UNIVERSIDAD AUTÓNOMA DE BAJA CALIFORNIA

FACULTAD DE CIENCIAS MARINAS
INSTITUTO DE INVESTIGACIONES OCEANOLÓGICAS

EFECTOS DE LA VARIABILIDAD OCEANOGRÁFICA EN LA COMUNIDAD DE PECES EN UN PERIODO DE 30 AÑOS EN LA LAGUNA COSTERA LOS PEÑASQUITOS

TESIS

QUE PARA CUBRIR PARCIALMENTE LOS REQUISITOS NECESARIOS PARA OBTENER EL GRADO DE

MAESTRO EN CIENCIAS EN OCEANOGRAFÍA COSTERA

PRESENTA

ABRAHAM GONZÁLEZ MENA

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RESUMEN

Los estuarios son ambientes costeros complejos en la interfaz tierra-océano-atmósfera amenazados por la variabilidad ambiental extrema, los procesos oceanográficos y el constante estrés antropogénico. Por consiguiente, los organismos que viven en estos ecosistemas pueden considerarse especies centinela. Específicamente, estudiar los ensambles de las comunidades de peces en los sistemas estuarinos es ideal para mejorar nuestra comprensión de los efectos del cambio climático. En este estudio, se analizaron los cambios en la comunidad de peces de la laguna costera Los Peñasquitos en función de la variabilidad oceanográfica de los últimos 30 años. Los resultados mostraron que las diferentes especies de peces tienen diferentes respuestas a las variaciones de los procesos oceanográficos y a las anomalías de los parámetros físico-químicos del agua. Los análisis estadísticos multivariantes sugieren que las principales causas de los cambios en la comunidad de peces han sido las condiciones de surgencia costera fuertes, las anomalías cálidas en la temperatura del agua, los eventos El Niño fuertes y los cierres de la boca de la laguna costera. Las surgencias costeras fuertes tuvieron un efecto negativo en las abundancias del lenguado de California, *Paralichthys californicus*, y el chupalodo grande, *Gillicthys mirabilis*. Las condiciones de El Niño y las anomalías cálidas de la temperatura del agua son favorables para las especies invasoras como el pez mosquito, *Gambusia affinis*, pero negativas para la especie dominante de la laguna, el pejerrey pescadillo, *Atherinops affinis*. Además, los resultados del análisis de las tendencias estadísticas en las series de tiempo sugieren una tendencia a la baja en las densidades de los peces chupalodo grande, *Gillicthys mirabilis*, y cabezón, *Leptocottus armatus*.

Estudios a largo plazo como éste son importantes para documentar las condiciones oceanográficas que dan forma a las comunidades de peces en los estuarios en diferentes escalas de tiempo. Los resultados proporcionan información valiosa para mejorar nuestra comprensión de la gestión de los estuarios y sus especies de peces en el contexto de los desafíos del cambio climático.

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DEDICATORIA

A Dios por su amor infinito, Creador del cielo, de la tierra y del océano.

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ABSTRACT

Estuaries are complex coastal environments at the land-ocean-atmosphere interface threaten by extreme variability, oceanographic processes, and constant anthropogenic stress. Consequently, organisms living in these ecosystems can be considered sentinels species. Specifically, fish community assemblages in estuarine systems are ideal to study to enhance our understanding of climate change effects. In this study, we analyzed changes in the fish community at Los Peñasquitos Lagoon as a function of oceanographic variability over the last 30 years. Our results showed that the different species of fish have different responses to oceanographic processes variations, and anomalies in the physical-chemical water parameters. Multivariate statistical analyses suggest that the principal causes of community changes have been strong coastal upwelling conditions, warm water temperature anomalies, strong ENSO events, and the lagoon's inlet closures. Strong coastal upwelling had a negative effect on the abundances of California halibut, *Paralichthys californicus*, and longjaw mudsucker, *Gillicthys mirabilis*. ENSO conditions and warm water temperature anomalies are favorable for the invasive species like mosquitofish, *Gambusia affinis,* but negative for the lagoon's dominant species, topsmelt, *Atherinops affinis.* Furthermore, time-series statistical trend analysis results suggest a downward trend in fish densities for the longjaw mudsucker, *Gillicthys mirabilis*, and staghorn sculpin, *Leptocottus armatus*.

Long-term studies like this are important to document how oceanographic drivers shape fish communities in estuaries at different time scales. Our results provide valuable information to enhance our understanding of estuaries management under climate change challenges.

Keywords: Estuary, coastal lagoon, Los Peñasquitos Lagoon, water physical and chemical parameters anomalies, oceanographic variability, oceanographic index, coastal upwelling, California Current Ecosystems, inlet closure, El Niño Southern Oscillation, fish assemblages, fish density

1 INTRODUCTION

Climate change effects on marine ecosystems are occurring globally threatening marine organisms at all latitudes and depths. It is expected an increase in frequency and intensity of the ocean warming, marine heatwaves, oxygen decrease leading to hypoxia events, in addition, ocean acidification and sea-level rise are threatening marine ecosystems, with direct consequences for ecosystem services, the ocean economy and human welfare (Hoegh-Guldberg and Bruno, 2010; Gao et al., 2019; Gaines et al., 2019). Climate change will influence estuaries temperatures with changes in ocean temperature, wind stress, and coastal upwelling (Brown et al., 2016). Other effects of climate change in estuaries are likely to be changes in precipitation patterns that alter freshwater input to the system, loss of marsh habitat, intrusion of marine waters and associated organisms, changes in circulation patterns that affect retention of resident or indigenous species, and increased hypoxia and storm surges (Kennedy, 1990).

Estuaries are marine ecosystems that provide important ecosystem services such as, carbon sequestration, nutrient cycling, water purification, coastal protection, and erosion control. For fisheries and fish ecology, estuaries worldwide are recognized as important habitats used as migration routes, refuge, nursery, and feeding areas (Elliot et al., 2007). For example, in the United States, estuaries are very important in economic terms because many of the shellfish and fish species most harvested are dependent on estuaries, some other species use estuaries at some stage of their life cycles, and serve as breeding and nursery habitats (Shultz and Ludwig, 2005; Barbier et al., 2011).

Estuarine systems host complex communities living at the land-sea interface and subject to a great deal of physical and chemical water parameters variations (James et al., 2008;

Feyrer et al., 2015). For example, salinity in a shallow well-mixed estuary can vary from low values typical of a river to salinity values observed in the open ocean. In contrast, salinity in the ocean generally stays the same on surface waters with minimum changes in salinity concentrations. Water temperature in estuaries is mainly influenced by the ocean water temperature in the tidal currents and the temperature of the freshwater that enters into the estuarine system, therefore, estuaries may present thermal gradients between the mouth and the head (Wooldridge and Deyzel, 2012). The temperature in shallow estuaries has great ranges of variations on a yearly and daily basis, seasonally the temperature reaches minimum values in winter and maximum values in summer, and temperature on a daily scale reaches lower values during the night. These variations in the physical-chemical parameters in the estuary make fish species assemblages an ideal study system to explore climate variability and its effects on complex coastal communities (Schwing et al., 1996; Sydeman et al., 2014; Feyrer et al., 2015).

Estuaries in the Northeast Pacific are temperate coastal ecosystems influenced by complex oceanographic processes at different and variant spatial and temporal scales (García-Reyes and Sydeman, 2017). For example, coastal upwelling in the California Current System has a seasonal influence with daily variations according to wind strength and direction, it is strongest during spring-summer seasons, generally between April-June when northwesterly winds are the strongest every year, and weaker or even null upwelling in fall-winter due to wind patterns variations (LaDochy et al., 2007; García-Reyes and Largier, 2012). At a larger inter-annual timescale, ENSO events with warm water El Niño phase occurring every 2 to 7 years alternating with the cold water phase La Niña, each event usually lasting between 6 to 18 months (Santoso et al., 2017).

Furthermore, due to climate change is expected an increase in the frequency and strength of El Niño, such as the 2015-2016 ENSO event (Santoso et al., 2017; Young et al., 2018). The largest time-spatial oceanographic influence on California coastal ecosystems is the Pacific Decadal Oscillation (PDO) with cyclical decadal variations in sea surface temperatures in the North Pacific Ocean with warm and cold phases that last decades (Easterbrook, 2016).

In addition to this variability, an extreme marine heatwave was recently documented in this region called the "Blob" followed by the 2015-2016 ENSO event created anomalously warm SST in the Northeastern Pacific (Bond et al., 2015; Di Lorenzo and Mantua, 2016). This extreme event has impacted coastal marine communities in this region changing the distribution and abundance of a great number of species (e.g. Cavole et al., 2016; Arafeh et al., 2019; Lonhart et al., 2019). Interestingly, there are models that predict marine heatwaves are expected to increase in both frequency and intensity and their impacts are still not well understood (Oliver et al., 2019).

One way to inform community-wide responses to climate variability is to identify patterns of change by integrating and analyzing long-term datasets (Hughes et al., 2017). Unfortunately, monitoring programs are very scarce, especially the ones that collect data for more than a decade of multi-species complexes. However, some long term monitoring programs exist such as the National Science Foundation Long Term Ecological Monitoring program or the National Oceanographic and Atmospheric Administration National Estuarine Research Reserve System (NERRs).

Los Peñasquitos Lagoon in Southern California is an estuarine system that has been monitored since 1986. The monitoring program was started by Dr. Zedler and the Pacific and Estuarine Research Laboratory (PERL) in 1986 and then the Tijuana River NERR inherited the monitoring program and monitors the: physical and chemical water parameters, vegetation, benthic invertebrates, and fish communities, and the lagoon’s mouth sedimentation and closures (Crooks et al., 2016). This long-term data from LPL can be used to register changing patterns in the physical-chemical parameters and its relationship to community changes in estuarine ecosystems. This will enhance our understanding and forecasting the estuary fish community responses to climate change.

Los Peñasquitos Lagoon (LPL) is an estuary with a barrier beach that experiences intermittent mouth closures and openings during the year. Tidal flow is the main factor that keeps the lagoon’s mouth open, especially when spring tides occur; nevertheless, the primary sources of sedimentation that leads to the lagoon closure are the sediment accumulated during neap tides and ebb tides. Followed by coastal processes such as wave run-up, littoral drift, cobbles and sand deposited by storm surge (Elwany, 2008; Jacobs et al. 2010). In addition, sediment loading from the watershed may increase the sand bar formation in the mouth area. During the rainy season, large floods open the lagoon’s mouth flushing sediments and nutrients out of the system. However, if these floods are not strong enough to break the barrier the lagoon remains closed and the upstream sediment and nutrients deposits in the lagoon’s channels and basins (Elwany, 2011). Consequently, after the inlet closure, the lagoon’s water quality diminishes decreasing salinity and lowering dissolved oxygen levels due to eutrophication resulting in hypoxic/anoxic conditions that lead to mass mortality events. However, to mitigate these effects and reestablish water quality conditions, since 1985 Los Peñasquitos Lagoon

Foundation has been dredging the inlet to restore connectivity with the ocean (Pratt, 2010). The inlet intermittent open-closure events not only have effects on the estuary's physical and chemical conditions, but it also has direct effects on fish assemblages (Gillanders et al., 2011; James et al., 2018). For example, closure events impede adult fish to migrate between the ocean and estuary, which reduces larval and juvenile recruitment (James et al., 2008). Moreover, when the lagoon is closed for a prolonged time, the extent and severity of hypoxic conditions reduce the quality and availability of fish habitat, hypoxic/anoxic deep waters make fish prone to surface predation and habitat loss for flatfish species in estuaries (Largier et al., 2019).

The aim of this study is to characterize the LPL fish community changes linked to oceanographic variability and anomalies in physical-chemical parameters in the last 30 years. Specifically, we are interested in 1) describing what is the structure of the fish community and how is its temporal variability; 2) How much the oceanographic indexes explain the fish community variability. And finally, 3) we assessed if there is an effect of the local water conditions on the fish community using water quality monitoring data from inside the lagoon.

2 METHODS

2.1 Study area

Los Peñasquitos Lagoon (LPL) is an intermittently closed and open lagoon, located in Southern California (32°56'3.46"N, 117°15'38.53"W) on a watershed area of approximately 24,281 Ha. Los Peñasquitos Lagoon is a small estuary of approximately

257Ha and is part of the Torrey Pines State Natural Reserve (Fig.1) and is one of the few remaining native salt marsh lagoons in California (Henning, 2012).

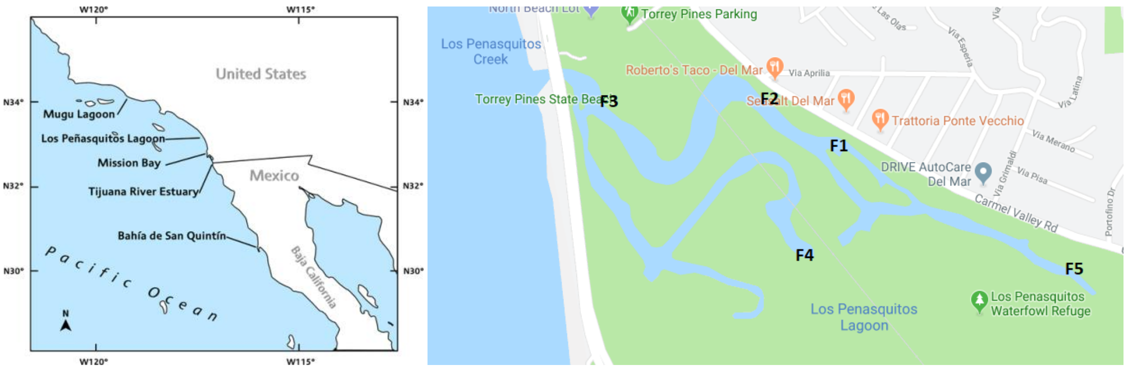


Figure 1. Los Peñasquitos Lagoon location and map showing fish sampling stations (F1-F5).

2.2 LPL Monitoring and data collection

All the monitoring information on fish surveys, days closures, and physical and chemical variables data used in this study were extracted from the annual reports (1986-2018) and electronic data repository of the Tijuana River National Estuarine Research Reserve.

PERL and TRNERR monitoring programs conducted have conducted fish surveys in five monitoring stations (F1-F5) from 1986 to date (Fig 1). Station F1 was sampled from 1986 to 2006, Stations F2 and F3 were sampled from 1986 to 2018, and stations F4 and F5 from 1996 to 2018.

Each station represents different habitats with different water salinities and sediment substrates, related to their distances to the mouth (Crooks et al., 2016). Stations F1 and F2 are located between the lagoon's inlet and the streams (Fig. 1), water salinity conditions vary in both stations and possess a substrate rich in organic matter and clay sediment. Station F3 is located close to the lagoon's mouth (Fig. 1), as a result, the station's conditions are similar to the marine environment with sediment composition mostly of sand. Stations F4 and F5 are located upstream (Fig. 1), hence these stations have lower salinities with clay substrates (Crooks et al., 2016). However, for the analyses we used the data combined from all stations to study the fish community of the whole lagoon.

2.3 Biological monitoring

Biological monitoring was conducted from 1986 to 2018. Seining was performed using a 6m wide purse seine with a 3-mm mesh and two blocking nets spaced approximately 5m apart (Crooks et al., 2016). The seine was swept three times. After the last swept, the blocking nets were swept towards shore, making a total of five passes. In each haul, fish were retrieved from the nets, placed in water buckets, identified to species, counted and released as soon as possible to reduce harming or killing them. We calculated the density of fishes using the swept area and the total fish counts per species. Fish densities time series were plotted in MATLAB R2014a.

2.4. Physical and chemical parameters

From 2004 to 2018 water quality parameters were recorded inside the lagoon at station W2 (Fig. 1) measuring physical and chemical parameters every 15 minutes by YSI ^{TR} multi-parameter sensors. The parameters recorded were: water temperature, salinity, dissolved oxygen, depth, conductivity, and pH. We plotted time series and calculated the annual anomalies for temperature, dissolved oxygen, and pH.

2.5. Oceanographic indices used for the study

We used ocean-climate indices to study the relationship between oceanographic variability and the LPL fish community. The indices we used in this study were: 1) Upwelling Index (UI) and 2) Upwelling Index Anomalies (UIA), both upwelling indices at 33°N 119°W from the National Oceanic and Atmospheric Administration's Pacific Fisheries Environmental laboratories (www.pfeg.noaa.gov/products/PFELData/upwell/monthly/upindex.mon) and (www.pfeg.noaa.gov/products/PFELData/upwell/monthly/upanoms.mon), 3) Oceanic Niño Index (ONI) from the National Oceanic and Atmospheric Administration's Ocean Climate Prediction Center (origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php), 4) Multivariate ENSO Index Version 2 (MEI.v2) from the National Oceanic and Atmospheric Administration's Earth System Research Laboratory Physical Sciences Division (www.esrl.noaa.gov/psd/enso/mei/), and 5) Multivariate Ocean Climate Indicator (MOCI) developed for California by The Farallon Institute. MOCI at 32-34.5°N (www.faralloninstitute.org/moci). For more information about MOCI refer to (Bjorkstedt et al.,2017; García-Reyes and Sydeman, 2017). MOCI data set starts in 1991, for this reason, it was included in the analysis period 2004-2018. All other indices were used in the analyses for the period 1986-2018.

2.6 Statistical analyses

We divided this study into two phases based on data availability. First, we used the oceanographic indices to test its effects on the fish community using the whole fish community data series from 1986-2018. Secondly, we used the water quality sensor data from 2004-2018 to look at the effect of the physical and chemical variables inside the lagoon and its effect on the fish community.

2.6.1 Analyses for the 1986-2018 period

Characterization of the fish community in composition, abundance trends, community structure, and diversity

Fish community abundance composition and time-series trends analysis

To characterize the fish community composition in the last 30 years, we first used total fish counts. Secondly, to analyze community composition based on life history and salinity tolerance we classified the fish species according to the ecological fish classification for Southern California and Northern Baja by Allen and collaborators (2016).

To find trends in the historical abundance variability of the fish community we used the nonparametric Mann–Kendall test to determine whether there was a monotonic trend on the time-series of fish species densities. This trend test was performed with XLSTAT 2019 and MATLAB R2014a. Mann-Kendall values were shown in the time-series only if there was a trend with a p-value ≤ 0.05.

Analysis of the fish community structure changes

To identify similarity over the years within the community structure and densities we used NMDS and Hierarchical cluster analysis for similarities percentages. Bray-Curtis similarity matrices were used to perform NMDS and Hierarchical Cluster Analysis.

The community diversity was analyzed with Shannon and Simpson diversity indexes (Appendix C). The Shannon diversity index to indicate mathematically the highest or lowest diverse year and Simpson diversity index to indicate the probability (%) to randomly pick two organisms from the same species in the sample. The four analyses were performed with the statistical software PRIMER v.5 (Clarke and Gorley, 2001).

Oceanographic variability effects on the fish community

For the statistical analyses to test the effect of oceanographic variability on the fish community from 1986 to 2018, we used the oceanographic indices as independent variables: Upwelling Index (UI), Upwelling Index Anomalies (UIA), Oceanic Niño Index (ONI), Multivariate ENSO Index (MEI); and factors: Days closed (DC), Interaction DC-UI, Interaction DC-UIA, Interaction DC-ONI, and Interaction DC-MEI.

Analysis of the oceanographic variability effects on the fish community

To find the best model that explained the effects of oceanographic variability on fish density (y), we analyzed the effects of oceanographic indices and factors on the fish community density based on the Akaike information criterion (AIC) with a Generalized Linear Model (GLM) with a Gamma distribution. The initial model analyzed:

$y^{l} = \beta_0 + \beta_1$ UI + β_2UIA + β_3 ONI + β_4 MEI + β_5 DC + β_6 Interaction DC-UI + β_7 Interaction DC-UIA + β_8 Interaction DC-ONI + β_9 Interaction DC-MEI.

This analysis was performed with STATISTICA 10.

Analysis of the oceanographic indices effects on the dissimilarities of the fish community and species

We used one way designed ANOSIM global and pairwise tests to determine which were the oceanographic variables that had effects in the dissimilarities on the fish community and SIMPER to determine species contribution to the dissimilarities. The factors used for SIMPER analyses were taken from the ANOSIM pairwise results with a statistical significance level of $p < 0.05$.

ANOSIM and SIMPER tests were performed for both study periods with the statistical software PRIMER v.5 (Clarke and Gorley, 2001). Fish densities data were log(1+y) transformed. Bray-Curtis similarity measure was used to produce the similarity matrices. The ANOSIM routine ran with a maximum of 1000 permutations.

2.6.2 ANALYSES FOR THE 2004-2018 PERIOD

Characterization of the fish community structure

Analysis of the fish community structure changes

To identify similarity over the years within the community structure and densities we used NMDS. Hierarchical cluster analysis was used to analyze linkages and percentage similarities of the years grouped by NMDS. Both analyses were performed with the statistical software PRIMER v.5 (Clarke and Gorley, 2001).

Oceanographic variability effects on the fish community

For the statistical analyses to test the effects of oceanographic variability on fish density from 2004 to 2018, we used the following independent variables: Lagoon's days closed

(DC), Multivariate Ocean Climate Indicator (MOCI), Water temperature anomalies (°C), Salinity anomalies (PSU), Dissolved oxygen anomalies (mg/l), and pH anomalies.

Physical and chemical parameters critical events, time-series variability, and anomalies

We identified lagoon’s critical events in the physical-chemical time-series parameters and calculated the annual anomalies for trends analysis. The data processing and time series plots were done in MATLAB R2014a and the anomalies Mann-Kendall trend test was performed with XLSTAT 2019. Mann-Kendall values were shown in the time series only if there was a trend with a p-value ≤ 0.05.

Effects of the physical-chemical parameters variability and oceanographic index on the fish community

To evaluate the effect of the physical and chemical parameters on the fish community we used Principal components analysis (PCA) to find the variance of the abiotic variables, and consequently the effects of the variability of the variables on the fish community every year. The PCA was performed with the statistical software STATISTICA 10. In order to meet the statistical assumptions for this test, the variables were standardized with the software standardization function. To obtain the best variance results the factor loadings were rotated varimax raw.

Analysis of the matrices correlation between oceanographic variables and the fish community

We used the BIOENV/BVSTEP nonparametric routines to attain the best model that maximizes the Spearman based correlations between the similarity matrices of the abiotic variables and fish densities. These routines were performed with the statistical software PRIMER v.5 (Clarke and Gorley, 2001).

Correlations between abiotic variables and fish species

In order to test the direct effects of the abiotic variables on the fish species densities, we performed Pearson correlation analysis with the statistical software STATISTICA 10. We only reported the results with statistical significance $p < 0.05$.

Analysis of the oceanographic indices effects on the fish community and species

To determine which were the oceanographic variables that had effects in the fish community dissimilarities we used one way designed ANOSIM global and pairwise tests and SIMPER to determine species contribution to the dissimilarities. The statistical software procedures and methodology criteria were the same as those used in the 1986-2018 study period.

3 RESULTS

3.1 Results 1986-2018

RESULTS OF THE FISH COMMUNITY CHARACTERIZATION

Fish community abundance composition

A total of 68,120 fish, belonging to ten families, and thirty-one species, were sampled between 1986 and 2018 (Appendix B. Table B.1). The fish were classified according to Allen (et al. 2006) into an ecological classification: freshwater and/or brackish (BR), estuarine residents (ER), marine migrants (MM), marine (M), and catadromous (C). We also added two categories to identify invasive species, the mosquitofish, *Gambusia affinis* (BRI), a brackish invasive species and the yellowfin goby, *Acanthogobius flavimanus,* (ERI) an estuarine resident invasive species.

Approximately 54% of the surveyed species during the 30 year study period were marine organisms (blue colors in Fig. 2a). These marine species (M, MM, and C) have their life histories tied to the ocean and survival inside the lagoon depends at least partially on the connectivity with coastal open waters. The rest 46% of species were resident species (BR and ER) more tolerant to different levels of salinity and/or brackish waters (greenish colors in Fig. 2a).

From the thirty-one fish species registered over the 30 years of the study period, eleven species or functional groups were used in the analyses (Fig. 2b). These species or functional groups are the dominant species (six fish species and a functional group represent 97% of the total fish abundance), invasive species (2 species), commercially important species (1 species), and one life history bioindicator species (1 species). The dominant species are topsmelt, *Atherinops affinis* 54%, Goby group 19.31%, mosquitofish, *Gambusia affinis* 7.2%, California killifish, *Fundulus parvipinnis* 5.74%, longjaw mudsucker, *Gillichthys mirabilis* 5.32%, deepbody anchovy, *Anchoa compressa* 2.52%, and staghorn sculpin, *Leptocottus armatus* 1.9%. Goby group represents at least four species of the Gobiidae family (arrow goby, *Clevelandia ios*, cheekspot goby, *Ilypnus gilberti*, bay goby, *Lepidogobius lepidus*, and shadow goby *Quietula y-cauda*) present in LPL, these species were grouped a functional group due to the physical similarities that made it difficult to identify them in the field. The Invasive fish species identified in LPL are yellowfin goby, *Acanthogobius flavimanus,* and mosquitofish, *Gambusia affinis.* California halibut, *Paralichthys californicus,* was the only species commercially important included in this research project. The Striped mullet, *Mugil cephalus,* was included because it is the only catadromous species present in LPL and finally the longtailgoby, *Ctenogobius sagittula,* was included in the list because this species appearance is linked to extreme El Niño events.

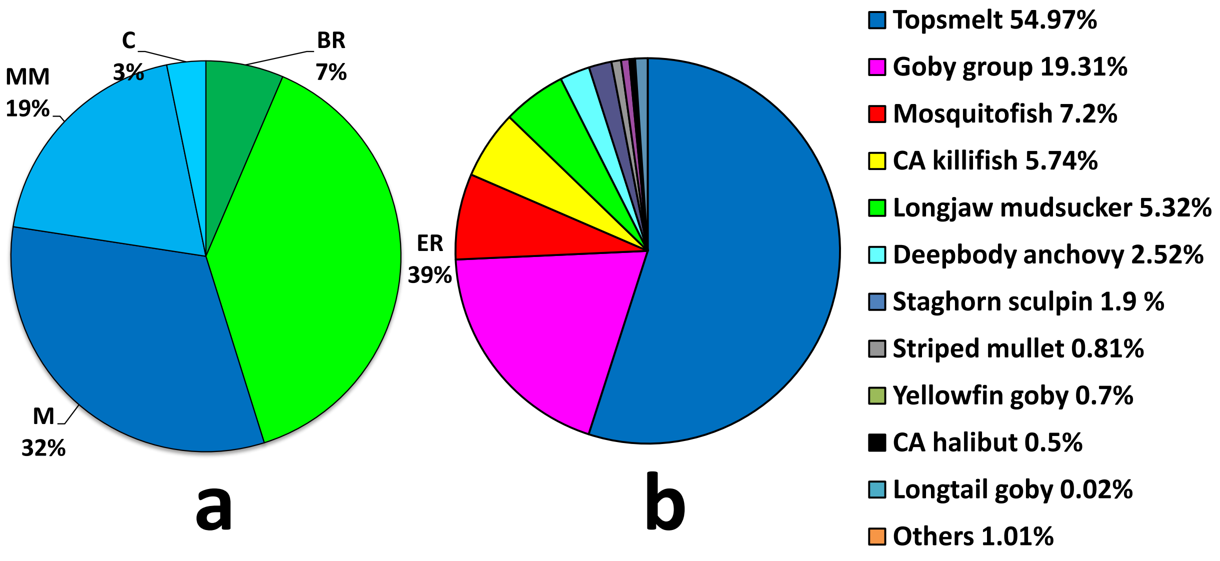


Figure. 2. LPL fish species classification composition (%) based on salinity tolerance and life history pattern between 1986 and 2018 (a). Blue colors represent fish species that enter and exit the lagoon: Marine migrants (MM), Marine (M), Catadromous (C). Green colors represent full-time residents estuarine or brackish fish species: Brackish (BR), Estuarine residents (ER)
Abundance composition (%) of fish species selected for this study (b)

Fish community variability and time-series trends

The overall fish community density varied every year, there was no evidence of a trend in this time series (Fig. 3a). However, after subtracting the dominant species topsmelt, *Atherinops affinis,* density, the fish community presented a positive trend (p= 0.021, τ= 0.297) (Fig. 3b).

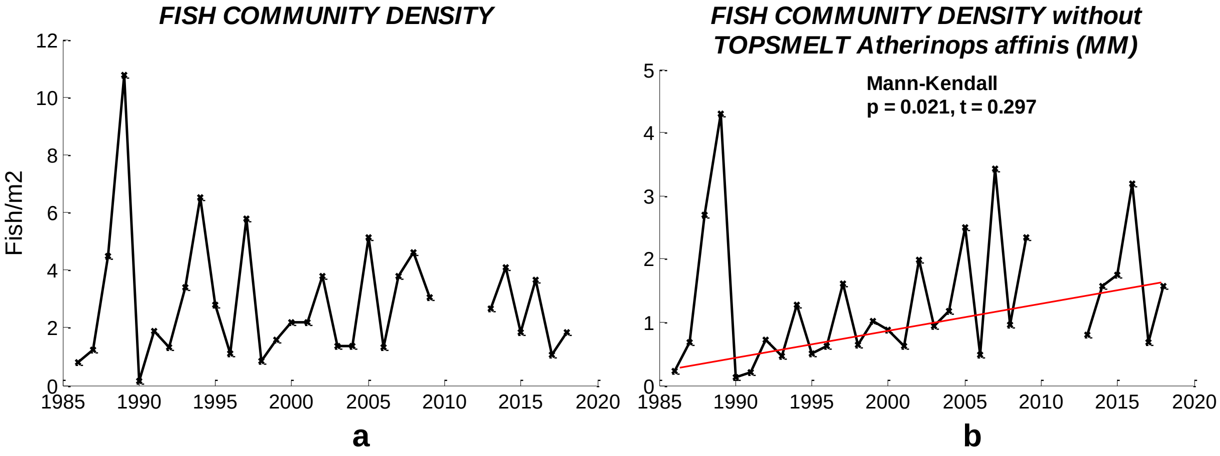


Figure **3**.Annual variability of the whole fish community density in Los Peñasquitos Lagoon between 1986 and 2018 (a). Annual variability of the fish community density without topsmelt, *Atherinops affinis,* in Los Peñasquitos Lagoon between 1986 and 2018. Mann-Kendall's trend test results with a statistical significance p-value (b).

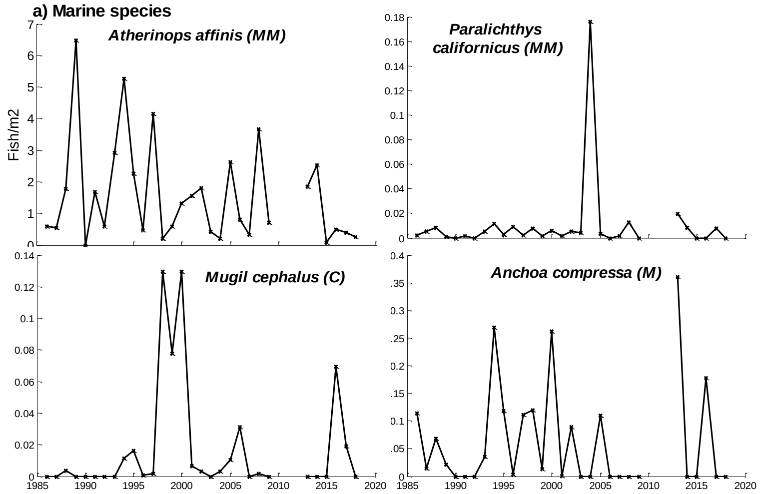
Fish species variabilities and time-series trends

All the marine fish species presented variability in their time-series (Fig. 4a), but none of these species showed a trend. The marine migrant CA halibut, *Paralichthys californicus,* had low density and presented a remarkable spike in 2004. The catadromous striped mullet, *Mugil cephalus,* was not registered every year and showed three major peaks in 1998, 2000 and 2016. However, the fishing technique used in the study underestimated the density of mullets since they are capable of jumping over the nets.

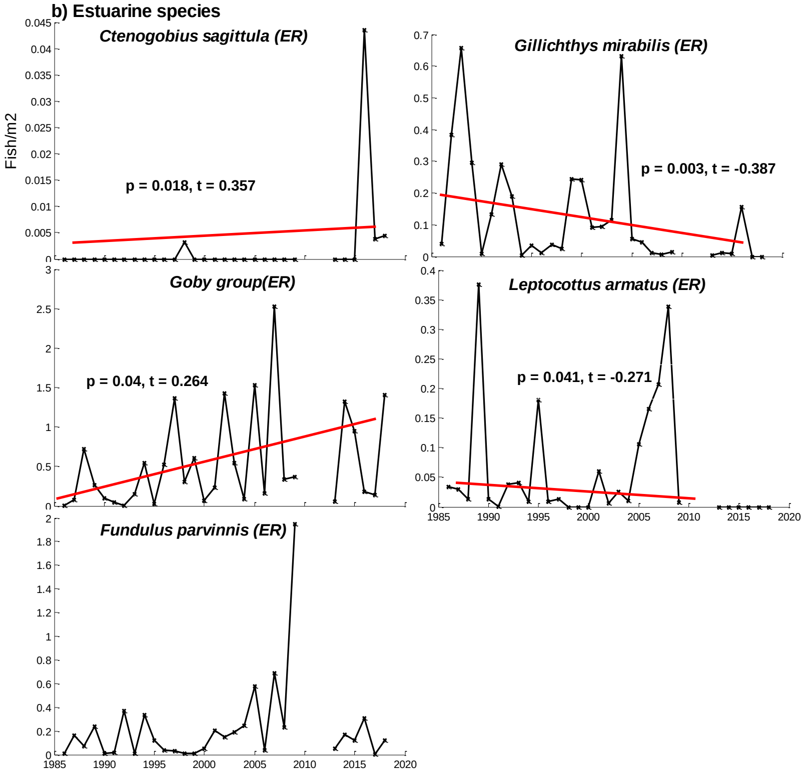
In the functional group estuarine species all the species presented a trend except the California killifish, *Fundulus parvipinnis* (Fig. 4b). The Upward trends were presented in the goby group ($p = 0.04$, $\tau = 0.264$) and Longtail goby *Ctenogobious sagittula* ($p = 0.018$, $\tau = 0.357$). The estuarine species that had negative trends were longjawmudsucker, *Gillicthys mirabilis* ($p = 0.003$, $\tau = -0.387$) and the staghorn sculpin, *Leptocottus armatus* ($p = 0.041$, $\tau = -0.271$), a fish that has not been registered since 2009.

The two invasive species of LPL presented variability (Fig. 4c). The brackish species mosquitofish, *Gambusia affinis* had two important spikes in 1989 and 2016. The estuarine resident yellowfin goby, *Acanthogobius flavimanus* showed peaks in 2000 and 2002.

a) Marine species



b) Estuarine species



c) Invasive species

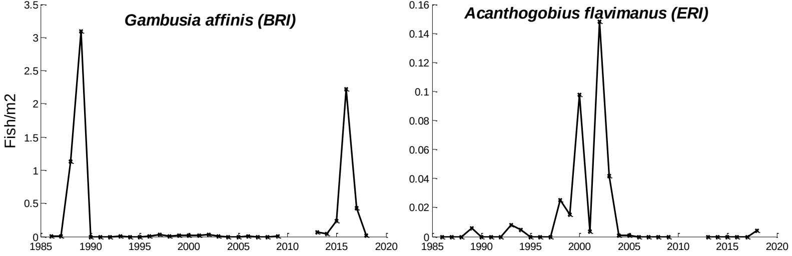


Figure. 4. The average annual density of fish species in Los Peñasquitos Lagoon between 1986 and 2018. Mann-Kendall’s trend test results with a statistical significance p-value. Species are separated according to their life histories in marine species (a), estuarine species (b), and invasive species (c).

Fish community structure changes

Non-metric multidimensional scaling (NMDS) (Fig. 5a) and Hierarchical Clusters Analysis were conducted for years and fish species (Fig 5b), they were grouped according to Bray-Curtis distances in similarities of fish species assemblages and their densities. Five similarity groups were identified in NMDS years analysis and the results of the Hierarchical cluster analysis presented the similarities percentage. The identified groups and their similarity percentage were: group A (1996, 1999, 2003) with a similarity of 77.32%; group B (1986,1987, 1992) a similarity of 81.64% without 1986 because this year was not grouped in the cluster analysis; group C (2015, 2018) with 75.4%; group D (1994, 1997, 2002, 2005, 2008, 2014) with 79.52%; and group E (1991, 1993, 1995, 2013) with 77.47%.

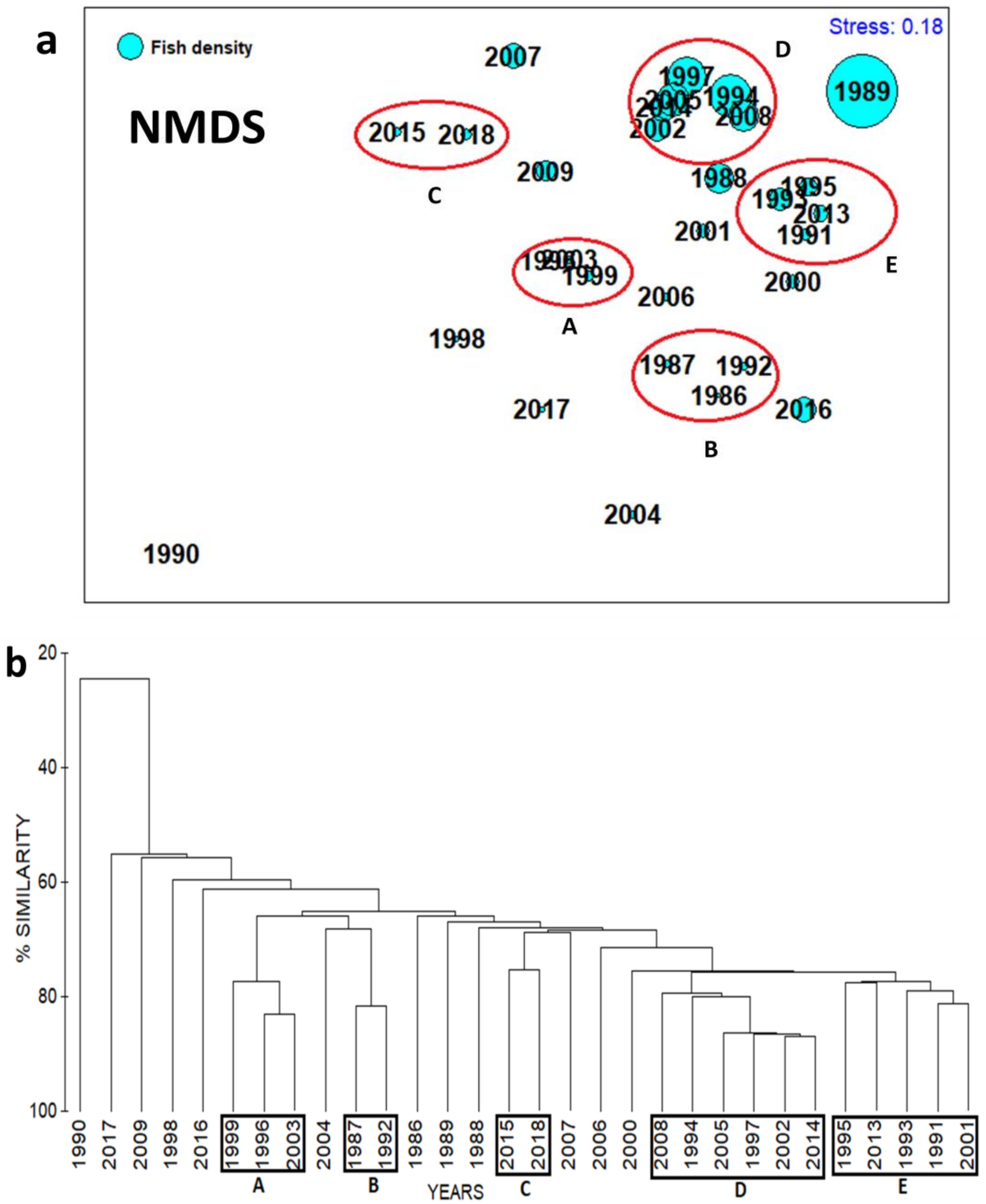


Figure. 5. Non-metric multidimensional scaling (NMDS) fish assemblages and densities similarities ordination of years 1986-2018 (a). The size of the blue bubble indicates fish density magnitude. Hierarchical clustering of years based on single linkage and % similarity of the fish assemblages and densities (b).

Fish community diversity variability

LPL fish community diversity varied each year (Fig. 6). Shannon and Simpson diversity indices showed similar results, the year with the highest diversity was 1998 with a probability of 23% that two randomly selected organisms from a sample were the same species (Appendix C.1. and C.2.). Both diversity indices also coincided that the year with the lowest diversity was1991 with a probability of 80% to pick two fish of the same species.

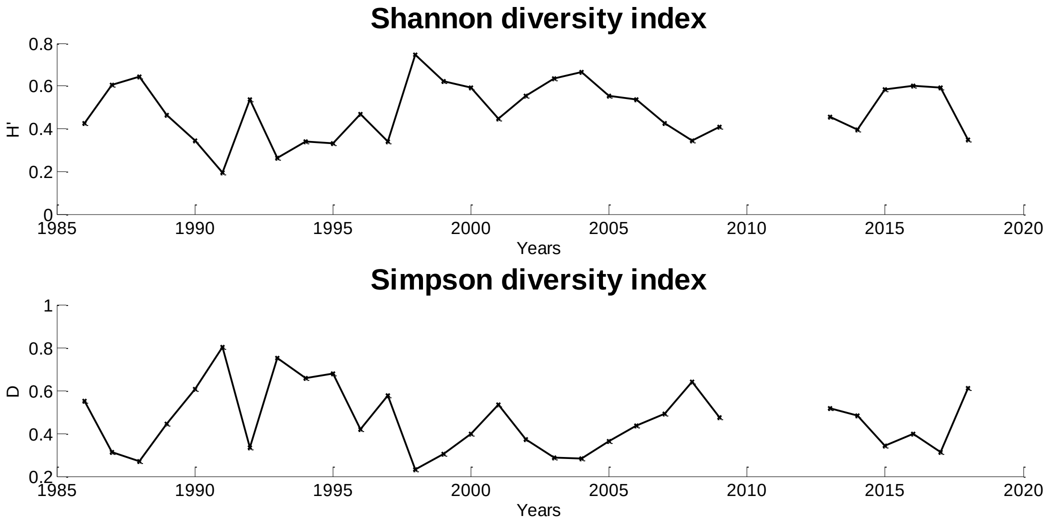


Figure 6. LPL Fish community diversity annual variability between 1986 and 2018, Shannon (H') and Simpson (D) diversity indices.

RESULTS OF OCEANOGRAPHIC VARIABILITY EFFECTS ON THE FISH COMMUNITY

Oceanographic variability effects on the fish density

The model building results of the GLM analysis suggested that according to the AIC = 126.58 and a $D^2 = 0.6336$, the best model that explains the effects of the oceanographic variability on the fish community densities was the Interaction of Days Closed-MEI with a statistical significance $p = 0.0381$.

Effects of the oceanographic indices on the fish community

The ANOSIM global test results for the independent variables ENSO, UIA, and DC showed evidence for similarities in the fish community, but the pairwise tests revealed slight dissimilarities in the fish community (Table I). Moderate dissimilarities were suggested with ENSO factors Normal conditions vs. Very Strong Niño, Low dissimilarities Normal conditions vs. Strong Niña; low dissimilarities with Upwelling Index Anomalies factors Strong Upwelling vs. Moderate Upwelling; moderate dissimilarities with Days Closures comparing factors 0 to 14 days vs. 186 to 216 days and 31 to 61 days vs. 155 to 185 days; and moderate dissimilarities resulted with Interactions DC-MEI with factors Moderate + vs. Low -, High + vs. Low -, High – vs. Low -. The variable Interaction DC-MEI was the only indicator that suggested low dissimilarities with the global test results and low to moderate dissimilarities with the pairwise test.

Table I. Period 1986-2018 ANOSIM results in global test and pairwise tests. ENSO= El Niño Southern Oscillation, UIA= Upwelling Index Anomalies, DC= Days Closed, INT.DC-MEI=Interaction of Days Closed-Multivariate Enso Index

	Global test			Pairwise test		
Variables	R	P value	Comparison Factors	R	P value	Results interpretation
ENSO	0.061	0.24				Similarities
			Normal vs. Very Strong Niño	0.353	0.042	Moderate dissimilarities
			Normal vs. Strong Niña	0.221	0.032	Low dissimilarities
UIA	0.066	0.15				Similarities
			Moderate Upwelling vs. Strong Upwelling	0.256	0.026	Low dissimilarities
DC	0.074	0.21				Similarities
			0-14 days vs. 186 - 216 days	0.709	0.048	Moderate dissimilarities
			31- 61 days vs. 155 - 185 days	0.634	0.044	Moderate dissimilarities
INT. DC-MEI	0.163	0.039				Low dissimilarities
			Moderate + vs. Low -	0.474	0.026	Moderate dissimilarities
			High + vs. Low -	0.357	0.047	Moderate dissimilarities
			High - vs. Low -	0.489	0.025	Moderate dissimilarities

Effects of the oceanographic indicators on fish species

SIMPER results for the study period 1986-2018 showed the fish species percentages contributions to dissimilarities caused by oceanographic factors previously analyzed in the ANOSIM routine. Furthermore, the SIMPER routine revealed that these factors had different effects on each species on their average abundances, which means factors were beneficial or harmful to the species and in some cases had a null/equal effect.

ENSO conditions effects on fish species

The comparisons of ENSO condition factors Very Strong Niño vs. Normal showed average dissimilarities 57.15% in the fish community and approximately an accumulated 78.56% of dissimilarities with contributions by four species: mosquitofish, *Gambusia affinis,* topsmelt, *Atherinops affinis*, goby group, and longjawmudsucker, *Gillichthys mirabilis.* Factor Very Strong Niño had a negative effect on the abundance of topsmelt, *Atherinops affinis*, goby group, CA killifish, *Fundulus parvipinnis*, staghorn sculpin, *Leptocottus armatus*, and yellowfin goby, *Acanthogobius flavimanus*. Although, the same factor had positive effects in mosquitofish, *Gambusia affinis*, longjawmudsucker, *Gillichthys mirabilis*, deepbody anchovy, *Anchoa compressa*, striped mullet, *Mugil cephalus*, and longtail goby, *Ctenogobius sagittula* (Table II).

Table II. SIMPER results analyzing variable ENSO conditions, factors Normal vs. Very Strong Niño. Species contributions to dissimilarities and comparisons of factor effects over species. Effects: Positive ↑, Negative ↓, Equal =.

SIMPER			Average dissimilarity = 57.15%	
	Factors effects		Dissimilarities	
Species	Normal	Very Strong Niño	Contribution %	Cumulated %
Mosquitofish *Gambusia affinis*	↓	↑	27.57	27.57
Topsmelt *Atherinops affinis*	↑	↓	21.11	48.68
Goby group	↑	↓	20.38	69.06
Longjaw mudsucker *Gillichthys mirabilis*	↓	↑	9.5	78.56
CA killifish *Fundulus parvipinnis*	↑	↓	6.82	85.38
Deepbody anchovy *Anchoa compressa*	↓	↑	6.32	91.71
Striped mullet *Mugil cephalus*	↓	↑	4.03	95.73
Staghorn sculpin *Leptocottus armatus*	↑	↓	2.08	97.81
Yellowfin goby *Acanthogobius flavimanus*	↑	↓	1.16	98.98
Longtail goby *Ctenogobius sagittula*	↓	↑	0.72	99.7
CA halibut *Paralichthys californicus*	=	=	0.3	100

The fish community presented an average dissimilarity of 59.74% with factor comparisons Strong Niña vs. Normal, and an accumulated 84% of dissimilarities in the fish community with contributions by the species topsmelt, *Atherinops affinis*, goby group, California killifish *Fundulus parvipinnis*, and mosquitofish, *Gambusia affinis.* Results from the factors comparisons showed that Strong Niña condition was favourable for the abundance of topsmelt, *Atherinops affinis*, California killifish, *Fundulus parvipinnis*, mosquitofish, *Gambusia affinis*, and staghorn sculpin, *Leptocottus armatus.* Whereas, negative effects on goby group, deepbody anchovy, *Anchoa compressa*, striped mullet, *Mugil cephalus*, yellowfin goby, *Acanthogobius flavimanus, and* California halibut, *Paralichthys californicus* (Table III).

Table III. SIMPER results in analyzing variable ENSO conditions with factors Normal vs. Strong Niña. Species contributions to dissimilarities and comparisons of factor effects over species. Effects: Positive ↑, Negative ↓, Equal =.

SIMPER			Average dissimilarity = 59.74%	
	Factors effects		Dissimilarities	
Species	Normal	Strong Niña	Contribution %	Cumulated %
Topsmelt *Atherinops affinis*	↓	↑	34.67	34.67
Goby group	↑	↓	26.29	60.97
CA killifish *Fundulus parvipinnis*	↓	↑	14.15	75.12
Mosquitofish *Gambusia affinis*	↓	↑	8.76	83.88
Staghorn sculpin *Leptocottus armatus*	↓	↑	5.49	89.37
Longjaw mudsucker *Gillichthys mirabilis*	=	=	5.37	94.74
Deepbody anchovy *Anchoa compressa*	↑	↓	3.38	98.12
Striped mullet *Mugil cephalus*	↑	↓	0.77	98.89
Yellowfin goby *Acanthogobius flavimanus*	↑	↓	0.76	99.65
CA halibut *Paralichthys californicus*	↑	↓	0.32	99.97
Longtail goby *Ctenogobius sagittula*	=	=	0.03	100

Upwelling Index Anomalies (UIA) effects on fish species

The SIMPER routine analyzed the factors Moderate Upwelling vs. Strong Upwelling, the fish community had average dissimilarities of 69.28% and the species that contributed with an approximate 80% of dissimilarities were topsmelt, *Atherinops affinis*, goby group, mosquitofish *Gambusia affinis*, and longjaw mudsucker, *Gillichthys mirabilis.* The factors comparison revealed positive effects of Moderate Upwelling in the abundances of topsmelt, *Atherinops affinis,* mosquitofish, *Gambusia affinis,* deepbody anchovy, *Anchoa compressa,* staghorn sculpin, *Leptocottus armatus, and* California killifish, *Fundulus parvipinnis* (Table IV). Whereas Strong Upwelling had positive effects over the abundances of the goby group, longjaw mudsucker, *Gillichthys mirabilis,* California halibut, *Paralichthys californicus,* striped mullet, *Mugil cephalus,* and yellowfin goby, *Acanthogobius flavimanus.*

Table IV. SIMPER results analyzing variable Upwelling Index Anomalies, factors Moderate Upwelling vs. Stong Upwelling. Species contributions to dissimilarities and comparisons of factor effects over species. Effects: Positive ↑, Negative ↓, Equal =.

SIMPER			Average dissimilarity = 69.28%	
	Factors effects		Dissimilarities	
Species	Moderate Upwelling	Strong Upwelling	Contribution %	Cumulated %
Topsmelt *Atherinops affinis*	↑	↓	46.21	46.21
Goby group	↓	↑	16.17	62.37
Mosquitofish *Gambusia affinis*	↑	↓	8.52	70.89
Longjaw mudsucker *Gillichthys mirabilis*	↓	↑	8.46	79.36
Deepbody anchovy *Anchoa compressa*	↑	↓	6.53	85.89
Staghorn sculpin *Leptocottus armatus*	↑	↓	4.82	90.71
CA killifish *Fundulus parvipinnis*	↑	↓	4.76	95.46
CA halibut *Paralichthys californicus*	↓	↑	2.18	97.64
Striped mullet *Mugil cephalus*	↓	↑	1.29	98.93
Yellowfin goby *Acanthogobius flavimanus*	↓	↑	1.02	99.95
Longtail goby *Ctenogobius sagittula*	=	=	0.05	100

Days Closed (DC) effects on fish species

The lagoon's mouth closure factors 0-14 day vs. 186-216 days had the effects in the fish community having as result an average dissimilarity of 55.61%. Only three species contributed with approximately 80% of the accumulated dissimilarities in the fish community, these species were topsmelt, *Atherinops affinis*, goby group, and California killifish, *Fundulus parvipinnis* (Table V). Closure 0 – 14 days presented positive effects to ten species in this study except for longjaw mudsucker, *Gillichthys mirabilis,* which the long period closure 186 – 216 days apparently had a positive impact on this goby fish, but negative effects to the rest of the species abundances.

See Appendix X for factors comparison results of 31 – 61 days vs. 155 – 185 days indicated an average dissimilarity of 75.35% in the fish community.

Table V. SIMPER results analyzing variable Days Closed, factors 0-14 days closed vs. 186-216 days closed. Species contributions to dissimilarities and comparisons of factor effects over species. Effects: Positive ↑, Negative ↓, Equal =.

SIMPER			Average dissimilarity = 55.61%	
	Factors effects		Dissimilarities	
Species	Closure 0 -14 days	Closure 186 - 216 days	Contribution %	Cumulated %
Topsmelt *Atherinops affinis*	↑	↓	38.06	38.06
Goby group	↑	↓	30.4	68.46
CA killifish *Fundulus parvipinnis*	↑	↓	11.2	79.66
Longjaw mudsucker *Gillichthys mirabilis*	↓	↑	7.69	87.35
Staghorn sculpin *Leptocottus armatus*	↑	↓	6.24	93.59
Deepbody anchovy *Anchoa compressa*	=	=	3.73	97.31
Yellowfin goby *Acanthogobius flavimanu*	↑	↓	1.52	98.84
Striped mullet *Mugil cephalus*	↑	↓	0.39	99.23
CA halibut *Paralichthys californicus*	↑	↓	0.39	99.62
Mosquitofish *Gambusia affinis*	↑	↓	0.38	100

Go to Appendix I to see results of SIMPER results of Interaction Days Closed-MEI effects on fish species

3.2 Results 2004-2018

RESULTS OF THE FISH COMMUNITY CHANGES

Fish community structure changes

Two similarity groups were identified in the NMDS years analysis and the results of the Hierarchical cluster analysis presented the similarities percentage. The identified groups and their similarity percentages were: group A (2007, 2015, 2018) had a similarity of 8.8%

and group B (2005, 2008, 2014) presented a similarity of 73.65%.

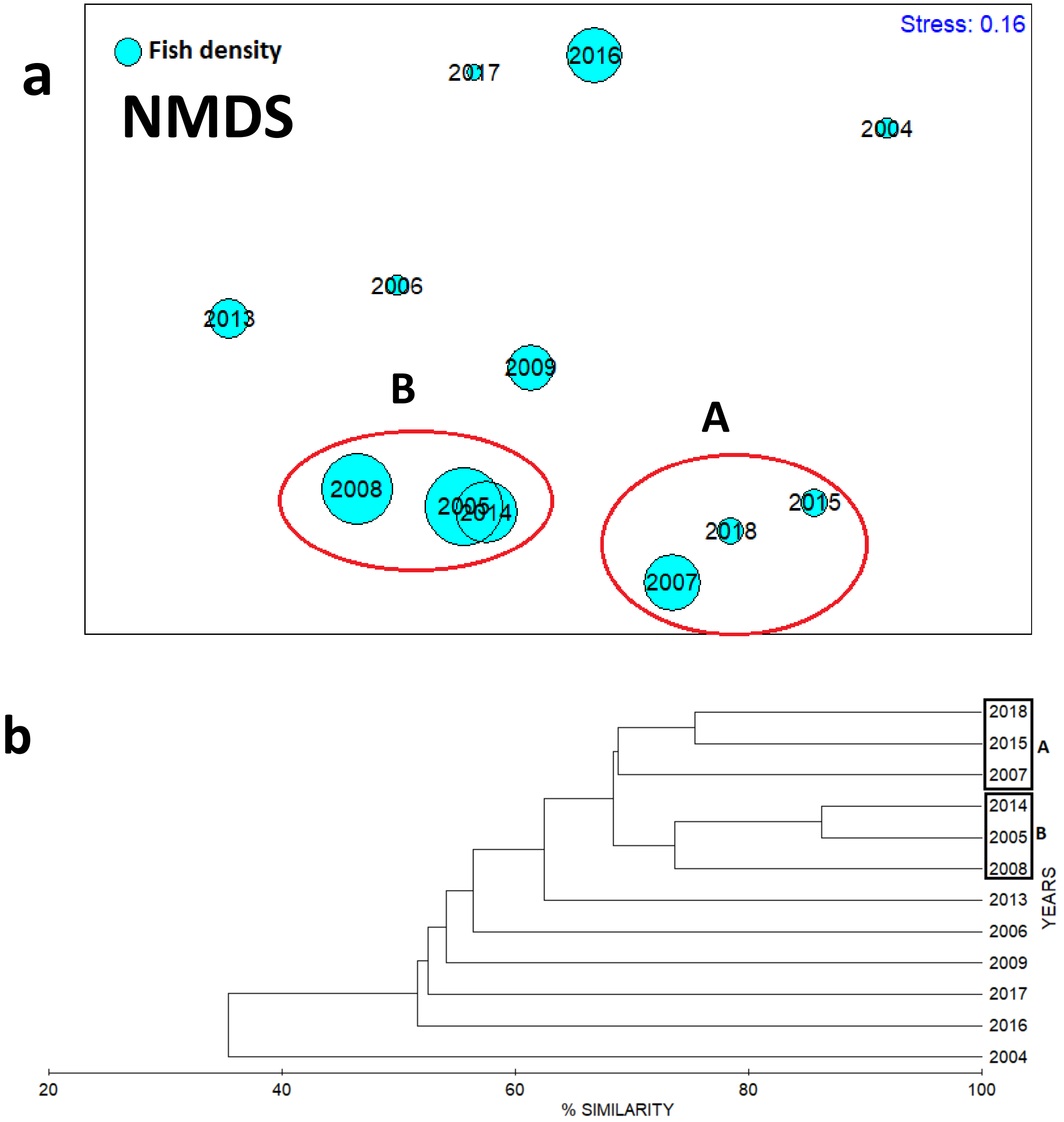


Figure. 7. Non-metric multidimensional scaling (NMDS) fish assemblages and densities similarities ordination of years 2004-2018 (a). The size of the blue bubble indicates fish density magnitude. Hierarchical clustering of years based on single linkage and % similarity of the fish assemblages and densities (b).

CHANGES IN PHYSICAL AND CHEMICAL VARIABLES

Physical and chemical parameters variability, critical events, and anomalies trends

The physical and chemical parameters within the lagoon presented variability from 2004 to 2018 (Appendix E.1.). Water temperature and salinity fluctuated seasonally, with warmer temperatures during late summer/early fall and lower salinities due to precipitations during winter typical of Southern California Mediterranean climate. The highest water temperatures events were registered in summer 2016 and the lowest in winter 2007. The concentrations of salinity reached the lowest values in 2016, and hypersaline conditions were not registered. Hypoxia conditions were identified along with the dissolved oxygen time series plot, but the lowest dissolved oxygen events reaching anoxia levels were detected in 2004, 2006, 2009, 2013, 2014 and 2016.

The only physical parameter anomaly that presented a trend according to the Mann-Kendall test was an upward trend in water temperature anomalies ($p = 0.03$ and $\tau = 0.41$) (Appendix E.2). Warm temperature anomalies started to rise at the end of the year 2013 due to the marine heatwave, Blob, then continuing rising temperatures with the 2015-2016 strong El Niño, and continued above-average through 2018. The chemical parameter pH anomalies were negative approximately from the end of 2011 to 2018. Dissolved oxygen anomalies and pH anomalies presented a similar pattern in the whole time series.

The highest value in MOCI was in 2015 due to strong El Niño conditions. In the year 2016, the inlet closed 225 days, in this year water temperature anomalies presented the highest spike and salinity the lowest level in the time series due to continuing freshwater input.

EFFECTS OF OCEANOGRAPHIC CONDITIONS AND PHYSICAL-CHEMICAL VARIABLES ON THE FISH COMMUNITY

Effects of the physical-chemical anomalies variability on the fish community

PCA results presented the abiotic variability every year, consequently, this variance had an effect on the fish community (Fig. 8). This test produced two principal components that together explained 72.55% of the total variance:

PC1 = 0.90water temperature anomalies + 0.60days closed + 0.89MOCI, these variables combined explained 51.60% of the total variance.

PC2 = 0.81Dissolved oxygen anomalies + 0.87Salinity anomalies, that explained 20.95% of the total variance.

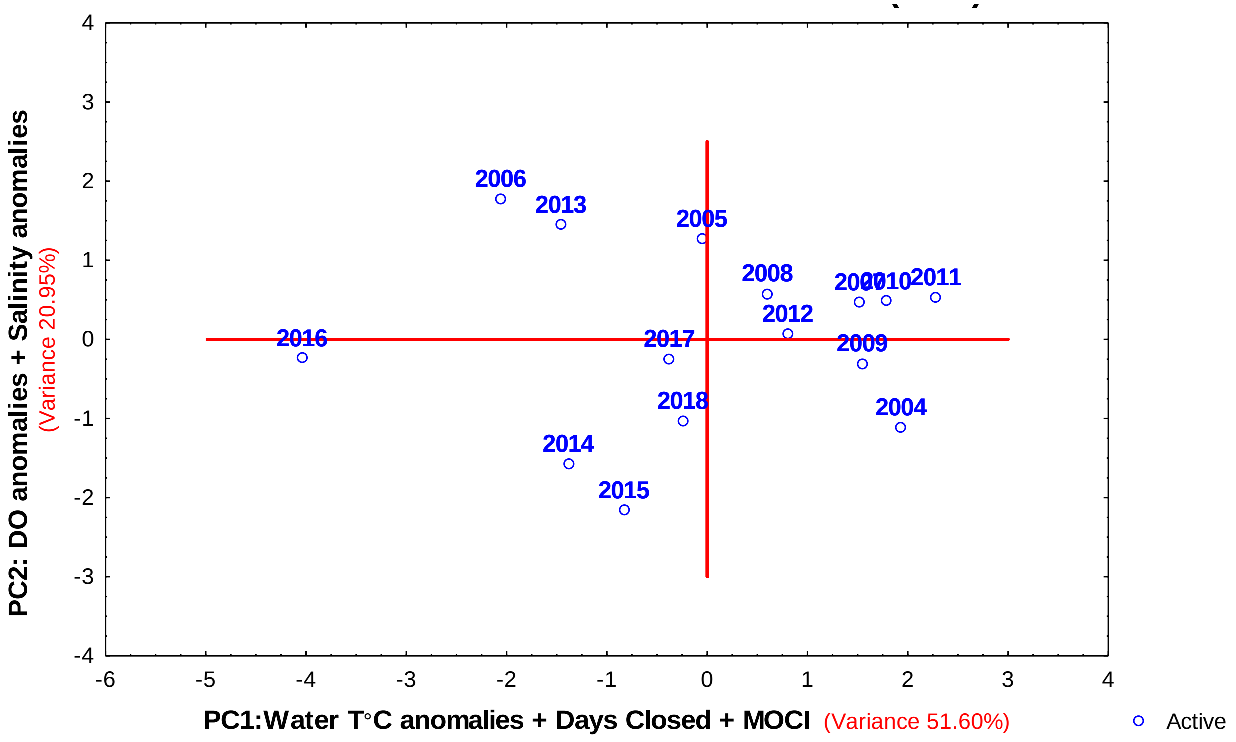


Figure. 8. PCA of the physical and chemical parameters anomalies and their annual variability in Los Peñasquitos Lagoon between 2004 and 2018.

Pearson correlations between abiotic variables and fish species

The Pearson correlations that showed statistical significance (α ≤ 5%) between oceanographic conditions or physical-chemical parameters with fish densities were (refer to Appendix G): Upwelling index had moderate correlations with the California halibut, *Paralichthys californicus* (r = - 0.544, p = 0.036) and Longjaw mudsucker, *Gillicthys mirabilis* (r = -0.574, p = 0.025) (Appendix Fig. G.1.). The chemical parameter dissolved oxygen anomalies had moderate correlations with California halibut, *Paralichthys californicus* (r = 0.658, p = 0.008) and Longjaw mudsucker, *Gillicthys mirabilis* (r = 0.623, p = 0.012) (Appendix Fig. G.3.). Days closed had very strong correlation with longtailgoby, *Ctenogobius sagittula* (r = 0.905, p = 0.0001), striped mullet, *Mugil cephalus* (r = 0.804, p = 0.0003), and mosquitofish, *Gambusia affinis* (r = 0.907, p = 0.0001) (Appendix Fig. G.5.). The physical parameter water temperature anomaly had moderate correlations with longtailgoby, *Ctenogobius sagittula* (r = 0.607, p = 0.016) and mosquitofish, *Gambusia affinis* (r = 0.608, p = 0.016) (Appendix Fig. G.5.). Salinity anomalies had strong correlation with striped mullet, *Mugil cephalus* (r = - 0.726, p = 0.002) (Appendix Fig. G.4.).

Results of the oceanographic indices effects on the fish community and species

Effects of water temperature anomalies on the fish community

The water temperature anomaly in the ANOSIM Global test showed an R= 0.349 and p= 0.049. This result suggested moderate dissimilarities, indicating water temperature anomalies had an effect on the fish community from 2004 to 2018.

Effects of water temperature anomalies on fish species

For the years 2004-2018 SIMPER analysis presented an average dissimilarity of 73.5% in the fish community as a result of the effects of water temperature anomalies with factors Strong – vs. Very Strong +. The species contribution of approximately 90% to cumulated dissimilarities resulted from topsmelt, *Atherinops affinis*, mosquitofish, *Gambusia affinis*, longjaw mudsucker, *Gillichthys mirabilis*, goby group, and California killifish, *Fundulus parvipinnis* (Table VI).

The factor very strong warm water temperature anomaly had a negative effect on almost all the fish species populations except on mosquitofish, *Gambusia affinis* and striped mullet, *Mugil cephalus*.

Table VI. Period 2004-2018 SIMPER results analyzing variable Water temperature anomalies °C with factors Strong - vs. Very Strong +. Species contributions to dissimilarities and comparisons of factor effects over species. Effects: Positive ↑, Negative ↓, Equal =.

SIMPER			Average dissimilarity = 73.50%	
	Factors effects		Dissimilarities	
Species	Strong -	Very Strong +	Contribution %	Cumulated %
Topsmelt *Atherinops affinis*	↑	↓	22.39	22.39
Mosquitofish *Gambusia affinis*	↓	↑	18.42	40.81
Longjaw mudsucker *Gillichthys mirabilis*	↑	↓	17.62	58.43
Goby group	↑	↓	15.82	74.25
CA killifish *Fundulus parvipinnis*	↑	↓	15.49	89.74
CA halibut *Paralichthys californicus*	↑	↓	5.32	95.06
Staghorn sculpin *Leptocottus armatus*	↑	↓	2.13	97.19
Deepbody anchovy *Anchoa compressa*	↑	↓	1.88	99.07
Striped mullet *Mugil cephalus*	↓	↑	0.69	99.76
Longtail goby *Ctenogobius sagittula*	=	=	0.2	99.96
Yellowfin goby *Acanthogobius flavimanus*	=	=	0.04	100

4 DISCUSSION

Los Peñasquitos Lagoon is an important coastal ecosystem in Southern California used by estuarine and marine fish species for reproduction, growth, and protection. In this Californian estuary, a total of 68,120 fish were sampled from 1986 to 2018. Our study results indicate that 54% of the surveyed fish species were marine species (Fig. 2a). The topsmelt, *Atherinops affinis*, a marine migrant fish was the most dominant species with an approximately 55% of the total sampled fish, followed by the estuarine residents, the goby group with 19% and in third place a 7% the invasive species, mosquitofish, *Gambusia affinis* (Fig 2b). The survival of these species and their population dynamics, especially marine species, depend on the lagoon's inlet intermittent closure-opening events. Closure events have an important effect on the estuary's physical and chemical conditions and also impede fish to migrate between the ocean and estuary, which reduces larval, juvenile and adult recruitment to the lagoon as well as organisms genetic exchange to other estuaries and coastal ecosystems on the California current system. The inlet open-closures events in coastal lagoons are an important factor that alters fish life histories, population structures, and abundance.

4.1 Fish community abundance composition and trends

Fish abundance in LPL showed annual density variability during the 30 years of the study period, although the time series did not show a trend in the fish community maximum spikes showed decreasing values over time, suggesting the possibility of declining numbers in the fish population abundance (Fig.3a). This abundance decrease could be associated with the declining pattern of maximum density values of the dominant fish species topsmelt, *Atherinops affinis*, (Fig.4a). However, after subtracting this species from the fish community density time-series, the rest of the fish community presented an upward trend in abundance (Fig. 3b). This could be explained due to the abundance increase in the time-series of the estuarine residents, the goby group, the second most dominant fish species in the lagoon (Fig. 4b). The switch between dominant fish species as well as the ecological functional group they represent could mean that the lagoon's abiotic conditions in the last years have not been favorable for marine fish species life histories inside LPL, but favorable to resident fish species and species more tolerant to brackish conditions such as the mosquitofish, *Gambusia affinis*.

4.2 Oceanographic variability effects on LPL fish community

LPL fish community varied through time due to the changing oceanographic conditions, such as El Niño or La Niña events, coastal upwelling anomalies, and inlet closures. These oceanographic variables and the interaction among them caused variability to the lagoon's water physical-chemical parameters, consequently, this variance had effects on the fish community (Fig. 8). This study indicates despite fish community structure and densities changed every year, some years presented similarities in these biotic variables (Fig. 5a), consequently, fish diversity in LPL presented variability (Fig. 6). This concurs with Williams (et al. 2001), in southern California estuaries, El Niño-associated events may affect shallow-water ecosystems physicochemical conditions, and their fish communities by modifying larvae supply with effects in the abundance, composition assemblages, and diversity. At a bigger scale, climatic and oceanographic patterns, such as North Atlantic Oscillation (NAO) in the Atlantic Ocean (Nyitrai et al., 2012), and NorthPacific Gyre Oscillation (NGO) and Pacific Decadal Oscillation (PDO) in the Pacific

Ocean (Feyrer et al., 2015), have had an influence on fish assemblages composition, as well as effects in the growth and abundance of marine fish during estuarine residency according to their life histories relationships with this coastal ecosystems.

4.3 Physical and chemical parameters anomalies effects on fish community

Warm water temperature effects on the fish community

Water temperature anomalies presented an increasing trend in the last 14 years of the study (Appendix Fig.E.2.), with warm water conditions in the last 6 years, due to marine heatwaves and a strong El Niño event. Our results showed that warm water temperature anomalies had negative effects on nine of the eleven species selected, including the dominant species topsmelt, *Atherinops affinis*. On the other hand, the only species favored with warm water anomalies were the invasive mosquitofish, *Gambusia affinis*, and the catadromous striped mullet, *Mugil cephalus* (Table VI). These results are consistent with those of Lonnhart (et al., 2019) that reports warm water conditions effects on fish in estuaries from 2013 to 2018 in central and southern California.

Warmer water temperatures in the future due to climate change will likely continue to have effects on the fish species in California (Hoegh-Guldberg and Bruno, 2010; Perkins et al., 2012; Frölicher and Laufkötter, 2018). Due to fish body temperature regulation depends on the environment, it is expected that water temperature rising globally and regionally will have effects on the life histories of marine and estuarine fish species and communities (Roessig et al., 2004; Jeffries et al., 2016).

Inlet closure effects on the fish community

Another important variable that had an effect on the fish community was the inlet closures. Due to urban runoff, LPL has a continuous freshwater input (Norbdy and Zedler, 1991), therefore during an inlet closure event lagoon's physical and chemical parameters change, the salinity, pH and dissolved oxygen decrease and water temperature increases (Appendix Fig. E.2.). These changes in the lagoon's abiotic parameters have effects on the fish species abundance. This study provided evidence that long periods of the lagoon's inlet closures had adverse effects on almost all LPL fish species, except for the estuarine resident, the longjaw mudsucker, *Gillicthys mirabilis,* and the invasive fresh/brackish species, mosquitofish, *Gambusia affinis* (Appendix Fig. G.5.).This result could be associated with the fish tolerance to brackish and hypersaline waters as well as to the capability to breathe air in low oxygen water conditions (Love, 2011). Previous studies have reported some negative effects of inlet closures due to changes in salinity and water temperature. It decreases growth rates of juvenile California halibut, lowers topsmelt food consumption rates 50%, and restricts the access of the California killifish, *Fundulus parvipinnis* to the intertidal marsh surface, (Madon, 2008). One of the most important factors that affect the estuarine ecosystem is inlet closure events, which have different effects on fish species behavior, physiology, and survival strategies (Tietze, 2016).

ENSO effects on the fish community

In Southern California, inlet closures events are likely to occur with more frequency in the following years due to sea-level rise (Doughty et al., 2017). In addition, as an effect of global warming on oceanographic conditions, increased stratification could increase the frequency of ENSO events and wave energy in general (Timmermann et al.,1999; Roessig et al., 2005; Young et al., 2018). In Southern California, strong ENSO events increments precipitation, elevates waves and sea level and increases the probability of mouth closures (Safran et al., 2017; Young et al., 2018).

Despite strong El Niño conditions had negative effects on the abundance of the majority of the fish species in our study, El Niño conditions were favorable for the longtailgoby *Ctenogobius sagittula*. This fish increases its abundance in strong El Niño years (Ruiz-Campos et al.,1999; Lea and Rosenbalt, 2000; Williams et al., 2001). For this reason, we suggest that the longtailgoby could be a bioindicator species of warming conditions (Lonhart et al.,2019).

Upwelling anomalies effects on the fish community

We identified that strong upwelling anomalies had negative effects on the abundance of California halibut, *Paralichthys californicus,* and longjawmudsucker, *Gillichtys mirabilis*. It is important to note that longjawmudsucker had a negative tendency in its abundance time-series which suggests that the species population at LPL could be decreasing. Another fish species that is likely to be decreasing is the staghorn sculpin, *Leptocottus armatus*, this fish presented a downward trend and has not been registered in LPL since 2009.

5 CONCLUSION

In conclusion, LPL fish species and community responded differently to oceanographic conditions, as well as to the variations or the physical and chemical parameters anomalies within the lagoon. The abundance of the fish community is likely to be declining due to the abundance decreasing values majorly of the dominant fish species, the topsmelt, *Atherinops affinis*. However, the second most abundant fish species, the goby group presented a positive trend in abundance. Our findings suggest that this negative effect on the fish community abundance is associated primarily with the increasingly warm water conditions from marine heatwaves and the strong El Niño that have affected Southern California coastal ecosystems in the last six years of this study. The results from our assessment indicates that changes on the fish community were driven principally by the warm water anomalies effects on the fish species, prolonged periods of the inlet closures that affects water quality turning to anoxic conditions that result in fish mass mortalities, and strong ENSO events that not only affect the estuary ecosystem with warm water temperatures but also to the precipitation increment that adds more freshwater to the system that consequently decreases drastically salinity concentrations. The climate-oceanographic processes that come along with strong ENSO conditions increase the probability of the lagoon's mouth closures due to the severity of storm surges and altered coastal sedimentation dynamics that are typical during this event. According to the scientific literature, due to climate change, it is expected that these events will be more frequent and strong in the region, therefore the California current fish communities in estuaries and coastal lagoons will be more stressed and threatened.

In order to have a better understanding of LPL fish community structure and ecology, we suggest complementing fish monitoring with more inclusive fish surveys that target also fish species related to the water column not only to the bottom. To have the whole spectrum of the oceanographic conditions and physical-chemical parameters effects on the fish community, we recommend to include in the monitoring and analyses other parameters such as nutrients, carbon dioxide concentration, chlorophyll, biochemical oxygen demand, harmful algal blooms events, and freshwater volume flow to the lagoon. This paper has highlighted the importance of long-term studies to understand LPL fish community changes caused by oceanographic variations over different spatial-time scales. This study provides useful information for Southern California coastal lagoons' current inlet management plans and fish species management. Furthermore, it provides valuable information for future challenges in environmental management planning addressing climate change expected estuaries scenarios.

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APPENDIX

Appendix A. Fish species classification based on salinity and life history

**Table A. 1. Fish species identified in LPL between1986 and 2018.
Classification based on salinity tolerance and life history pattern (Allen et al., 2006).**

FAMILY	COMMON NAME	SCIENTIFIC NAME	CLASSIFICATION
ATHERINOPSIDAE	Topsmelt	*Atherinops affinis*	MM
BOTHIDAE	CA halibut	*Paralichthys californicus*	MM
CENTRARCHIDAE	Green sunfish	*Lepomis cyanellus*	BR
	Unid. Bass	*Micropterus spp.*	M
COTTIDAE	Staghorn sculpin	*Leptocottus armatus*	ER
CYPRINODONTIDAE	CA killifish	*Fundulus parvipinnis*	ER
EMBIOTOCIDAE	Shiner surfperch	*Cymatogaster aggregate*	MM
ENGRAULIDIDAE	Unid. anchovy spp.	*Unid. anchovy spp.*	M
	Deepbody anchovy	*Anchoa compressa*	M
	Northern anchovy	*Engraulis mordax*	M
GIRELLIDAE	Opaleye	*Girella nigricans*	M
GOBIIDAE	Yellowfin goby	*Acanthogobius flavimanus*	ERI
	Arrow goby	*Clevelandia ios*	ER
	Longtail goby	*Ctenogobius sagittula*	ER
	Longjaw mudsucker	*Gillichthys mirabilis*	ER
	Cheekspot goby	*Ilypnus gilberti*	ER
	Bay goby	*Lepidogobius Lepidus*	ER
	Shadow goby	*Quietula y-cauda*	ER
	Unid. goby spp.	*Unid. goby spp.*	ER
MUGILIDAE	Striped mullet	*Mugil cephalus*	C
PLEURONECTIDAE	Diamond turbot	*Hypsopsetta guttulata*	MM
	Spotted turbot	*Pleuronichthys ritteri*	MM
POECILIDAE	Mosquitofish	*Gambusia affinis*	BRI
SCIAENIDAE	Yellowfin croaker	*Umbrina roncador*	MM
	CA corbina	*Menticirrhus undulates*	M
SERRANIDAE	Barred sandbass	*Paralabrax nebulifer*	M
	Spotted sandbass	*Paralabrax maculatofasciatus*	M
	Kelpbass	*Paralabrax clathratus*	M
SYNGNATHIDAE	Bay pipefish	*Syngnathus leptorhynchus*	ER
	Barred Pipefish	*Syngnathus auliscus*	ER
UROLOPHIDAE	Round Stingray	*Urolophus halleri*	M

Appendix B. Total fish species densities

Table B.1. Los Peñasquitos Lagoon yearly fish densities (fish/m²) 1986-2018. Years 2010, 2011, and 2012 were not sampled. Goby group = arrow goby, *Clevelandia ios*, cheekspot goby, *Ilypnus gilberti*, bay goby, *Lepidogobius lepidus*, and shadow goby, *Quietula y-cauda*.

Common name	Scientific name	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995
Topsmelt	*Atherinops affinis*	0.5900	0.5349	1.7859	6.4676	0.0	1.6882	0.5991	2.9175	5.2660	2.2725
CA halibut	*Paralichthys californicus*	0.0019	0.0051	0.0086	0.0010	0.0	0.0013	0.0	0.0054	0.0113	0.0027
Green sunfish	*Lepomis cyanellus*	0	0	0	0	0	0	0	0	0	0
Unid. Bass	*Micropterus spp.*	0	0	0	0	0	0	0	0	0	0
Staghorn sculpin	*Leptocottus armatus*	0.0338	0.0296	0.0135	0.3753	0.0125	0.0013	0.0378	0.0405	0.0091	0.1808
CA killifish	*Fundulus parvipinnis*	0.0113	0.1595	0.0748	0.2366	0.0083	0.0147	0.3697	0.0081	0.3372	0.1215
Shiner surfperch	*Cymatogaster aggregata*	0	0	0	0	0	0	0	0	0	0.0027
Unid. anchovy spp.	*Unid. anchovy spp.*	0	0	0	0	0	0	0	0	0	0
Deepbody anchovy	*Anchoa compressa*	0.1147	0.0141	0.0687	0.0210	0	0	0	0.0351	0.2693	0.1188
Northern anchovy	*Engraulis mordax*	0	0	0	0	0	0.0040	0.0027	0	0	0
Opaleye	*Girella nigricans*	0.0003	0	0	0	0	0	0.0027	0	0.0045	0
Yellowfin goby	*Acanthogobius flavimanus*	0	0	0	0.0060	0	0	0	0.0081	0.0045	0
Goby group	*Various Gobies spp.*	0.0094	0.0823	0.7212	0.2695	0.0958	0.0441	0.0027	0.1484	0.5409	0.0243
Longtail goby	*Ctenogobius sagittula*	0	0	0	0	0	0	0	0	0	0
Longjaw mudsucker	*Gillichthys mirabilis*	0.0409	0.3832	0.6575	0.2945	0.0083	0.1324	0.2915	0.1889	0.0045	0.0351
Striped mullet	*Mugil cephalus*	0	0	0.0037	0	0	0	0	0	0.0113	0.0162
Diamond turbot	*Hypsopsetta guttulata*	0.0003	0.0039	0.0135	0	0	0	0.0135	0	0.0362	0
Spotted turbot	*Pleuronichthys ritteri*	0	0	0	0	0	0.0013	0	0	0	0
Mosquitofish	*Gambusia affinis*	0.0019	0.0090	1.1383	3.0886	0	0	0	0.0027	0	0
Yellowfin croaker	*Umbrina roncador*	0	0	0	0	0	0	0	0	0	0.0027
CA corbina	*Menticirrhus undulatus*	0	0	0	0	0	0	0	0	0	0
Barred sandbass	*Paralabrax nebulifer*	0	0	0	0	0	0.0013	0	0	0	0
Spotted sandbass	*Paralabrax maculatofasciatus*	0	0	0	0	0	0	0	0	0.0068	0
Kelpbass	*Paralabrax clathratus*	0	0	0	0	0	0	0	0	0.0045	0
Bay pipefish	*Syngnathus leptorhynchus*	0.0075	0	0.0025	0	0	0.0013	0	0.0216	0.0362	0
Barred Pipefish	*Syngnathus auliscus*	0	0	0	0	0	0	0	0	0	0
Round Stingray	*Urolophus halleri*	0	0	0	0	0	0	0	0	0	0
TOTAL Density per year		0.811875	1.2216136	4.4880837	10.760062	0.125	1.8902306	1.3197492	3.376291	6.5423373	2.7772379
Species richness		11	9	11	9	4	10	8	10	14	10

Table B.1. Continued

Common name	**Scientific name**	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
Topsmelt	*Atherinops affinis*	0.4660	4.1541	0.2044	0.5849	1.3190	1.5614	1.8092	0.4264	0.1958	2.6390
CA halibut	*Paralichthys californicus*	0.0089	0.0024	0.0080	0.0018	0.0060	0.0013	0.0052	0.0041	0.1758	0.0037
Green sunfish	*Lepomis cyanellus*	0	0	0.0008	0	0	0	0	0	0	0
Unid. Bass	*Micropterus spp.*	0	0	0	0.0006	0	0	0	0	0	0
Staghorn sculpin	*Leptocottus armatus*	0.0083	0.0128	0	0	0	0.0597	0.0065	0.0255	0.0100	0.1056
CA killifish	*Fundulus parvipinnis*	0.0392	0.0337	0.0103	0.0134	0.0489	0.2058	0.1463	0.1908	0.2475	0.5798
Shiner surfperch	*Cymatogaster aggregata*	0	0	0	0	0	0	0.0195	0	0	0
Unid. anchovy spp.	*Unid. anchovy spp.*	0	0	0	0	0	0	0	0	0	0
Deepbody anchovy	*Anchoa compressa*	0.0030	0.1116	0.1193	0.0128	0.2618	0.0013	0.0897	0	0	0.1107
Northern anchovy	*Engraulis mordax*	0	0	0	0	0	0	0	0	0	0
Opaleye	*Girella nigricans*	0	0.0008	0	0	0.0015	0	0	0	0.0017	0.0293
Yellowfin goby	*Acanthogobius flavimanus*	0	0	0.0254	0.0152	0.0978	0.0038	0.1483	0.0418	0.0008	0.0007
Goby group	*Various Gobies spp.*	0.5261	1.3644	0.3061	0.6073	0.0625	0.2338	1.4242	0.5478	0.0875	1.5284
Longtail goby	*Ctenogobius sagittula*	0	0	0.0032	0	0	0	0	0	0	0
Longjaw mudsucker	*Gillichthys mirabilis*	0.0125	0.0385	0.0254	0.2429	0.2423	0.0927	0.0943	0.1143	0.6316	0.0564
Striped mullet	*Mugil cephalus*	0.0006	0.0016	0.1296	0.0777	0.1294	0.0064	0.0033	0	0.0033	0.0103
Diamond turbot	*Hypsopsetta guttulata*	0.0065	0.0120	0.0103	0.0085	0.0023	0	0.0065	0.0112	0.0100	0
Spotted turbot	*Pleuronichthys ritteri*	0	0	0	0	0	0	0	0	0	0
Mosquitofish	*Gambusia affinis*	0.0024	0.0329	0.0024	0.0200	0.0150	0.0127	0.0306	0.0020	0	0
Yellowfin croaker	*Umbrina roncador*	0	0	0	0	0	0	0	0	0	0
CA corbina	*Menticirrhus undulatus*	0	0	0.0016	0	0	0	0	0	0	0
Barred sandbass	*Paralabrax nebulifer*	0	0	0	0	0	0.0013	0	0	0	0
Spotted sandbass	*Paralabrax maculatofasciatus*	0	0	0	0	0	0	0	0	0	0
Kelpbass	*Paralabrax clathratus*	0	0	0	0	0	0	0	0	0	0
Bay pipefish	*Syngnathus leptorhynchus*	0.0137	0.0008	0.0048	0.0158	0.0038	0.0076	0.0163	0	0.0150	0.0784
Barred Pipefish	*Syngnathus auliscus*	0	0	0	0	0	0	0	0	0	0
Round Stingray	*Urolophus halleri*	0	0	0	0	0	0	0	0	0	0
TOTAL Density per year		1.0871956	5.7656038	0.8516425	1.6009134	2.1903193	2.1878057	3.7998915	1.36399	1.3789254	5.1423134
Species richness		11	12	14	12	12	12	13	9	11	11

Table B.1. Continued

Common name	Scientific name	2006	2007	2008	2009	2013	2014	2015	2016	2017	2018
Topsmelt	*Atherinops affinis*	0.8220	0.3384	3.6639	0.7095	1.8602	2.5247	0.0759	0.4870	0.3955	0.2476
CA halibut	*Paralichthys californicus*	0	0.0018	0.0125	0	0.0194	0.0086	0	0	0.0077	0
Green sunfish	*Lepomis cyanellus*	0	0	0	0	0	0	0	0	0	0
Unid. Bass	*Micropterus spp.*	0	0	0	0	0	0	0	0	0	0
Staghorn sculpin	*Leptocottus armatus*	0.1654	0.2070	0.3388	0.0074	0	0	0	0	0	0
CA killifish	*Fundulus parvipinnis*	0.0409	0.6913	0.2294	1.9502	0.0505	0.1677	0.1215	0.3087	0.0038	0.1194
Shiner surfperch	*Cymatogaster aggregata*	0	0	0	0	0	0	0	0	0	0
Unid. anchovy spp.	*Unid. anchovy spp.*	0	0	0.0143	0	0	0	0	0	0	0
Deepbody anchovy	*Anchoa compressa*	0	0	0	0	0.3612	0	0	0.1783	0	0
Northern anchovy	*Engraulis mordax*	0	0	0	0	0	0	0	0	0	0
Opaleye	*Girella nigricans*	0.0033	0	0	0	0.2369	0	0.4000	0	0	0
Yellowfin goby	*Acanthogobius flavimanus*	0	0	0	0	0	0	0	0	0	0.0044
Goby group	*Various Gobies spp.*	0.1621	2.5239	0.3334	0.3640	0.0583	1.3204	0.9468	0.1826	0.1382	1.4017
Longtail goby	*Ctenogobius sagittula*	0	0	0	0	0	0	0	0.0435	0.0038	0.0044
Longjaw mudsucker	*Gillichthys mirabilis*	0.0458	0.0108	0.0054	0.0149	0.0039	0.0129	0.0101	0.1565	0	0
Striped mullet	*Mugil cephalus*	0.0311	0	0.0018	0	0	0	0	0.0696	0.0192	0
Diamond turbot	*Hypsopsetta guttulata*	0	0	0.0018	0	0	0	0	0	0	0.0044
Spotted turbot	*Pleuronichthys ritteri*	0	0	0	0	0	0	0	0	0	0
Mosquitofish	*Gambusia affinis*	0.0082	0	0	0.0111	0.0621	0.0387	0.2380	2.2174	0.4263	0.0221
Yellowfin croaker	*Umbrina roncador*	0	0	0	0	0	0	0	0	0	0
CA corbina	*Menticirrhus undulatus*	0	0	0	0	0	0	0	0	0	0
Barred sandbass	*Paralabrax nebulifer*	0	0	0	0	0	0	0	0.0043	0	0
Spotted sandbass	*Paralabrax maculatofasciatus*	0	0	0	0	0.0039	0	0	0.0043	0.0077	0
Kelpbass	*Paralabrax clathratus*	0	0	0	0	0	0	0	0	0	0
Bay pipefish	*Syngnathus leptorhynchus*	0.0180	0.0018	0.0233	0	0.0039	0	0	0.0087	0	0.0221
Barred Pipefish	*Syngnathus auliscus*	0	0	0	0	0	0.0258	0.0253	0.0087	0.0768	0
Round Stingray	*Urolophus halleri*	0	0	0	0	0	0.0043	0	0	0	0
TOTAL Density per year		1.2968724	3.7750455	4.6246505	3.0572065	2.6601942	4.1032258	1.8177215	3.6695652	1.0791091	1.8262215
Species richness		9	7	10	6	10	8	7	12	9	8

Appendix C. Shannon and Simpson Diversity Indices LPL 1986-2018

In order to analyze diversity during the 30 year study period, we calculated the Shannon and Simpson diversity indexes for each year using the software PRIMER v.5 (Clarke and Gorley, 2001).

Shannon diversity index formula (H') is

$H' = -\Sigma pi \ln pi$

(p_i) = number of species

Simpson diversity formula (D) is

$D = 1 – (\Sigma(n\text{-}1)/N(N\text{-}1))$

n = number of individuals of one species

N= total number of all individuals

Table C.1. Diversity rank based on the Shannon diversity index.

Shannon diversity index					
Diversity rank	**Year**	**Index**	**Diversity rank**	**Year**	**Index**
1	1998	0.7458	16	1989	0.4661
2	2004	0.6638	17	2013	0.4551
3	1988	0.6423	18	2001	0.4451
4	2003	0.6343	19	1986	0.4254
5	1999	0.6211	20	2007	0.4254
6	1987	0.6045	21	2009	0.4083
7	2016	0.601	22	2014	0.3946
8	2000	0.5944	23	2018	0.3487
9	2017	0.5943	24	1990	0.3453
10	2015	0.5824	25	2008	0.3427
11	2002	0.5556	26	1997	0.3392
12	2005	0.5529	27	1994	0.3391
13	1992	0.5364	28	1995	0.3303
14	2006	0.5363	29	1993	0.2617
15	1996	0.4698	30	1991	0.1961

Table C.2. Diversity rank based on the Simpson diversity index.

(%) indicates the probability of picking two fish of the same species in the sample

Simpson diversity index					
Diversity rank	**Year**	**Index(%)**	**Diversity rank**	**Year**	**Index(%)**
1	1998	0.2318	16	1989	0.4468
2	1988	0.2705	17	2009	0.475
3	2004	0.2826	18	2014	0.484
4	2003	0.287	19	2007	0.4916
5	1999	0.3033	20	2013	0.5168
6	2017	0.3123	21	2001	0.5322
7	1987	0.3125	22	1986	0.5528
8	1992	0.3343	23	1997	0.5756
9	2015	0.3433	24	1990	0.6067
10	2005	0.3657	25	2018	0.6121
11	2002	0.3715	26	2008	0.6407
12	2000	0.396	27	1994	0.6591
13	2016	0.397	28	1995	0.6778
14	1996	0.4196	29	1993	0.7521
15	2006	0.4367	30	1991	0.8032

Appendix D. Oceanographic indices charts used to make factor categories for ANOSIM and SIMPER analyses

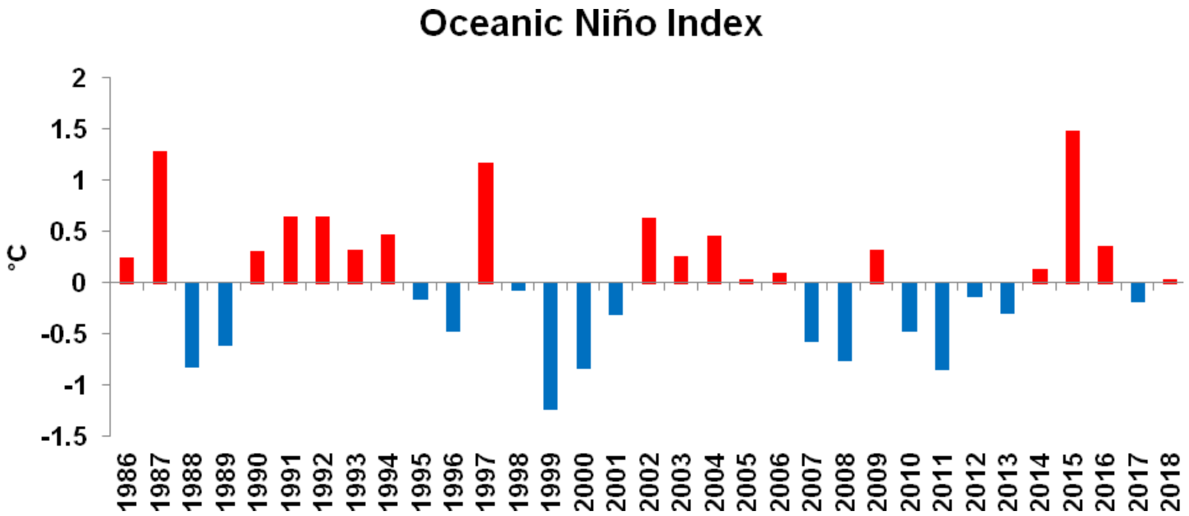

Figure D.1. Oceanic Niño Index (ONI) between 1986 and 2018, blue bars indicate cold water temperatures and red bars warm water temperatures.

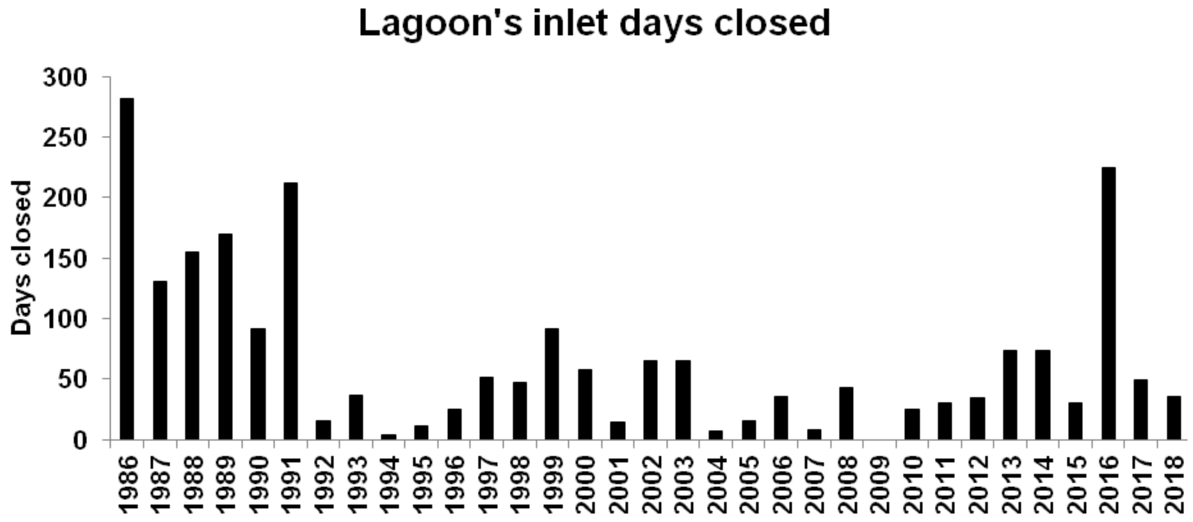

Figure D.2. Los Peñasquitos Lagoon inlet days closed between 1986 and 2018.

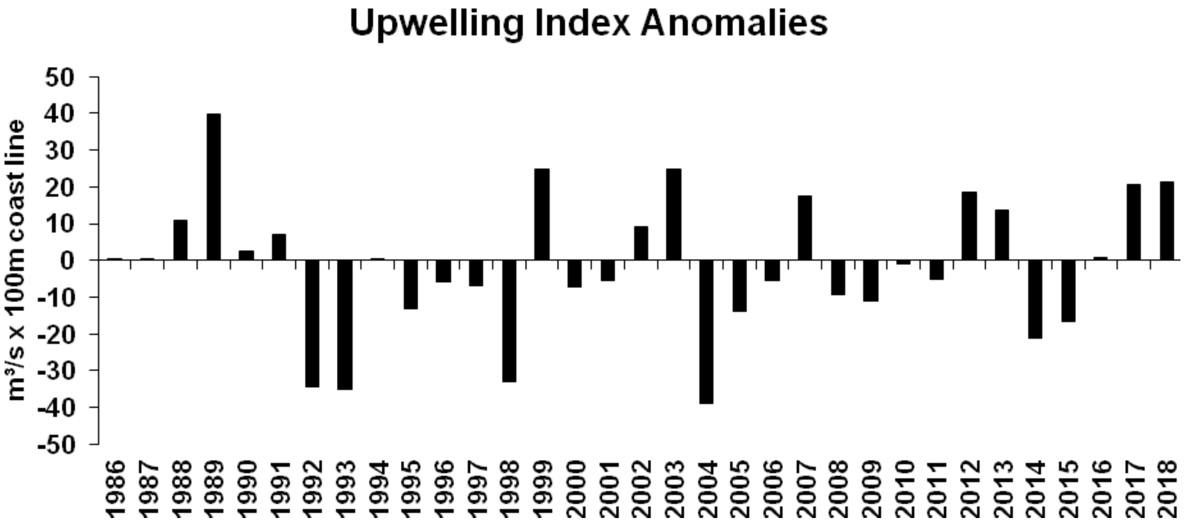

Figure D.3. Upwelling Index Anomalies (UIA) in southern California between 1986 and 2018.

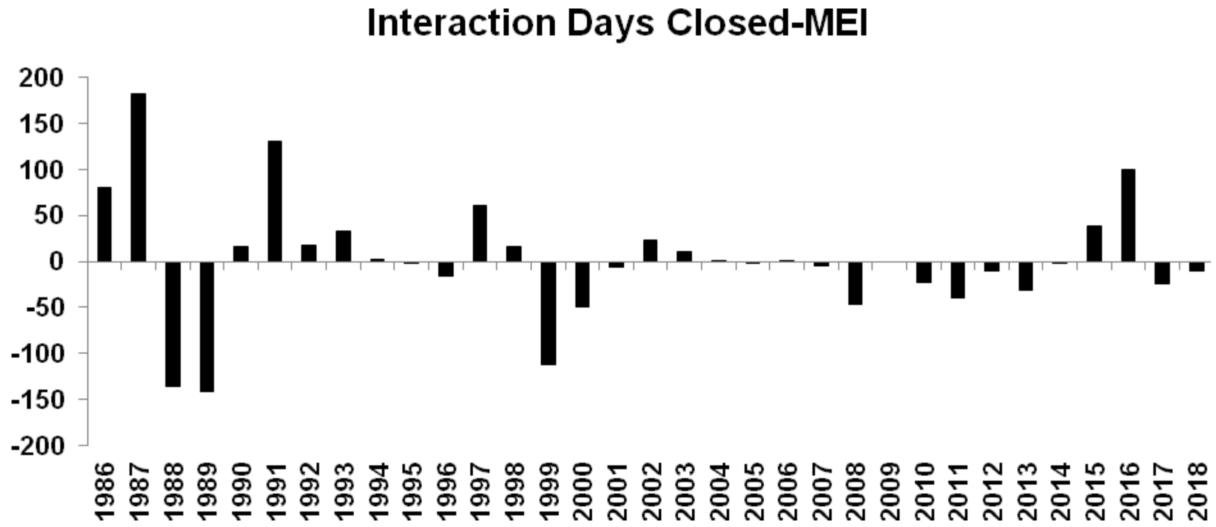

Figure D.4. Interaction days closed-MEI between 1986 and 2018.

Table D.1. Variables categorized in factors for the ANOSIM tests in the study period 1986-2018. ENSO= El Niño Southern Oscillation, UIA= Upwelling Index Anomalies, DC= Days Closed, INT.DC-MEI=Interaction of Days Closed-Multivariate Enso Index.

Variables	Comparison Factors	Values in chart	Variables	Comparison Factors	Values in chart
ENSO (ONI)	Very Strong Niño	1 or +	UIA	Strong upwelling	20 or +
	Strong Niño	0.5 to 1		Moderate upwelling	10 to 20
	Moderate Niño	0.25 to 0.5		Weak upwelling	0 to 10
	Normal conditions	0 to ±0.25		Weak downwelling	0 to -10
	Moderate Niña	- 0.25 to -0.5		Moderate downwelling	-10 to -20
	Strong Niña	- 0.5 to – 1		Strong downwelling	-20 or -
	Very strong Niña	-1 or -			
INT.DC-MEI	High positive	100 or +	DC	0-14 days	
	Moderate positive	50 to 100		15-30 days	
	Low positive	0 to 50		31-61 days	
	Low negative	0 to -50		62-92 days	
	Moderate negative	-50 to -100		93-123 days	
	Lower negative	-100 or -		124-154 days	
				155-185 days	
				186-216 days	
				217-247 days	
				248-278 days	
				279-309 days	

Appendix E. Physical and chemical variables time series

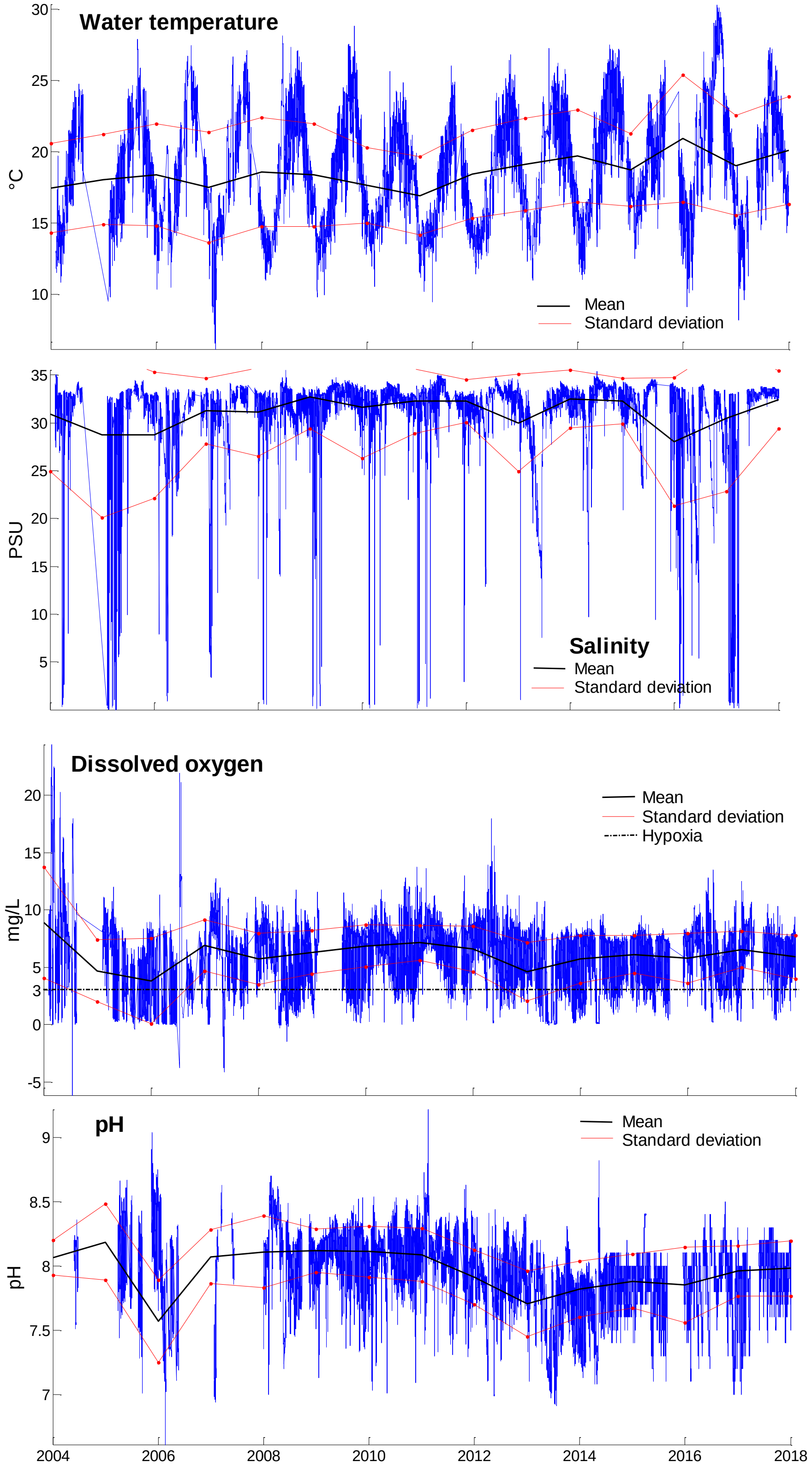

Figure E.1. Annual variation of the physical and chemical parameters (2004-2018).

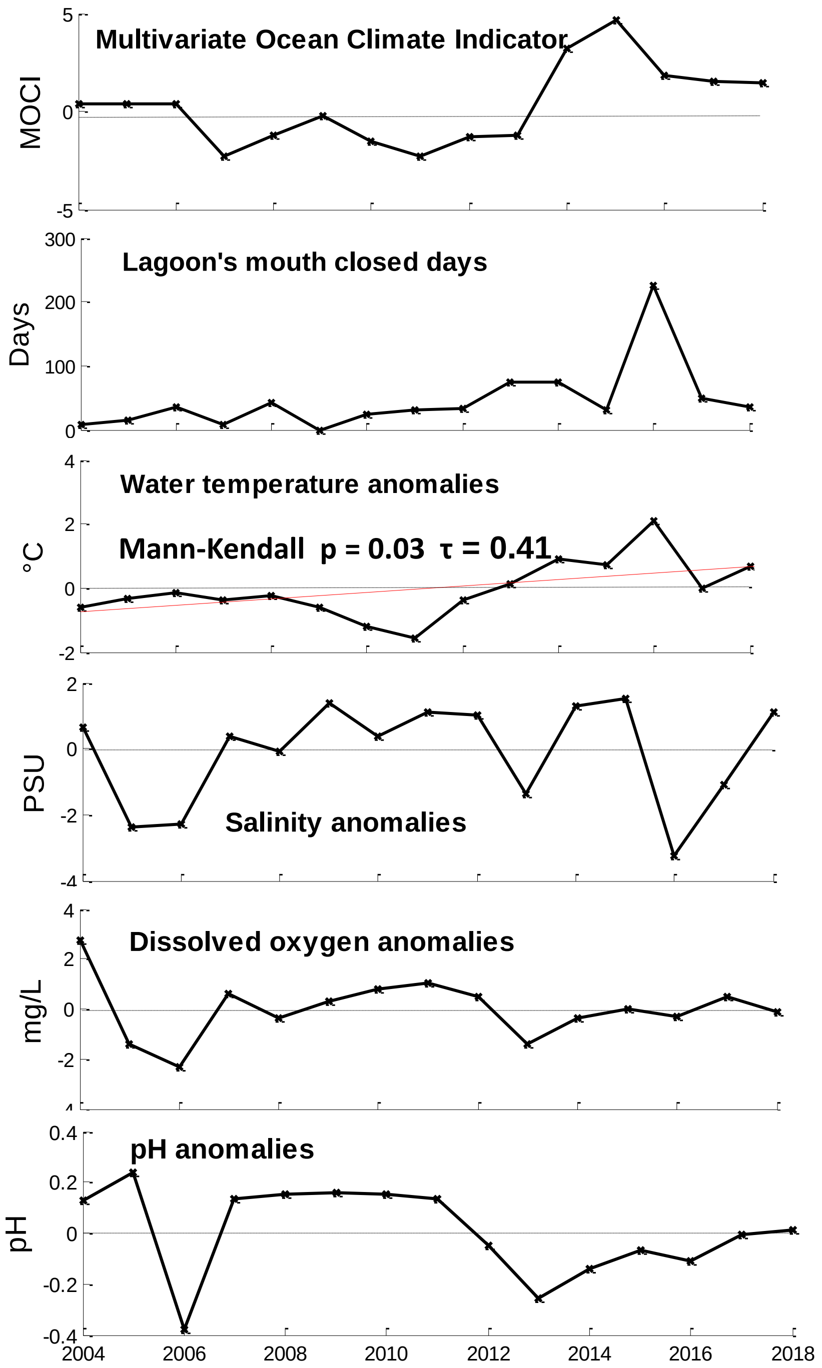

Figure E.2. Annual variation of southern California MOCI, days closed, physical and chemical parameters anomalies (2004-2018). The only statistically proven trend was the parameter water temperature anomaly.

Appendix F. Pearson correlations between abiotic variables

Moderate Pearson correlations were found between the abiotic variables: salinity anomalies and days closed (r = -0.56, p = 0.029), salinity anomalies and dissolved oxygen anomalies (r = 0.56, p = 0.028), and dissolved oxygen anomalies and ph anomalies (r = 0.56, p = 0.028). The strongest Pearson correlations corresponded to water temperature anomalies and days closed (r = 0.76, p = 0.001), water temperature anomalies and MOCI (r = 0.71, p = 0.003), and water temperature anomalies and interaction days closed-MOCI (r = 0.83, p = 0.0001).

Appendix G. Pearson correlations between fish species and abiotic variables

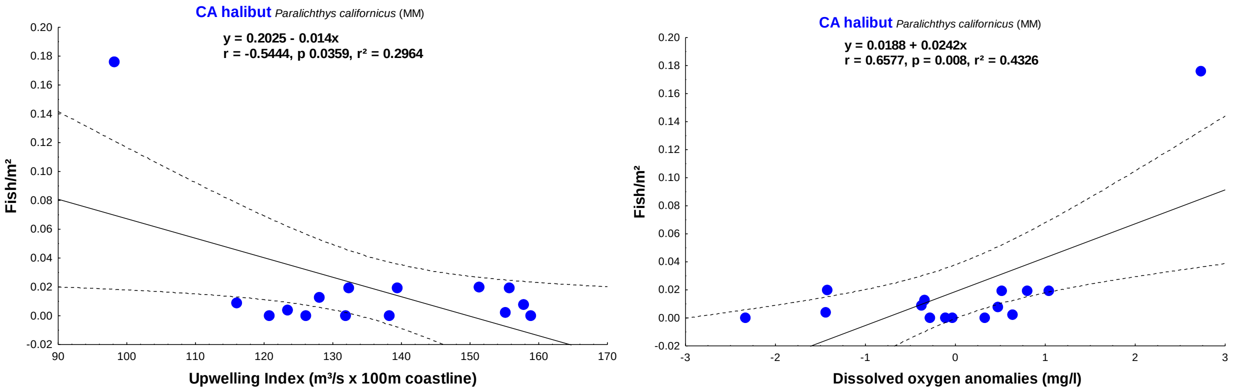

Figure. G.1. Influence of the upwelling index and dissolved oxygen anomalies in the density of CA halibut, *Paralichthys californicus* in Los Peñasquitos Lagoon between 2004 and 2018.

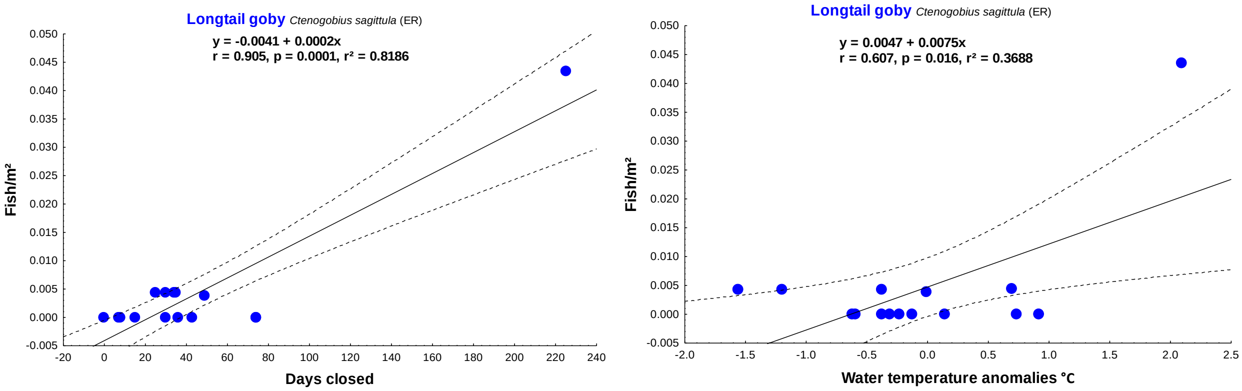

Figure. G.2. Influence of days closed and water temperature anomalies in the density of longtail goby *Ctenogobius sagittula* in Los Peñasquitos Lagoon between 2004 and 2018.

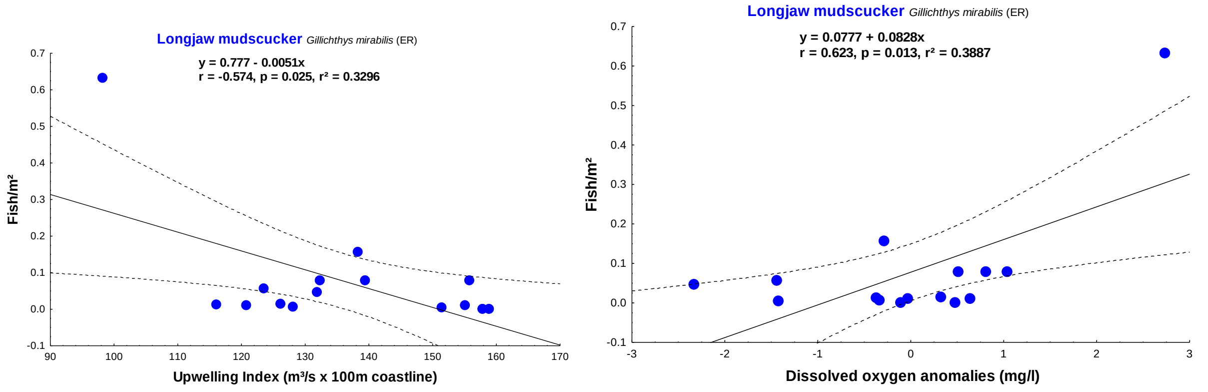

Figure. G.3. Influence of the upwelling index and dissolved oxygen anomalies in the density of longjaw mudscucker, *Gillichthys mirabilis* in Los Peñasquitos Lagoon between 2004 and 2018.

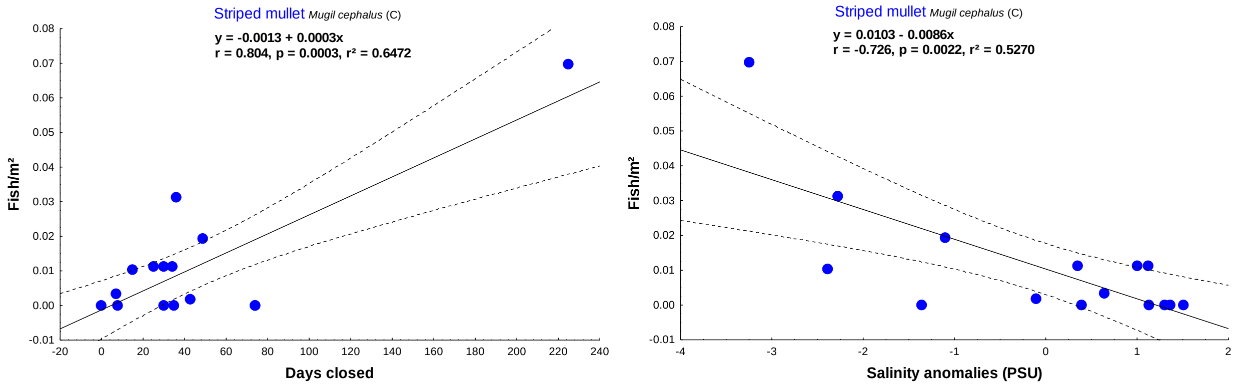

Figure. G.4. Influence of days closed and water temperature anomalies in the density of striped mullet, *Mugil cephalus* in Los Peñasquitos Lagoon between 2004 and 2018.

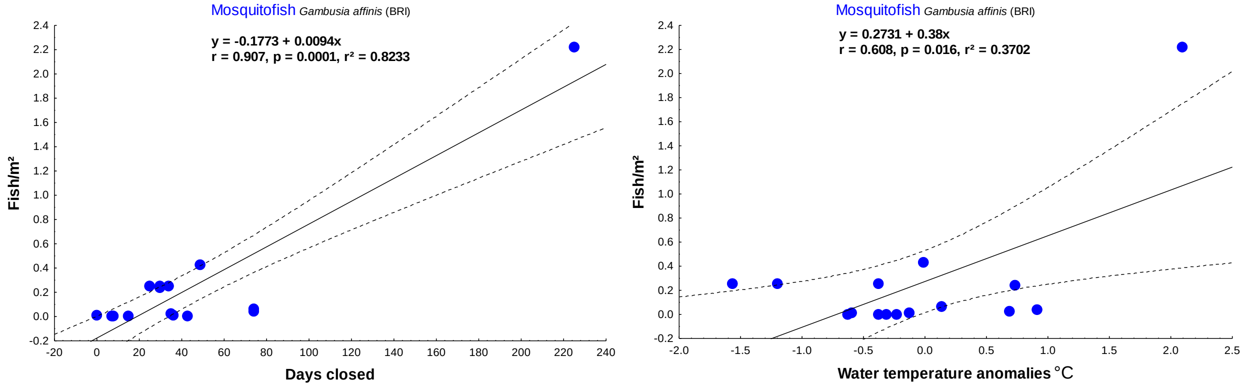

Figure. G.5. Influence of days closed and water temperature anomalies in the density of mosquitofish, *Gambusia affinis* in Los Peñasquitos Lagoon between 2004 and 2018.

Appendix H. BIOENV/BVSTEP results in LPL 2004-2018

The BIOENV/BVSTEP routines presented a model that maximized correlations between the abiotic variables and fish densities.

The best model was Dissolved oxygen anomalies + Days closed + MOCI that showed a moderate Spearman correlation r = 0.411. The second-best model was Water temperature anomalies + Dissolved oxygen anomalies + Days closed + MOCI, with a moderate Spearman correlation r = 0.375.

Appendix I. Complementary SIMPER results

For the 30 year study period, the factor comparison results of 31 – 61 days vs. 155 – 185 days indicated an average dissimilarity of 75.35% in the fish community. Four species contributed with 84% of the accumulated dissimilarities, these species were topsmelt, *Atherinops affinis*, goby group, mosquitofish, *Gambusia affinis,* and California killifish, *Fundulus parvipinnis.* Factor 31 – 61 days had positive effects in the species goby group, California killifish, *Fundulus parvipinnis,* deepbody anchovy, *Anchoa compressa,* California halibut, *Paralichthys californicus,* striped mullet, *Mugil cephalus,* and yellowfin goby, *Acanthogobius flavimanus* (Table I.1.). Factor 155 – 185 days had positive effects in topsmelt, *Atherinops affinis*, mosquitofish, *Gambusia affinis,* staghorn sculpin, *Leptocottus armatus,* and longjaw mudsucker, *Gillichthys mirabilis.*

Table I.1. SIMPER results analyzing variable Days Closed, factors 31-61 days closed vs. 155-185 days closed. Species contributions to dissimilarities and comparisons of factor effects over species. Effects: Positive ↑, Negative ↓, Equal =.

SIMPER			Average dissimilarity = 75.35%	
	Factors effects		Dissimilarities	
Species	Closure 31- 61 days	Closure 155 -185 days	Contribution %	Cumulated %
Topsmelt *Atherinops affinis*	↓	↑	38.84	38.84
Goby group	↑	↓	18.5	57.33
Mosquitofish *Gambusia affinis*	↓	↑	15.84	73.17
CA killifish *Fundulus parvipinnis*	↑	↓	11.26	84.43
Staghorn sculpin *Leptocottus armatus*	↓	↑	4.34	88.77
Deepbody anchovy *Anchoa compressa*	↑	↓	4.25	93.02
Longjaw mudsucker *Gillichthys mirabilis*	↓	↑	4.21	97.22
Striped mullet *Mugil cephalus*	↑	↓	1.97	99.2
Yellowfin goby *Acanthogobius flavimanus*	↑	↓	0.46	99.65
CA halibut *Paralichthys californicus*	↑	↓	0.28	99.93
Longtail goby *Ctenogobius sagittula*	=	=	0.07	100

SIMPER results with Interaction Days Closed – Multivariate ENSO Index (INT. DC-MEI)

The factors comparison Moderate + vs. Low - analyzed in the SIMPER routine indicated an average dissimilarity of 57.94%. Four fish species together contributed 82% of the accumulated dissimilarities in the fish community, the species were topsmelt, *Atherinops affinis*, goby group, longjaw mudsucker, *Gillichthys mirabilis*, and California killifish, *Fundulus parvipinnis*. Moderate + had positive effects in the species longjaw mudsucker, *Gillichthys mirabilis,* deepbody anchovy, *Anchoa compressa,* and striped mullet, *Mugil cephalus.* The factor Low - presented positive effects on topsmelt, *Atherinops affinis*, goby group, California killifish, *Fundulus parvipinnis*, staghorn sculpin, *Leptocottus armatus*, and mosquitofish, *Gambusia affinis* (Table I.2.).

Table I.2. SIMPER results analyzing variable Interaction Days Closed – Multivariate ENSO Index, factors Moderate + vs. Low -. Species contributions to dissimilarities and comparisons of factor effects over species. Effects: Positive ↑, Negative ↓, Equal =.

SIMPER			Average dissimilarity = 57.94%	
	Factors effects		Dissimilarities	
Species	Moderate +	Low -	Contribution %	Cumulated %
Topsmelt *Atherinops affinis*	↓	↑	36.49	36.49
Goby group	↓	↑	24.17	60.66
Longjaw mudsucker *Gillichthys mirabilis*	↑	↓	10.63	71.29
CA killifish *Fundulus parvipinnis*	↓	↑	10.55	81.84
Deepbody anchovy *Anchoa compressa*	↑	↓	5.56	87.4
Striped mullet *Mugil cephalus*	↑	↓	4.47	91.87
Staghorn sculpin *Leptocottus armatus*	↓	↑	3.48	95.35
Mosquitofish *Gambusia affinis*	↓	↑	2.68	98.03
Yellowfin goby *Acanthogobius flavimanus*	=	=	1.45	99.48
CA halibut *Paralichthys californicus*	=	=	0.39	99.88
Longtail goby *Ctenogobius sagittula*	=	=	0.12	100

The fish community had an average dissimilarity of 56.11% resulted from factors comparison High + vs. Low -. The fish species topsmelt, *Atherinops affinis*, goby group, mosquitofish, *Gambusia affinis*, and longjawmudsucker, *Gillichthys mirabilis*, contributed together with approximately 82% of the dissimilarities in the fish community. The effects over the community showed that Low- was more beneficial than High+ because six species presented positive effects against three species in the case of High+. Low- had positive effects on topsmelt, *Atherinops affinis*, goby group, California killifish, *Fundulus parvipinnis*, staghorn sculpin, *Leptocottus armatus*, deepbody anchovy, *Anchoa compressa*, and yellowfin goby, *Acanthogobius flavimanus*. High+ had positive effects in mosquitofish, *Gambusia affinis*, longjawmudsucker, *Gillichthys mirabilis*, and striped mullet, *Mugil cephalus* (Table I.3.).

Table I.3. SIMPER results analyzing variable Interaction Days Closed – Multivariate ENSO Index, factors High+ vs. Low -. Species contributions to dissimilarities and comparisons of factor effects over species. Effects: Positive ↑, Negative ↓, Equal =.

SIMPER			Average dissimilarity = 56.11%	
	Factors effects		Dissimilarities	
Species	High +	Low -	Contribution %	Cumulated %
Topsmelt *Atherinops affinis*	↓	↑	27.75	27.75
Goby group	↓	↑	23.34	51.09
Mosquitofish *Gambusia affinis*	↑	↓	17.75	68.84
Longjaw mudsucker *Gillichthys mirabilis*	↑	↓	11.83	80.67
CA killifish *Fundulus parvipinnis*	↓	↑	11.75	92.42
Staghorn sculpin *Leptocottus armatus*	↓	↑	3.01	95.43
Deepbody anchovy *Anchoa compressa*	↓	↑	2.91	98.35
Yellowfin goby *Acanthogobius flavimanus*	↓	↑	0.63	98.98
Striped mullet *Mugil cephalus*	↑	↓	0.59	99.57
CA halibut *Paralichthys californicus*	=	=	0.33	99.9
Longtail goby *Ctenogobius sagittula*	=	=	0.1	100

The results of the comparisons between High- vs. Low- indicated an average dissimilarity of 65.94% in the fish community and an accumulated dissimilarity of 81% with contributions to the dissimilarity of four fish species, topsmelt, goby group, mosquitofish, and California killifish (Table I.4.). High- was the factor with effects in more fish species, seven in total, these were topsmelt, *Atherinops affinis*, mosquitofish, *Gambusia affinis*, longjaw mudsucker, *Gillichthys mirabilis*, deepbody anchovy, *Anchoa compressa*, staghorn sculpin, *Leptocottus armatus*, striped mullet, *Mugil cephalus*, and yellowfin goby, *Acanthogobius flavimanus*. Factor Low- had positive effects in only three species, goby group, California killifish, *Fundulus parvipinnis*, and California halibut, *Paralichthys californicus*.

Table I.4. SIMPER results analyzing variable Interaction Days Closed – Multivariate ENSO Index, factors High- vs. Low -. Species contributions to dissimilarities and comparisons of factor effects over species. Effects: Positive ↑, Negative ↓, Equal =.

SIMPER			Average dissimilarity = 65.94%	
	Factors effects		Dissimilarities	
Species	High -	Low -	Contribution %	Cumulated %
Topsmelt *Atherinops affinis*	↑	↓	38.36	38.36
Goby group	↓	↑	21.21	59.57
Mosquitofish *Gambusia affinis*	↑	↓	13.13	72.69
CA killifish *Fundulus parvipinnis*	↓	↑	8.56	81.25
Longjaw mudsucker *Gillichthys mirabilis*	↑	↓	5.49	86.74
Deepbody anchovy *Anchoa compressa*	↑	↓	4.8	91.54
Staghorn sculpin *Leptocottus armatus*	↑	↓	4.36	95.9
Striped mullet *Mugil cephalus*	↑	↓	2.01	97.91
Yellowfin goby *Acanthogobius flavimanus*	↑	↓	1.79	99.7
CA halibut *Paralichthys californicus*	↓	↑	0.27	99.97
Longtail goby *Ctenogobius sagittula*	=	=	0.03	100