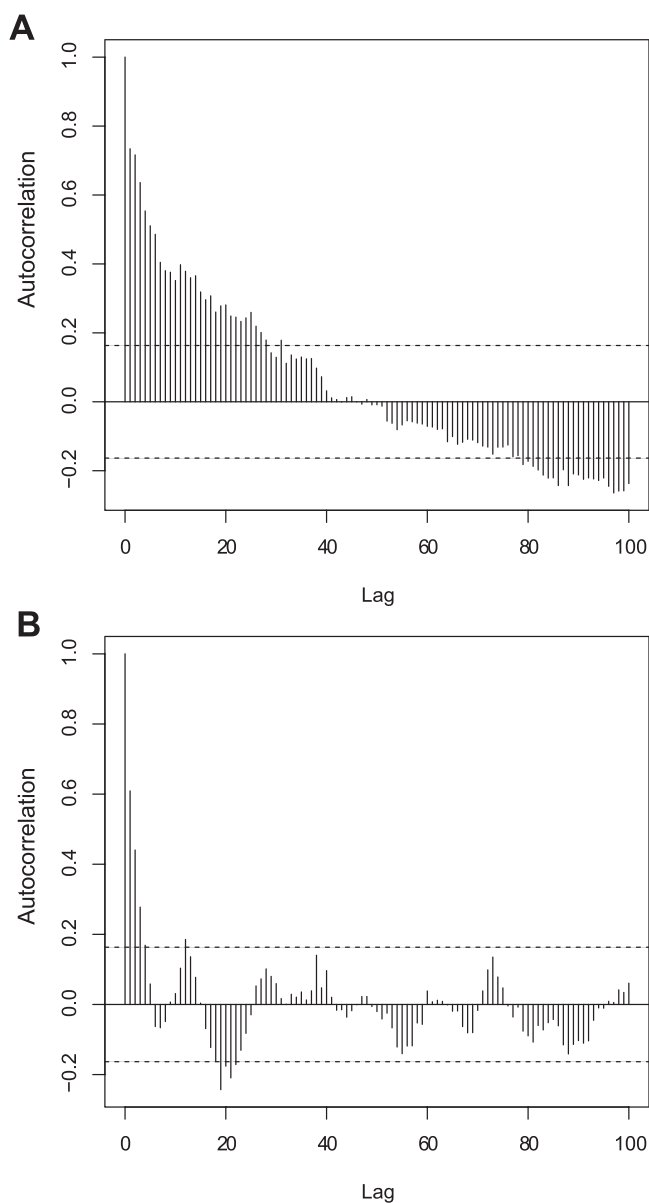ows some temporal stability and explains 71% of the temporal variation (Table 2, Fig. 3A). In contrast, the standardized landings of *D. gahi* show abrupt oscillations that explain 30% of the temporal variability (Table 2, Fig. 3B). The thermal anomalies of El Niño1 + 2 did not have a significant effect on the catches of *D. gigas* and *D. gahi* (Table 2, Fig. 3C and D).

For *D. gigas* the ACF shows a non-stationary pattern. There is a significant correlation in the first 30 months with a delay of one month (Fig. 4A). For *D. gahi*, the ACF has a stationary pattern with a significant delay of one month and an unclear periodicity ranging from minimum to maximum catches every 6–15 months (Fig. 4B). The PACF showed that the species have different endogenous dynamics as the negative correlations occur at different times (Fig. 5A and B).

From the point of view of the population dynamics, there seems to be a first order regulation feedback affecting the *D. gigas* population. This can be deduced from the significant inverse relationship (Table 3) between the per capita population growth rate and the abundance observed in the previous year (Fig. 6A). In addition, this relationship indicates that the annual growth rate change in abundance can be modelled as a function of density observed in previous years; this explains 55% of the variation. For *D. gahi,* the R-function was significant (Table 3) (Fig. 6B) and explains 49% of the variation. From this, it is seen that the *D. gahi* landings represent a popu-

Fig. 3. Standardized squid catches in northern Peru. Dots correspond to CPUE and the trend line corresponds to the adjusted model (GAM) ±95% confidence interval. Squid catches versus time (A and B) and SSTA at Niño1 + 2 (C and D) for *Dosidicus gigas* and *Doryteuthis gahi*, respectively.

A

B

Fig. 4. Autocorrelation function (ACF) of the standardized time series of the squids (A) *Dosidicus gigas* and (B) *Doryteuthis gahi*.

lation with first order dynamics. Second order dynamics have no significant effect in either squid species (Table 3).
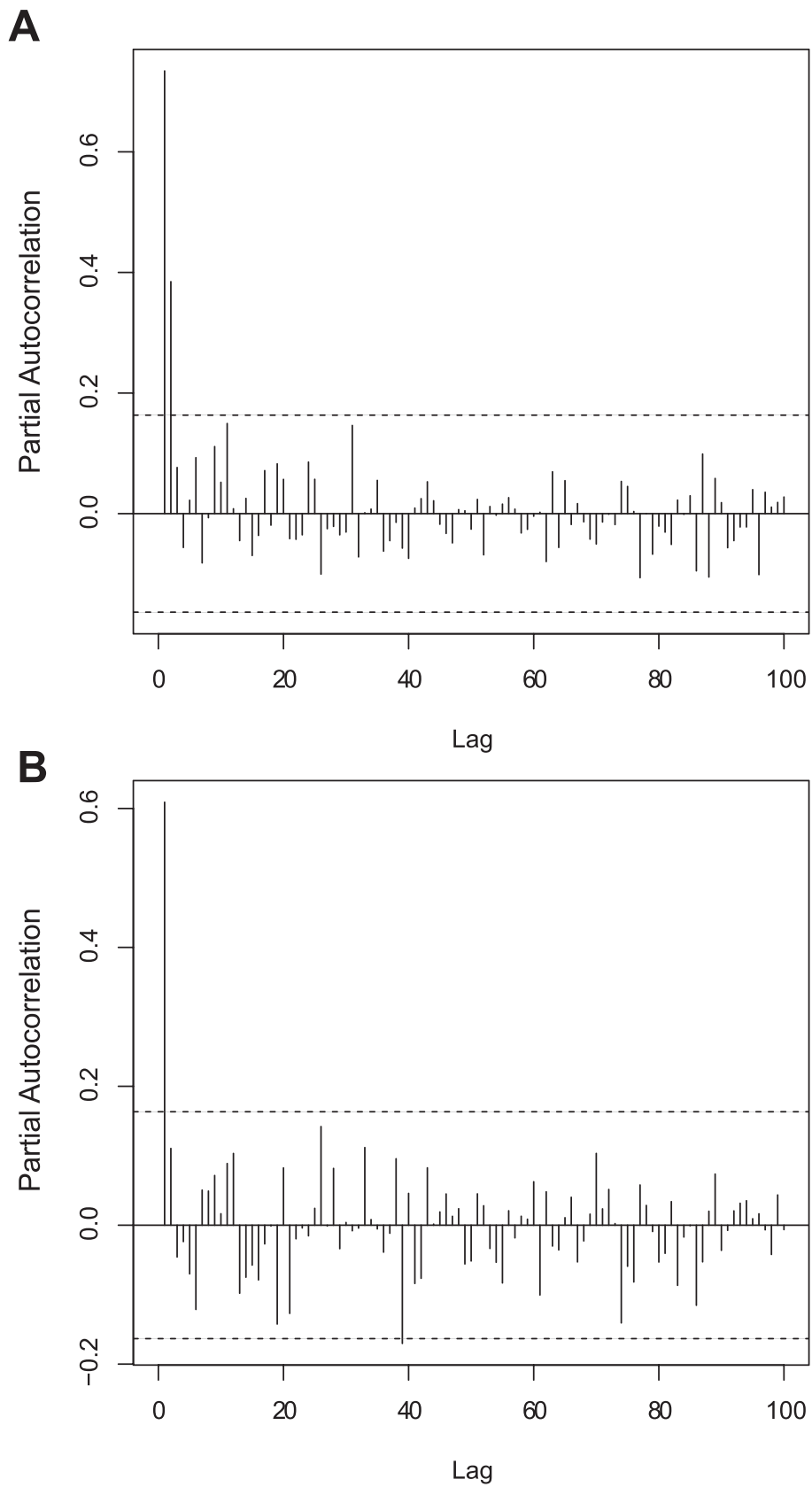
4. Discussion

The catch data presented indicate different patterns of population dynamics for the two squid species studied. The *D. gigas* catch time series shows an increase of catches from 1999 to 2010 and this increase is not related to SSTA, but rather there are signals of endogenous factors regulating the population dynamics. On the other hand, *D. gahi* showed a fluctuating pattern of catches related to endogenous factors, which nevertheless explained only 30% of variance. For *D. gahi*, the population dynamics observed could be the result of interactive effects of endogenous and exogenous factors. In the Northern Hemisphere, variable population responses of two species of ommastrephid and loliginid squids have been reported for populations subjected to similar oceanographic variation (e.g., NAO) (Dawe et al., 2007). Recently, it has been suggested that climate-related events (e.g., El Niño and La Niña) could alter not

only the size of a population but they could affect in the distribution (both horizontal and vertical) of marine populations (Camus, 2008).
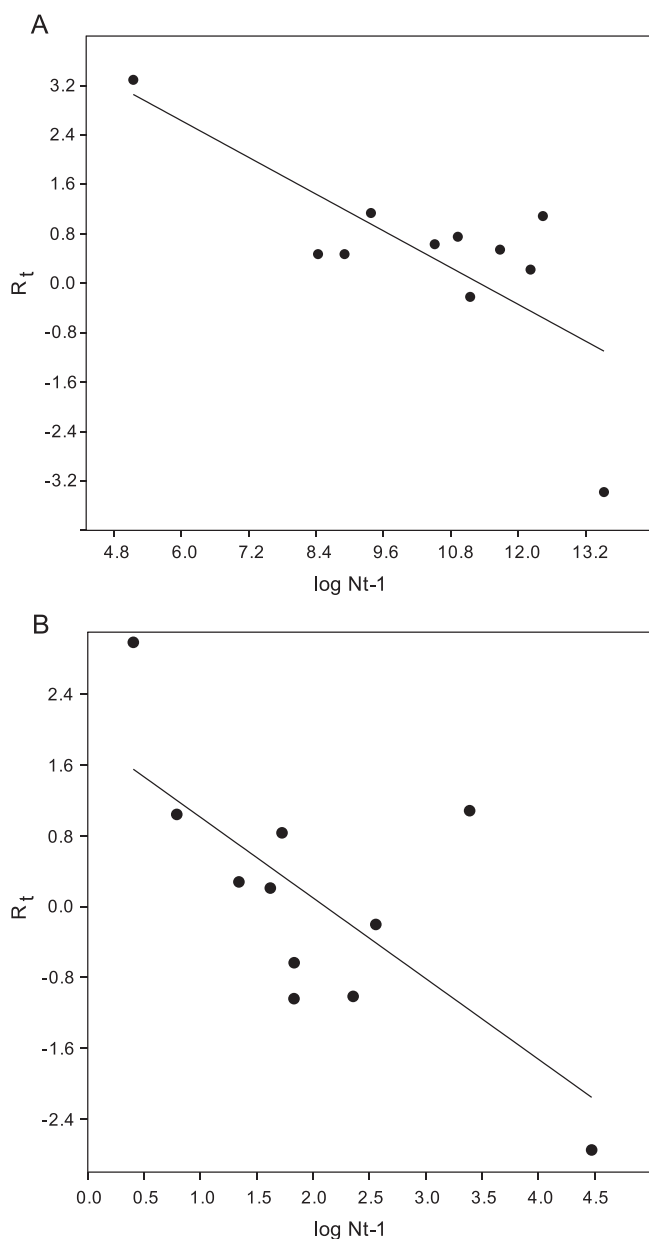
Population fluctuations are complex and may be caused by an interaction of direct and indirect processes, which can be both physical and biological. Traditionally, there are two opposing hypotheses that attempt to explain population dynamics. The first suggests that exogenous factors, or so-called density-independent factors such as climate variability, determine population abundance (Lima, 1995; Lima et al., 2000). The second holds that the observed variability in many populations is explained by endogenous factors that represent feedback events generated by the interaction between individuals within populations or between populations. These are known as density-dependent factors and are the accurate regulators of natural populations (Turchin and Taylor, 1992; Berryman, 1999; Pedraza-García and Cubillos, 2008). It is accepted that the dynamics of natural populations are the consequence of the interaction between endogenous (density-dependent) and exogenous (density-independent) factors (Royama, 1992; Lima, 1995, 2001; Lima et al., 1999; 2000). To study such interactions, a detailed knowledge of ecological systems and climate variability is required. Therefore, the density-dependent and density-independent factors interacting with climate must be well understood (Stenseth et al., 2002). Climate phenomena such as the NAO and ENSO have been shown to have an impact on a variety of ecological processes in marine and terrestrial systems and these effects are detectable at various spatial and temporal scales (Stenseth et al., 2002, 2003). In this study, SSTA variation was not the best adjustment for both squid species time series. Instead, it is thought that a strong first order feedback dominates the population dynamics. Previous studies have found a significant association between catch data and SSTA, but these studies have included the 1997–98 ENSO event data (Waluda et al., 2006; Waluda and Rodhouse, 2006). However, these studies do not explore the feedback structures of the population dynamics and their results are only associative. Knowing what factors determine squid population fluctuations is also needed to examine others results of the same species or other phylogenetically-related species. In addition, studies of other ecosystems and studies using more complex models (e.g., non-linear, interactive effects) could benefit from a firm knowledge of the factors that shape populations.

It has been proposed that environmental factors and particularly El Niño and La Niña events alter the abundance of *D. gigas* and *D. gahi* in Peru and Chile (Villegas, 2001; Rodhouse, 2001; Anderson and Rodhouse, 2001; Taipe et al., 2001). Nevertheless, our results indicate that these species respond differently to environmental variability. This is potentially associated with the different life history strategies of ommastrephid and loliginid squids. These differing life history characteristics include the type of spawning, the related dispersal potential (O'Dor and Webber, 1991; Boyle and Rodhouse, 2005), as well as the squid habitat use (see Arkhipkin, 2013). Loliginid squids inhabit coastal areas and their populations are likely to be affected by local or mesoscale variations of ENSO. Ommastrephid squids, which are typically oceanic, may migrate to more stable environmental conditions. In this study we did not consider the 1997–98 ENSO period, because the related thermal anomaly strongly affected several economically important species landings. It was assumed that considering this time period would produce a statistical artifact resulting in a spurious significant relationship. The analyzed study period (i.e., 1999–2010) consisted of environmental conditions that were very different from the conditions present before the 1997–98 ENSO event. This study shows that fishery time series of squid populations are not completely influenced by local SSTA, and density-dependent processes may be more important to the population dynamics than are environmental fluctuations. Nevertheless, SSTA can be considered to be a *proxy*

A

B

Fig. 5. Partial autocorrelation function (PACF) of the standardized time series of the squids (A) *Dosidicus gigas* and (B) *Doryteuthis gahi*.

A

B

Fig. 6. Instantaneous population growth rate of the standardized time series of the squids (A) Do*sidicus gigas* and (B) *Doryteuthis gahi*.

variable for ecosystem productivity. This has been assumed to be the explanation for spatial and temporal changes in the distribution and abundance of *D. gigas* in the Humboldt Current System. It is thought that these fluctuations are a consequence of changes in the trophic system provoked by fisheries and environmental changes (Keyl et al., 2008). The Patagonian squid *D. gahi* spawns in coastal zones in spring and summer (Villegas, 2001) when the water temperature increases. Thus, juveniles could be easily caught in this peak fishing period. Rather than thermal anomaly variation, this biological characteristic may better explain the different catch patterns seen of *D. gahi*.

From an ecological point of view, squid populations fluctuate in response to environmental changes and feedback structures. From an evolutionary perspective, the genetic evidence suggests that changes in the distribution and abundance of *D. gigas* and *D. gahi* squids could be related to historical variation in productivity and sea temperature in the last 40,000 years. It has been assumed that more favorable environmental conditions following the last glacia-

tion period have led to an increase in abundance of both species (Ibáñez et al., 2011, 2012; Ibáñez and Poulin, 2014).

References

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control 19, 716–723.

Anderson, C.I.H., Rodhouse, P., 2001. Life cycles, oceanography and variability: ommastrephid squid in variable oceanographic environments. Fish. Res. 54, 133–143.

Arkhipkin, A.I., 2013. Squid as nutrient vectors linking South West Atlantic marine ecosystems. Deep-Sea Res. II 95, 7–20.

Berryman, A.A., 1999. Principles of Population Dynamics and their Applications. Stanley Thornes Publishers, Cheltenham.

Boyle, P.R., Boletzky, S.V., 1996. Cephalopod populations: definition and dynamics. Phil. Trans. Royal Soc. London Serie B 351, 985–1002.

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

Camus, P.A., 2008. Understanding biological impacts of ENSO on the eastern Pacific: an evolving scenario. Int. J. Environ. Health 2, 5–19.

Cardoso, F., 1991. Los calamares y potas (Cephalopoda: Teuthoidea) del mar peruano. Biota 15, 2–13.

Cardoso, F., Baltazar, P., Bautista, J., 2005. The early development of the Patagonian squid *Loligo gahi* d'Orbigny, 1835 in Peruvian Waters (Cephalopoda: Loliginidae). Rev. Peru. Biol. 12, 369–376.

Cardoso, F., Tarazona, J., Paredes, C., 1998. Aspectos biológicos del calamar patagónico *Loligo gahi* (Cephalopoda: Loliginidae) en Huarmey, Perú. Rev. Peru. Biol. 5, 9–14.

Chong, J., Oyarzún, C., Galleguillos, R., Tarifeño, E., Sepúlveda, R.D., Ibáñez, C.M., 2005. Parámetros biológico-pesqueros de la jibia, *Dosidicus gigas* (Orbigny, 1835) (Cephalopoda: Ommastrephidae) frente a la costa de Chile central 29°S y 40°S durante el periodo 1993–1994. Gayana 69, 319–328.

Dawe, E.G., Hendrickson, L.C., Colbourne, E.B., Drinkwater, K.F., SHowell, M.A., 2007. Ocean climate effects on the relative abundance of shortfinned (*Illex illecebrosus*) and long-finned (*Loligo pealeii*) squid in the northwest Atlantic Ocean. Fish. Oceanogr. 16, 303–316.

Field, J.C., Baltz, K., Phillips, A.J., Walker, W.A., 2007. Range expansion and trophic interactions of the jumbo squid, *Dosidicus gigas*, in the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 48, 131–146.

Ibáñez, C.M., Cubillos, L.A., 2007. Seasonal variation in the length structure and reproductive condition of the jumbo squid *Dosidicus gigas* (d'Orbigny, 1835) off Central-South Chile. Sci. Mar. 71, 123–128.

Ibáñez, C.M., Poulin, E., 2014. Genetic structure and diversity of squids with contrasting life histories in the Humboldt Current system. Hidrobiológica 24, 1–9.

Ibáñez, C.M., Cubillos, L.A., Tafur, R., Argüelles, J., Yamashiro, C., Poulin, E., 2011. Genetic diversity and demographic history of *Dosidicus gigas* (Cephalopoda: Ommastrephidae) in the Humboldt Current System. Mar. Ecol. Prog. Ser. 431, 163–171.

Ibáñez, C.M., Argüelles, J., Yamashiro, C., Adasme, L., Céspedes, R., Poulin, E., 2012. Spatial genetic structure and demographic inference of the Patagonian squid *Doryteuthis gahi* in the Southeastern Pacific Ocean. J. Mar. Biol. Assoc. UK 92, 197–203.

Jereb, P., Roper, C.F.E., 2010. Cephalopods of the world. An annotated and Illustrated catalogue of species known to date. FAO Species Catalogue for Fishery Purposes, 4, 51–55.

Keyl, F., Argüelles, J., Mariátegui, L., Tafur, R., Wolff, M., Yamashiro, C., 2008. A hypothesis on range expansion and spatio-temporal shifts in size-at-maturity of jumbo squid (*Dosidicus gigas*) in the eastern Pacific Ocean. Calif. Coop. Ocean. Fish. Invest. Rep. 49, 119–128.

Lima, M., 1995. Regulación poblacional, denso-dependencia y métodos para su detección en series de tiempo. Rev. Chil. Hist. Nat. 68, 251–269.

Lima, M., 2001. The dynamics of natural populations: feedback structures in fluctuating environments. Rev. Chil. Hist. Nat. 74, 317–332.

Lima, M., 2006. Los efectos ecológicos de las fluctuaciones climáticas. Invest. Cienc. 2006, 46–52.

Lima, M., Keymer, J.E., Jaksic, F.M., 1999. ENSO-driven rainfall variability and delayed density dependence cause rodent outbreaks in western South America: linking demography and population dynamics. Am. Nat. 153, 476–491.

Lima, M., Brazeiro, A., Defeo, O., 2000. Population dynamics of the yellow clam (*Mesodesma mactroides*): recruitment variability, density-dependence and stochastic processes. Mar. Ecol. Prog. Ser. 207, 97–108.

Montecino, V., Strub, P.T., Chavez, F.P., Thomas, A.C., Tarazona, J., Baumgartner, T., 2005. Chapter 10 Bio-physical Interactions off Western South America. The

Sea. In: Robinson, A.R., Brink, K.H. (Eds.). Harvard University Press, Cambridge, pp. 329–390.

Nigmatullin, Ch. M., Nesis, K.N., Arkhipkin, A.I., 2001. A review of the biology of the jumbo squid *Dosidicus gigas* (Cepahlopoda: Ommastrephidae). Fish. Res. 54, 9–19.

O'Dor, R.K., Webber, D.M., 1991. Invertebrates athletes: tradeoffs between transport efficiency and power density in cephalopod evolution. J. Exp. Biol. 160, 93–112.

Pedraza-García, M., Cubillos, L.A., 2008. Population dynamics of two small pelagic fish in the central-south area off Chile: delayed density-dependence and biological interaction. Environ. Biol. Fish. 82, 111–122.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rocha, F., Vega, M.A., 2003. Overview of cephalopod fisheries in Chilean waters. Fish. Res. 60, 151–159.

Rocha, F., Guerra, A., González, A.F., 2001. A review of reproductive strategies in cephalopods. Biol. Rev. 76, 291–304.

Rodhouse, P.G., 2001. Managing and forecasting squid fisheries in variable environments. Fish. Res. 54, 3–8.

Rosa, R., Yamashiro, C., Markaida, U., Rodhouse Waluda, P.G.K.C.M., Salinas-Zavala, C.A., Keyl, F., O'Dor, R., Stewart, J.S., Gilly, W.F., 2013. *Dosidicus gigas*, Humboldt squid. In: Rosa, R., O'Dor, R., Pierce, G. (Eds.), Advances in Squid Biology: Ecology and Fisheries, Part II Oegopsid squids. Nova Science Publishers, Inc., New York, pp. 169–206.

Royama, T., 1992. Analytical Population Dynamics. Chapman and Hall, London, United Kingdom, 371 pp.

Semmens, J.M., Pecl, G.T., Gillanders, B.M., Waluda, C.M., Shea, E.K., Jouffre, D., Ichii, T., Zumholz, K., Katugin, O.N., Leporati, S.C., Shaw, P.W., 2007. Approaches to resolving cephalopod movement and migration patterns. Rev. Fish Biol. Fish. 17, 401–423.

Staaf, D.J., Camarillo-Coop, S., Haddock, H.D., Nyack, A.C., Payne, J., Salinas-Zavala, C.A., Seibel, B.A., Trueblood, L., Widmer, C., Gilly, W.F., 2008. Natural egg mass deposition by the Humboldt squid (*Dosidicus gigas*) in the Gulf of California and characteristics of hatchlings and paralarvae. J. Mar. Biol. Assoc. UK 88, 759–770.

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S., Lima, M., 2002. Ecological effects of climate fluctuations. Science 297, 1292–1296.

Stenseth, N.C., Ottersen, G., Hurrell, J.W., Mysterud, A., Lima, M., Chan, K.-S., Yoccoz, N.G., Dlandsvik, B., 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. Proc. R. Soc. London B 1529, 2087–2096.

Taipe, A., Yamashiro, C., Mariategui, L., Rojas, P., Roque, C., 2001. Distribution and concentrations of jumbo squid (*Dosidicus gigas*) off Peruvian coast between 1991 and 1999. Fish. Res. 54, 21–32.

Thiel, M., Macaya, E., Acuña, E., Arntz, W., Bastias, H., Brokordt, K., Camus, P., Castilla, J.C., Castro, L.R., Cortés, M., Dumont, C.P., Escribano, R., Fernández, M., Lancelloti, D., Gajardo, J.A., Gaymer, C.F., Gomez, I., González, A.E., González, H.E., Haye, P.A., Illanes, J.E., Iriarte, J.L., Luna-Jorquera, G., Luxoro, C., Manríquez, P.H., Marín, V., Muñoz, P., Navarrete, S.A., Pérez, E., Poulin, E., Sellanes, J., Sepúlveda, A., Stotz, W., Tala, F., Thomas, A., Vargas, C.A., Vásquez, J.A., Vega, A., 2007. The Humboldt current system of northern and central Chile oceanographic processes, ecological interactions and socioeconomic feedback. Oceanography Mar. Biol. An Ann. Rev. 45, 195–344.

Turchin, P., Taylor, A.D., 1992. Complex dynamics in ecological time series. Ecology 73, 289–305.

Villegas, P., 2001. Growth, life cycle and fishery biology of *Loligo gahi* (d'Orbigny 1835) off the Peruvian coast. Fish. Res. 54, 123–131.

Waluda, C.M., Rodhouse, P.G., 2006. Remotely sensed mesoscale oceanography of the Central Eastern Pacific and recruitment variability in *Dosidicus gigas*. Mar. Ecol. Prog. Ser. 310, 25–32.

Waluda, C.M., Yamashiro, C., Rodhouse, P.G., 2006. Influence of the ENSO cycle on the light-fishery for *Dosidicus gigas* in the Peru current: an analysis of remotely sensed data. Fish. Res. 79, 56–63.

Zeidberg, L.D., Robison, B.H., 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. Proc. Natl. Acad. Sci. 104, 12948–12950.

Zúñiga, M.J., Cubillos, L.A., Ibáñez, C.M., 2008. Synchronous pattern of periodicity in the monthly catch of Jumbo squid (*Dosidicus gigas*) along the Chilean coast (2002–2005). Cienc. Mar. 34, 91–99.