

1 The recruitment dynamics of the nylon shrimp
2 *Heterocarpus reedi*, effects of climate and predation off
3 Chile

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16 **Abstract**

17 Climate variability and predation influence the fluctuations in the recruitment of exploited
18 marine populations. This study analyses the dynamics of the recruitment of the nylon shrimp
19 (*Heterocarpus reedi* Bahamonde 1955) over the period 1968 and 2015, considering the influence
20 of climate variability and the biomass of common hake (*Merluccius gayi*), as a proxy for

predation in its distribution area. We collected the Humboldt Current Index (HCI) and Southern Oscillation Index (SOI) time series as climate variables and estimates of recruitment and spawning biomass of nylon shrimp, as well as biomass of Chilean hake. Annual deviations in nylon shrimp recruitment showed increased sensitivity to climate variability from the late 1990s onwards, expressed through a significant cumulative correlation over time ($P < 0.05$). Generalized Linear Models showed that climatic variables and biomass of common hake were responsible for the recruitment rate ($r^2 = 0.873$, $P < 0.05$). A path diagram with structural equation models (SEM) showed that the recruitment rate is being influenced by the greater or lesser biomass of common hake, either through the consumption of juveniles in the year of formation of the annual class or on adult spawners, in interaction with climate variability.

Key words: Recruitment, shrimp, climate, predation, sensitivity, trawl fishery

Introduction

In general, fishing and/or the environment influence the large fluctuations experienced by the stocks, directly or indirectly affecting the magnitude of recruitment, which expresses through the entry of juveniles into the exploitable fraction (Gómez et al., 2012; Hsieh et al., 2006). Likewise, the pre-recruitment phases can be sensitive to favorable or unfavorable environmental factors (Hidalgo et al., 2011; Perry et al., 2010; Planque et al., 2010). Fluctuations in recruitment are caused not only by climate forcing and fishing but also due to ecological interactions such as predator-prey (???, ???, ???, ???), particularly the shrimp-gadoid relationship (Björnsson et al., 2017, 2011; Drinkwater et al., 2010; Worm and Myers, 2003).

Climate variability occurs on different time scales, from the seasonal, interannual cycle with irregular periods of 1 to 3 years associated with El Niño-Southern Oscillation (ENSO), aperiodic decadal variability between 5 to 50 years to centennial and longer-term periods (Chavez et al., 2003; Overland et al., 2010; Perry et al., 2010). There is evidence that this variability influences the status and functioning of marine ecosystems and is closely related to population distribution, migration, and abundance (Lehodey et al., 2006). It has also been shown that fishing and other human activities have an impact on exploited and unexploited

species (Hsieh et al., 2006; Planque et al., 2010), and can modify the structure, size, and functioning of ecosystems (Cury et al., 2000).

In the upwelling ecosystem of the Humboldt Current System, there have been seasonal and decadal changes in populations of small pelagic fish such as anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*), which demonstrate the almost immediate impact of the environment and synchrony over a wide latitudinal range (Alheit and Niquen, 2004; Cubillos et al., 2007; Yañez et al., 2008). In the central-southern zone, the inter-annual variability of ENSO influences pelagic fish populations, for example, on the recruitment of the common sardine *Strangomera bentincki* (Gómez et al., 2012). El Niño and La Niña considerably modify the neritic environment, and we observed that in cold years (La Niña) there is an increase in the recruitment of typical sardines as a result of an increase in biological production (Parada, 2013). In turn, climatic conditions influence faunal changes in plankton, zooplankton, and predators, mainly in the pelagic ecosystem (Alheit and Niquen, 2004; Ayón et al., 2011; Chavez et al., 2003; van der Lingen et al., 2009; Xu et al., 2019), whose greater or lesser predation would have a direct effect on the benthic and demersal system (Cury et al., 2000). However, few studies have aimed at assessing the role of climate influence on benthic crustaceans distributed in deep waters over the continental platform and upper slope.

Nylon shrimp inhabit the continental platform and slope along the coast of Chile, between 200 and 500 m deep, associated with the Peru-Chile Subsurface Current flowing towards the pole, and the mixing of water masses between the Antarctic Intermediate Water (oxygenated and cold water, 11-12 °C) and the Equatorial Subsurface Water ($O_2 < 1 \text{ ml L}^{-1}$, 12-13 °C, 35 psu) (Arana, 2012; Bahamonde and Henri'quez, 1970; Silva, 2012). South of its distribution, river discharges, and upwelling events determine the availability of organic matter that could favor adult feeding. Likewise, the northward circulation of the Humboldt Current may explain the presence of juveniles in the north of its current distribution through processes of survival and recruitment by larval or juvenile dispersal (C Canales et al., 2016). C Canales et al. (2016) suggested that the shrimp population is likely to be a metapopulation structure with at least two subunits located north and south of 32°S, and whose connectivity would be explained by larval drift.

The shrimp fishery is located between 25°S and 37°10'S, with two stock units (C. M. Canales et al., 2016; Montenegro and Branco, 2016): a northern stock between 25°S and 32°S and a southern stock from 32°S to 37°10'S (Fig. 1). The fishery involves a fleet of small industrial trawlers on the slope and the continental platform. The available data have made it possible to evaluate this resource from 1940 to 2015 through stock assessment models structured by length (C.M. Canales et al., 2016). Biomass indices are available from biomass evaluation by the swept area method, which show an increasing trend south of 32°S from 2006 (Acuña et al., 2012). According to (C Canales et al., 2016), positive trends in biomass could be influenced by the reduction in exploitation levels, the closure of some fishing areas since 2000, and by the depletion of Chilean hake (*Merluccius gayi gayi*) after 2003. The common hake is one of the most abundant and important predators of the demersal system in which shrimp and prawns live (Arana and Williams, 1970; Arancibia and Neira, 2008; Cubillos, 2007), and it could be an additional factor influencing the variability of long-term recruitment of nylon shrimp.

According to the above, understanding and taking into account these sources of variability and their interactions represent a challenge for modern fisheries management. This work aimed to evaluate the hypothesis that the changes observed in the recruitment and biomass of nylon shrimp could be influenced by their population dynamics and the trophic interaction with common hake in a changing environment.

Material and Methods

Source of data and information

We obtained the time series of spawning biomass and shrimp recruitment from (C.M. Canales et al., 2016), who considered data from the northern and southern fishery unit in a spatial stock assessment model. For the analysis, we discarded the estimates of spawning biomass and recruitment for the years 1945 to 1960 because these early estimates do not account for variability but rather for expected recruitment. Besides, one of the climate indices began in 1968, conditioning the study period (see below).

The variations in the recruitment of the northern and southern fishing units are identical, with slight differences in the time series. This is due to the stock assessment model that considers shrimp recruitment to be a function of the same signal and spatially segregated by a proportion that defines connectivity between areas (C.M. Canales et al., 2016). Using in this context, the sum of northern and southern recruitment in subsequent analyses.

We used two climate indices to study the influence of environmental variability on shrimp recruitment, the Humboldt Current Index (HCI) (Blanco-García, 2004), and the Southern Oscillation Index (SOI). The HCI measures the atmospheric circulation between Rapa Nui (27°6'16.8"S, 109°21'37.7"S) and Antofagasta (23°38'39"S, 70°24'39"S) and it is an index of the decadal climate variability of the Humboldt Current System. The SOI is a standardized index based on observed sea level pressure differences between Tahiti and Darwin, Australia, which measures Walker's atmospheric circulation. These indicators make it possible to detect decadal and interannual changes in the climate that could restructure the ecosystem, which is associated with long-lasting periods of hot or cold temperature anomalies, related to the approach or retreat of warm subtropical oceanic waters to the coast of Chile (Alheit and Niquen, 2004).

Hake biomass as a proxy for predation on shrimp

We used hake biomass as a proxy to study the effects of predation on nylon shrimp. To analyze the fraction of the biomass that influences the predation of nylon shrimp, we considered the biomass estimates of Chilean hake by age reported by Tascheri et al. (2017) and covering the period 1968-2015. We obtained the age selection of Chilean hake preying on shrimp from the relationship between predator weight and prey weight using the Ursin size-selection index (Ursin, 1973). For this purpose, we used data on stomach contents of common hake documented by Arancibia et al. (1998), where we calculated prey size-selectivity using the following expression:

$$\alpha(jx, is) = \exp \left(-\frac{(\log(W_{x,j}/W_{s,i}) - \eta)^2}{2\sigma^2} \right)$$

where $W_{x,j}$ is the average weight of predator x at age j , $W_{s,i}$ is the average weight of prey s at age i . The constant η represents the average weight ratio between prey and predator, and σ represents the range of prey size in the predator's diet. Once obtained this index, we analyzed the age range of the Chilean hake affecting the size-selectivity of shrimp.

Recruitment sensitivity

We removed the mean from each time series of the variables used and divided it by the standard deviation. We used these anomalies to detect the sensitivity of shrimp recruitment to climatic indices HCI and SOI, and to hake biomass (H) at the time of formation of the annual classes (two years earlier). A proxy for increased sensitivity overtime was to calculate cumulative correlations over time. The cumulative correlation analysis began with the first 5 years of the series (1968-1972) and then added one year sequentially until all available years (1968-2015, $n=48$) were completed (Cahuin et al., 2013). The critical correlation coefficients for the cumulative correlation decrease with the addition of each year, which allowed to know the significance of the cumulative correlation in time, starting from $r = 0.878$ ($P = 0.025$, $df = 3$ years) to $r = 0.288$ ($P = 0.025$, $df = 46$ years).

Modeling the shrimp recruitment rate

We used Generalized Linear Model to model the shrimp recruitment rate as a function of the spawning stock, climate variables, and common hake biomass. We used the log-recruitment rate $\log(R_t/S_{t-ar})$ as a dependent variable, where R_t is the recruitment at year t , S_{t-ar} is the spawning biomass at year $t - ar$, and ar is the age of recruitment ($ar = 2$). Spawning biomass was the sum of the north and south zones, i.e., $S_t = S_{t,north} + S_{t,south}$ (C.M. Canales et al., 2016). We analyzed the phase or lagging effects of climate variables and hake biomass. We consider a phasing effect when a variable acts in the year of recruitment and a lagging effect when a variable acts two years before recruitment, i.e., in the year of formation of the annual class. We utilized GLM with link identity (McCullagh and Nelder, 1989) and the package MASS of Venables and Ripley (2002) and considered nine models differentiated in

the combination of predictor variables. The best model was selected by applying the Akaike's information criterion (AIC) (Akaike, 1973) and weighed according to Buckland et al. (1997).

Path diagram

Structural equation modeling (SEM) allowed us to understand the phase or lagging relationship between nylon shrimp recruitment, climate indices, and hake biomass as a proxy for predation. This technique (SEM) is a statistical approach for parameterizing and testing causal models that describe hypothetical relationships between multiple variables, to solve a set of equations involved in a path diagram (Grace et al., 2010; Grace and Bollen, 2005). Because SEM, based on maximum likelihood, uses a correlation matrix, it assumes that all relationships are linear and additive (Grace and Bollen, 2005). As in the GAM models, the recruitment rate could be related to the effects of climate variability and predation in the phase ($\text{lag} = 0$, or direct effects), or in lag ($\text{lag} = 2$) during the year of formation of the annual classes.

Results

During the study period, the Humboldt Current Index (HCI) showed positive values in the periods 1970-1978 and 1997-2015, associated with a strengthening of the Pacific Anticyclone (Fig. 2). Between 1979 and 1996, the index remained negative, implying a period of warmer conditions. In turn, the Southern Oscillation Index (SOI) shows high inter-annual variability with El Niño events expressed with negative values of the SOI in the years 1972, 1977-1980, 1982-84, 1986-87, 1990-95, 1997-98, 2002-06, 2009, 2012, 2014 and 2015 (Fig. 2). It also identifies La Niña events (positive SOI values) in the years 1970, 1973-76, 1981, 1985, 1988-89, 1996, 1999-2001, 2007-08, 2010-11 and 2013. It should be noted that the length of a period in which negative values prevail between 1977 and 1997 is consistent with the same period identified in the HCI (Fig. 2).

Anomalies of recruitment for both stocks were similar to each other, showing negative fluctuations for the period from 1976 to 1998, and then remaining at positive values (Fig.

3A). However, we observe fluctuations in the spawning biomass of the northern stock that differs from that of the southern stock, the latter being more fluctuating throughout the period where negative values prevail for years similar to those observed in the recruitments (1976-1998) (Fig. 3B).

The Chilean hake biomass has a sustained increase from 1970 to mid-90s, dramatically decreasing from 2003 to 2004 and remain at low values from 2005 to 2015. Thus, we observe opposite trends between the spawning biomass of shrimp and the biomass of common hake (Fig. 3C). Along with the above, from the model of predation hake-shrimp, the fraction of shrimp that goes from 0 to 3 years is depredated by all ages of common hake, however, from age 2 + we observe a higher selectivity by hake over 4 years (Table 1).

The recruitment was not sensitive to the variability represented by SOI throughout the study period (Fig. 5). However, the sensitivity began to be significant and positive with the HCI, mainly between 1981-1987 and 1994-2013. The sensitivity of shrimp recruitment to changes in the biomass of common hake showed a significant negative correlation in the periods 1974-1975, 1978-1988, 1991-1994, and from 2005 to 2013.

Out of nine GLM models, the models that considered shrimp spawning biomass and hake biomass in the year of recruitment, along with the climate indicator (HCI or SOI) in the year of annual class formation, better explained the variations in shrimp nylon recruitment during the study period (Table 2). The models M4, M5, and M6, which include the Chilean hake effects on the year of recruitment plus either delayed or direct effects of the HCI, were the models that best represented the variation in shrimp recruitment. However, of the models selected, the model with the lowest AIC was the M6 model, which considers the negative effects of the Chilean hake biomass directly on the recruitment rate, and to a lesser extent the indirect effects of the HCI on the year of recruitment (Table 2).

The SEM analysis was based on the linear correlation between variables (Table 3) and showed that Chilean hake biomass (Hake) had significant negative effects on shrimp spawning biomass in the year of recruitment and annual-class formation (Hake.lag). To a lesser extent, we observed a lagged effect of the HCI on the spawning biomass (Figure 6). There is evidence that the predator (Hake) was negatively and significantly related to the spawning biomass in the

year of recruitment, and in the shrimp recruitment rate, in turn, Hake.lag and HCI.lag related to the shrimp spawning biomass with a two-year lag, the first negatively and significantly, and the second positively, but with low significance.

Discussion

The challenge for modern fisheries management is to understand and take into account environmental variables and their interactions with exploited populations, leading to a more holistic view of the processes that influence the dynamics of exploited marine populations. In this study, we found that the recruitment of nylon shrimp is being influenced by the higher or lower biomass of common hake, either through consumption of juveniles in the year of formation of the annual class or on adult spawners, in interaction with the interannual climate variability reflected through the ENSO-associated HCI during spawning.

The low influence of the spawning biomass itself on the recruitment rate and the climatic indicators HCI and SOI on shrimp spawning biomass in the year of formation of the year class are highlighted, both in the path diagram (SEM) and in the GAM models. The year-to-year changes between the indicators show the close relationship between the climate indices and negative values for HCI (periods of warm conditions) compared to existing positive values for SOI (El Niño phase). However, HCI only manifests itself as a decadal trend in the prevailing environmental conditions, while SOI represents the interannual variation ENSO (El Niño-Southern Oscillation) (Blanco-García, 2004).

The climate variables analyzed here should be considered as indicating large-scale changes at the atmospheric level and in the ocean's climate through ocean-atmosphere interaction. The influence at the habitat level of the nylon shrimp on the continental slope is unknown. However, climatic influence could likely influence the alteration in the circulation patterns of the Peru-Chile Subsurface Current and the distribution of physical properties associated with the mixing of present water mass, i.e., Subsurface Equatorial and Antarctic Intermediate (Nelson S. and Neshyba, 1979). These water mass intensify or weaken during either El Niño or La Niña events, and influence the subsurface dynamics where the nylon shrimp live

(Hormazabal et al., 2013).

The significance of these indicators is conditional and increases when the incidence of common hake on spawning biomass in the year of formation, and the recruitment rate is incorporated. Nevertheless, from GLM models, we conclude that common hake would explain more than 90% of the variations in the recruitment rate. Recruitment sensitivity analysis showed that common hake presented more considerable significance, which expressed itself through a significant negative correlation in the periods 1973-1975, 1977-1986, and from 2005 to 2011. These results are consistent with (C Canales et al., 2016) in that the increase (decrease) in shrimp biomass could be modulated in part by the depletion (increase) of common hake. The biomass of common hake showed an increasing trend in the first years of the series, with significant increases in 1972-1977, 1980-1984, 1991-1996, and 1998-2000 (Tascheri et al., 2017). These periods coincide with the years of the highest association between hake and the recruitment of nylon shrimp. Opposing trends between the biomasses of common hake and spawning biomasses of nylon shrimp are consistent with findings by Worm and Myers (2003), who show that the abundance of northern shrimp (*Pandalus Borealis*) was negatively related to Atlantic cod (*Gadus morhua*) populations. These authors found that cod correlated with temperature, and they found that changes in predator populations can have substantial effects on prey populations in the ocean food networks and that the intensity of these interactions can be sensitive to changes in mean ocean temperature (Worm and Myers, 2003). Björnsson et al. (2011) found that seasonal migratory activity of immature *G. morhua* was affected both by the location of the local shrimp stock, and the seasonal and spatial differences in temperature.

We found that the incidence of shrimp in the diet of hake is generally low (Arancibia et al., 1998; Cubillos et al., 2003), which could be related to deeper distribution of nylon shrimp. Nevertheless, size selectivity coefficients indicated that common hake from 2 to 4 years of age preys preferentially on 1 to 3-year-old nylon shrimp (shrimp juveniles, recruits, and spawning individuals, as reported by Canales et al. (1999)). These results are consistent with those found by Cubillos (2007), who conclude through the same analysis that hakes over 4 years old prey on red squat lobster (*Pleuroncodes monodon*) and yellow squat lobster (*Cervimunida*

johnei) over 2 years old. It is important to note that after 2003, the biomass of common hake decreased significantly and there was also a juvenilization of the age structure, supported by specimens from 2 to 5 years of age, in addition to a decrease in the size at maturity (Lillo et al., 2015). These demographic changes in the predator could relax probable predation effects favoring the recruitment of nylon shrimp.

With the above, studies of the fauna accompanying the direct assessment cruises of common hake, point to nylon shrimp as one of the main species within the faunal group of the demersal assembly (Acuña et al., 2019; Lillo et al., 2015), the same occurs in the direct assessment cruises of shrimp, where common hake and prawns, make up the main species associated with the captures, with the former showing the most significant recurrence in the captures throughout the entire sampling area (Acuña et al., 2012, 2002, 2019; Arana et al., 2006).

The aforementioned suggests that the interaction in the biological components would have a more significant impact on the biological processes of the component species than the prevailing environmental conditions.

Credit authors

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