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Biology, fisheries and population status of ispi *Orestias ispi* (Vertebrata: Ciprinodontidae) on Lake Titicaca, Peru

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Summary: The ispi (*Orestias ispi*) is one of the species targeted by artisanal fishing in Lake Titicaca. The aim of this study was to understand the most important aspects of ispi biology and fishing, to offer an evaluation of its population situation and degree of exploitation, and to contribute to fisheries management. Information on official fish landings from the Ministry of Production and Puno Regional Production Directorate (1981–2021) and capture, effort and biological data from the Peruvian Sea Institute (2008–2021) were used. Fish landings show an established pattern, with values below 1500 t/year and a biomass of 42336 t for 2021. The size structure was 3.5 a 9.5 cm total length (TL) and the mean size range was 6.1 to 7.1 cm TL, showing a non-significant negative trend in relation to the minimum catch size. Growth parameters showed a maximum asymptotic length (L_{inf}) of 9.76 cm TL and a growth rate (K) of 1.01 year^{-1}. The gonadosomatic index showed greater intensity of reproductive activity between July and October, and the size at maturity (LM50%) was 5.2 cm TL. Simulations carried out with the method based on catch maximum sustainable yield indicate that the ispi is at the full exploitation level.

Keywords: catch maximum sustainable yield; degree of exploitation; length-based assessment; *Orestias ispi*; size at maturity.

Biología, pesca y estado población del ispi *Orestias ispi* (Vertebrata: Ciprinodontidae) en el lago Titicaca, Perú

Resumen: El *Orestias ispi* es una de las especies de la pesca artesanal en el lago Titicaca. El objetivo fue entender los aspectos más relevantes de la biología y la pesca del ispi, así como ofrecer una evaluación de su situación poblacional y grado de explotación, y coadyuvar en la gestión pesquera. Se utilizó información de desembarques oficiales del Ministerio de la Producción y Dirección Regional de Producción Puno (1981-2021), captura, esfuerzo y datos biológicos del Instituto del Mar del Perú (2008-2021). Los desembarques presentan un patrón establecido con valores por debajo de los 1500 t/año y una biomasa de 42336 t para el 2021. Con una estructura por tamaños de 3,5 a 9,5 cm LT, con rango valores de talla media de 6,1 a 7,1 cm LT que mostraron una tendencia negativa no significativa. Con parámetros de crecimiento de longitud máxima asintótica (L_{inf}) en 9,76 cm LT y tasa de crecimiento (K) de 1,01 año^{-1}. El índice gonadosomático (IGS) mostró mayor intensidad de la actividad reproductiva entre julio y octubre y la talla madurez (LM50%) fue 5,2 cm LT. Las simulaciones realizadas con el método basado en captura y máximo rendimiento sostenible (CMSY) indican que el ispi se encuentra en nivel de plena explotación

Palabras clave: Evaluación basada en longitud; grado de explotación; método basado en captura; *Orestias ispi;* talla de madurez.

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INTRODUCTION

At 3810 m above sea level, Lake Titicaca is the highest navigable lake on the planet (Wirrmann 1991). It is home to a wide range of plant and animal species, and the large number of native fish include more than 30 species of the genus *Orestias* and two of the genus *Trichomycterus* (Sarmiento et al. 1987) (Fig. 1).

The ispi (*Orestias ispi*) is a native fish of the *Orestias* group (Chura 2012). Its rapid growth allows us to infer that recruitment to the fishing gear occurs between 7 months and 1 year of age, at sizes of 4 to 6 cm total length (TL). During the day they remain at less than 50 m depth, whereas at night they move between 25 and 45 m depth They approach the shore to reproduce, feed and find shelter (IMARPE 2016, 2018), and their diet is principally zooplankton (Gutiérrez 2013). The ispi supports the lake's pelagic fishery and greatly exceeds the Argentine silverside (*Odontesteshes bonariensis*) in biomass and landings (IMARPE 2010, IMARPE 2019, PRODUCE 2021).

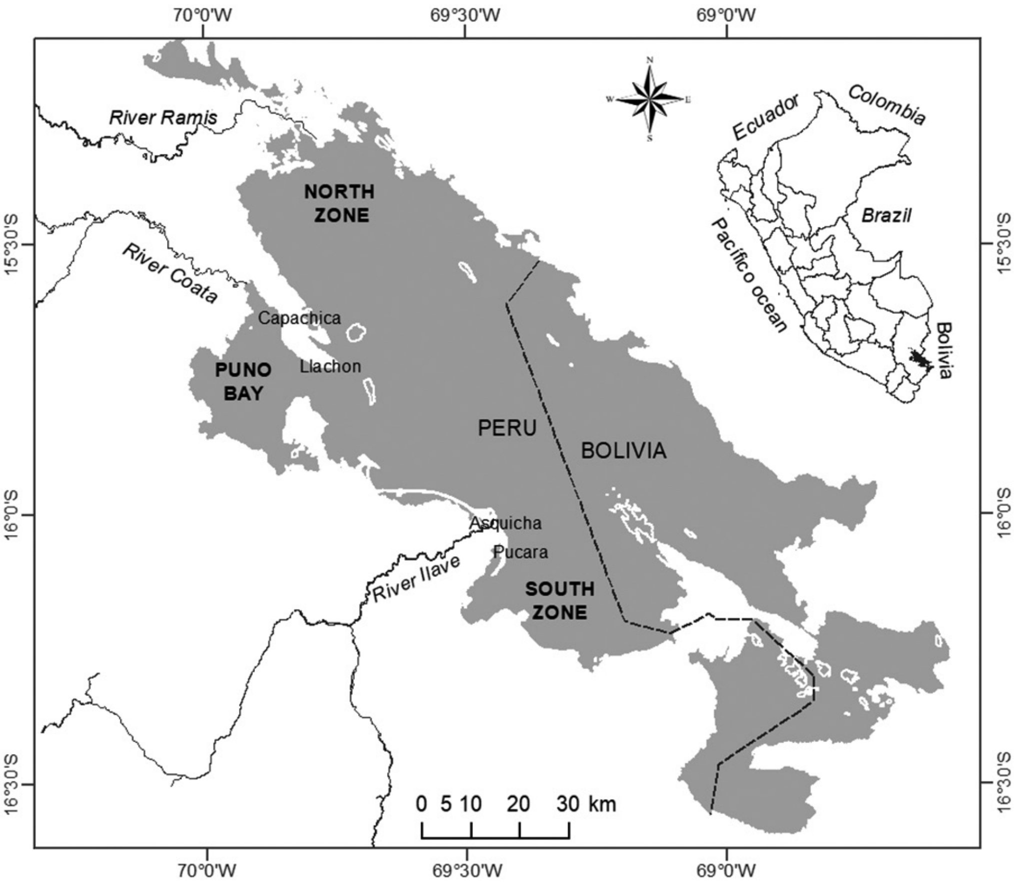

Fig. 1. – Location map of Lake Titicaca.

Fishing in Lake Titicaca plays a crucial role in the local economy and is complemented by agriculture and livestock in the Puno area (IMARPE 2008, Santiago et al. 2013). Currently, fishing activity has shown technological changes, including the use of wooden and fibreglass boats with outboard motors, very effective fishing gear and gear (monofilament nylon nets) and changes in the mesh sizes of curtain nets, and the fishers have extensive knowledge of the behaviour of the fishery resources (Ocola et al. 2021). The total number of fishers in the Peruvian sector of Lake Titicaca in 2006 was 1562, divided into (i) permanent fishers, who fish more than 200 days a year; (ii) temporary fishers, who fish between 100 and 200 days, and (iii) sporadic fishers, who fish fewer than 100 days a year, linking their activity to the agricultural cycles (Segura et al. 2013). For the year 2019, the number of fishers in Lake Titicaca was estimated at 1549, a figure very similar to that of 2006 (Ocola et al. 2021).

Due to the high demand for the ispi resource for both direct and indirect human consumption, the Ministry of Production implemented control standards to regulate its exploitation, such as a minimum catch size (MCS) of 6.3 cm TL and a minimum mesh size (curtain net) of 15.3 mm mesh length through Ministerial Resolution (MR) No. 271-2010-PRODUCE. Fishing is also prohibited during the breeding season through MR N° 022-2010-PRODUCE.

The aim of the study was to understand the main biological and fishery aspects of the ispi and to present an overview of its population status and exploitation level in order to contribute to the management of this resource.

MATERIALS AND METHODS

Fisheries indicators

We used annual landings extracted from the landing fish yearbooks of Puno Regional Production Department from 1981 to 2012, as well as from the fisheries and aquaculture statistical yearbooks of Ministry of Production between 2013 and 2021. We also used records of the ispi biomass evaluations in Lake Titicaca carried out by Peruvian Institute of the Sea (IMARPE) and the Lake Titicaca Special Project (PELT) between 1985 and 2021 using acoustic techniques (Castillo et al. 2009) applied to the entire surface of the lake. The evaluations were conducted annually in the month of July.

Biological indicators

The biological and size analyses were based on information obtained through IMARPE (the data collection system of the Lake Titicaca Fisheries Monitoring from IMARPE) corresponding to the period 2008–2021. For this purpose, monitoring records were used from 24 landing points distributed along the Peruvian circumlacustrine ring, organized into three macrozones: Puno Bay, North and South zones. The collection of biological and size information at the landing points was subject to the availability of the ispi resource, since at certain times of the year it was not accessible for fishing due to its migrations within the lake (Valdés and Cuadros 2022).

Structure by size and the information on landing sites were examined and confirmed. A weighting procedure was then performed by month (*mo*) and landing site (*fa*) according to the following description:

$$fp_{(mo,fa,s)} = \sum fabs_{(mo,\mathrm{fa,s})} * \frac{\sum d_{(mo,\mathrm{fa})}}{\sum p_{sample(mo,fa)}}$$

where $fp_{(mo,\mathrm{fa,s})}$ is the adjusted frequency for size s; $f\,abs_{(mo,\mathrm{fa,s})}$ is the absolute frequency; $p_{samble\,(mo,fa)}$ is sample weight (kg) and $d_{(mo,\mathrm{fa})}$ is total landings (kg).

The purpose of this procedure is to determine the relevance of the composition by size of commercial fishing, considering the amount of catch in each macrozone according to the landings sites and months of the year.

The average size was estimated as proposed by Sparre and Venema (1997), calculated by dividing the aggregate size distribution by the sum of the frequencies of all class marks. The global average fluctuation sizes were calculated by year and macrozone. Then a simple linear regression analysis was performed to assess the significance of the trend in average annual catch size. A t-test was performed to compare the average annual catch size in relation to the MCS.

The juvenile fishery incidence rate was the proportion of fish caught below the MCS (6.3 cm TL) relative to the total catch. The MCS was established in MR No. 271-2010-PRODUCE.

For ispi commercial fishing, monofilament nylon curtain nets are used in sizes from 40 to 60 m length and 0.6 to 0.8 m height, and the most commonly used mesh sizes are 13 and 16 mm. The nets are placed in the afternoon and collected in the early hours of the day, remaining in the water for 12 to 13 hours (IMARPE 2016, Ocola et al. 2021, Huamán and Alarcón 2025). Curtain nets of different mesh sizes are characterized by being selective by mainly catching a range of commercial fish sizes (3.5 to 9.5 cm TL). The study was complemented with information from ispi samplings from scientific cruises carried out in 2019 (1.5 to 7.5 cm TL) using trawls at depths greater than 50 m (Ninaraqui et al. 2022, Valdés and Cuadros 2022).

Based on the selected data, the following indicators were calculated:

The gonadosomatic index (GSI) was calculated according to the formula of Vazzoler (1982):

$$GSI = \left(\frac{Wg}{We}\right) * 100$$

where *Wg* is the weight of the gonad (g) and *We* is the eviscerated weight of the fish (g). The monthly fluctuation of this indicator allowed the recognition of the reproductive cycle. A Kruskal-Wallis test (a non-parametric ANOVA) was used to determine significant differences in reproductive season.

The reproductive condition was determined using the gonadal development scale for teleost fishes (Johansen 1924), which distinguishes eight phases.

The application of this technique for size at gonadal maturity (LM_{50}%) included the following steps:

a) Establishment of length at maturity from a wide range of sizes, including small and large specimens, based on biological data from commercial fisheries and assessment cruises.

b) Classification of females into two sub-groups: the immature group, which showed gonadal maturity phases I and II; and the mature group, which showed phases III and IV. Other stages of maturity were not taken into account because they were in spawning and/or recovery situations, since the purpose of this study was to establish the length of change between immature and mature.

To calculate LM_{50}%, the *matSize* package created by Torrejón-Magallanes (2020) in the R tool was used, based on the formulas of Roa et al. (1999). The probability of reaching maturity at a specific size was assessed by logistic regression using bootstrap resampling and allowing repetition, in order to calculate the average probability and its confidence interval.

$$\mathrm{PL} = \frac{1}{1+e^{-(\beta_0+\beta_1 l)}}$$

where PL is the probability of a mature fish having a length l, β_0 is the slope and β_1 is the intercept.

$$\mathrm{LM}_{50}\% \text{ was calculated: } = -\frac{\beta_0}{\beta_1}$$

The *TropFishR* package (Mildenberger et al. 2017) of the R software (R Core Team 2023) was used to analyse the annual size structure between 2008 and 2018, following the procedure indicated by Sparre and Venema (1997). This package features improvements to the FAO-ICLARM Stock Assessment Tools II (FISAT II) functions (Gayanilo et al. 2005, Pauly 1980), incorporating some new approaches used in growth parameter estimation, along with new optimization methods (Taylor and Mildenberger 2017) and a comprehensive set of methods for the evaluation of size frequency data.

The length-based stock assessment method explained by Sparre and Venema (1997) and *TropFishR* (Mildenberger et al. 2017) were carried out within a bootstrap framework (Schwamborn et al. 2019). This made it easier to determine the range of uncertainty for all parameters and prevent the seed effect. This step was followed by length frequency data adjustments with an algorithm optimization function (ELEFAN GA and SA start-up; Schwamborn et al. 2019), which made it possible to calculate the uncertainties associated with the growth projections.

Total lengths grouped into class ranges of 0.5 cm TL were used to analyse growth parameters using a von Bertalanffy growth function that varies with the seasons (Pauly and Gaschutz 1979, Somers 1988):

$$L_t = L_{inf}\left(1 - e^{-(K(t-t_o)+S(t)-S(t_o))}\right)$$

where L_t is the total length (cm) at time t, L_{inf} is the asymptotic length of the fish (cm), K is the speed at which L_t approaches L_{inf}, t_0 is the hypothetical age of the fish at the time when L_t is zero, $S(t) = (cK/2\pi) \sin 2\pi(t - t_s)$, c represents a constant indicating the extent of the fluctuation, which usually ranges from 0 to 1 (a value >1 implies phases of decrease in height, which is uncommon), and t_s is the fraction of a year (relative to the age of recruitment, t=0) in which the sinusoidal oscillation begins (i.e. it becomes positive).

Growth parameters were assessed using a moving average. Since the parameters are known to be sensitive to moving average settings (Taylor and Mildenberger 2017), ELEFAN GA and SA bootstrapped function was executed for each assessment with 5 and 7 moving averages.

The estimated values of L_{inf} and K were used to determine the growth performance index (phi, φ) which was defined by (Pauly and Munro 1984) as:

$$\emptyset = logK + 2logL_{inf}$$

The theoretical age of the fish (t_o), was determined by the formula of Pauly (1979):

$$\log(-t_o) = -0.392 - 0.275 * logL_{inf} - 1.038 * logK$$

The beginning of the growth curve was aligned with the month of greatest reproductive activity. To obtain a suitable adjustment of the growth curve, length data were collected monthly during 2008 and 2018 using the methodology used by Palomares et al. (1987).

Natural mortality (M) was calculated using the empirical formula of Pauly (1980), which relates the average water temperature and the growth parameters (K and L_{inf}) and was determined in the following equation:

$$\mathrm{Log}_{10}\,\mathrm{M} = -0.0066 - 0.279\, log_{10}\, L_{inf} + 0.6543\, log_{10}\, K + 0.4634\, log_{10}\, T$$

where L_{inf} and K are von Bertalanffy's growth parameters and T is the average surface temperature (14.3°C) for 2008 to 2018.

Stock indicators

To calculate the catch per unit of effort (CPUE), we used data from daily landing and effort records of the artisanal fishing fleet in Lake Titicaca during the period 2008–2021 from 24 landing sites grouped into three macrozones (Puno Bay, North and South zones) provided by IMARPE. Information was primarily used from curtain nets, due to the amount of data available and their relevance to catches (~97%) (IMARPE 2022).

The CPUE represents a value proportional to the average abundance, expressed as

$$CPUE_{(kg/h)} = \frac{\sum C_{(kg)}}{\sum E_{(h)}}$$

where CPUE (*kg/h*) is the catch per unit effort, *C* is the agglomerated catch (kg), and *E* is fishing effort (cumulative hours). It should be noted that the unit of effort used to calculate the CPUE was the hours spent on the fishing trip.

Artisanal fishing provides limited information about population abundance, CPUE and historical catches (Fenner 2012), and low data quality (Ault et al. 2018), factors that hinder making estimates in stock assessment. In this context, it is useful to use assessment models with "poor data", which consider population parameters (sexual maturity, mortality, growth and longevity) to determine the status of the stock (Gedamke and Hoenig 2006). Access to such information is therefore essential in order to ensure effective management of fisheries resources (Fry et al. 2006).

Spawning potential ratio (SPR) was defined as the ratio of the number of eggs generated by a cohort throughout its life in a fishing context to the number of eggs that would have been generated during its life in a no-fishing situation. SPR values range from 0 to 1, usually presented as a percentage, and are frequently used to determine limit and target reference criteria for fishing activity (Clark 2002, Restrepo and Powers 1999).

Among the most widely used models is the length-based spawning potential ratio (LB-SPR) (Hordyk et al. 2015, Ault et al. 2018), whose principle is to determine a relationship between the reproductive potential of a stock without fishing (SPR 100%) and the stock after fishing (Prince et al. 2015). This method considers information on sizes and population parameters such as $LM_{50}\%$, L_{95}, M/K and L_{inf}, following the methodology of Hordyk et al. (2015). It is based on the equilibrium hypothesis and assumes that the observed size composition does not deviate from the expected structure due to fluctuation in mortality or recruitment. It also states that (1) growth is correctly represented by von Bertalanffy's formula, and (2) the size structure determined in the catch reflects the population, that is, the structure is not influenced by domed selectivity or incomplete sample of the population.

The studies were carried out using the *LB-SPR* package designed for the R platform, which can be found at: https://cran.r-project.org/web/packages/LBSPR/vignettes/LBSPR.html

The catch maximum sustainable yield method (CMSY) (Froese et al. 2017) uses Monte-Carlo simulations to estimate reference points—maximum sustainable yield (MSY), fishing mortality at MSY (F_{MSY}) and biomass at MSY (B_{MSY}). It also estimates the relative stock size (B/B_{MSY}) and the exploitation rate (F/F_{MSY}) based on catch data. In addition, it presents a Bayesian implementation of the Schaefer model (BSM), which is fitted to catch data together with an abundance index (CPUE or biomass).

The basic dynamics of biomass is defined by the following formula:

$$B_{t+1} = B_t + r\left(1 - \frac{B_t}{K}\right)B_t - C_t$$

where B_{t+1} is the biomass exploited in the subsequent year t+1, B_t is the current biomass, C_t is the catch in the year *t*, *K* is carrying capacity and *r* is the intrinsic growth rate. This approach provides suitable estimates of the relative biomass and rate of resource extraction, having been implemented in 400 fish and invertebrate groups from ten ecoregions in European seas (Froese et al. 2017). The R code to use this approach can be accessed at: https://oceanrep.geomar.de/id/eprint/52147/

The initial dataset used to apply this method used landings from 1981 to 2021. A priori values for the intrinsic growth rate (*r*) of 0.6 to 1.0 were also taken into account. Similarly, it was decided to use a relative stock size in the first year (B_{1981}/K), with an amplitude that varied between 0.6 and 0.8 K (beginning of fishing activity) and for the last year (B_{2021}K) from 0.4 to 0.6K. Nominal CPUE (2008–2021) was incorporated in order to generate suitable predictions about relative biomass and exploitation rate. Data from the abundance indices of the historical biomass series of research cruises (1985–2021) were removed because they were not separated specifically for the Peru sector.

RESULTS

Fishery indicator

Fish landings do not show a random order (R=15; p=0.04) but follow an established pattern. Landings below 100 t were recorded between 1989 and 1991, followed by the years 1996, 1999, 2002 and 2021. Landings below 500 t were recorded in the years 1995, 2000, 2015 and 2016 and landings above 500 t in the years 1983, 1993, 2007, 2011 and 2017. (Fig. 2).

There are no time series data on biomass in the Peruvian sector of the lake, which made it difficult to analyse its evolution and trends. The highest biomass value for Lake Titicaca was recorded in 2017 (76844 t) and the lowest in 1996 (27240 t). Between 2011 and 2017, a gradual increase from 42273 to 76844 t was recorded. For 2021, a biomass of 42336 t was recorded (Fig. 2).

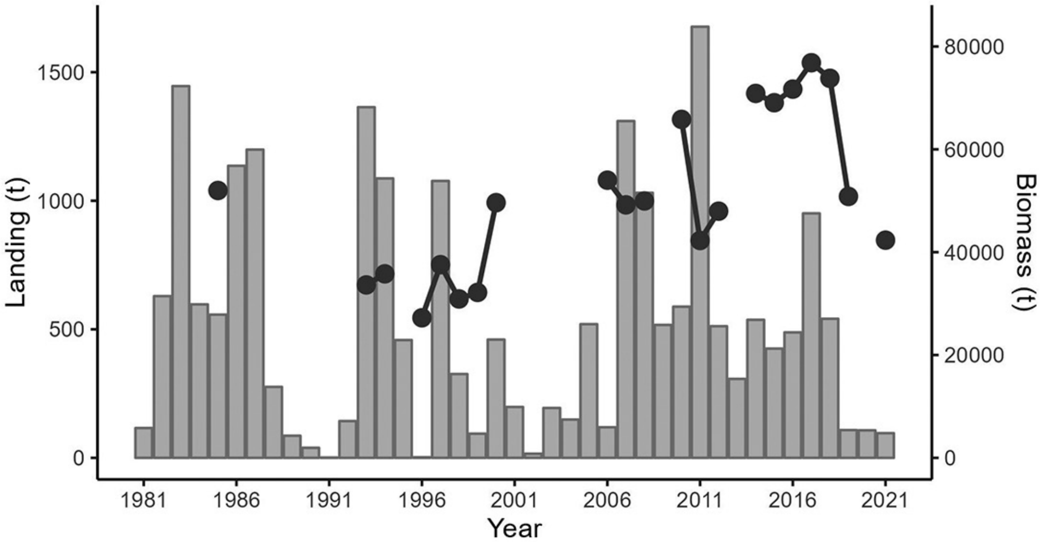

Fig. 2. – Ispi landings and biomass in the Peruvian sector of Lake Titicaca 1981–2021 (IMARPE and PRODUCE).

Biological indicators

Size structure showed a breadth of lengths between 3.5 and 9.5 cm TL from the measurement of 131443 individuals, while the weighted mean length ranged from 6.1 cm TL (2021) to 7.1 cm TL (2008).

The average annual catch size values were not statistically different from the established MCS (t_{14} = 0.99, p=0.3499). However, the trend the average annual catch showed a significant negative trend (r^2=0.29; p=0.04). In 2009, 2013, 2016 and 2019–2021, mean sizes were below the MCS (6.3 cm TL), whereas in 2008, 2011, 2012 and 2014 they were above the MCS (Fig. 3).

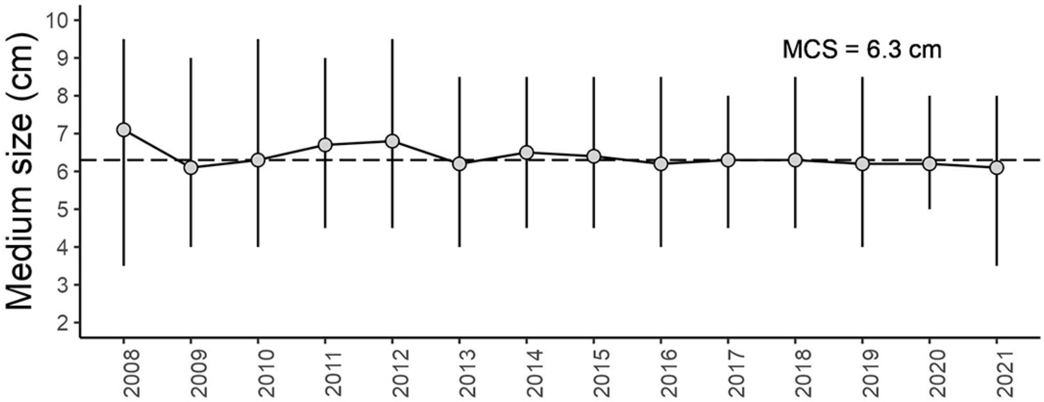

Fig. 3. – Weighted average and extreme sizes (minimum and maximum) in the landings of the ispi (2008-2021). Horizontal dashed line is the minimum catch size (MCS).

According to the macrozones analysis (Fig. 4), the following was evident:

In Puno Bay, mean sizes were below the MCS for the years 2009 (6.1 cm TL), 2013 (6 cm TL), 2016 (6.2 cm TL), and 2021 (6.1 cm TL), and above the MCS in 2008 (7 cm TL), 2012 (6.6 cm TL) and 2015 (6.4 cm TL). The series shows a slight non-significant negative trend (r^2=0.15; p=0.17). In the North zone, mean size did not show a clear trend, with values below the MCS in 2013 (6.1 cm TL) and 2016 (6.1 cm TL) and values above the MCS in 2012 (6.8 cm TL), 2015 (6.6 cm TL), and 2020 (6.6 cm TL).

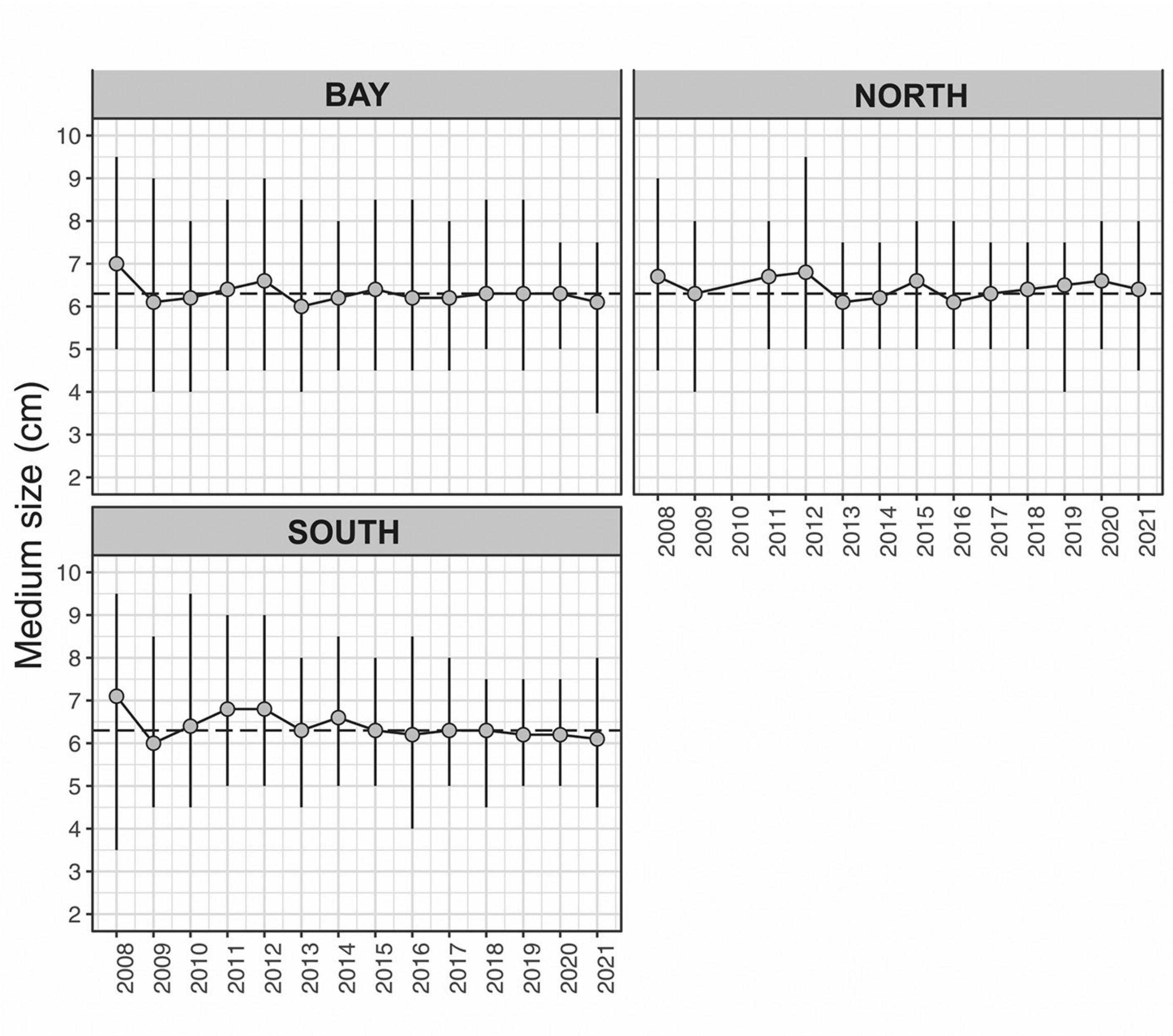

Fig. 4. – Average catch size of the ispi by area of Lake Titicaca, 2008–2021; whiskers indicate maximum and minimum sizes. The horizontal dashed line represents the minimum catch size (MCS).

In the southern zone, mean size values were above the MCS in 2008 (7.1 cm TL), 2011 (6.8 cm TL) and 2014 (6.6 cm TL) and below the MCS in 2009 (6 cm TL), 2016 (6.2 cm TL), and 2019–2021 (6.2 to 6.1 cm TL). The trend in mean size was negative and significant (r^2=0.32; p=0.03).

The trend in the rate of individuals with a length below the MCS in landings was positive but not significant (r^2=0.25, p=0.07), with the minimum value in 2008 and the maximum in 2013 and with values below 50% between 2014 and 2021, except 2016 (Fig. 5).

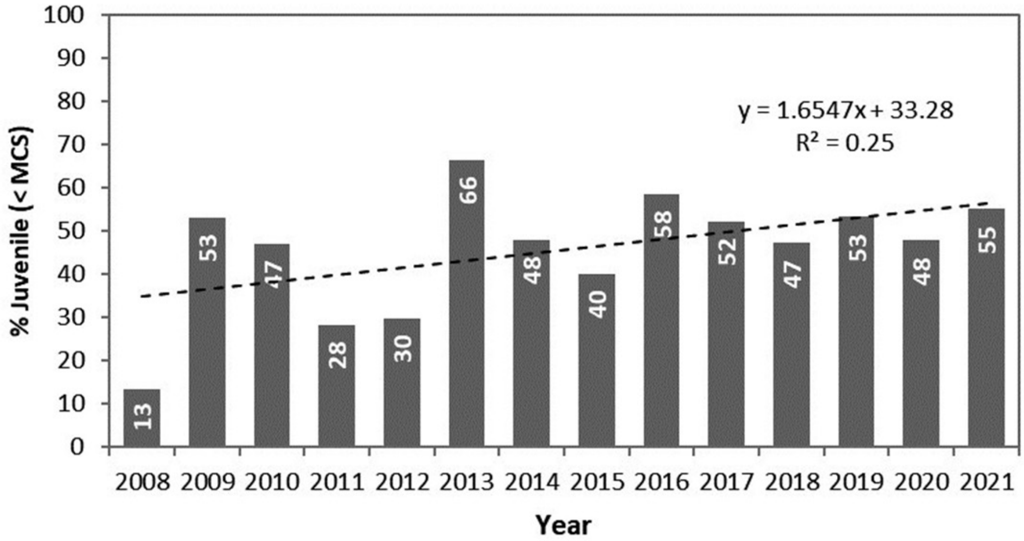

Fig. 5. – Percentage incidence of specimens of ispi smaller than the minimum catch size in landings in Lake Titicaca (2008–2021). Dashed line represents a trend.

The GSI varied throughout the year ($p<0.05$, ANOVA Kruskal-Wallis test). From the analysis of the monthly progression of the GSI (Fig. 6) in females between 2008 and 2018, high values were recorded from July to October, with a peak in September, which is interpreted as the period of greatest spawning intensity. With respect to MR N° 022-2011-PRODUCE, which establishes the reproductive closure period in two periods, from March to April and from September to October, the length values observed in this study differed between the beginning and end of the spawning season.

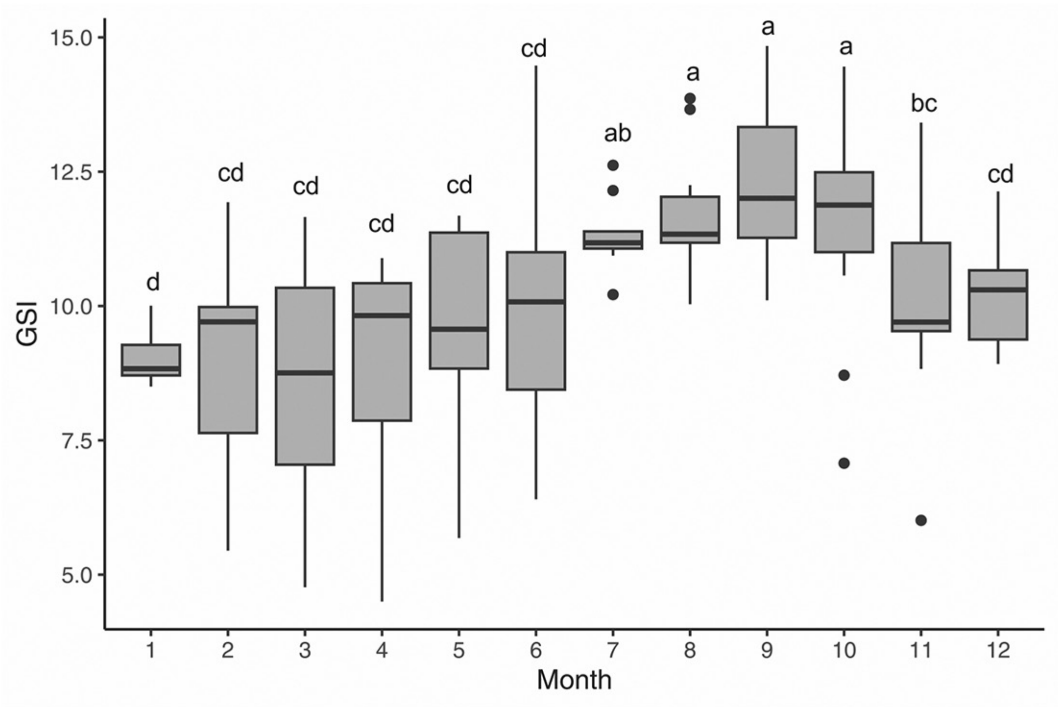

Fig. 6. – Multiannual monthly variation of gonadosomatic index in ispi females, multimonthly (2008–2018). Values with different letters (a, b, c, d) indicate significant differences ($p<0.05$; Kruskal-Wallis test).

The multiannual value of LM_{50}% between 2008 and 2021 for females was calculated at 5.2 cm TL (r^2=0.63) (Fig. 7).

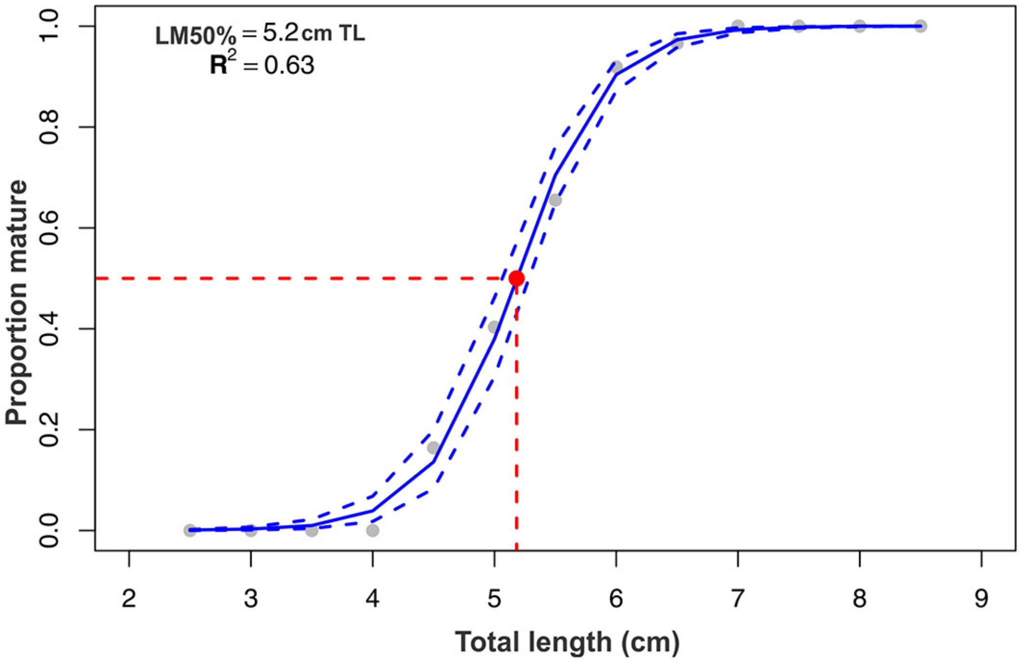

Fig. 7. – Logistic curve for the length at maturity (LM50%) in ispi females (2008–2021).

The estimated growth parameters were L_{inf} at 9.76 cm TL, a K value of 1.01 year^{-1} and a growth index (∅) of 1.99.

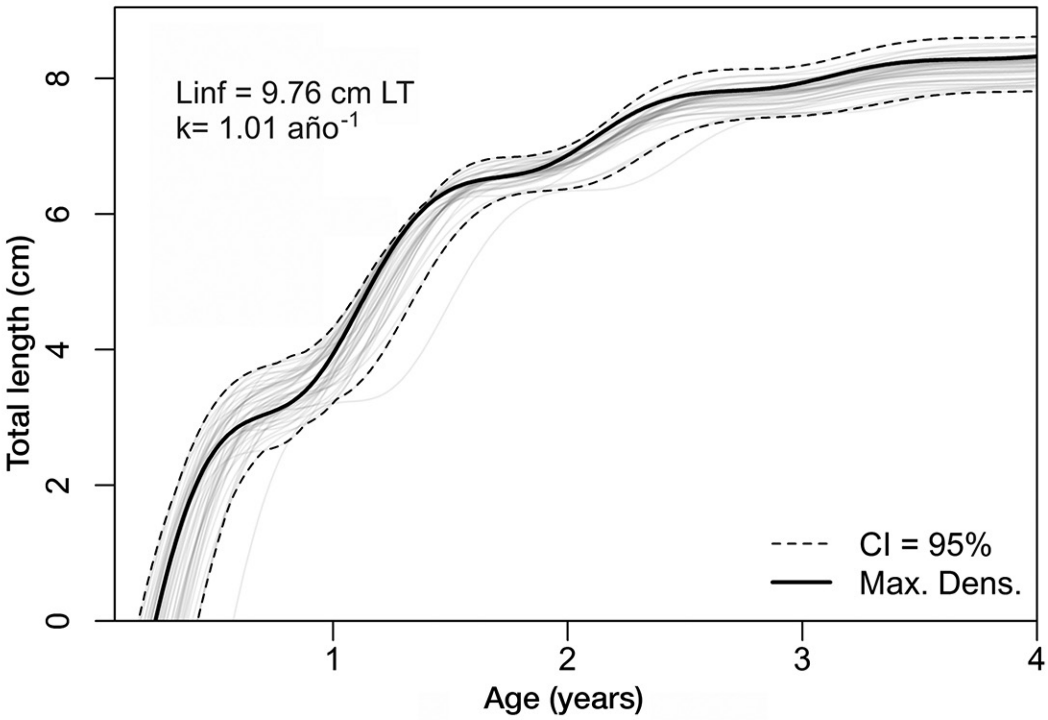

Fig. 8. – Growth curve based on the frequency of sizes of the ispi using data from the period 2008–2018.

Stock indicators

The results of the selectivity analysis of the LB-SPR model for the period 2008–2018, (Fig. 9A) show that 50% of the individuals captured had lengths between 6.0 and 6.3 cm TL, and 95% had lengths of less than 7.4 cm TL. In all years the size was above LM_{50}% (Fig. 10). The results show a gradual decrease in selectivity of 50% and 90% from 2008 to 2016, followed by a gradual recovery until 2021. Meanwhile, the ratio of fishing mortality to natural mortality (F/M) showed a progressive increase from 2.6 to 4.7 (Fig. 9B), representing a slight increase in fishing pressure on the ispi.

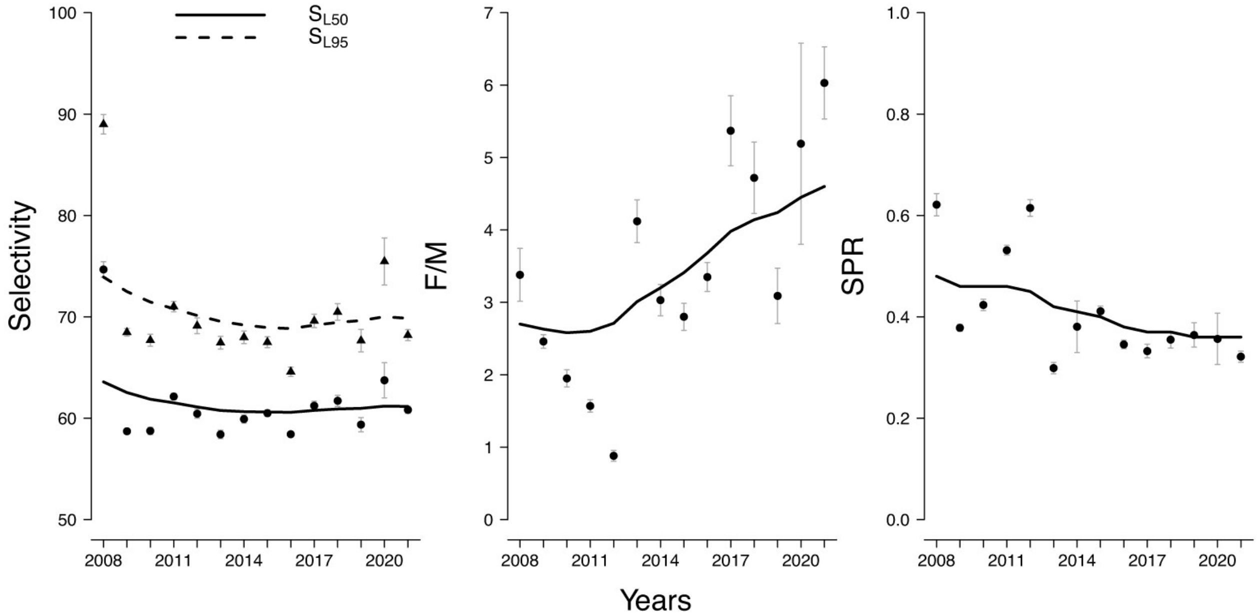

Fig. 9. – Annual length-based spawning potential ration (LB-SPR) estimates of (A) selectivity parameters (SL_{50} and SL_{95}), (B) fishing mortality over natural mortality (F/M) and (C) SPR (with confidence intervals) for ispi. Points with error bars represent yearly estimates with their associated uncertainty; the solid line represents the fitted trend.

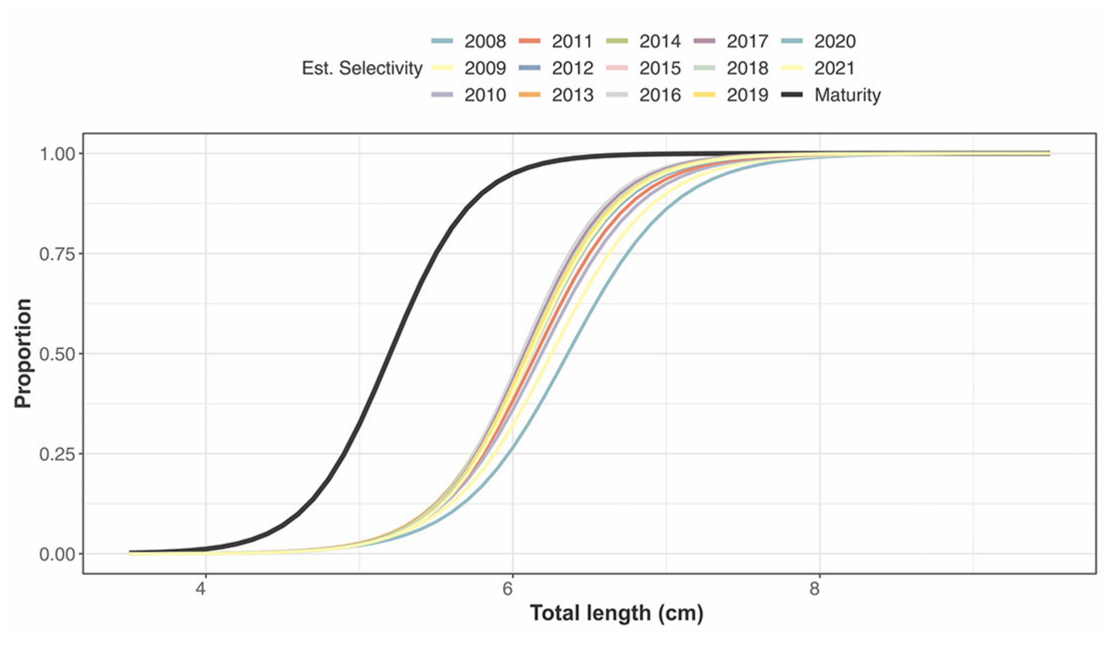

Fig. 10. – Cumulative selectivity curves by year and maturity curve of ispi for the period 2008–2021

The SPR indices were estimated between 0.48 (2008) and 0.36 (2021) (Fig. 9C), which is interpreted as showing no signs of overfishing by recruitment for the study period.

The CPUE value series showed a weak random order (R=6, p=0.09) for the period 2008 and 2021, highlighting two peaks in the years 2011 and 2017. A multi-year CPUE of 4.5 kg h^{-1} was calculated, showing annual changes with a maximum value (8 kg h^{-1}) in 2017 and a minimum (1.6 kg h^{-1}) in 2021 (Fig. 11). The trend between 2008 and 2021 showed a slight stability, with a gradual increase from 2009 to 2017 and a peak in 2011 (7.9 kg h^{-1}), followed by a gradual decrease from 8 to 1.6 kg h^{-1} from 2017 to 2021.

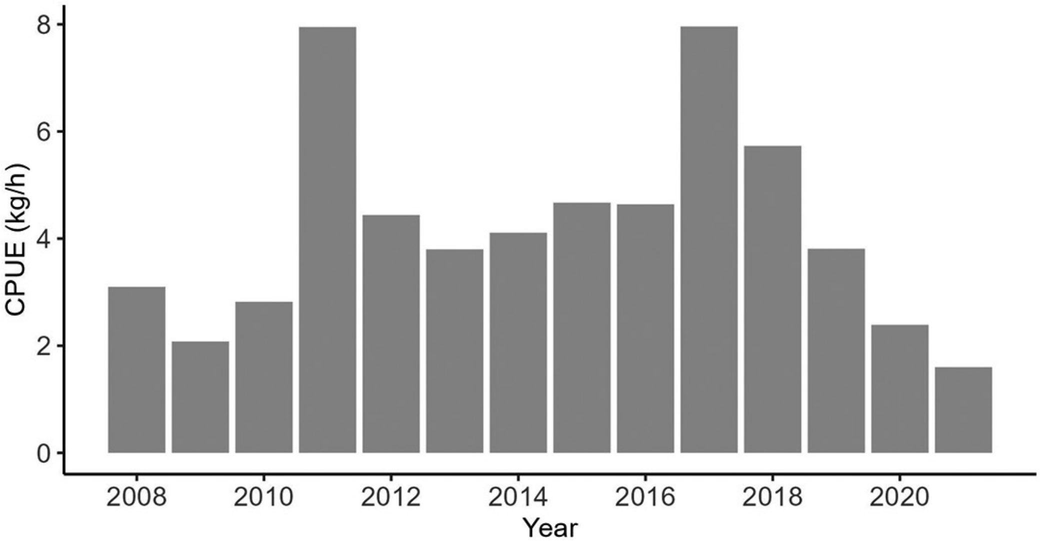

Fig. 11. – Variation in the catch per unit of effort (CPUE) of the ispi in Lake Titicaca, 2008–2021.

The population parameters and biological reference points estimated by the CMSY model are shown in Table 1. The value of *r* was estimated at 0.723 and was within the a priori value range, the value of K was estimated at 3340 t and the MSY was estimated at 603 t.

Table 1. – Population parameters and biological reference points estimated through catch maximum sustainable yield with their 95% credible interval values for ispi.

Parameters	Average	Units	Confidence intervals
r	0.723	$year^{-1}$	0.582–0.899
K	3340	t	2720–4090
MSY	603	t	526–692
B_{MSY}	1670	t	1360–2050
F_{MSY}	0.362	$year^{-1}$	0.291–0.449
B_{2021}/B_{MSY}	1.30		0.855–1.59
F_{2021}/F_{MSY}	0.139		0.102–0.223

The annual landings showed values above the MSY in the years 1983–1988, 1993, 2011–2012 and 2017 and values below the MSY in the years 1990, 1996, 2003, 2015 and 2021 (Fig. 12A). Biomass had a maximum value in 1982, followed by a decrease in 1989, then an increase until 2005, a decrease until 2019 and a recovery until 2021; between 1992 and 2021 the biomass was above the B_{MSY} (Fig. 12B). Fishing mortality showed values above the reference level (F_{MSY}) in the years 1987, 2012 and 2018 and values below it from 1990 to 2010 and from 2019 to 2021 (Fig. 12C). Finally, the Kobe diagram shows the trajectories of B/B_{MSY} and F/F_{MSY}, indicating that the fishery is currently fully exploited (B_{2021}/B_{MSY}=1.30 and F_{2021}/F_{MSY}=0.139) (Fig. 12D).

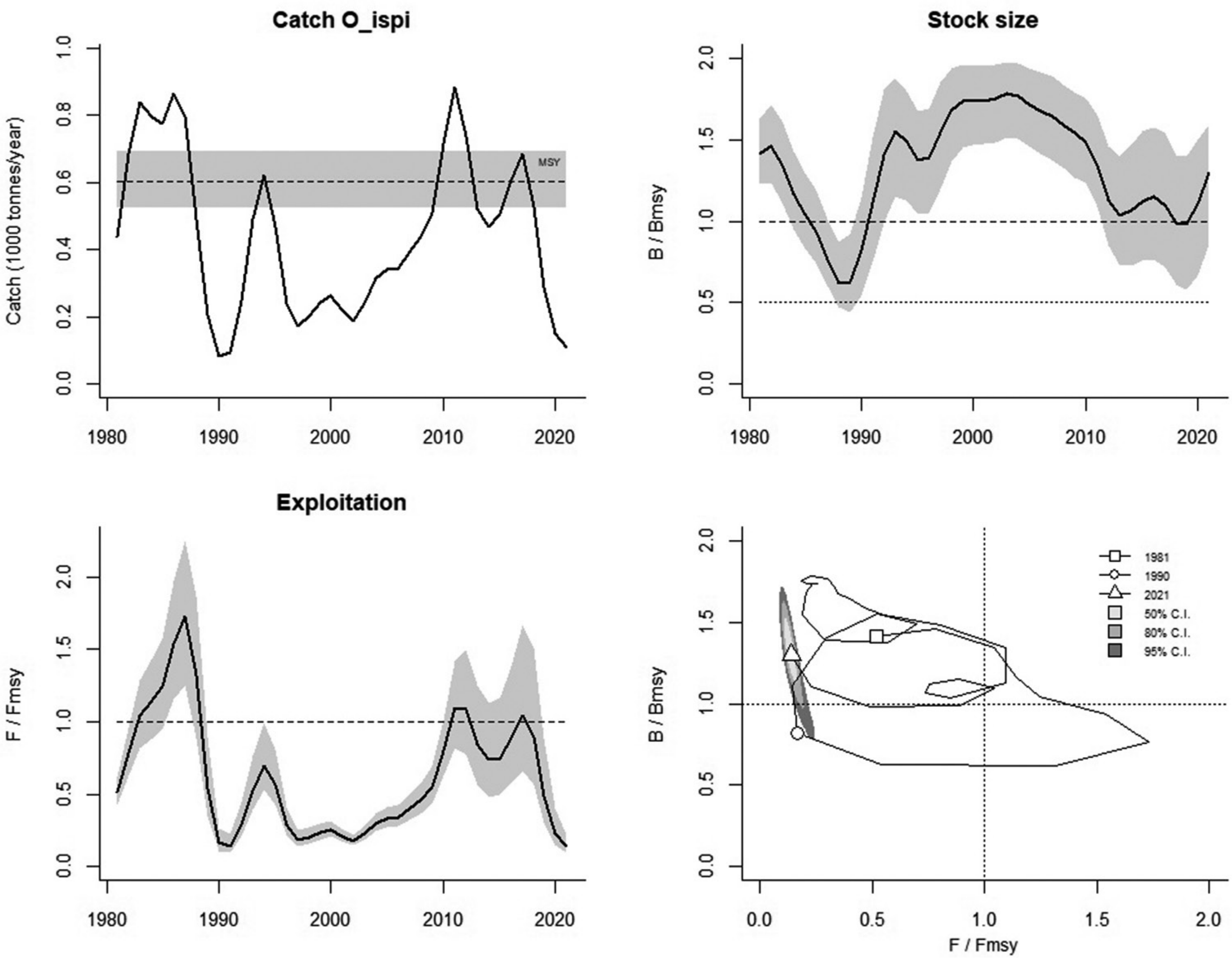

Fig. 12. – A, capture series for ispi with the maximum sustainable yield and its confidence ranges (black dotted line and grey band, respectively). B, biomass series (B) with respect to maximum sustainable yield biomass (B_{MSY}). C, fishing mortality series (F) with respect to maximum sustainable yield fishing mortality (F_{MSY}). D, Kobeplot.

In 1981–1982, 1991–2010, 2013–2016 and 2020–2021, the ispi population was subjected to low fishing pressure, with allowable catch levels and a healthy population capable of generating yields close to the MSY (green colour). In 1983–1985, 2011–2012 and 2017, it went through periods of depletion in which catches were above the B_{MSY} (orange) and showed a risk of falling into overfishing. In 1986–1988 there was evidence of overfishing, which is reflected in very low levels of biomass in depletion (red colour) that did not produce the MSY. From 1989 to 1992 the stock showed low levels of biomass, although the fishing pressure was reduced, which means that it was in the process of recovery (yellow colour) (Fig. 13).

The ispi fishery has gone through all the aforementioned situations, and in the last year (2021), it is presented in the green area, where uncertainty (cream 50%, grey 80%, dark grey 95%) at a confidence level of 95% does not show significant differences with respect to other scenarios. In addition, according to the analysis carried out (Fig. 10), there is an 8.1% probability that biomass will return to the yellow area and a probability of 91.9% that it will be fully exploited (green area).

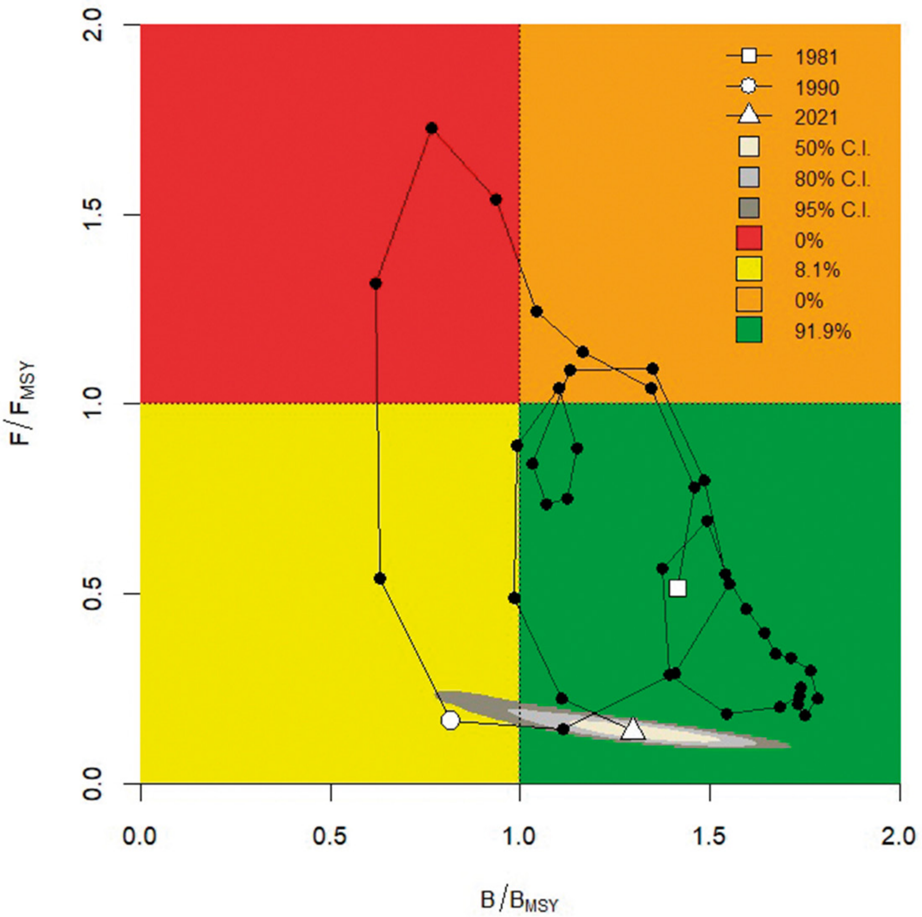

Fig. 13. – Catch maximum sustainable yield results for ispi presented in a Kobeplot. $F/F_{MSY,}$ fishing mortality series with respect to maximum sustainable yield fishing mortality.

DISCUSSION

Fishery indicator

Artisanal fishing in Lake Titicaca is an important occupation complemented by agriculture and livestock farming, and the ispi is the species with the largest landing volumes (IMARPE 2013). Between 2008 and 2018, fishing for ispi in the Peruvian sector of the lake represented 50.3% of the accumulated fish landings, with large catches in the South, Puno Bay and North Zones (IMARPE 2022). Annual fluctuations in landings could be related to the abundance and availability of ispi in the coastal zone, where they are caught by the artisanal fishing fleet (Treviño et al. 1984, Avila et al. 1991, IMARPE 2013). They could also be related to the abundance of Argentine silverside and rainbow trout (*Oncorhynchus mykiss*). Chura (2012) found a significant negative relationship between the biomass of ispi and Argentine silverside, with the decrease (increase) of the ispi influencing the increase (decrease) of the silverside. Added to this is the predation of rainbow trout on the ispi (Everett 1973, IMARPE 2022), which is the exclusive prey of adult trouts (Sarmiento et al. 1987, IMARPE 2016).

The fishery of ispi and other fish species dates back a long time, to when the first cultures settled in the circumlacustrine ring and used it for food and barter (Leviel and Orlove 1990). The use of curtain nets for ispi fishing in Lake Titicaca is reported by Quiroz et al. (1979), and fishers today have introduced major modifications in the use of materials and the assembly of nets. Segura et al. (2013) and Ocola et al. (2021) indicate that the curtain nets used by fishers vary between 50 and 100 m, with heights of less than 1 m and mesh sizes of 5.0 to 6.5 mm. The nets are placed in the coastal area in the afternoon and collected in the morning hours, remaining in the water for 12 to 13 hours (IMARPE 2013, Ninaraqui et al. 2022).

Biological indicators

The size of organisms is a central factor of ecological processes. Changes in size distribution can have many causes, including environmental variability, the genetics of life history, pre-capture relationships and competitive interactions (Yunne-Ja et al. 2005).

After the period 2013 to 2019, a drop in average length from 5.5 cm TL (2013) to 3.5 cm TL (2019) was recorded, followed by to 4.9 cm TL in 2021. In addition, between 1993 and 1994 average sizes of 6.6 and 6.2 cm TL were recorded, whereas in 1998 and 1999 the values increased to 7.5 and 7.6 cm TL (PELT-CEIDAP 1994, PELT 1999).

Although the weighted average size series showed a negative trend during the period analysed, this trend was probably influenced by changes in the mesh size of the curtain nets (97% of those used by fishers) and lake level fluctuations in the period. It is important to note that artisanal fishers in the southern zone and Puno Bay mention that they have had to change the mesh size from 16 a 13 mm due to fluctuations in the availability of the ispi to obtain greater catches on their fishing trips.

The maximum percentage tolerance of individuals with lengths below the MSC in the catches was 10% (MR No. 271-2010-PRODUCE). However, the fraction of specimens with sizes below the MCS recorded by the artisanal fishing fleet was greater than 30%, except for the years 2008 and 2011. The results of this analysis reveal non-compliance with the MCS and could describe an unfavourable scenario for the sustainability of the resource.

The monthly series of the GSI for females for the period 2008 and 2018 show no pause in the reproductive process. In fertility research, the existence of three types of eggs (mature, in the process of maturation and immature) was determined, which is a reproductive characteristic of the *Orestias* group (Treviño et al. 1984, IMARPE 2013). The fluctuation of the GSI peaks between 2008 and 2018 in reference to RM N° 022-2011-PRODUCE, which establishes two reproduction cycles, could be determined by the conditions of the aquatic environment, which generate considerable variability in reproductive tactics (Barnabe 1986, Saborido-Rey 2008). Furthermore, a reproductive mismatch is affected by patterns of photoperiod and temperature change that vary in one or more months: the larger the lag in the photothermal cycles, the greater the advance or delay in the spawning of the broodstock. In contrast, if this environmental gap is smaller, the spawning period of the groups tends to align (Carrillo 2012).

The established maturity length differs from 7.4 cm TL reported by Cruz-Cornejo (1984), the 6.3 cm TL reported by IMARPE (2013) and Sarmiento et al. (1987), and the 5.5 cm TL reported by Bocángel and Larrea (1999) and Lauzanne (1981. A possible variation could be due to overexploitation, which could be causing an evolution or adaptation in the average length of sexual maturity (Hutchings 2005, Cerna 2011). Another possible reason could be environmental variations, especially those related to temperature or other conditions that affect food availability (Trippel et al. 1997).

The ispi is a small fish compared with other species of *Orestias* in the lake, with a high annual growth rate (IMARPE 2013). Smaller fish tend to show a faster growth rate than larger fish (Ziegler et al. 2007, Haddon 2011). The parameters of age and growth determined in our study show differences from those of previous research. The asymptotic length of 9.76 cm TL observed in 2008–2018 was lower than that of 10.6 cm TL reported for the year 2000 by Paca et al. (2002); this difference could be associated with alterations in environmental conditions (Clark et al. 1999, Goicochea and Arrieta 2008) and variations in the mesh length of curtain nets.

Stock indicators

Prince et al. (2015) point out that an SPR of 40% is a conservative (optimal) proxy for MSY, based on a meta-analysis of quantitatively evaluated fisheries. Conversely, an SPR of less than 20% indicates that recruitment rates are being affected and that the resource is in a state of overexploitation and/or overfishing. On the recommendation of Hordyk et al (2015), an SPR of 35% was adopted, considering that it is a small fish with rapid growth (K= 1.01 year^{-1}), which ensures a population renewal rate in the short term.

Influence of lake level on ispi abundance and availability

Chura (2012) reported that, on a monthly scale, changes in lake level have an adverse impact on availability for fishing, with a one-month lag, followed by a positive response after 8 to 9 months, possibly enhanced by migration to the coast for breeding purposes. On an annual scale, the same authors observed a negative relationship with a lag of 4 to 6 years in the variation of landings

Development of fisheries and aquaculture in the coastal area of Lake Titicaca

IMARPE (2008) established that fishing occurs in two regions of Lake Titicaca: the coastal zone and the pelagic zone, each with environmental conditions that influence the existence of stocks, although they are considered similar. Fishing is carried out mainly in the coastal zone, which covers the edge of the circumlacustrine ring up to approximately 25 m depth, an area with the presence of submerged macrophytes that is used for the reproductive process (Chura 2012). Trout farming in Lake Titicaca has emerged as the fastest growing economic practice in Puno

(Chura and Mollocondo 2009, Barra 2018) and is carried out mainly in the coastal zone. According to information from the aquaculture cadastre of the Ministry of Production (http://catastroacuicola.produce.gob.pe/web/), there are more than 290 rights of use of concessioned aquatic areas and more than 21530 hectares enabled for aquaculture (PRODUCE 2021). Of the total aquaculture infrastructure installed in the lake, more than 40% is below the 15 m depth isobath. There is also a large informal aquaculture sector.

The unregulated development of aquaculture is also putting at risk the habitat of native ichthyofauna (*Orestias* and *Trichomycterus*) and is causing an ecological imbalance, with adverse effects on the ecosystem in the coastal zone. Therefore, it is necessary to review and/or modify the General Aquaculture Law regarding the authorization of aquatic areas, particularly in relation to Lake Titicaca and high Andean lagoons.

Several reports indicate that aquaculture has been leading to changes in the limnological conditions of coastal aquatic environments, particularly in areas where floating cages have been installed for longer periods. Mariano et al. (2010), Siguayro et al. (2022) and Vásquez et al (2015) report changes in the chemical properties of the water and the macroinvertebrate community, especially involving elements associated with eutrophication, such as ammonium, carbon dioxide and phosphorus, which are directly related to the alteration or modification of the habitat of native fish of coastal habits of the *Orestias* group. The ispi, which uses the coastal zone for reproductive processes, is particularly affected by these changes, which appear to be leading to a decrease in the rate of stock renewal.

In recent years, conflicts have arisen between fishers and aquaculturists over the use of aquatic space and hydrobiological resources in various sectors of Lake Titicaca, particularly regarding the installation of floating cages in Cachipucara and Asquicha (South zone) and Llachón (Puno Bay). Fishers also criticize the fact that fish farmers use ispi, Argentine silverside and carachi juveniles as food for rainbow trout (Ocola et al. 2021).

CONCLUSIONS

Ispi fishing is mainly carried out with curtain nets, with annual landings below 1500 t and a biomass for 2021 of 42336 t.

The average annual catch size showed a negative significant trend and was not statistically different from the minimum catch size.

A single yearly breeding period was observed, beginning in July and ending in October.

The length at maturity (LM50%) of females was 5.2 cm TL.

The ispi stock in the Peruvian sector of Lake Titicaca is in full exploitation.

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DECLARATION OF COMPETING INTEREST

All authors declare that they have no conflict of interest.

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AUTHORS' CONTRIBUTION STATEMENT

René Chura Cruz: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – review and editing. **Hilda Faustina Ninaraqui Lupaca:** Formal analysis, Investigation, Methodology and Writing – original draft. **Sheila Yuliana Godoy Suárez:** Formal analysis, Investigation, Methodology and Writing – original draft

REFERENCES

Ault J.S., Smith S.G., Bohnsack J.A., et al. 2018. Length-based risk analysis for assessing sustainability of data-limited tropical reef fisheries ICES. J. Mar. Sci. 76(1): 165-180. https://doi.org/10.1093/icesjms/fsy123

Avila L., Charaja M., Paz P., et al. 1991. Importancia socioeconómica de la pesca en la bahía de Puno, parte III Eutroficación y la economía de los recursos acuáticos. In: Northcote T., Morales S., Levy D., et al (eds). Contaminación en el Lago Titicaca: capacitación, investigación y manejo. pp. 139-164.

Barnabe G. 1986. Aquaculture. Lavoisier, Paris. 522 pp.

Barra P. 2018. Acuicultura en el Lago Titicaca: las ventajas y dificultades de cultivar trucha a 3800 metros sobre el nivel del mar. Revista Mundo Acuícola. 115: 22-25.

Bocángel D., Larrea D. 1999. Algunos aspectos sobre la prevalencia del plerocercoide de *Ligula intestinalis* en *Orestias ispi* del lago Titicaca. Ecología en Bolivia. 32: 23-27.

Carrillo M.A. 2012. La reproducción de los peces: aspectos básicos y su aplicación en la acuicultura. Ediciones Mundi-Prensa, Madrid, 718 pp.

Castillo P.R., Peraltilla S., Aliaga A., et al. 2009. Protocolo técnico para la evaluación acústica de las áreas de distribución y abundancia de recursos pelágicos en el mar peruano. Informe Inst. Mar Perú. 36(1-2): 7-28.
Cerna F. 2011. Changes in size and age maturity of Chilean hake population (*Merluccius gayi gayi*) in the Pacific southeast off Chile: An effect compensatory, environmental or evolutionary? master's thesis, Univ. de Concepción. 65 pp.
Chura R. 2012. Fluctuaciones en el nivel de agua del lago Titicaca y precipitación en relación con dos pesquerías de importancia comercial en el sector peruano del lago (1981- 2010). Thesis magister, Univ. de Concepción, 112 pp. http://repositorio.udec.cl/jspui/handle/11594/755
Chura R., Mollocondo H. 2009. Desarrollo de la acuicultura en el Lago Titicaca (Perú). Revista AquaTIC. 31: 6-19.
Clark W. 2002. F35% Revisited Ten Years Later. North Am. J. Fish. Manage. 22: 251–257 https://doi.org/10.1577/1548-8675(2002)022<0251:FRTYL>2.0.CO;2
Clark W.G., Hare S.R., Parma A.M., et al. 1999. Decadal changes in growth and recruitment of Pacific halibut (*Hippoglossus stenolepis*). Can. J. Fish. Aquat. Sci. 56(2): 242-252. https://doi.org/10.1139/f98-163
Cruz-Cornejo J.M. 1984. Estudio de la fecundidad de *Orestias sp* "ispi" en Llachón, Lago Titicaca. Thesis Licenciatura, Univ. Nacional del Altiplano, 76 pp.
Everett G.V. 1973. The rainbow trout *Salmo gairdneri* (Rich.) fishery of Lake Titicaca. J. Fish Biol. 5(4): 429–440. https://doi.org/10.1111/j.1095-8649.1973.tb04472.x
Fenner D. 2012. Challenges for managing fisheries on diverse coral reefs. Diversity. 4(1): 105-160. https://doi.org/10.3390/d4010105
Froese R., Demirel N., Coro G., et al. 2017. Estimating fisheries reference points from catch and resilience. Fish Fish. 18(3): 506–526. https://onlinelibrary.wiley.com/doi/abs/10.1111/faf.12190
Fry G.C., Brewer D.T., Venables W.N. 2006. Vulnerability of deepwater demersal fishes to commercial fishing: Evidence from a study around a tropical volcanic seamount in Papua New Guinea Fish. Res. 81(2-3): 126-141. https://doi.org/10.1016/j.fishres.2006.08.002
Gayanilo F.C., Sparre P., Pauly D. 2005. FAO-ICLARM Stock assessment Tools II (FiSAT II). Revised version. User's guide. FAO Computerized Information Series (Fisheries) N° 8. Rome. 126 pp. https://openknowledge.fao.org/handle/20.500.14283/y5997e
Gedamke T., Hoenig J.M. 2006. Estimating mortality from mean length data in nonequilibrium situations, with application to the assessment of goosefish Trans. Am. Fish. Soc. 135(2): 476-487. https://doi.org/10.1577/T05-153.1
Goicochea C., Arrieta S. 2008. Variaciones en el crecimiento de la anchoveta peruana expresadas en los radios de los otolitos. Inf. Prog. Inst. Mar Peru, 35(3): 241-244. https://hdl.handle.net/20.500.12958/1974
Gutiérrez R.M. 2013. Análisis de contenido estomacal de ispi (*Orestias ispi*). Bachelor's thesis, Univ. Mayor de San Andrés, 108 pp.
Haddon M. 2011. Modelling and quantitative methods in fisheries. Chapman and Hall/CRC, New York, 452 pp. https://doi.org/10.1201/9781439894170.
Hordyk A.R., Ono K., Valencia S.R., et al. 2015. A novel length-based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small scale, data-poor fisheries. ICES J. Mar. Sci., 72(1): 217-231. https://doi.org/10.1093/icesjms/fsu004
Huamán M., Alarcón J. 2025. Determinación de la selectividad de la red de enmalle a partir de la morfología de la sección transversal del "ispi" (*Orestias ispi* Lauzanne, 1981) en el lago Titicaca para una gestión pesquera sostenible. Thesis magister, Uni. Nacional del Callao. 99 pp. https://hdl.handle.net/20.500.12952/10551
Hutchings J.A. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 62(4): 824-832. https://doi.org/10.1139/f05-081
IMARPE (Instituto del Mar del Perú). 2008. Anuario Científico Tecnológico IMARPE. Callao. 174 pp. https://hdl.handle.net/20.500.12958/1198
IMARPE (Instituto del Mar del Perú). 2010. Anuario Científico Tecnológico. Callao. 205 pp. https://repositorio.imarpe.gob.pe/handle/20.500.12958/1966
IMARPE (Instituto del Mar del Perú). 2013. Anuario Científico Tecnológico. Callao. 214 pp. https://repositorio.imarpe.gob.pe/handle/20.500.12958/2298
IMARPE (Instituto del Mar del Perú). 2016. Anuario Científico Tecnológico. Callao. 276 pp. https://hdl.handle.net/20.500.12958/3180
IMARPE (Instituto del Mar del Perú). 2018. Estudio poblacional del recurso ispi en la zona litoral y pelágica en el Lago Titicaca con fines de aprovechamiento racional y sostenible (2016-2017). Informe Técnico. 53 pp.
IMARPE (Instituto del Mar del Perú). 2019. Opinión técnica sobre grado de explotación de los recursos hidrobiológicos en la cuenca del Lago Titicaca, parte peruana. Informe técnico. 25 pp.
IMARPE (Instituto del Mar del Perú) 2022. Evolución de indicadores biológico-pesqueros y estado actual de los recursos pesqueros en el Lago Titicaca, sector peruano (2008-2018). Documento 1. Estudio Complementario 16: Análisis de la situación de pesquería del Lago Titicaca. Proyecto GIRH-TPDS. 59 pp. https://alt-perubolivia.org/?wpdmpro=analisis-de-situacion-de-las-pesquerias-en-el-lago-titicaca-bolivia
Johansen A.C. 1924. On the summer and autumn spawning herring in the North Sea. Medel. Forum. Havunders. Fishery. 7(5): 119.
Lauzanne L. 1981. Description of Three New Orestias from Lake Titicaca, *O. ispi* N. Sp., *O. forgeti* N. Sp. and *O. tchernavini* N. Sp. (Pisces, Cyprinodontidae). Cybium. 5(3): 71-91.
Leviel D., Orlove B. 1990. Local control of aquatic resources: Community and Ecology in Lake Titicaca, Peru. Am. Anthropol. 92: 362-382. https://doi.org/10.1525/aa.1990.92.2.02a00070
Mariano M., Huamán P., Mayta E, et al. 2010. Contaminación producida por piscicultura intensiva en lagunas altoandinas de Junín, Perú. Rev. Peru. Biol. 17(1): 137-140. https://doi.org/10.15381/rpb.v17i1.63
Mildenberger T.K., Taylor M.H., Wolff M. 2017. TropFishR: an R package for fisheries analysis with length-frequency data. Methods Ecol. Evol. 8(11): 1520-1527. https://doi.org/10.1111/2041210X.12791
Ninaraqui H., Anahua I., Hilasaca L. 2022. Aspectos biológicos pesqueros de las especies capturadas durante operaciones de pesca en el lago Titicaca (CR. 1907). Inf. Inst. Mar Perú. 49(4): 532-537
Ocola J., Escalante J., Ñahuincopa A. 2021. Diagnostico binacional pesquero y acuícola en el ámbito del sistema hídrico lago Titicaca, rio Desaguadero, lago Poopó y salar de Coipasa – TDPS. Volumen I. Autoridad Binacional del Lago Titicaca, La Paz, 317 pp.
Paca F., Paca R., Atencio S., et al. 2002. Desarrollo de programas de pesca artesanal en el ámbito Peruano del sistema TDPS. 135 pp.
Palomares M.L., Muck P., Mendo J., et al. 1987. Growth of the Peruvian Anchoveta (*Engraulis ringens*), 1953 to 1982. PROCOPA Contributions. 15: 117-141.
Pauly D. 1979. Theory and Management of tropical Multispecies Stocks: A review, with emphasis on the Southeast Asian demersal fisheries. ICLAR Stud. Rev. 1: 35
Pauly D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. ICES J. Mar. Sci. 39(2): 175–192. https://doi.org/10.1093/icesjms/39.2.175
Pauly D., Gaschutz G. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculators. I.C.E.S.C.M. 1979/G: 24
Pauly D., Munro J.L. 1984. Once more on the comparison of growth in fish and invertebrates. Fishbyte. 2(1): 21.
PELT (Proyecto Especial Lago Titicaca). 1999. Evaluación de los recursos pesqueros en el lago Titicaca, Crucero 9907-08. Informe técnico. Lima. 60 pp.
PELT (Proyecto Especial Lago Titicaca), CEIPAD (Centro de Investigación y Desarrollo Agropesquero). 1994. Evaluación electroacústica de los recursos pesqueros en el lago Titicaca, Crucero 9409-9412. Informe técnico. Lima. 68 pp.
Prince J., Victor S., Kloulchad V., et al. 2015. Length based SPR assessment of eleven Indo-Pacific coral reef fish populations in Palau. Fish. Res. 171: 42-58. https://doi.org/10.1016/j.fishres.2015.06.008
PRODUCE. 2021. Anuario estadístico pesquero y acuícola. Lima, 189 pp. https://www.gob.pe/produce

Quiroz A., Villaverde F., Saravia P. 1979. Artes y métodos de pesca en las riberas del lago Titicaca. Inf. Inst. Mar Perú nº65, 28 pp.
R Core Team. 2023. R: A language and environment for statistical computing. In: R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
Restrepo V., Powers J. 1999. Precautionary control rules in US fisheries management: specification and performance. ICES J. Mar. Sci. 56: 846-852. https://doi.org/10.1006/jmsc.1999.0546
Roa R., Ernst B., Tapia F. 1999. Estimation of size at sexual maturity: an evaluation of analytical and resampling procedures. Fish. Bull. 97(3): 570-580.
Saborido-Rey F. 2008. Ecología de la reproducción y potencial reproductivo en las poblaciones de peces marinos. PhD thesis, Universidad de Vigo, 71 pp. http://hdl.handle.net/10261/7260
Santiago J., Ambrosio L., Fresno M.C. 2013. Estudio de las actividades y mejora de las condiciones de producción acuícola en el lago Titicaca (Perú). Proyecto Apoyo al Desarrollo del Sector Pesquero y Acuícola del Perú. Informe técnico. 117 pp.
Sarmiento J., Azabache L., Mariño L., et al. 1987. Sinopsis biológica de las Principales Especies Ícticas del Lago Titicaca. OLDEPESCA-Documento de Pesca nº 07, 173 pp.
Schwamborn R., Mildenberger T.K., Taylor M.H. 2019. Assessing sources of uncertainty in length-based estimates of body growth in populations of fishes and macroinvertebrates with bootstrapped ELEFAN. Ecol. Modell. 393: 37-51. https://doi.org/10.1016/j.ecolmodel.2018.12.001
Segura M., Guardia A., Cervantes L. 2013. Encuesta de la pesca artesanal en el lago Titicaca (junio-diciembre 2006). Inf. Inst. Mar Perú. 40(3-4): 274-290.
Siguayro H., Pasapera J., Villanueva C., et al. 2022. Evaluación de fuentes contaminantes en el anillo circunlacustre del lago Titicaca (sector peruano), 2017. Bol. Inst. Mar Perú. 37(2): 361-386. https://hdl.handle.net/20.500.12958/6544
Somers I. F. 1988. On a seasonally oscillating growth function. Fishbyte. 6(1): 8-11.
Sparre P., Venema S.C. 1997. Introduction to tropical fish stock assessment. Part 1: Manual. FAO Fisheries technical paper, nº 306/1, 420 pp.
Taylor M.H., Mildenberger T.K. 2017. Extending electronic length frequency analysis in R. Fish. Manage. Ecol. 24(4): 330-338. https://doi.org/10.1111/fme.12232
Torrejón-Magallanes J. 2020. sizeMat: An R package to estimate size at sexual maturity.
Treviño H., Torres J., Levy D.A., et al. 1984. Pesca experimental en aguas negras y limpias del litoral de la Bahía de Puno, Lago Titicaca, Perú. Bol. Inst. Mar Perú. 8(6): 34-34.
Trippel E.A., Kjesbu O.S., Solemdal P. 1997. Effects of adult age and size structure on reproductive output in marine fishes. In: Chambers RC, Trippel EA. (eds), Early life history and recruitment in fish populations. Chapman and Hall, London, pp. 31-62. https://doi.org/10.1007/978-94-009-1439-1_2
Vásquez W., Talavera M., Inga M. 2015. Evaluación del impacto en la calidad de agua debido a la producción semi intensiva de trucha (*Oncorhynchus mykiss*) en jaulas flotantes en la Laguna Arapa – Puno. Rev Soc. Quim. Perú. 81(1): 15 -28. https://doi.org/10.37761/rsqp.v82i1.41
Vazzoler A.E. 1982. Manual de métodos para estudos biológicos de populações de peixes: reprodução e crescimento. CNPq, Sao Paulo, 106 pp.
Wirrmann D. 1991. Morfología y batimetría. In: Dejoux C, Iltis A. (eds), El Lago Titicaca: síntesis del conocimiento limnológico actual. ORSTOM-HISBOL, La Paz, pp 31-38.
Yunne-Jai S., Marie-Joëlle R., Simon J., et al. 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. ICES J. Mar. Sci. 62(3): 384–396. https://doi.org/10.1016/j.icesjms.2005.01.004
Ziegler P.E., Lyle J.M., Haddon M., et al. 2007. Rapid changes in life-history characteristics of a long-lived temperate reef fish. Mar. Freshw. Res. 58(12): 1096-1107. https://doi.org/10.1071/MF07137