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Age, growth and reproduction of the Galapagos sailfin grouper *Mycteroperca olfax* (Jenyns, 1840): an overdue and needed comprehensive baseline

Paolo Usseglio, Alan M. Friedlander, Edward E. DeMartini, Anna Schuhbauer, Pelayo Salinas de Léon

The Galapagos Sailfin grouper, *Mycteroperca olfax*, locally known as bacalao and listed as vulnerable by IUCN, is culturally, economically, and ecologically important to the Galapagos archipelago and its people. It is regionally endemic to the Eastern Tropical Pacific, and, while an important fishery resource that has shown substantial declines in recent years, to date no effective management regulations are in place to ensure the sustainability of its Galapagos fishery. Previous estimates of longevity and size of maturity for bacalao are inconsistent with estimates for congeners, which questions the accuracy of prior estimates. We set out to rigorously assess the age, growth, and reproductive biology of bacalao in order to provide more accurate life history information to inform more effective fisheries management for this species. The oldest fish in our sample was 24 years old, which is 2-3 times greater than previously reported estimates of longevity. Parameter estimates for the von Bertalanffy growth function (k= 0.07, L_∞= 119.1 cm TL, and t_o= -2.33 years) show bacalao to grow much slower and obtain substantially larger asymptotic maximum length than previous studies. Mean size at maturity (as female) was estimated at 61.1 cm TL, corresponding to an age of 7.8 years. As a protogynous hermaphrodite, size at sex change (from adult female to adult male) occurred at 83.7 cm TL, corresponding to 15.2 years of age. We found that sex ratios were extremely female biased (0.015 M:1F), with a large majority of the individuals in our experimental catch being immature (73%). Our results show that bacalao grow slower, live longer, and mature at a much larger size and greater age than previously thought, with very few mature males in the population. These findings have key implications for the fishery of this valuable species and urge for a long-due species management plan to ensure its long-term sustainability.

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Age, growth and reproduction of the Galapagos sailfin grouper *Mycteroperca olfax* (Jenyns, 1840): an overdue and needed comprehensive baseline

Paolo Usseglio[1,2*#], Alan M. Friedlander[1,3], Edward E. DeMartini[4,5], Anna Schuhbauer[6,7], Pelayo Salinas de Léon[6]

Affiliations

[1] Fisheries Ecology Research Lab, University of Hawai'i at Manoa, Honolulu, Hawai'i, USA
[2] Fundacion In-nova Castilla la Mancha, Toledo, España
[3] Pristine Seas, National Geographic Society, Washington, DC, USA
[4] NOAA Fisheries – Pacific Islands Fisheries Science Center
Fisheries Research and Monitoring Division, Life History Program
Honolulu, Hawai'i, USA
[5] Hawai'i Institute of Marine Biology
University of Hawai'i, School of Earth Science and Technology
Kaneohe, Hawai'i, USA
[6] Department of Marine Sciences, Charles Darwin Research Station, Galapagos Islands, Ecuador
[7] University of British Columbia, Vancouver, British Columbia, Canada

*Corresponding author:

[#] Current Address:
Fisheries Ecology Research Lab, University of Hawai'i,
Edmondson Hall, Room 216,
Honolulu, HI 96822.
Phone:+1-808 956 8350
usseglio@hawaii.edu

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Abstract

The Galapagos Sailfin grouper, *Mycteroperca olfax*, locally known as bacalao and listed as vulnerable by IUCN, is culturally, economically, and ecologically important to the Galapagos archipelago and its people. It is regionally endemic to the Eastern Tropical Pacific, and, while an important fishery resource that has shown substantial declines in recent years, to date no effective management regulations are in place to ensure the sustainability of its Galapagos fishery. Previous estimates of longevity and size of maturity for bacalao are inconsistent with estimates for congeners, which questions the accuracy of prior estimates. We set out to rigorously assess the age, growth, and reproductive biology of bacalao in order to provide more accurate life history information to inform more effective fisheries management for this species. The oldest fish in our sample was 24 years old, which is 2-3 times greater than previously reported estimates of longevity. Parameter estimates for the von Bertalanffy growth function ($k = 0.07$, $L_{\infty} = 119.1$ cm TL, and $t_o = -2.33$ years) show bacalao to grow much slower and obtain substantially larger asymptotic maximum length than previous studies. Mean size at maturity (as female) was estimated at 61.1 cm TL, corresponding to an age of 7.8 years. As a protogynous hermaphrodite, size at sex change (from adult female to adult male) occurred at 83.7 cm TL, corresponding to 15.2 years of age. We found that sex ratios were extremely female biased (0.015 M:1F), with a large majority of the individuals in our experimental catch being immature (73%). Our results show that bacalao grow slower, live longer, and mature at a much larger size and greater age than previously thought, with very few mature males in the population. These findings have key implications for the fishery of this valuable species and urge for a long-due species management plan to ensure its long-term sustainability.

Keywords

Galapagos grouper, Life history, Management, Age and growth, Maturity.

Introduction

The Galapagos Sailfin grouper, *Mycteroperca olfax*, has high cultural, economic, and ecological importance to the people and the marine ecosystem of the Galapagos Archipelago. It is one of the most sought after species in the artisanal hand-line fishery and is prized in its dried form for a traditional dish called “fanesca” that is consumed during Easter (Nicolaides et al., 2002). With a trophic level of 4.2, bacalao is the third top predator of the Galapagos (Okey et al., 2004). The species is a protogynous hermaphrodite (Rodriguez, 1984; Coello & Grimm, 1993), and it is regionally endemic to the Eastern Tropical Pacific (ETP), where it is commonly found throughout the Galapagos, and to lesser degrees at Cocos Island, Costa Rica, and Malpelo Island off the west coast of Colombia (Grove & Lavenberg, 1997).

The artisanal hand-line fishery that targets *M. olfax* dates back to the late 1920's, when Norwegians introduced the butterfly method of salting and drying fish that gives bacalao (cod in Spanish) its name (Reck, 1983). Over the years bacalao has been one of the most sought after species, representing almost 100% of the finfish landings in the 1940's (Reck, 1983), to 89% of the total finfish catch in the 1970's, and only 17% in recent years (Reck, 1983; Nicolaides et al., 2002; Schiller et al., 2014). A very limited geographical range, and clear evidence of fisheries declines have led the International Union for the Conservation of Nature (IUCN) to list bacalao as Vulnerable (VU) (Bertoncini et al., 2008).

Fishing regulations in the Galapagos Marine Reserve include a zonation scheme, with no-take areas (Heylings, Bensted-Smith & Altamirano, 2002), licensing system, gear restrictions (e.g. spearfishing and long-lining), a ban on industrial fishing vessels, and a ban on capture and marketing of sharks (Castrejón et al., 2014). However, these regulations are poorly enforced and not well adhered to by many in the fishing community, which has resulted in overfishing of a number of prized species (Usseglio et al., In review; Bustamante et al., 2000; Ruttenberg, 2001; Edgar et al., 2010). While bacalao has historically been the most important finfish fishery in the Galapagos, and despite suggestions of overfishing (Usseglio et al., In review; Schiller et al., 2014), to date there are no management regulations specifically aimed at its fishery (e.g. total allowable catch, size limits, fishing seasons).

Fisheries are often managed to lessen the consequences of uncontrolled fishing, which can lead to collapse of a fishery, economic inefficiency, loss of employment, habitat degradation and decreases in the abundance of rare species (Jennings, Kaiser & Reynolds, 2009). Fishery models use basic life history information (e.g., age, growth, reproduction) as inputs to determine how species are affected by fishing. Models such as virtual population analysis are used to calculate mortality rates of age-based cohorts, making it critical to accurately assign the correct age to an individual of a given size. However in the case of bacalao previous studies have provided conflicting results that are inconsistent with what is known about similar members of this genus (Heemstra & Randall, 1993). For example, previous estimates of longevity range between 7 and 11 years (Rodriguez, 1984; Froese & Pauly, 2000; Gagern, 2009), which is two to three times lower than what has been reported for other mycteropercids (Froese & Pauly, 2000). Similarly, various studies have provided dissimilar estimates of size at sexual maturity that range from 47-67 cm TL (Rodriguez, 1984; Coello, 1989; Heemstra & Randall, 1993). Underestimation of longevity leads to overestimation of growth and mortality rates (Mills & Beamish, 1980), which can in turn affect the outcome of population models used to formulate management of fish stocks (Tyler, Beamish & McFarlane, 1989; Reeves, 2003).

Because of the uncertainty in important life history parameters, our goal was to rigorously determine the longevity, growth rate, and size at maturity of bacalao in the Galapagos Islands in order to provide more accurate information for better management of this species.

Methods

Study site

The Galapagos Archipelago is located 1000 km off the coast of Ecuador, and comprises thirteen islands and over 100 islets (Snell, Stone & Snell, 1996). The Galapagos Marine Reserve (GMR) encompasses approximately 133,000 km^2 and was the first marine reserve established in Ecuador in 1998, being recognized in 2001 as a UNESCO World Heritage Site (Heylings, Bensted-Smith & Altamirano, 2002). While there is a ban on industrial fishing vessels in the GMR, artisanal fishing is allowed in fishing areas delimited by the GMR zonation scheme (Castrejón et al., 2014).

Despite this status, artisanal fishing occurs throughout much of the archipelago.

Sample collection

Biological samples were collected by both accompanying fishers on fishing trips, and sampling landings at the port in Puerto Ayora, on Santa Cruz Island. Biological samples were collected in June 2011, February 2012, and from September 2012 to April 2013. Samples were obtained from major fishing locations centred on Santa Cruz Island (Fig. 1).

Sample processing

Total (TL) and standard length (SL) of bacalao were measured to the nearest cm, and total weight was taken to the nearest gram. Sagittal otoliths were extracted from fish, cleaned in 95% ethanol, and then washed in water prior to dry-storage. The right sagittal otolith was weighted to the nearest 0.1 g and its maximum length and width recorded to the nearest 0.1 mm. Otoliths were then fastened to a 2 x 2 cm square of plywood using acrylic glue, and a single transverse section ~300 µm thick was cut at low speed using a Buehler™ IsoMet saw with two parallel blades separated by a shim. Sections were then mounted on glass slides using clear adhesive (Crystalbond™), ground for a few seconds with sand paper 400grit, polished with 15 µm lapping film, and viewed immersed in water against a dark background at low power on a dissecting microscope using two reflected light sources angled at 45 degrees. The number of clear bands observed in the transverse sections was counted, as well as the appearance of the outer margin (clear vs. opaque).

Gonads were removed from the fish and weighted to the nearest 0.1 g. A 0.5 mm transverse section from the middle of the gonad was cut and placed inside a tissue-embedding cassette before being fixed in 10% buffered formalin for 7 days, after which the samples were transferred to 70% ethanol. Tissue samples were embedded in plastic resin (JB-4™) following previously established protocols (Sullivan-Brown, Bisher & Burdine, 2011). Embedded samples were sectioned into 1-2 µm slices using an automated microtome with a glass knife blade. Following sectioning, samples were stained with toluidine blue and viewed under a dissecting microscope using transmitted light at 100x magnification.

Samples were assigned to reproductive stages following key milestones in the reproductive cycle previously proposed by (Brown-Peterson et al., 2011) (**Error! Reference source not found.**).

Data analysis

Age and growth

The proportion of otolith samples with clear (translucent) margins was calculated for each month and this edge analysis used to deduce the timing and periodicity of yearly increment formation. The relationship between the formation of the clear otolith bands and water temperature was explored by scaling each variable between 0 and 1, and plotting them against one another following the methods outlined by (Newman & Dunk, 2003). Monthly temperature was recorded on Santa Cruz Island using *in situ* data loggers (Hobo pendant™) set to record at hourly intervals.

Ageing consisted of assigning each fish a count of annual growth increments that comprised a ring of alternating clear and opaque sections. These were counted with no reference to time of collection or fish length. Each otolith was read three times to compare counts, if they differed, the otolith section was re-read and the previous counts re-assessed. If no consensus was reached among counts, or if the otolith appeared irregular, or had poorly defined growth increments, the otolith was discarded from all further analyses.

Growth was modelled using the von Bertalanffy growth function (Bertalanffy, 1938):

$$L_t=L_\infty(1-e^{-k(t-t_o)})$$

Where L_t is the expected length at time t, L_∞ is the asymptotic maximum length, k is the Brody growth rate coefficient, and t_0 is the theoretical age at which length is 0. Starting parameters for the model were determined using a Ford-Walford plot (Ford, 1933; Walford, 1946). Confidence intervals for the model parameters were estimated via bootstrapping with 1000 iterations. The previous analyses were done using the R package FSA (Ogle, 2015)

Length–weight relationship for bacalao was obtained by fitting the power function $W= aL^b$ to weight and length data where: W is the total wet weight, L total length, and a and b are constants determined empirically.

Reproduction

The adult sex ratio was calculated using all sexually mature females and males. A chi square test was used to assess whether sex ratios differed significantly from 1:1. Mean size at sexual maturity (L_{50}) was calculated by fitting a logistic model to the proportion of mature fish binned in 5 cm size classes. The logistic model follows the formula: log (p/1-p)=a+TL, where p is the probability of being mature, TL is total length, and a is a fitting constant.

Confidence intervals for the predicted model parameters were estimated via bootstrapping with 1000 iterations. Mean age at first maturity was estimated using the same method. Additionally, an estimate of L_{50} was obtained from the empirical relationship between L_{50} and L_∞ derived using the equation $\log L_{50} = 0.9469 * \log L_\infty - 0.1162$ (Froese, 2000).

All analyses were done using the statistical software R (R Development Core Team, 2008). Data manipulation was performed using the reshape package (Wickham, 2007), and graphing was conducted with the package ggplot2 (Wickham, 2009).

Results

We sampled a total of 297 bacalao, with a mean TL of 49.8 cm (±11.1 sd) and size range from 18 to 100 cm TL. The length (TL) to weight (g) relationship resulted in estimates for a=6.471e^{-5}, b=3.158, and provided a good model fit (r^2=0.94).

Age and growth

After discarding otoliths that were considered unreadable, or where counts differed and were unresolvable, a total of 141 out of 174 bacalao otolith specimens were used for growth analysis. These fish contained the full size range of the overall sample; mean size across all samples (49.8 cm ±11.1 sd) and of the otolith subsample (50.5 ±12.8 sd, Fig. 2) did not differ significantly ($t_{(256)}$= -0.466, $p > 0.05$). Sectioned sagittal otoliths, when viewed under a dissecting microscope with reflected light, showed alternating clear and opaque bands (Fig. 3), and the clear bands formed once yearly around April-June when sea temperature reaches its minimum yearly values (Fig. 4).

Growth modelling and length at age

Age estimates from otoliths ranged from 1-24 years. The estimated von Bertalanffy growth model parameters were k= 0.07 (0.05 - 0.09 95% CI), L_∞= 119.1 cm (TL) (106.9 - 140.8 95% CI), and t_o= -2.33 years (-3.13 - -1.73 95% CI) (Fig. 5).

Reproduction

Logistical constraints only allowed for the assessment of a subsample of 200 (197 female, and 3 male) out of the 297 tissue samples collected. Mean TL of the subsample was 51.6 cm TL (±10.8 sd), with a range between 34-100 cm TL (Fig. 6). Lengths of subsample fish did not differ significantly ($t_{(451)}$= -1.71, $p > 0.05$) from the parent sample of fish. The sex ratio was significantly female skewed (χ^2= 188.2, $p < 0.01$), with 0.015 males per female.

Immature fish represented 73% of the sampled individuals (n=146) (Fig. 7a) and had a mean TL of 48.2 (±7.5 sd) cm. Mature bacalao, including fish that were developing, spawning capable or that were regressing and whose ovaries contained regenerating oocyte stages (Fig. 7b,c), represented 27% of the samples (n=54). These fish had a mean TL of 60.1 (±13.1 sd) cm. There were only three males in our samples (Fig. 7d), ranging in size from 81 to 100 cm TL.

Size at which 50% of the population reached sexual maturity (L_{50}) was estimated from the logistic regression model as 61.1 cm TL (58.3-65.1 95% CI), while age at maturity was 7.8 years (7.1-8.6 95% CI, Fig.8). The empirical equation proposed by (Froese, 2000) estimated size at maturity for females as 70.7 cm TL (53.4 – 93.6 se). Size at sex change was estimated as 83.7 cm TL, corresponding to an age of 15.2 years (Fig. 9), because of the low number of males seen in the study it was not possible to calculate confidence intervals around these values.

Discussion

Our estimates of maximum age of bacalao (24 years) were two to three times higher than those previously reported. The large proportion of immature individuals in our samples, as well as the low number of larger individuals, and highly biased sex ratio suggests that the resource has undergone, and is probably still experiencing, severe overfishing. We have provided more accurate estimates of size-at-age, growth, and size and age at sex change of bacalao, and these estimates should need to be urgently incorporated into management plans for this species.

Age and growth

Previous age estimates of bacalao ranged between 7 and 11 years (Rodriguez, 1984; Froese & Pauly, 2000; Gagern, 2009). Longevity for other mycteropercids such as *Mycteroperca bonaci* (Max TL 150 cm) is 34 years, while *M. macrolepis* (Max TL 145 cm) and *M. phenax* (Max TL 107 cm) reach 22 and 21 years, respectively (Froese & Pauly, 2000). Our maximum recorded age of 24 years is closer to what would be expected of a mycteropercid grouper, and while our biggest fish was only 100 cm TL, bacalao is reported to reach 120 cm TL (Walford, 1937), suggesting that it is likely that longevity for this species be closer to 30 years. Differences in age between our study and previous works very likely stem from difficulties in reading bacalao otoliths. Rodriguez (1984) reported that 90% of the otoliths collected were considered unreadable due to the presence of a large number of false rings, or the lack of rings that he attributed to demineralization. Similarly, Gagern (2009) reported finding a large number of rings that he presumed were formed on a monthly basis. It was clear in the present study that bacalao otoliths are not necessarily easy, but we found that cross-sections can be read more easily using a dissecting microscope with reflected light against a dark background than with transmitted light and a compound microscope. Both Rodriguez and Gagern employed transmitted light and a compound microscope for their readings. The results of our edge analysis validation clearly show that the rings that we counted were structures that formed once yearly.

Estimation of age and growth in marine teleosts is useful for a variety of purposes such as estimating mortality (Pauly, 1980), predicting responses to exploitation (Jennings, Reynolds & Mills, 1998; Jennings, Kaiser & Reynolds, 2009), and developing fisheries sustainability (Frisk, Miller & Dulvy, 2005). However, inaccurate estimates of these key parameters can result in models that do not accurately represent exploitation of the species. For instance, in the case of the orange roughy (*Hoplostethus atlanticus*), initial estimates of longevity were 24 years, while later validated estimates were nearly 100 years (Andrews, Tracey & Dunn, 2009), resulting in dramatically different estimates of natural mortality and exploitation rates (Tracey & Horn, 1999).

Our Brody growth rate coefficient estimate of 0.07 was less than half of that reported previously (k=0.18) by Rodriguez (1984). Our corresponding estimate of longevity was 24 rather than 9-11 years, which is consistent with other large, long lived species (Jennings, Kaiser & Reynolds, 2009). We also estimated L_∞ to be 28% larger. Overestimating growth rates results in greater risk of over-exploitation because models will assume a faster recovery from exploitation than is actually occurring.

Reproduction

Previous studies of the reproductive biology of bacalao have produced contrasting results in key life history parameters. While both Rodriguez (1984), and Coello and Grimm (1993) found evidence for protogyny in bacalao and identified peak spawning between the months of September and November. Size at maturity yielded different estimates of 47.5 cm TL (Coello, 1989) and as 63 cm TL (Rodriguez, 1984). Fishbase (www.fishbase.org), on the other hand, reports size at maturity as 67 cm, citing Heemstra and Randall (1993) as the source. However, we did not find any reference to size at maturity for bacalao in the latter paper. Both Rodriguez and Coello staged gonads based solely on gross (macroscopic) morphology, which is known to produce inaccurate estimates of reproductive size (West, 1990) and even of sexual identity in protogynous groupers (DeMartini, Everson & Nichols, 2011).

Our estimates of size at maturity, while consistent with those published by Rodriguez (1984), are 13% below empirical estimates derived from Froese's equations (70 cm) (Froese, 2000). Although it is recognized that the predictive model of Froese (2000) has a high level of uncertainty, the difference we observed may suggest an effect of earlier maturation caused by fishing induced changes in life history (Conover & Munch, 2002; Baskett et al., 2005; Enberg et al., 2012; Sharpe, Wandera & Chapman, 2012). Signs of overexploitation of bacalao include a decrease in mean landed size since the 1970's (Reck, 1983; Nicolaides et al., 2002), a marked increase in the proportion of immature fish in landings from 35% in 1993 (Coello & Grimm, 1993) to 73% in our study, and an overall decline in the catch of bacalao from 89% of the total finfish catch in the 1970's to only 17% in recent years (Reck, 1983; Nicolaides et al., 2002; Schiller et al., 2014). Declines in the bacalao catch might also reflect a diversification of the fisheries and a shift to pelagics such as tuna and wahoo (Schiller et al., 2014). This may particularly be a preference for these species by the local tourist industry and export market, but might also reflect a decline in nearshore fish stocks.

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Fishery effects on bacalao quite likely also include impacts on adult sex ratio and size-at-sex change. The highly skewed sex ratio we observed (0.015) is consistent with those reported previously (0.021: Coello & Grimm, 1993; 0.017: Reck, 1983), suggesting that adult sex ratio had likely been altered by fishing down of the larger bacalao prior to the 1980s, specially by targeting spawning aggregations (Salinas-de-León, Rastoin & Acuña-Marrero, 2015). Although there has not been a decline in catch rates in the bacalao fishery over time (Nicolaides et al., 2002), this might represent expansion of the fishery to new unfished areas. In the 1980s fishers reported that larger fish were caught mostly on “far” offshore banks such as Banco San Luis, which is located only 30 km from the main fishing port on Santa Cruz Island (Reck, 1983). In contrast, the largest fish in our study, as well as 2 of the 3 males we collected, were caught at Wolf Island, located in the far north bio-region of the GMR, nearly 300 km north of Santa Cruz Island.

Size-selective fishing mortality typically results in the differential loss of larger and older males in protogynous groupers (Sadovy, 1996). Major implications of severely skewed sex ratios include reduction in the probability that females will survive to sex change (Armsworth, 2001), loss of productivity due to sperm limitation (Bannerot et al., 1987; Koenig et al., 1996), and ultimately reproductive failure as males become too rare to effectively mate with females (Allee effect) (Bannerot et al., 1987; Huntsman & Schaaf, 1994).

Conclusions

Protogynous species have been suggested to be at particular risk of overexploitation, even when fishing mortality rates are low (Huntsman & Schaaf, 1994; Alonzo & Mangel, 2004; Heppell et al., 2006). This is especially relevant in an area such as the Galapagos where there are no management regulations specific to bacalao (e.g. allowable catch, size limits, fishing seasons). Conservative management approaches, especially for hermaphrodites, should include a mix of control over catch and fishing effort and realized no-take spatial closures (Heppell et al., 2006). Currently, the only protection for bacalao occurs in no-fishing zones which are yet to show positive evidence of protection ((Usseglio et al., In review). The results from this paper provide needed inputs for fisheries models in order to determine adequate levels of catch and fishing effort that are desperately needed to ensure the long term sustainability of the bacalao fishery and reduce current levels of discards and bycatch associated with it (Zimmerhackel et al., 2015). Creating management regulations, however, is often easier than implementing them. This is especially true in developing countries (McClanahan, Maina & Davies, 2005; King, 2013), where using collaborative approaches is necessary to ensure compliance to management regulations (Yochum, Starr & Wendt, 2011; Usseglio, Schuhbauer & Friedlander, 2014). By working with the local fishing community to develop more accurate estimates of age, growth, and reproduction of bacalao, our results are more credible to them, and therefore more likely to be accepted in any future management decisions.

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Table 1(on next page)

Reproductive stages used to assess maturity

Reproductive stages, histological features, and maturity rating used to assess the maturity of female bacalao. Stages follow key milestones in the reproductive cycle (modified from (Brown-Peterson et al., 2011)).

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Phase	Histological features	Maturation
Immature (never spawned)	Small ovaries, often clear, blood vessels indistinct. Only oogonia and primary growth oocytes present. No atresia or muscle bundles. Thin ovarian wall and little space between oocytes.	Immature
Developing (ovaries developing but not yet ready to spawn)	Enlarging ovaries, blood vessels becoming more distinct. Primary growth, cortical alveolar, vitellogenic stages 1 or 2. No evidence of vitellogenic stage 3 or postovulatory follicles.	Mature
Spawning capable	Large ovaries, blood vessels prominent, Vitellogenic stage 3 oocytes and postovulatory follicles present. Early stage maturation oocytes might be present. Atresia or early vitellogenic oocytes might be present.	Mature
Regressing	Atresia at any stage, postovulatory follicles present. Blood vessels prominent. Some cortical alveolar and or vitellogenic oocytes stages 1 or 2 present.	Mature
Regenerating	Small ovaries, blood vessels reduced but present. Only oogonia and primary growth oocytes present. Muscle bundles, enlarged blood vessels, thick ovarian wall, atresia, old degenerating postovulatory follicles, may be present.	Mature

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Figure 1(on next page)

Study area

Study area of the Galapagos archipelago, red dots represent sampling sites; inset map shows the location of the Galapagos archipelago.

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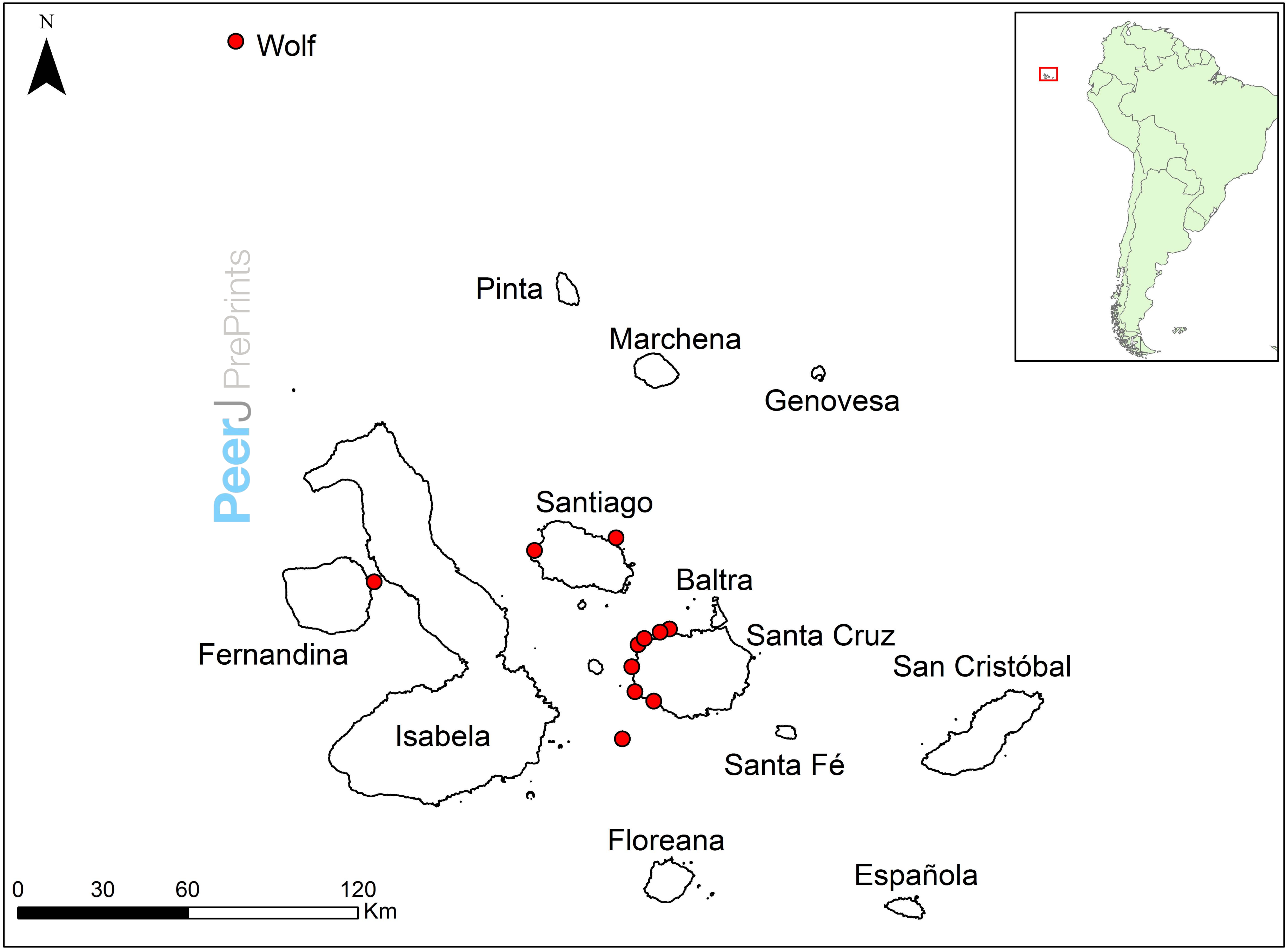

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Figure 2(on next page)

Size class distribution of fish used to assess growth

Size class distribution of otolith sub-sample fish (n= 141). Black dashed line represents mean TL (50.4 cm ± 12.8 sd).

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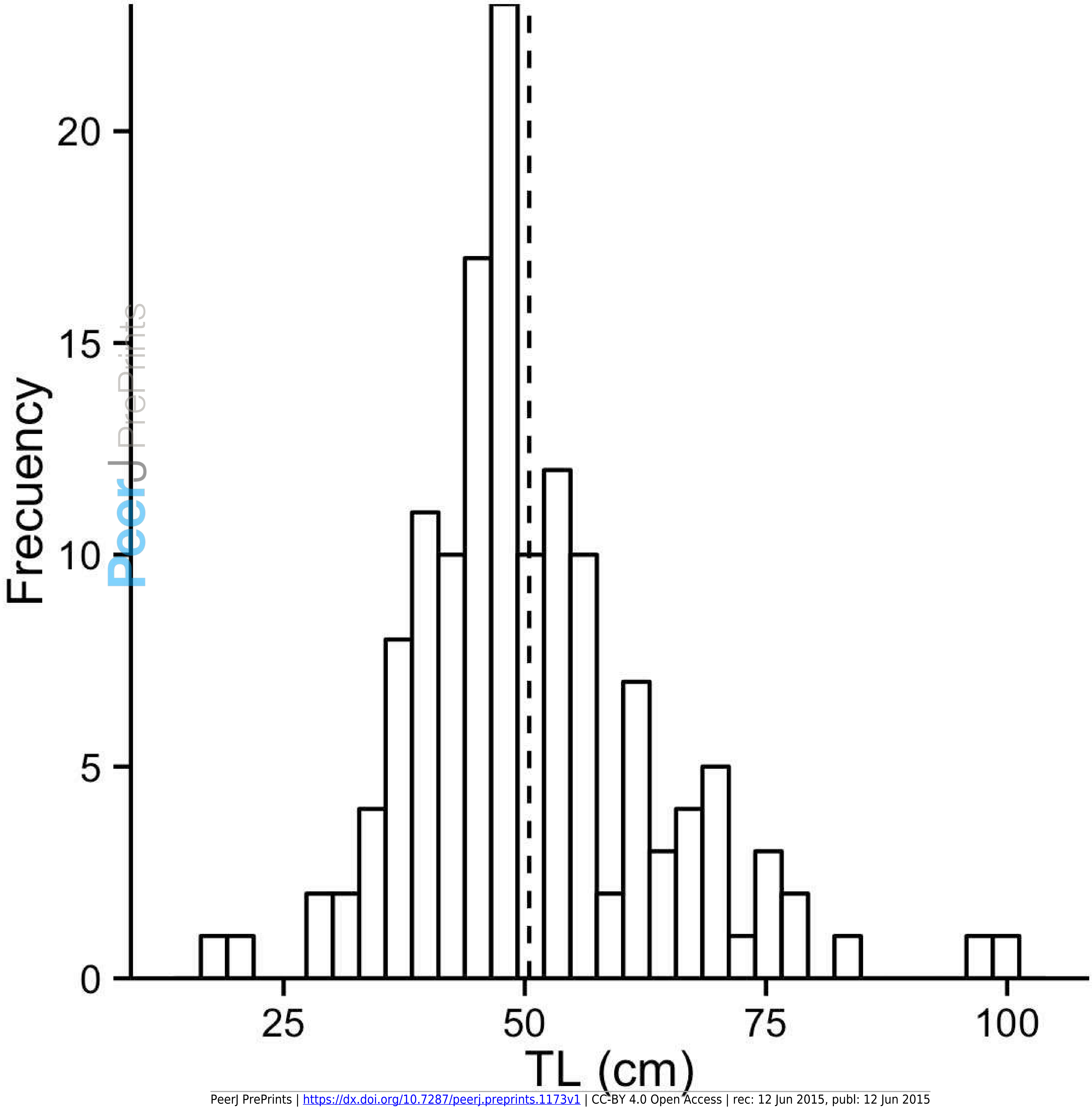
Frecuency
TL (cm)
0
5
10
15
20
25
50
75
100

3

Photomicrograph of otolith cross section

Photomicrograph of an otolith cross section from a 49 cm, 5 year old bacalao, as viewed through a dissecting scope against a dark background with reflected light from two sources placed at opposing sides at a 45 degree angle. Red dots represent yearly rings.

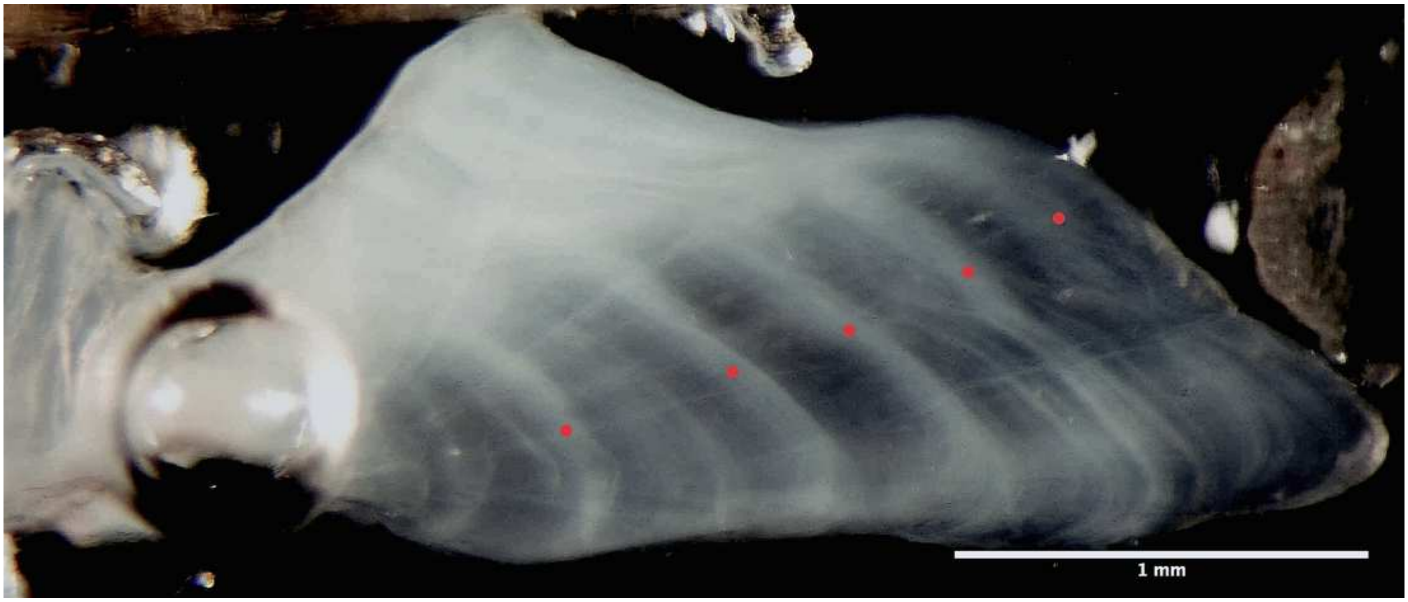

Figure 4(on next page)

Otoliths with clear margins and monthly sea water temperatures.

Proportion of otoliths with clear margins grouped by month (n = 141) and monthly sea water temperatures. Values have been standardised and rescaled to a maximum of one to allow for direct comparison of the trends.

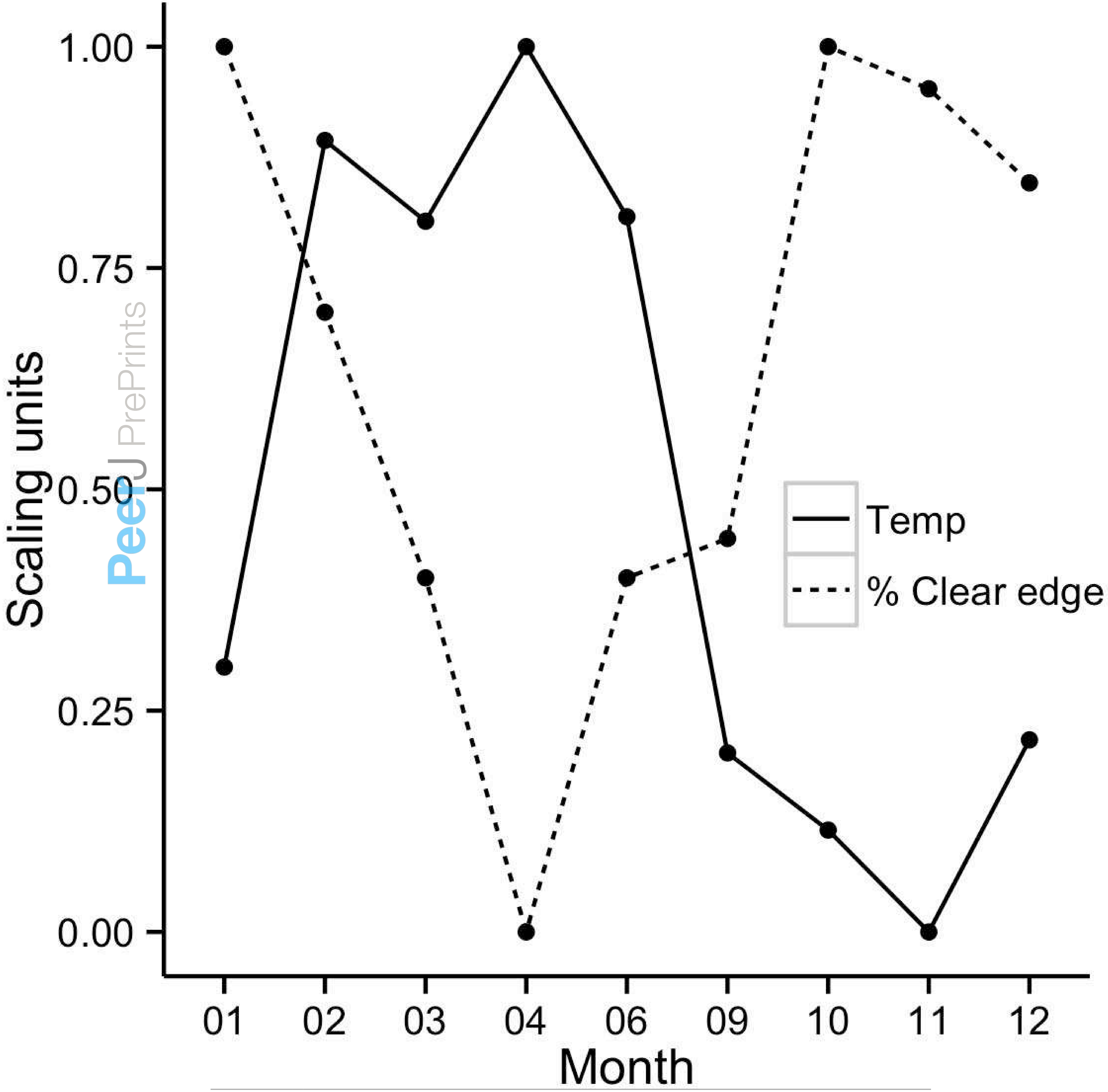

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Figure 5(on next page)

von Bertalanffy growth function for bacalao

The von Bertalanffy growth function fit to size at age data for bacalao in the Galapagos (n=141).

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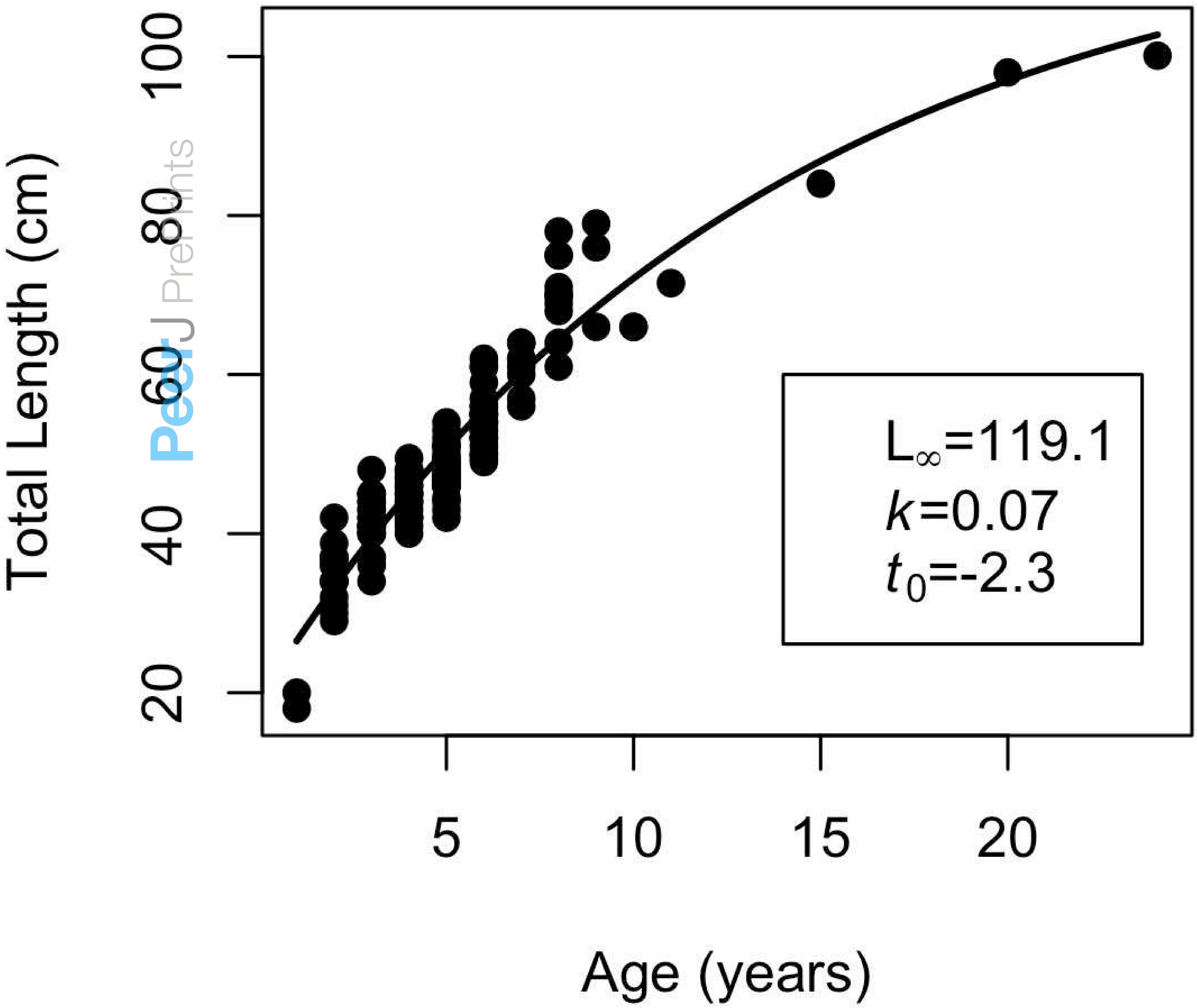

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Figure 6(on next page)

Size class distribution of bacalao sampled for gonads

Size class distribution of bacalao sampled for gonads, by sex (n= 200). Black dashed line represents mean TL (51.6 cm ±10.8 sd).

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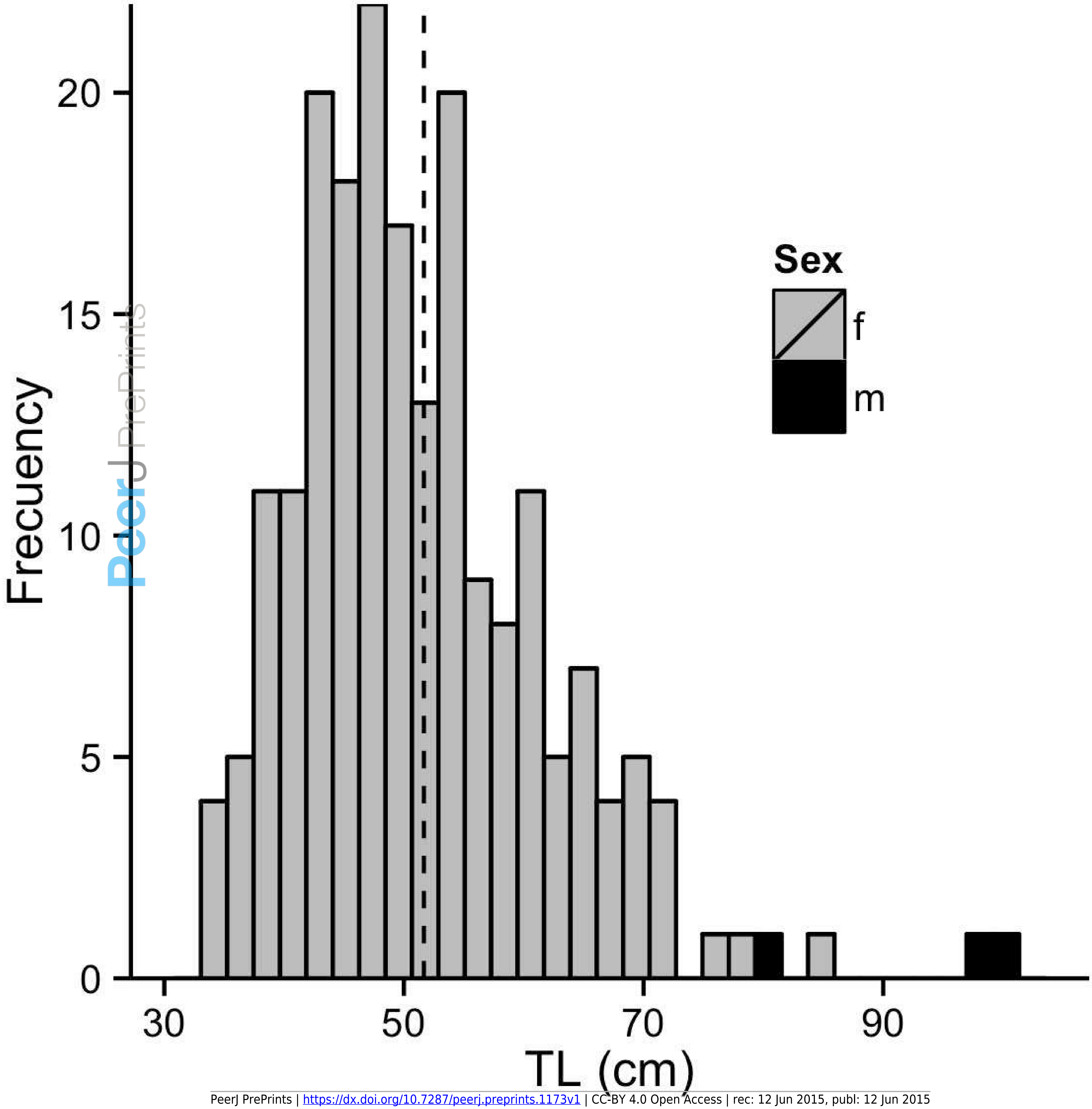

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Figure 7(on next page)

Photomicrograph of toluidine blue stained gonad cross sections

Photomicrograph of toluidine blue stained gonad cross sections of Mycteroperca olfax: a) immature 46 cm TL female exhibiting primary growth oocytes (PG) and weakly developed ovarian lamellae (L), b) spawning capable 70 cm TL female with oocytes in vitellogenic stage 3 (Vt3) and atresia (At), c) spawning capable 84 cm TL female with oocytes in vitellogenic stage 3 (Vt3) and hydrated (Hy), d) male 98 cm TL with spermatocytes (Sc). Scale bars 100 µm.

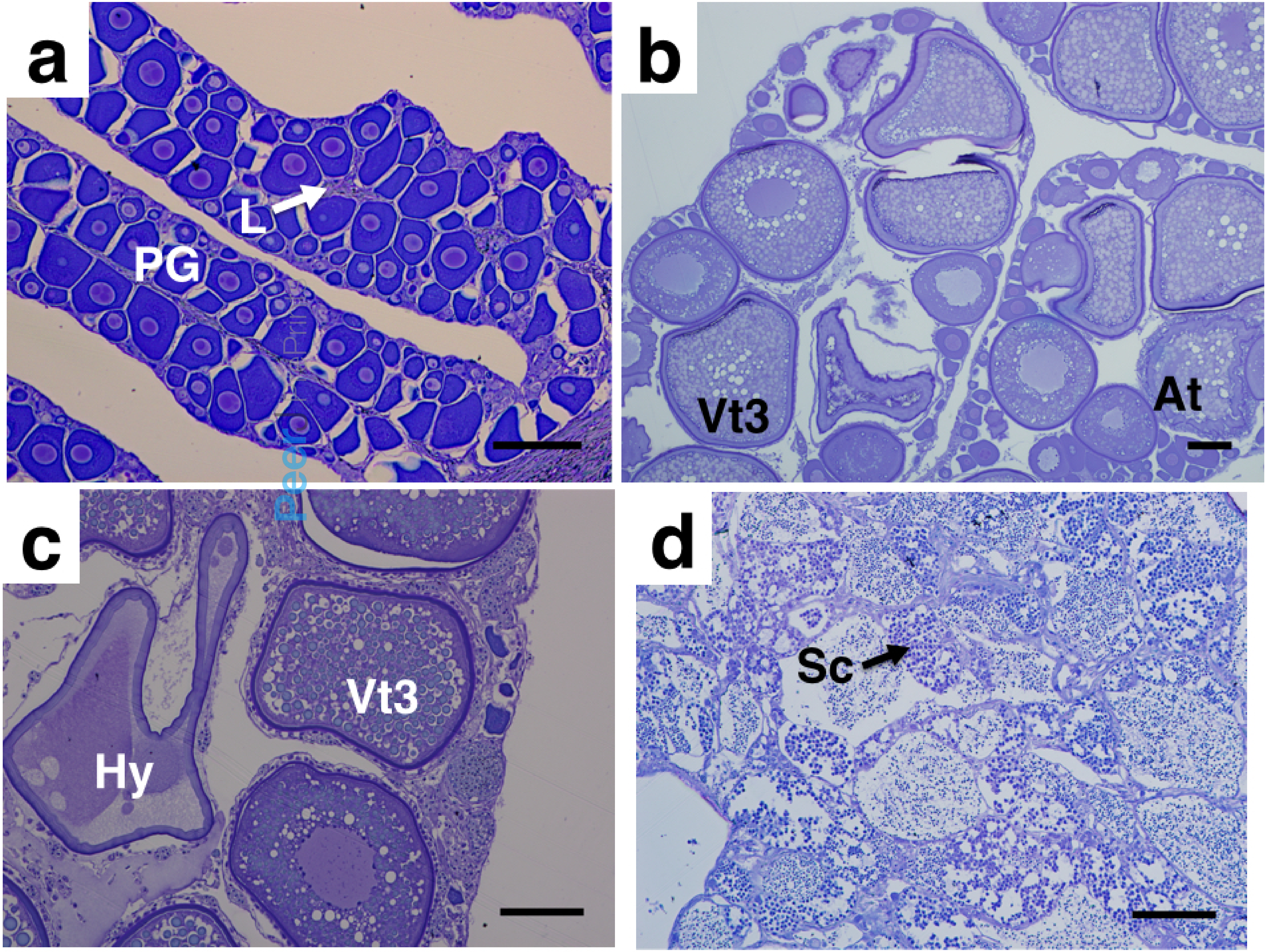

a
L
PG
b
Vt3
At
c
Vt3
Hy
d
Sc

Figure 8(on next page)

Ogive for size and age of sexual maturity

Maturity ogives for female bacalao (n=197), left: size (TL) at which 50% of the population matures (L50 = 61.1 cm TL, 58.3-65.1 95% CI), right: age at which 50% of the population matures (7.8 years, 7.1-8.6 95%CI). Blue dashed lines represent size and age at which 50% of the population matures; red line is the resulting logistic model, black squares are proportions of categorized values.

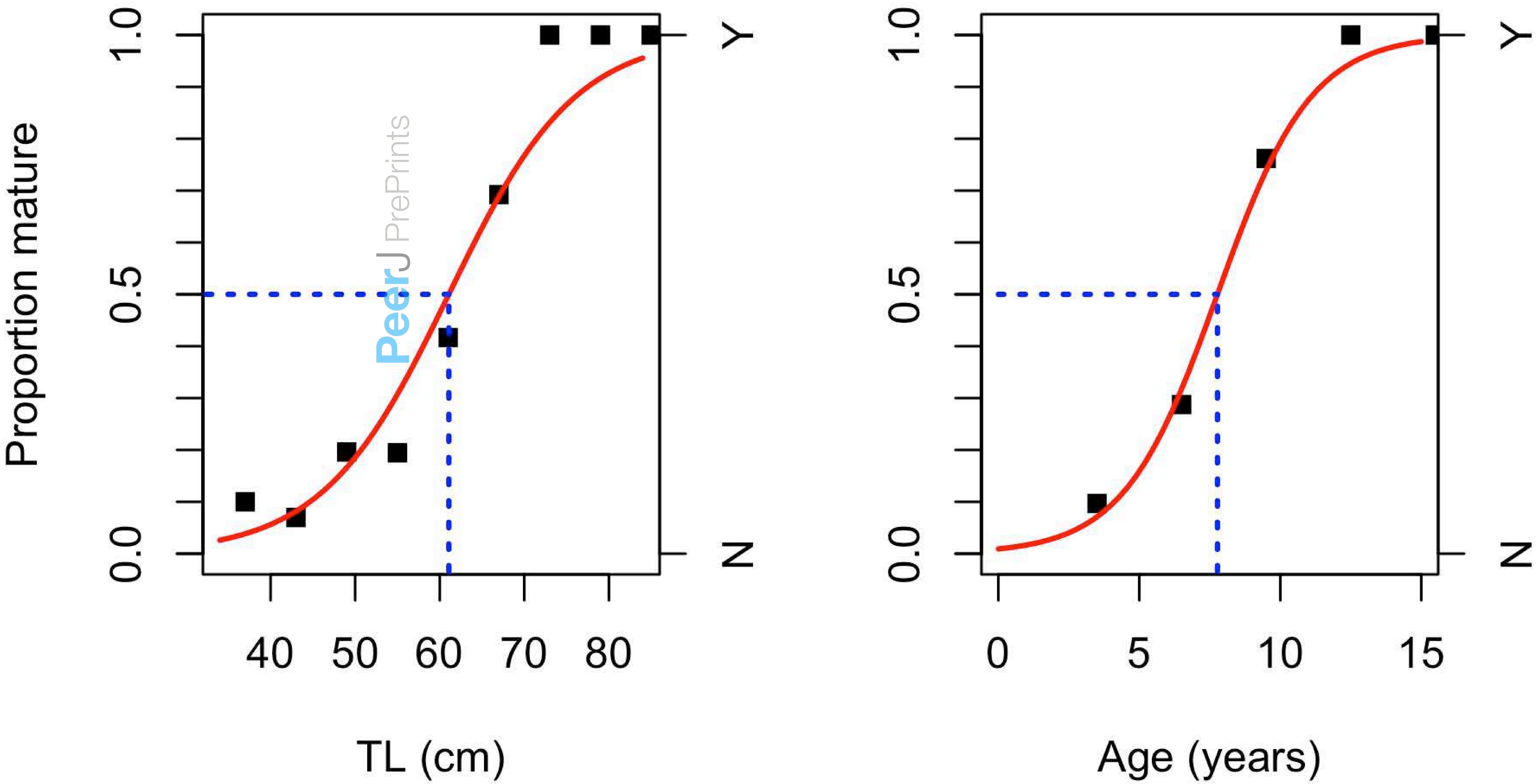
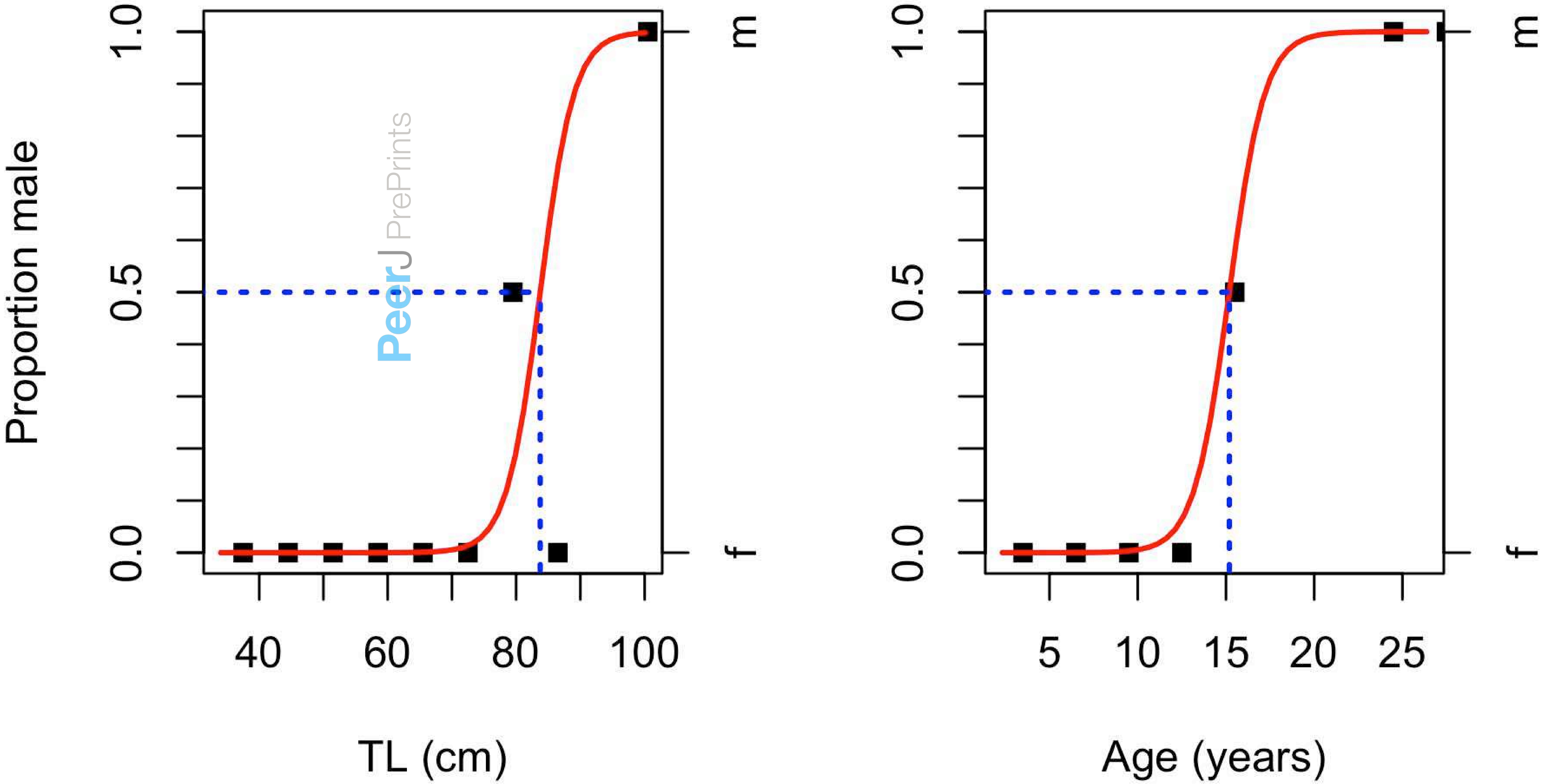

Proportion mature
1.0
0.5
0.0
Y
N
40
50
60
70
80
TL (cm)
1.0
0.5
0.0
Y
N
0
5
10
15
Age (years)

Figure 9(on next page)

Ogives for size and age of sex change in bacalao.

Maturity ogives for bacalao in the Galapagos (n=200); left: size (TL) at which 50% of the population changes sex (83.7 cm TL), right: age at which 50% of the population changes sex (15.1 years). Blue dashed lines represent size and age at which 50% of the population changes sex, red lines are the resulting logistic models, black squares are proportions of categorized values.


Proportion male
0.0
0.5
1.0
m
f
40
60
80
100
TL (cm)
0.0
0.5
1.0
m
f
5
10
15
20
25
Age (years)