

Package: mustelus (via r-universe)

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Title Chondrichthyan Fisheries Biology

Version 0.0.0.9000

Description Tools for analysing the life history of chondrichthyan fishes (sharks, rays and chimaeras), covering length-weight relationships, length or age at maturity and maternity, fecundity, clasper elongation, and von Bertalanffy growth.

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URL <https://alharry.github.io/mustelus/>,
<https://github.com/alharry/mustelus>

BugReports <https://github.com/alharry/mustelus/issues>

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Contents

blacktip	2
clasp_length	4
fecundity	5
growth	6
growth_region	8
len_weight	10
maternity	11
maturity	12
sandbar	13
spottail	14
Index	16

blacktip	<i>Common blacktip shark data</i>
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Description

A dataset containing life history information for 475 common blacktip sharks, *Carcharhinus limbatus*, collected from south-east Queensland and northern New South Wales, Australia, between 2004 and 2013. These are the data analysed by Harry et al. (2019), including the corrections made in that study.

Usage

blacktip

Format

A data frame with 475 rows and 24 variables:

source Data source: "QLD 2004–2007", Moreton Bay survey; "QLD 2007", neonates purchased from a Moreton Bay commercial fisher; "NSW 2008–2010" and "NSW 2013", observer surveys of the New South Wales Ocean Trap and Line Fishery

date Date collected

month Month, integer form

year Calendar year

tag Identification number

FL Fork length (cm)

STL Stretched total length (cm), measured with the upper caudal lobe depressed in line with the body axis

PCL Pre-caudal length (cm)

wgt Weight (kg)

sex 2 level factor

umb_scar Umbilical scar open? Yes, no or partially

neonate Known age-zero individual, TRUE where the umbilical scar was open or partially healed

clasp_length Outer length of male claspers (mm)

clasp_calc Were claspers calcified? Yes, no or partially

uter_stage Macroscopic staging of female uterus, 1 to 6 (recorded as A to F in the original data)

maturity_stage Binary maturity stage: 0, immature; 1, mature

maternity_stage Binary female maternity stage: 0, non-maternal; 1, maternal

emb Number of embryos

embTL Mean total length of embryos (mm)

male_emb Number of male embryos

female_emb Number of female embryos

reader1 Age from the first reader, adjusted for date of birth

reader2 Age from the second reader, adjusted for date of birth

age_agree Consensus age estimate, adjusted for date of birth

Details

The data combine four sources that used different fishing gears and sampled different parts of the population. Sharks from Moreton Bay, Queensland, were mostly neonates and small juveniles, sampled by fishery-independent methods and by a commercial gillnet fisher. Sharks from New South Wales were mostly larger than 150 cm and were caught on demersal setlines by the Ocean Trap and Line Fishery. Vertebrae were collected only from the 2008 to 2010 New South Wales survey, and umbilical scars were recorded only in Queensland. Species identity in the 2008 to 2010 survey was determined genetically, and individuals of hybrid ancestry with *C. tilstoni* are included, as in the original study.

Ages are counts of growth zone pairs on sectioned vertebrae, read independently by two readers, plus the fraction of a year between an assumed birth date of 1 November and the start of the month of capture. The same fraction is added to both readings and the consensus age, so they can be passed directly to `growth()`.

Source

<https://github.com/alharry/limbatus>

References

Harry, A.V., Butcher, P.A., Macbeth, W.G., Morgan, J.A.T., Taylor, S.M. and Geraghty, P.T. (2019) Life history of the common blacktip shark, *Carcharhinus limbatus*, from central eastern Australia and comparative demography of a cryptic shark complex. *Marine and Freshwater Research* **70**(6), 834-848. doi:10.1071/MF18141

clasp_length	Analyse clasper length as a function of length or age
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Description

Fits a nonlinear (logistic) model of clasper length against a continuous predictor such as body length or age, describing the rapid elongation of claspers that accompanies maturation in male chondrichthyans. The model is

Usage

```
clasp_length(clasp, x, calc = NULL, data, times = 1000, start = NULL)
```

Arguments

clasp	Numeric vector of clasper lengths
x	Continuous predictor variable (e.g. length, age)
calc	Optional clasper calcification stage, conventionally coded "n" (not calcified), "p" (partially calcified) and "y" (calcified). Used only for plotting, where points are shaded white, grey and black respectively; it does not enter the model.
data	A data frame containing the above variables
times	Number of bootstrap replicates (default 1000)
start	Optional named list of starting values for a, b, L50 and L95. If NULL (the default) these are derived from the data.

Details

$$CL = b + (a - b) \left(1 + e^{-\log(19)(x - L_{50}) / (L_{95} - L_{50})} \right)^{-1}$$

where b and a are the juvenile and adult asymptotes, and L50 and L95 are the values of the predictor at which clasper length reaches 50 and 95 percent of the way between them. It is fitted on the log scale via `nls()`, giving multiplicative error, so the fitted curve describes median rather than mean clasper length.

Confidence intervals on the parameters and on the fitted curve are obtained by bootstrap resampling with `rsample`. Prediction intervals combine the bootstrap variance of the curve with the residual variance of the fit.

Records with missing or non-positive clasper length are dropped, so passing a data frame containing both sexes is safe provided females are recorded as NA.

Value

A one row tibble of class "clasp_length" containing the list columns data, coefs, preds, mods and boot_coefs.

Examples

```
library(ggplot2)
data(spottail)

cl <- clasp_length(clasp_length, length, clasp_calc, data = spottail, times = 200)

summary(cl)

plot(cl) + xlab("Total length (mm)") + ylab("Clasper length (mm)")
```

fecundity

*Analyse fecundity as a function of length or age***Description**

Fits a linear regression of fecundity (e.g. number of *in utero* embryos) against a continuous predictor such as length or age. Essentially a wrapper for `lm()` and `predict.lm()` that tabulates useful summary statistics and returns the predicted mean with 95 percent confidence and prediction intervals, in the style of Walker (2005).

Usage

```
fecundity(fec, x, data)
```

Arguments

fec	Numeric vector of fecundity counts (e.g. number of embryos)
x	Continuous predictor variable (e.g. length, age)
data	A data frame containing the above variables

Details

Records with zero or negative fecundity are dropped before fitting, since a count of zero indicates a non-gravid animal rather than a fecundity of zero. The number dropped is reported as a message. Predictions therefore span the length or age range of gravid animals only.

Value

A one row tibble of class "fecundity" containing the list columns data, coefs, preds, and mods.

References

Walker, T.I. (2005) Reproduction in fisheries science. In: Hamlett, W.C. (ed) *Reproductive Biology and Phylogeny of Chondrichthyes*.

Examples

```
library(ggplot2)
data(spottail)

fec <- fecundity(emb, length, data = spottail)

summary(fec)

plot(fec) + xlab("Total length (mm)") + ylab("Number of embryos")
```

growth	<i>Analyse growth from length at age data</i>
--------	---

Description

Fits a von Bertalanffy growth model to length at age data, following Harry et al. (2019), which builds on Cope and Punt (2007). The curve is parameterised by length at birth rather than t_0 :

Usage

```
growth(
  len,
  age,
  grouping_var = NULL,
  data,
  neonate = NULL,
  reads = NULL,
  cv_age = NULL,
  start = NULL
)
```

Arguments

len	Numeric vector of lengths
age	Numeric vector of ages. Used directly when ageing error is off, and as the starting value for true age when it is on.
grouping_var	Optional grouping variable (typically sex). Separate L_{inf} and K are estimated per group; L_0 and CV_L are shared.
data	A data frame containing the above variables
neonate	Optional indicator for individuals of known age zero. Anything coercible to logical, e.g. <code>umb_scar %in% c("y", "p")</code> .
reads	Optional replicate age reading columns, e.g. <code>c(reader1, reader2)</code> . Switches on ageing error. Readings must be on the same scale as age: where ages include an adjustment for birth date, the same adjustment should be added to each reading. Readings must be greater than zero.

cv_age	Optional ageing CV supplied directly. An alternative to reads when only a consensus age is available.
start	Optional named list of starting values for Linf, K, L0 and CV_L. Derived from the data if NULL.

Details

$$L_{i,g}(a) = L_0 + (L_{\infty,g} - L_0)(1 - e^{-K_g a_{i,g}})$$

where $L_{\infty,g}$ and K_g may differ between groups (typically sexes) while L_0 is shared. Observed length is normally distributed about the curve with a standard deviation proportional to expected length, $\sigma_L = CV_L L_{i,g}$, so variability in length at age grows with size.

Two optional extensions from the paper can each be switched on independently.

Ageing error. Supplying reads, two or more columns of replicate age readings, treats true age as a random effect. Observed readings are linked to true age by $A_{i,j} = a_i + \epsilon$, with $\epsilon \sim N(0, (CV_a a_i)^2)$. The ageing CV is computed from the replicate readings outside the likelihood and held fixed. Alternatively cv_age supplies that CV directly, which is useful where only a consensus age is available but the ageing CV is known from elsewhere. With neither argument, age is treated as measured without error.

Neonates. Supplying neonate, an indicator for individuals of known age zero such as those with an unhealed umbilical scar, adds their lengths as direct information on L_0 through $L_{0,i} \sim N(L_0, (CV_L L_{0,i})^2)$. Flagged individuals are used only for this term: any that also carry an age are removed from the length at age data, since an age-zero observation and a length at birth observation carry the same information and including both would count it twice.

Estimation is by maximum likelihood using RTMB, with the random effects integrated out by the Laplace approximation. Confidence intervals on the fitted curve come from the delta method via sdreport; prediction intervals add the individual variability CV_L .

Value

A one row tibble of class "growth" containing the list columns data, coefs, preds, mods and neonates. coefs has one row per group, with L0 and CV_L repeated since they are shared. mods holds the RTMB objective, the nlminb result and the sdreport.

References

- Cope, J.M. and Punt, A.E. (2007) Admitting ageing error when fitting growth curves: an example using the von Bertalanffy growth function with random effects. *Canadian Journal of Fisheries and Aquatic Sciences* **64**(2), 205-218. doi:10.1139/f06179
- Harry, A.V., Butcher, P.A., Macbeth, W.G., Morgan, J.A.T., Taylor, S.M. and Geraghty, P.T. (2019) Life history of the common blacktip shark, *Carcharhinus limbatus*, from central eastern Australia and comparative demography of a cryptic shark complex. *Marine and Freshwater Research* **70**(6), 834-848. doi:10.1071/MF18141

Examples

```
library(ggplot2)
data(spottail)

# Sex-specific growth, with neonates informing length at birth
g <- growth(length, age_agree, sex, data = spottail,
            neonate = umb_scar %in% c("y", "p"))

summary(g)

plot(g) + xlab("Age (years)") + ylab("Total length (mm)")

# Ageing error from two readers, as in Harry et al. (2019)
data(blacktip)
g2 <- growth(STL, age_agree, sex, data = blacktip, neonate = neonate,
            reads = c(reader1, reader2))

summary(g2)
```

growth_region

Likelihood confidence regions for growth parameters

Description

Constructs approximate joint confidence regions for L_∞ and K from a [growth](#) fit, following Kimura (1980). Unlike an ellipse drawn from the covariance matrix of the estimates, the region follows a contour of equal likelihood and need not be symmetrical about the estimates.

Usage

```
growth_region(x, level = 0.95, profile_L0 = FALSE, n_steps = 50)
```

Arguments

x	An object returned by growth
level	Confidence level
profile_L0	Re-estimate L_0 at each point rather than holding it at its estimate
n_steps	Number of values of K at which the boundary is found

Details

Kimura (1980) defined the region by the residual sum of squares,

$$S(L_\infty, K, t_0) \leq \hat{S} \left(1 + \frac{p}{N-p} F_{p, N-p}(1-\alpha) \right)$$

with $p = 3$ parameters and N observations, and displayed it as the two-dimensional cross-section for L_∞ and K with t_0 held at its estimate. `growth()` maximises a likelihood with a standard deviation that changes with length, so the same criterion is applied to the log-likelihood ℓ :

$$2 \left[\hat{\ell} - \ell(L_\infty, K) \right] \leq N \log \left(1 + \frac{p}{N-p} F_{p, N-p}(1 - \alpha) \right)$$

For a single group with constant variance this is identical to Kimura's criterion. N is the number of aged individuals in the group.

L_0 takes the place of t_0 and is held at its estimate, as are the parameters of the other groups. CV_L is re-estimated at each point, as σ effectively is in the ratio of sums of squares. As Kimura noted, holding the third parameter fixed gives a cross-section of the region rather than a true confidence region, since more extreme values of L_∞ and K may occur at a different value of it. Setting `profile_L0 = TRUE` re-estimates L_0 at each point as well, giving the projection of the full three-parameter region onto L_∞ and K . The two are close when L_0 is well determined, for example by neonates. When it is not, the projection can be noticeably wider, mainly in K .

As in Kimura (1980), the boundary is found by stepping through values of K and solving for the two values of L_∞ at which the likelihood reaches the critical value. This follows regions that are strongly curved, as they often are when few old animals have been aged. For models with ageing error each evaluation of the likelihood includes the Laplace approximation, and the calculation takes longer.

Value

A tibble of class "growth_region" with one row per group, holding the estimates, the number of aged individuals `n`, the critical value `crit`, and the boundary of the region in the list column `region`. `summary()` gives the range of L_∞ and K within each region.

References

Kimura, D.K. (1980) Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin* 77(4), 765-776.

Examples

```
library(ggplot2)
data(blacktip)

g <- growth(STL, age_agree, sex, data = blacktip, neonate = neonate)
r <- growth_region(g)

summary(r)

plot(r) + labs(x = "Linf (cm)", y = "K (per year)", linetype = "Sex")
```

len_weight	<i>Analyse weight-length relationship</i>
------------	---

Description

Function for running a log-linear regression model to analyse body mass as a function of length. Essentially just a wrapper for `lm()` and `predict.lm()` that tabulates some useful summary statistics. Also returns the predicted mean, 95 percent confidence intervals and prediction intervals, corrected for bias due to log transformation, and the fitted `lm()` objects.

Usage

```
len_weight(weight, length, grouping_var = NULL, data)
```

Arguments

weight	Numeric vector of weights
length	Numeric vector of lengths
grouping_var	Categorical variable containing two or more unique variables (e.g. sex). Will be converted into a factor.
data	A data frame containing, minimally, variables for length and weight, and optionally sex or another grouping variable

Value

results A list containing the `lm` model, coefficients and other useful info, predicted mean and raw data

Examples

```
library(ggplot2)
data(spottail)

lw <- len_weight(wgt, length, sex, data = spottail)

summary(lw)

p <- plot(lw)

p$f + xlab("Total Length (mm)") + ylab("Weight (kg)")
```

maternity	Analyse length or age at maternity
-----------	------------------------------------

Description

Fits the three-parameter logistic maternity function of Walker (2005) to binary data on female maternal condition, as described in Harry et al. (2024):

Usage

```
maternity(matern, x, data, pmax = NULL, times = 1000, start = NULL)
```

Arguments

matern	Binary maternal condition variable (0 = not maternal, 1 = maternal), defined following Walker (2005) as whether a female would give birth or lay eggs in the current year.
x	Continuous predictor variable (e.g. length, age)
data	A data frame containing the above variables
pmax	Upper asymptote. NULL (the default) estimates it from the data; a value in (0, 1] fixes it.
times	Number of bootstrap replicates (default 1000)
start	Optional named list of starting values for m50, m95 and pmax. Derived from the data if NULL.

Details

$$E[Y_i] = P_{Max} \left(1 + e^{-\ln(19)(x_i - x_{50})/(x_{95} - x_{50})} \right)^{-1}$$

where Y_i is a Bernoulli random variable indicating whether female i is in maternal condition, x_{50} and x_{95} are the lengths (or ages) at which 50 and 95 percent of the maximum proportion P_{Max} are in maternal condition, and P_{Max} itself is the proportion of females contributing to recruitment in a given year. The model reduces to the familiar two-parameter maturity ogive when $P_{Max} = 1$.

Two methods from Harry et al. (2024) are available. With `pmax = NULL` the asymptote is estimated from the data (*3PLF-estimated*). Supplying a value fixes it and estimates only `m50` and `m95` (*3PLF-fixed*), the approach of Walker (2005) where the asymptote is chosen from knowledge of the ovarian and uterine cycles, e.g. 0.5 for a biennial cycle or 1/3 for a triennial one. Fitting both and comparing AIC provides a formal test of reproductive periodicity.

The model is implemented in RTMB and estimated by maximum likelihood. Confidence intervals on the parameters and on the fitted curve are obtained by bootstrap resampling with `rsample`, refitting the model to each resample; replicates that fail to converge or contain no maternal females are dropped and the number reported.

Harry et al. (2024) found that sample sizes of roughly 100-200 maternal females were typically required to estimate P_{Max} accurately. With fewer, fixing `pmax` from independent information is likely to be the better choice.

Value

A one row tibble of class "maternity" containing the list columns data, coefs, preds, mods and boot_coefs. mods holds the RTMB objective function, the nlminb result and the sdreport. coefs reports asymptotic standard errors alongside the bootstrap intervals, and convergence is FALSE if any parameter is poorly identified.

References

Harry, A.V., Baremore, I.E. and Piercy, A.N. (2024) Quantifying maternal reproductive output of chondrichthyan fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **81**(10), 1481-1494. doi:10.1139/cjfas20240031

Walker, T.I. (2005) Reproduction in fisheries science. In: Hamlett, W.C. (ed) *Reproductive Biology and Phylogeny of Chondrichthyes*. Science Publishers, Enfield, NH, pp. 81-127.

Examples

```
library(ggplot2)
data(sandbar)

# Estimate the asymptote
mt <- maternity(maternity_stage, FL, data = sandbar, times = 200)
summary(mt)

# Fix it at 0.5, as for a biennial cycle, and compare by AIC
mt_biennial <- maternity(maternity_stage, FL, data = sandbar,
                          pmax = 0.5, times = 200)
summary(mt_biennial)

plot(mt) + xlab("Fork length (cm)") + ylab("Proportion in maternal condition")
```

maturity	Analyse length or age at maturity
----------	-----------------------------------

Description

Fits a logistic regression model (binomial GLM) of maturity stage as a function of length, age, or another continuous predictor. Bootstrap confidence intervals are computed via rsample.

Usage

```
maturity(mat, x, grouping_var = NULL, data, times = 1000)
```

Arguments

mat	Binary maturity variable (0 = immature, 1 = mature)
x	Continuous predictor variable (e.g. length, age)
grouping_var	Optional categorical grouping variable (e.g. sex). Will be converted to a factor.
data	A data frame containing the above variables
times	Number of bootstrap replicates (default 1000)

Value

A nested tibble of class "maturity" with one row per group, containing list columns data, coefs, preds, and mods, each named by the grouping variable level.

Examples

```
library(ggplot2)
data(spottail)

lm50 <- maturity(maturity_stage, length, sex, data = spottail, times = 100)

summary(lm50)

plot(lm50)
```

sandbar	<i>Sandbar shark data</i>
---------	---------------------------

Description

A dataset containing maturity and maternity data from 1087 female sandbar sharks, *Carcharhinus plumbeus*, collected from the Gulf of Mexico and western north Atlantic Ocean. Data from two studies were combined and maternal condition assigned to each individual for the empirical case study of Harry et al. (2024).

Usage

```
sandbar
```

Format

A data frame with 1087 rows and 4 variables:

- FL** Fork length (cm)
- maturity_stage** Binary maturity stage: 0, immature; 1, mature
- maternity_stage** Binary maternity stage: 0, non-maternal; 1, maternal
- source** Originating study: "Baremore" or "Piercy"

Source

<https://doi.org/10.1139/cjfas-2024-0031>

References

- Baremore, I.E. and Hale, L.F. (2012) Reproduction of the sandbar shark in the western North Atlantic Ocean and Gulf of Mexico. *Marine and Coastal Fisheries* **4**(1), 560-572. doi:10.1080/19425120.2012.700904
- Harry, A.V., Baremore, I.E. and Piercy, A.N. (2024) Quantifying maternal reproductive output of chondrichthyan fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **81**(10), 1481-1494. doi:10.1139/cjfas20240031
- Piercy, A.N., Murie, D.J. and Gelsleichter, J.J. (2016) Histological and morphological aspects of reproduction in the sandbar shark *Carcharhinus plumbeus* in the U.S. south-eastern Atlantic Ocean and Gulf of Mexico. *Journal of Fish Biology* **88**(5), 1708-1730. doi:10.1111/jfb.12945

 spottail

Spot-tail shark data

Description

A dataset containing life history information for 659 spot-tail sharks, *Carcharhinus sorrah*, collected from north-eastern Australia.

Usage

spottail

Format

A data frame with 659 rows and 27 variables:

month Month, integer form
year Calendar year
date Date collected
jday Day of year
tag Identification number
FL Fork length (mm)
TL Total length (mm)
PCL Pre-caudal length (mm)
length Preferred length measurement (STL)
wgt Weight (mm)
sex 2 level factor, NA if unavailable
umb_scar Umbilical scar open? Yes, no or partially
clasp_length Outer length of male claspers (mm)
clasp_calc Were claspers calcified? Yes, no or partially
gonad_stage Macroscopic staging of male testes (Not used)

run_sperm Running sperm present? Yes, no or partially (Not used)
MOD Maximum diameter of the largest ovarian follicle
yolky_ova Number of yolky ovarian follicles (Not used)
uter_stage Macroscopic staging of female uterus
maturity_stage Binary maturity stage: 0, immature; 1, mature
maternity_stage Binary female maternity stage: 0, non-maternal; 1, maternal
emb Number of embryos
embTL Mean total length of embryos
embryo Is individual an embryo? TRUE/FALSE
male_emb Number of male embryos
female_emb Number of female embryos
vertebrae Vertebrae collected? TRUE/FALSE
age_agree Consensus age estimate, adjusted for date of birth

Source

<http://dx.doi.org/10.1071/MF12142>

Index

* datasets

- blacktip, [2](#)
- sandbar, [13](#)
- spottail, [14](#)

blacktip, [2](#)

clasp_length, [4](#)

fecundity, [5](#)

growth, [6](#), [8](#)

growth_region, [8](#)

len_weight, [10](#)

maternity, [11](#)

maturity, [12](#)

sandbar, [13](#)

spottail, [14](#)