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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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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;

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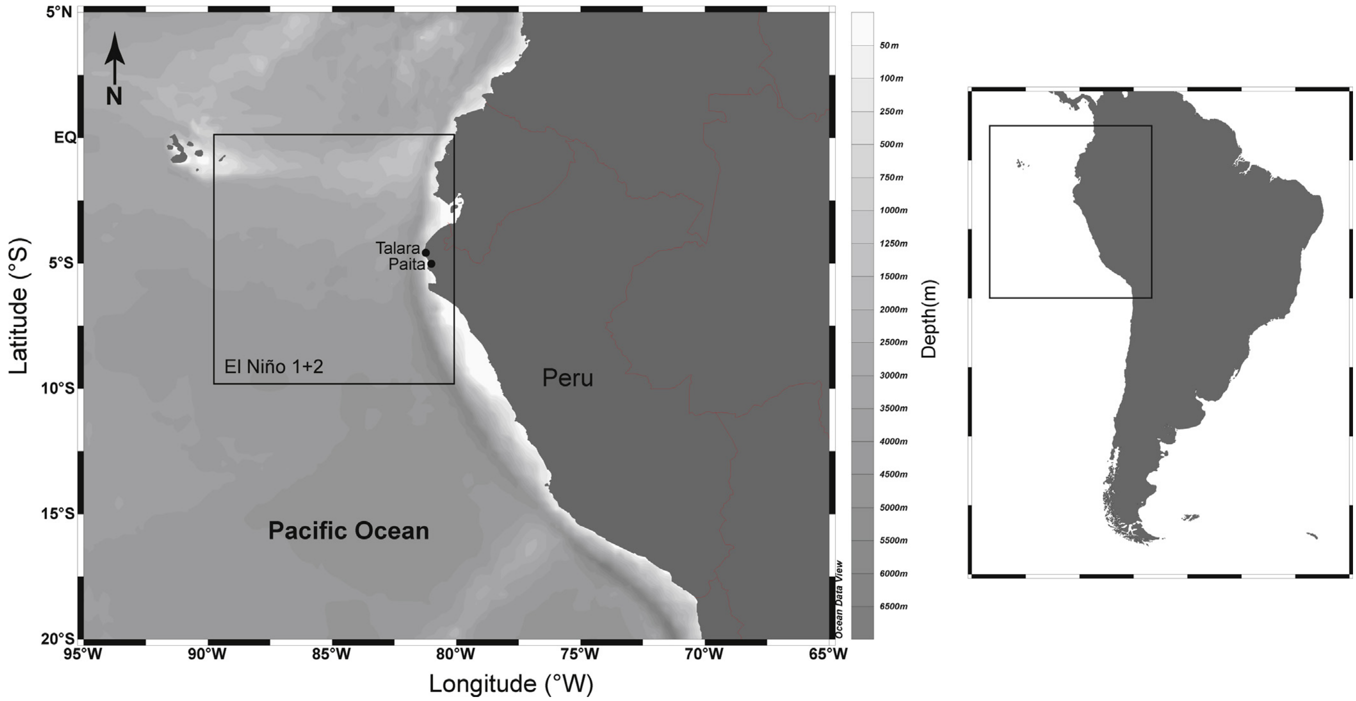

Fig. 1. Map showing the fishing zone where *Dosidicus gigas* and *Doryteuthis gahi* were captured by artisanal fleets in northern Peru.

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

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