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CHANGES IN THE PREDOMINANCE OF PHENOTYPIC GROUPS OF JUMBO FLYING SQUID *Dosidicus gigas* AND OTHER INDICATORS OF A POSSIBLE REGIME CHANGE IN PERUVIAN WATERS

by

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SUMMARY

The jumbo flying squid *Dosidicus gigas* is a neritic-oceanic species widely distributed in the Eastern Pacific. Has a high phenotypic plasticity that is expressed through the presence of three population groups, distinguishable by their maximum size and the size at which they reach sexual maturity. The three phenotypic groups tend to have somewhat different distribution areas and environmental preferences, which may overlap partially, and the three groups are be found in the northern part of the Peruvian Current ecosystem, within Peruvian national waters, although not necessarily at the same time and space. Monthly biological and fisheries information on *Dosidicus gigas* caught during commercial and scientific research fishing operations in Peruvian waters is analyzed, together with coastal sea temperature data since 1989. Changes in predominance of these three phenotypic groups in Peruvian waters are examined while trying to establish if the sea surface temperature could be used as indicator of the most likely environmental driver of the observed changes in the predominance of the population groups of *Dosidicus gigas* in Peruvian waters, and its possible relationship with regime changes observed for other species. The information available indicates that at least one decadal or regime change has occurred in the predominance of the phenotypic groups of *Dosidicus gigas* in Peruvian waters in the last 30 years, and that possibly another one may be in the making in recent years. The phenotypic groups that mature at small and medium sizes predominated in Peruvian waters during the decade of 1989-1999, identified as a warmer period. The phenotypic group that matures at large sizes predominated during more than a decade, between 2000 and 2016, identified as a colder period. And, since 2017 there are indicators of a possible shift into another regime, probably of shorter duration, with the predominance of the phenotypic groups that mature at small and medium sizes in coincidence with what is being identified as another warmer period. It is also noted that, in addition to the changes in the predominant body sizes, these decadal changes are having an impact on the catch rates and abundance indexes of *Dosidicus gigas*. With higher biomass abundance indexes and total catches when the phenotypic group maturing at large sizes predominates, and lower biomass abundance indexes and catches when the groups maturing at small and medium size are the ones to predominate. It is expected that this information will be of use in adjusting fisheries management strategies to make the best use of this important and fluctuating fishery resource, guaranteeing its sustainability.

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1. INTRODUCTION

The northern part of the Peruvian Current ecosystem, also known as the Humboldt Current ecosystem even though Alexander von Humboldt was personally opposed to having this Current named after him, and he had good reasons for it (Csirke *et al.* 2018), is one of the world's most productive marine ecosystems in terms of fish production (Chavez *et al.* 2008). However, this part of the Peru Current ecosystem is also impacted by a high climatic variability, at different spatial and temporal scales, which can affect all or only part of the marine ecosystem and Peruvian fishery resources within seasonal, interannual and interdecadal time-frames (Sharp and Csirke 1983; Csirke and Sharp 1984; Csirke 1988, 1995; Morón 2000; Chávez *et al.* 2003; Bertrand *et al*. 2004; Graco *et al.* 2007).

Seasonal and interannual climate variability usually causes fluctuations in the productivity of the ecosystems and, as a consequence, also in the abundance and productivity of the fishery resources. Which can be quite noticeable and disturbing, but of limited duration and, if proper fisheries management actions are taken, can yield short-term benefits if of positive sign; or, if of negative sign, can produce short-term loses, which tend to be easy to recover from. Whereas climatic variability at decadal scales causes changes, also known as regime change, of longer duration in ecosystem productivity and in the abundance and productivity of fishery resources. With some frequency, it has also been observed that regime changes comprising a longer-lasting increase in the abundance of one or more groups of species or population groups, may follow or are followed by changes in the opposite direction of other groups, as has been shown for various groups of neritic fish resources off Peru and elsewhere by, among others, Jordan *et al.* (1978), Kawasaki (1983), Csirke and Sharp (1984), Csirke (1984, 1988, 1995), Csirke *et al.* 1996; Lluch-Belda *et al.* (1989), Schwartzlose *et al.* (1999), Bertrand *et al.* (2011), Espino (2013), Flores *et al.* (2013).

As highlighted in Csirke *et al.* (2009) *"The effects of large-scale, environmentally driven changes on the distribution and abundance of fish populations have been a major source of concern for fishery scientists and managers for decades, particularly those dealing with the assessment and management of small pelagic fisheries"*. It is however clear that this concern and interest in detecting and having an early diagnosis on whether a regime change is in fact taking place, and in having enough information to explain it and to adapt fishery management measures accordingly, is applicable to any fishery resource exposed to changes at decadal scales or regime changes lasting one or more decades. It is also clear that environmentally-induced fluctuations and longer-term changes can hardly be regulated and, therefore, the alternative is to adapt to these fluctuations (and long-term changes) and try to take as much benefits as possible from periods of high abundance or, contrariwise, reduce possible losses during periods of low abundance, …all will longer-term interests in mind.

It is therefore of crucial importance for fisheries managers to ascertain whether an observed large and unexpected change in the distribution, composition and abundance of one or more fishery resources being exploited under their watch is or will be of short duration, or if it is indicative of a regime change, which could last one or more decades. Since, as explained in Csirke (1984), the perception of the type of fluctuation pattern being observed and its most likely duration (*i.e.,* …it is a short-term fluctuation or a longer-term regime change?) can strongly influence management strategies and decision-making, and can even alter management objectives.

In this respect, it has been noted that if a large and unexpected positive change in abundance and catch rates is perceived as a short-lived pulse, the normal reaction will be to try to take advantage of that greater temporary abundance, but without incurring in major long-term investments or commitments; or, if the pulse were negative, there will be a similar attitude of not making major long-term changes, and try to weather out the temporary low period with the available means. On the other hand, if the change in abundance and catch rates are perceived as the initial phase of a longer-lasting regime change, this will most likely trigger an increased interest and better disposition to expand and incur in major long-term investments, contracts and other commitments if the changes were of a positive sign; or, if the changes were of negative sign, the most likely response will be to reduce expectations, postponing planned investments and reducing costs and installed capacity.

However, if the diagnosis about the nature and duration of the changes were mistaken, and the fisheries management erroneously reacts to what in reality is the initial phase of a long-term regime change as if it were just a temporary pulse, there would be a delay in adjusting to the new situation and, until this happens, some potential benefits would be lost if the changes were of a positive sign; while incurring in higher costs and some risk of overexploitation if the changes were of a negative sign.

On the contrary, if a temporary positive pulse is mistakenly perceived as if it were part a longer-lasting regime change, it may erroneously trigger greater investments and other long-term commitments which, after a short initial period of increased benefits, would be followed by longer term losses, social and economic upheavals and other consequences of overinvestment, which may even include overfishing of the resource base if proper fisheries management measures and constrains are not timely introduced. While if the temporary pulse were of negative sign, any premature steps to adjust to a false long-lasting situation of scarcity could lead to unnecessary reductions in existing fishing, storage and processing capacity, which would lead to lost benefits in the short term, developing into a constrained situation that shouldn't be too difficult to revert without compromising long-term benefits once the mistaken perception is recognized.

The mechanisms that trigger and govern these decadal regime changes in the distribution and abundance of fish stocks are still poorly understood, although there is strong evidence of the important role played by observed environmental changes, primarily identified through changes in temperature, salinity, food availability, availability of dissolved oxygen, among others, as already demonstrated in the case of pelagic species such as anchoveta (*Engraulis ringens*), sardine (*Sardinops sagax*), Jack mackerel (*Trachurus murphyi*) and some other species in the northern system of the Peruvian Current (Chavez *et al*. 2003, 2008, 2009; Graco *et al.* 2007; Bertrand *et al.* 2008, 2011; Dioses 2013; Espino 2013; Flores *et al.* 2013; Gerlotto and Dioses 2013).

Another species of great importance in the northern part of the Peruvian Current ecosystem is the jumbo flying squid *Dosidicus gigas*, which is the cephalopod of greatest ecological and economic importance for Perú (and others), given its role as prey and predator and for its important contribution to food production, foreign exchange earnings and employment.

The high variability in the catch per unit of effort (CPUE) and other abundance indices was something noticeable soon after the commercial scale fishery for jumbo flying squid in Peruvian waters started in 1989 and, as time passed-by, it was clear that this high variability was in response to the seasonal, interannual and interdecadal environmental changing

conditions that impact the Peruvian marine ecosystem. Moreover, it was also noted that some of the interannual and longer-term changes in jumbo flying squid distribution and abundance were closely associated with changes in the predominance of the three phenotypic groups identifiable by the size at which they reach sexual maturity described for Peruvian waters (Nigmatullin *et al.* 2001; Arguelles and Tafur 2010; Csirke *et al.* 2015, 2018). This is similar to what has been observed in some other squid species, in which changes in growth and size at maturity have been found to be related to changes in sea temperature (Hatfield 2000; Jackson and Moltschaniwskyi 2002; Forsythe 2004).

In this regard, Arkhipkin *et al.* (2015) have shown indications of a weak but significant negative relationship between the sea surface temperature during the early life-history stages of *Dosidicus gigas* on the duration of its life cycle. Which would be shorter (living up to a year) when exposed to higher temperatures, and longer (living a year or more, and up to two years) with lower temperatures. However, the same authors recognize that more and longer time series of observations are required before firmer causal mechanisms relating environmental variables with observed changes in the biology of a species could be inferred, even more so considering the broad food spectrum of the jumbo flying squid and, in particular, that its habitat is characterized by its demonstrated broad tolerance to a wide range of water temperatures, salinities and dissolved oxygen concentrations, and that can be found over a very large vertical and horizontal spatial range.

The Peruvian Institute of Marine Research (IMARPE, Instituto del Mar del Peru) has a well-established monitoring system of the Peruvian jumbo flying squid stocks and fisheries (Yamashiro *et al.* 2018). And through this observation system it has been noted that over the last 3-4 years there has been an increased presence of smaller squids in the size frequency distributions of the commercial landings, and that there is a noticeable decrease in the catch rates, the catch per unit of effort (CPUE) and other abundance indicators.

In other types of fisheries, this would be interpreted as a sign of possible overfishing, but in the case of jumbo flying squid, mid-to-long-term changes in distribution and abundance have been associated with changes in the predominance of the three phenotypic groups that have been described for the Peruvian waters and are identifiable by the size at which they reach sexual maturity. And, with this work we will try to establish if there is in fact a change in the predominance of the above-mentioned phenotypic groups in recent years and, if possible, throw some light into whether we may be facing a regime change, while possibly exploring further into the possible relationship between the sea temperature and the observed changes observed in the population structure of *Dosidicus gigas* in Peruvian waters.

2. MATERIAL AND METHODS

For this study we analyze catch data and mantle length-frequency data in catch totals and of mature females only, of jumbo flying squid *Dosidicus gigas* collected as part of IMARPE's regular monitoring and research programmes, provided through regular observation and sampling of catches taken by commercial as well as by scientific research vessels in Peruvian waters. We also analyze sea surface temperature data from IMARPE coastal laboratories and research stations along the Peruvian coast.

The study area covers the entire distribution area of jumbo flying squid in Peruvian waters. The squid mantle length-frequency includes monthly data that extends over a period of 30 years, from 1989, when the Peruvian fishery specifically targeting on *Dosidicus gigas* started,

to mid-2019. While the sea surface temperature data includes monthly data from January 1989 to December 2018.

2.1. Oceanographic data

The Peruvian Oscillation Index (POI) proposed by Purca (2005) was taken as the likely best representation of the integrated variability of the sea surface temperature (SST) along the Peruvian coast (Purca 2005; Purca *et al.* 2005, 2010; Quispe and Tam 2010). SST data from 9 selected IMARPE coastal stations distributed along the Peruvian coast, between 5°S and 17°S, is used for the POI estimation. Daily SST data from these 9 coastal stations from January 1950 to December 2018 was processed and analyzed for this paper.

After calculating the mean monthly SST for each coastal station from the daily SST records, the monthly anomaly of the SST (SSTA) was calculated for each station, by calculating the deviation of the observed monthly SST mean from a long-term monthly standard SST, where the long-term monthly standard SST is the monthly average SST of 68 years, between 1950 and 2017. Nine SSTA time series, one for each coastal station was therefore obtained.

The first principal component of the 9 time-series was then calculated once a monthly SSTA series for each of the 9 stations was available, and the first principal component was retained, as it explains most of the SSTA variability, and used for this paper as the POI.

2.2. Biological data

The mantle length (ML) of *D. gigas* caught during the commercial jigging fishery by larger industrial fishing vessels and by smaller artisanal vessels operating in Peruvian waters was recorded both on board (mostly in the case of the industrial fleet) and on the landing sites (mostly in the case of the artisanal fleet), and samples were taken for further biological and biometric examination, including sex and stage of gonadal maturity following the sampling protocol described by Tafur *et al*. (2016, 2019). The same protocol was followed on board scientific research vessels. Monthly time series of mantle length-frequency distributions of *D. gigas* caught in Peruvian waters from 1989 throughout May 2019 were therefore obtained.

Monthly and annual time series of mantle length-frequency distributions of mature females of *Dosidicus gigas* were then obtained by estimating an average of females in mature and spawning stages (stages III+IV) by size interval, also following the protocol for biological sampling described by Tafur *et al*. (2016, 2019).

3. RESULTS

3.1. Total catch length-frequency distributions

The observed mantle length-frequency distributions in the total catch of *D. gigas* shows that in Peruvian waters there have been significant changes over time, both in the predominant modal sizes as well as in the amplitude of the observed size-frequency ranges (Figure 1). Where it is possible to identify up to three time-periods or "regimes" by the observed length-frequency distributions in the catch totals. The first from 1989 to 1999, the second from 2000 to 2016, and a third one from 2017 to 2019.

During the first period or decadal regime (1989-1999), the catches were made mainly by the industrial fleet, and the body sizes or mantle length (ML) observed were most frequently between 20 and 50 cm of ML, and generally didn't exceed 70 cm of maximum ML size. Except in 1992, when larger ML sizes were recorded.
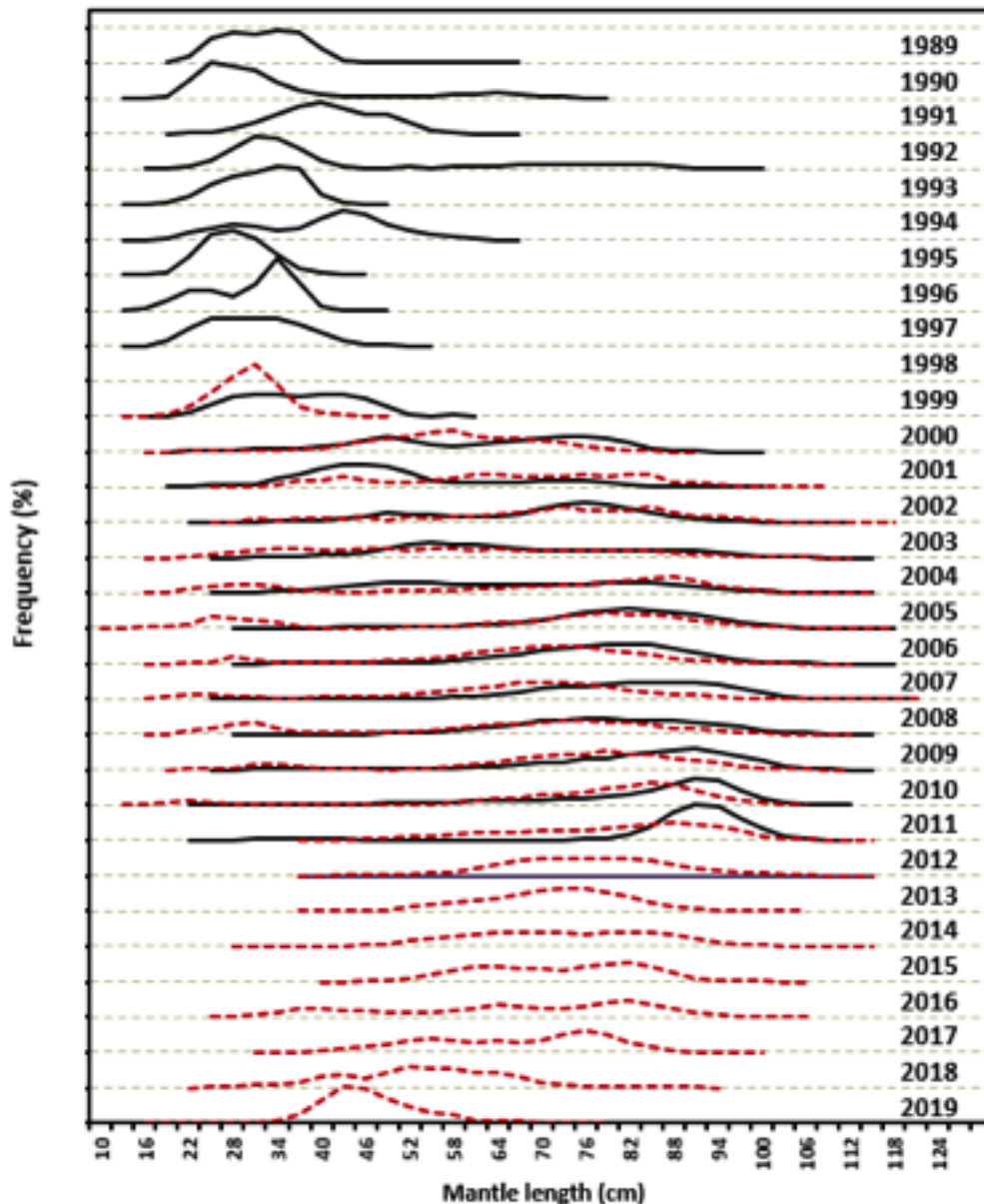
Figure 1.- Length-frequency distribution of *Dosidicus gigas* in the catches made by the artisanal jigger fleet (broken red lines) and the industrial jigger fleet (continuous black lines) in Peruvian waters, in mantle length (ML) by year, years 1989-2019 (updated from Arguelles *et al*. 2017)

During the second period or decadal regime (2000-2016), the catches were made by both the artisanal and industrial fleet until 2011, and only by the artisanal fleet from 2012 onwards. In this period the ML sizes presented a wider range, between 10 and 118 cm of ML, and in some years, one may be able to identify up to three modal groups, but with a predominance of squids larger than 50 cm of ML.

During the third period (2017-2019), the catches were all made by the artisanal fleet and, especially as of 2018, it is observed that small- and mid-sizes predominate in the catches. In 2018 the ML sizes varied between 22 and 94 cm of ML, with a predominance size groups between 50 and 65 cm of LM. While in 2019 the observed sizes were between 29 and 67 cm of LM, with modal size in the 43 cm of LM.

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3.2. Length-frequency distribution of mature females

The observed length-frequency distribution of mature females of *D. gigas* in Peruvian waters between 1989 and 2019 is shown in Figure 2. Mature females are used because adult males usually remain active, with high percentages of mature or evacuating specimens throughout the year. While females also tend to remain active throughout the year, but with much lower overall percentages of mature or spawning specimens, in general, and clearer and better-defined reproductive cycles, with the higher percentages of mature and evacuating females concentrated in a few months, usually in the spring (October-December). And, furthermore, there is a need to separate males and females in order to identify their phenotypic groupings by their size at maturity because females grow larger and the ranges of mantle length at adult stage defining each phenotypic group of males and females don't coincide.
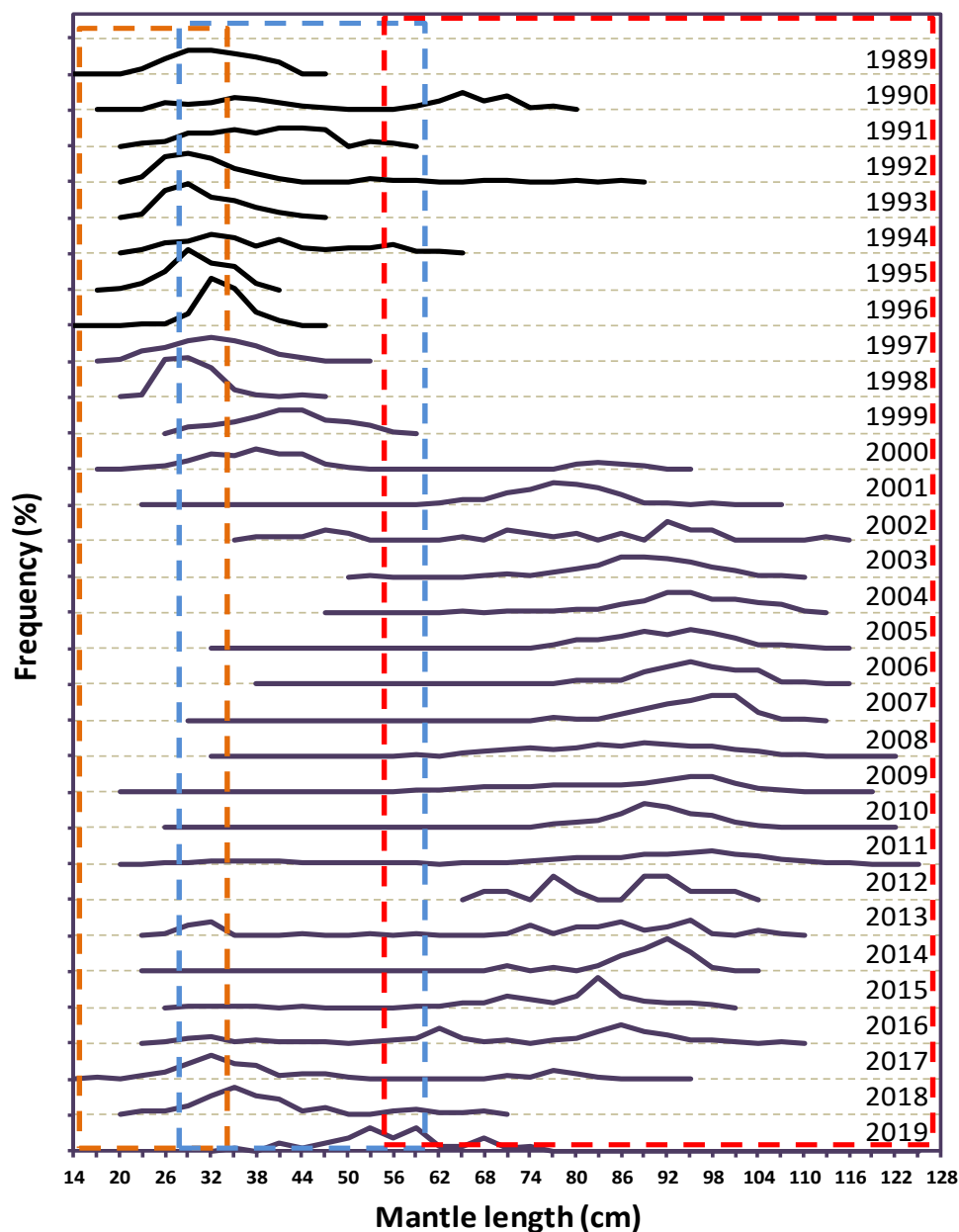

Figure 2.- Mantle length-frequency distribution of mature females of Dosidicus gigas caught in Peruvian waters, in percentage (%), years 1989 to 2019. The shaded areas indicate the size ranges of the three size-at- maturity groups proposed by Nigmatullin et al. (2001) (updated from Csirke et al. 2018)

Therefore, the preference to use the percentages of mature females in the size-frequency distributions when trying to identify the phenotypic groups of *D. gigas* described by Nigmatullin *et al.* (2011) and reported further for Peruvian waters by Arguelles and Tafur (2010) and Csirke *et al.* (2015, 2018), and to then show the interannual variations in their presence and predominance in Peruvian waters over time.

It is noted that there is a close relationship between the observed interannual variations of length-frequency distributions of mature females in Figure 2, and the length-frequency distributions of all males and females in Figure 1. But, nevertheless, the presence and changes in predominance of the modal size-groups representing each of the three phenotypic groups are more easily identified in Figure 2, where the three periods or regimes indicated above, from 1989 to 1999, from 2000 to 2016, and from 2017 to 2019 appear with more clarity.

It is also noted that the predominant phenotypic group between 1989 and 1999 was the one characterized by maturing at mid-size, with some presence of those maturing at small-size over the whole period and some presence of the group maturing at large-size in 1990 and 1992. Subsequently, from 2000 to 2016, the large-size maturing group was the predominant one, with only small proportions of those maturing at mid-sizes and almost negligible presence of the small-size maturing group. Then, in 2017 there is a shift towards the predominance of the mid-size maturing group the becomes more evident in 2018 and 2019. Suggesting a possible shift into a regime similar to the one observed between 1989 and 1999.

3.3. Changes in catch volumes and observed mean mantle size

When examining and trying to explain the fluctuations in annual catch volumes of *D. gigas,* a positive close relationship was found with the observed mean mantle size of squids caught the same year (Figure 3), where higher annual catches tend to occur when the larger size groups are present.
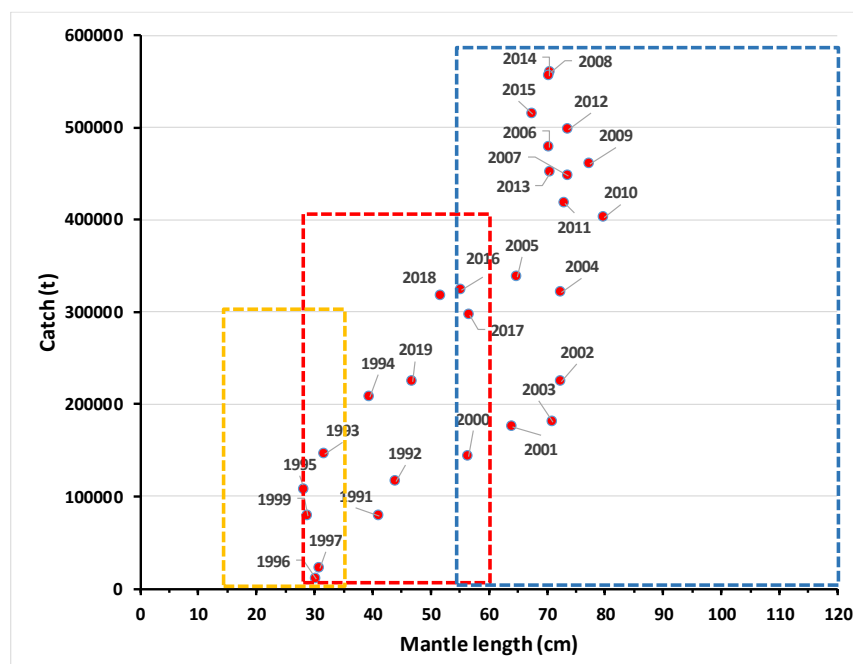

Figure 3.- Annual catch volumes and mean mantle size of *Dosidicus gigas* caught in Peruvian waters between 1991 and 2019 (until May 2019 only). Shaded areas bordered by orange, red and blue broken lines delimit the size ranges of phenotypic groups or possible population units of mature females (according to phenotypic groups described by Nigmatullin *et al.* 2011)

The lowest catches (less than 50 000 t) were recorded in 1996 and 1997, when the observed mean size was 30 cm ML and two climatic anomalies such as the moderate 1995-1996 La Niña and the very strong 1997-1998 El Niño occurred. Annual catch levels between 50 000 and 300 000 t were recorded in the period 1991-1999, when the observed *D. gigas* mean sizes where between 30 and 50 cm ML; and in 2000-2003, when observed mean sizes were between 50 and 75 cm ML. While annual catch volumes over 300 000 t and up to 560 000 t were observed in 2004-2015, in years when observed *D. gigas* mean sizes varied between 60 and 85 cm ML. In 2016, and particularly in 2017-2018 annual catch volumes were barely over 300 000 t, similarly to 2004-2005, but with smaller mean sizes, between 50-55 cm ML. Smaller mean size (of 48 cm ML) are being observed in 2019 (until May 2019) but the annual totals are still to be seen.

3.4. Interannual variation of the Peruvian Oscillation Index

The Peruvian Oscillation Index (POI) proposed by Purca (2015) has been adopted as the composite index of choice to reflect the temporary variation of the SST along the whole Peruvian coast, since it integrates the variability of the SST of nine selected coastal stations distributed along the Peruvian coast, between 5° and 17°S.

Through this POI (or IOP, for "Indice de Oscilación Peruano"), it becomes clear that between 1989 and 2019 there have been four multiannual and possibly decadal periods or "regimes". Two dominated by positive anomalies of the SST and two periods dominated by negative anomalies (Figure 4). There are two clear periods with negative POI values, a short and weak one during 1989-1990 and a stronger and longer-lasting one, during 2000-2012; and two periods with positive POI values, one during 1992-1999 and the other between 2014 and 2018, so far.
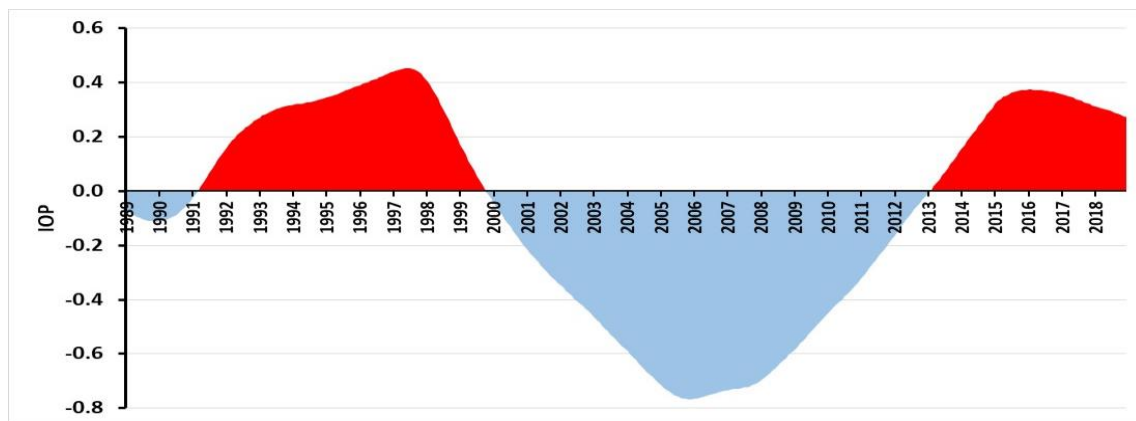

Figure 4.- . Interannual variation of the Peruvian Oscillation Index (POI) for the period January 1989 – December 2018, representing the integrated sea surface water (SST) variations along the Peruvian coast, between 5° and 17°S (updated from Purca 2005).

During the first "colder" period, of short duration, the negative POI values did not exceed -0.2; while during the second "colder" period, that lasted more than a decade, from 2000 to 2012, the maximum negative POI values were close to -0.7 between 2005 and 2007. On the other hand, the first "warmer" period with positive POI values, during 1992-1999, presented two maximum values, at +0.3 in 1993 and almost +0.5 in 1997; while during the second "warmer" period, starting in 2013 and still noticeable towards the end of 2018, and apparently the beginning of 2019, there is so far a single maximum, of almost +0.4 in 2015-2016.

4. DISCUSSION

The various responses of fish populations to environmental changes in marine ecosystems have been under close scrutiny for many years. Fish population responses to environmental changes are usually noted through observable changes in the distribution, abundance and species or intra-specific groups composition within a given area or marine ecosystem. However, in most cases, the specific causal mechanisms of environmentally driven changes in these fish populations are still not well known, although most of the ongoing research on the matter point out to processes that determine reproduction and recruitment success, survival throughout the successive life-history stages, somatic growth and development and/or stock displacements in search of more favorable habitats (Barber *et al.* 1982; Sharp and Csirke 1983; Csirke and Sharp 1984; Barry *et al.* 1995; Csirke 1995; Chavez *et al.* 2003; Alheit and Ñiquen 2004; Green and Fisher 2004; Csirke *et al.* 2009; Ayon and Correa 2013; Ayon 2018).

The northern part of the Peruvian Current ecosystem, off Peru, is one of the most productive of the world (Chavez *et al.* 2008). The main neritic pelagic fish populations being exploited in this area are the anchoveta (*E. ringens*), sardine (*S. sagax*), Jack mackerel (*T. murphyi*) and chub mackerel (*Scomber japonicus*); and their wide variability at interannual and decadal scales, in relation to interannual climatic phenomenon such as El Niño and La Niña, and in relation to longer-term interdecadal climatic phenomenon such as "El Viejo" and "La Vieja" (Chavez *et al.* 2008) have been well documented (Csirke 1995; Csirke *et al.* 1996, Chávez et al. 2003, Alheit and Ñiquen 2004; Bertrand *et al.* 2004; Ayón *et al.* 2011; Ayón and Correa 2013; Espino 2013; Flores 2013). Similar changes, with some of biological characteristics, such as their mean size, being temporarily modified in relation to decadal changes in sea temperature have also been described for demersal species such as for the Peruvian hake (*Merluccius gayi*) in the same area (Wosnitza-Mendo *et al.* 2004; Guevara-Carrasco 2004; Guevara-Carrasco and Lleonart 2008).

Temperature, and in particular sea surface temperature (SST), is the environmental variable most frequently used to relate and try to explain environmentally driven changes in abundance and other biological variables of exploited fish populations. And that's because temperature is most frequently and more easily recorded marine environmental parameter, and relatively long historic records for key marine sites are usually kept by marine research and other maritime institutions. However, there are other biological variables that could be good indicators of possible regime changes, such as the changes in diet composition, such as reported for Jack mackerel by Alegre *et al.* (2013), or the changes in distribution and abundance larvae in relation to some environmental parameters, such as reported for Jack mackerel by Ayon *et al.* (2013).

Larval and early juvenile stages are the most critical phases in the development and subsequent abundance of fish populations. And several studies have been carried out trying to determine the effects of sea temperature on the development, growth and mobility of fish and squid larvae (Green and Fisher 2004; Forsythe 1993). Particularly considering that temperature has demonstrated effects on live organisms' metabolism and physiological processes in general, having an effect on somatic growth, particularly important in early life-history stages, as shown for salmon by Nicieza and Metcalfe (1997). Also, Green and Fisher (2004) found that lower temperatures lead to slower larval development, longer duration at

larval stage, slower growth rates and slower swimming speeds in the larval stage of fish, which can easily translate into slower escapement speeds (from predators) and thus higher mortality rates.

Squid larvae are also affected by changes in sea temperature during their development, as proposed by Forsythe (1993), and changes in temperature affecting growth will also lead to increased mortality. Also, Ayon (2018) examined the occurrence of cephalopod paralarvae in Peruvian waters between 1980 and 2014, and reported a much frequent occurrence of paralarvae from 2000 onwards.

Although Ayon didn't differentiate the cephalopod species, the greater abundance of *D. gigas* in comparison to other cephalopod species throughout the observed period would lead to the conclusion that most of the observed paralarvae were *D. gigas*. Once surviving the larval stages, the main component of the survival success of juveniles towards recruitment will be associated with the access to suitable food, and with finding themselves in areas with optimal or closer to optimal conditions for food retention.

For instance, Ichii *et al.* (2004) reported differences in body size of two cohorts of *Ommastrephes bartramii* in the North Pacific, and proposed that the autumn cohort grows to larger sizes because they happen to develop in a food-richer habitat, unlike the winter-spring cohort that happens to develop in a habitat that is not as food-rich.

Therefore, if we are prepared to accept that changes in environmental factors trigger differences in the development of the successive life-history stages of a given cohort or groups of cohorts; it can be supposed that, in the case of jumbo flying squid off Peru, the predominance of the phenotype maturing at larger sizes (and probably also maturing at an older age) observed between 2000 and 2011, and also the slightly smaller but still within the large-size at maturity phenotypic group observed in 2012-2016 (Figure 2), is closely related to the colder and food-richer conditions (colder conditions are indicative of stronger coastal upwelling, and increased food production) observed in Peruvian waters between 2000 and 2013, as indicated by the negative sign of the Peruvian Oscillation Index (Figure 4) during those years.

While, for the same time-series, the predominance of the small- and mid-size at maturity phenotypic groups observed between 1989 and 1999 would be related to warmer and not as food-rich conditions (fewer cold upwelled waters along the cost equals weaker coastal enrichment processes) represented by the positive sign of the Peruvian Oscillation Index in those years. Similarly, the predominance of the mid-size at maturity phenotypic group being observed between 2017 and 2019 occurs shortly after the sign of the Peruvian Oscillation Index flipped from being negative to being positive in 2013 (Figure 4).

Is this a new regime shift, going in the opposite direction of the one observed in 1999-2000? How long the new regime will last? The recent observed change in length-frequency distribution, towards the predominance of the mid-size at maturity phenotypic group, and the shift in the CPUE abundance index observed at about the same time, early in 2016 (Figure 5) would suggest that, in fact, a regime shift has occurred, although the duration of this new regime is still uncertain. The declining trend in the POI values from 2016 onwards suggest that the duration of this warmer less productive period for jumbo flying squid may not last much longer, but this suggestion has to be taken with great caution at least until we can develop better POI predictive capabilities.
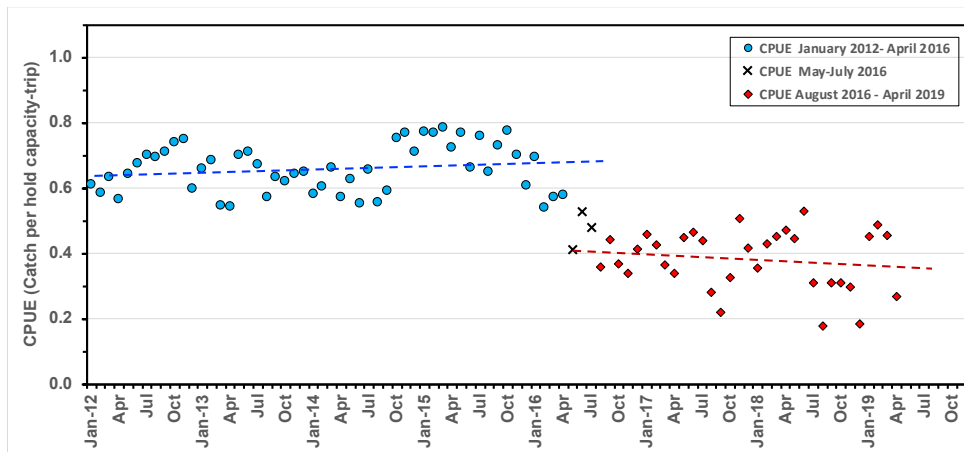
Figure 5.- Estimated monthly Catch by Unit of Effort (CPUE) in tons per m³ hold capacity-trip of the Peruvian artisanal fleet fishing jumbo flying squid (*Dosidicus gigas*) between January 2012 and April 2019, with indication of the observed trends of this CPUE abundance index in two distinct periods, between January 2012 and April 2016 and between August 2016 and April 2019 (adapted from IMARPE-PRODUCE 2019)

It is also noted that in order to reach the large sizes reached by squids in the large-size at maturity phenotypic group, and for the population to attain such large biomasses as observed between 2000 and 2016, jumbo flying squid in Peruvian waters must have had access to larger amounts and higher concentrations of food-prey in the water column during those years. Therefore, further examination of the food-prey and other variables such as the depth of the minimum oxygen layer and its temporal variations at interannual and decadal could throw some extra light into the role of, for instance, prey abundance in the water column in determine possible regime changes affecting in jumbo flying squid distribution, abundance and phenotype groups composition.

It is stressed that in order to better understand the observed spatial and temporal changes in the abundance and population structure of *D. gigas* in Peruvian waters, we need more information on the characteristics of the habitat of each of the phenotypic groups already described, and on the physical (salinity, thermocline) and chemical parameters (oxygen, minimum oxygen zone) that characterize each phenotypic predominance period or regimes observed so far. We need to know more on the parameters that characterize the most suitable habitat of each phenotypic group, keeping in mind that the parameters or characteristics of what would be the optimal habitat for each life-history stage may be different, both between and within each phenotypic group.

It is also clear that jumbo flying squid observed in Peruvian waters carries a genetic variability that is flexible enough to allow it to thrive under various environmental regimes by adopting diverse and distinguishable phenotypic expressions of a common, highly flexible genetic pool.

The great question here is whether this high genetic flexibility is built into the genes of each and every single individual, which are then expressed differently, through the predominance of different phenotypic groups, depending on when and where (under which environmental conditions) those individuals carrying the common genes happened to find themselves during their early life-history stages.

Or, whether this high genetic flexibility is achieved by the spreading of slightly differentiated genes into different structured populations, or sub-population units, with slightly different phenotypes (up to three according to Nigmatullin *et al.* 2011), each one with slightly different habitat requirements, which still allows them to coexist at certain times and space, but with

only one taking over or thriving more than the others according to the prevailing environmental conditions in a particular space and time-frame. Thus leading to the changes in the predominance of phenotypic groups described above. It is expected that the type of genome analyses proposed by Sotil and Cueva (2019) will contribute to throw some additional light into this important matter.

On this, it is worth noting that the observed length-frequency distributions shown in Figure 2 above, are characterized by the presence of discrete phenotypic groupings, which would be more consistent with a type of on/off response of different genotypic groupings to the observed decadal changes in environmental conditions in Peruvian waters; while the case of individual's genetic flexibility responding to changes in environmental conditions would most likely be reflected through more of a continuum change in the observed size at maturity. Nevertheless, only further in-depth analyses of the jumbo flying squid genomics and habitat preferences in Peruvian and adjacent high sea waters would provide enough elements to better assess the validity of the two hypotheses mentioned above.

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