1   Investigating photoreceptor densities, potential visual acuity, and cone mosaics of shallow water,

2   temperate fish species

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4   D. E. Hunt*[1]

5   N. J. F. Rawlinson[1]

6   G. A. Thomas[2]

7   J. M. Cobcroft[3,4]

8

9   [1] Northern Hub, Institute for Marine and Antarctic Studies, University of Tasmania, Locked Bag

10   1370, Launceston, TAS 7250, Australia

11   [2]University College London, Torrington Place, London, WC1E 7JE

12   [3] Fisheries and Aquaculture Centre, Institute for Marine and Antarctic Studies, University of

13   Tasmania, Private Bag 49, Hobart, TAS 7001, Australia

14   [4] University of the Sunshine Coast, Locked Bag 4, Maroochydore DC, Queensland 4558, Australia

15   *Corresponding author: Tel.: +61431 834 287; email address: darcieh@amc.edu.au

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[1] Contact: (03) 6324 3801; email: darcieh@amc.edu.au

ABSTRACT

The eye is an important sense organ for teleost species but can vary greatly depending on the adaption to the habitat, environment during ontogeny and developmental stage of the fish. The eye and retinal morphology of eight commonly caught trawl bycatch species were described: *Lepidotrigla mulhalli*; *Lophonectes gallus*; *Platycephalus bassensis*; *Sillago flindersi*; *Neoplatycephalus richardsoni*; *Thamnaconus degeni*; *Parequula melbournensis*; and *Trachurus declivis*. The cone densities ranged from 38 cones per 0.01 mm^2 for *S. flindersi* to 235 cones per 0.01 mm^2 for *P. melbournensis*. The rod densities ranged from 22 800 cells per 0.01 mm^2 for *L. mulhalli* to 76 634 cells per 0.01 mm^2 for *T. declivis* and potential visual acuity (based on anatomical measures) ranged from 0.08 in *L. gallus* to 0.31 in *P. melbournensis*. Higher rod densities were correlated with maximum habitat depths. Six species had the regular pattern of four double cones arranged around a single cone in the photoreceptor mosaic, while *T. declivis* had only rows of double cones. *P. melbournensis* had the greatest potential ability for detecting fine detail based on eye anatomy. The potential visual acuity estimates and rod densities can be applied to suggest the relative detection ability of different species in a commercial fishing context, since vision is a critical sense in an illuminated environment for perceiving an oncoming trawl.

Keywords: potential visual acuity; rod density; cone density; cone mosaic; minimum separable angle.

1. INTRODUCTION

The eye is an essential tool for fish and is utilised for capture of prey, detection of predators, schooling, and the courtship involved in reproduction (Gurthrie & Muntz, 1993). The structure of the eye can vary depending on the adaptation to the habitat, environmental conditions during ontogeny (e.g. temperature, nutrition, light intensity), and developmental stage (Powers & Raymond ,1990). Although the teleost eye is very similar to that of terrestrial vertebrates, common variations between species occur within the retina, particularly in the abundance of the different photoreceptor

43   cells and potential visual acuity (VA) (Wagner, 1990). There are also various morphological

44   specialisations of the teleost eye in different species, such as having more than one lens, oblong

45   eyeballs, degeneration (no cornea or lens), and even the use of adipose eyelids (Gailliet, et al.,

46   1996). These adaptions of the teleost eye are suited to optimise visual ability underwater.

47   Most fish that inhabit shallow waters can detect colours and patterns with well-developed eyes

48   (Gurthrie & Muntz, 1993). Pigments (rhodopsin and porphyropsin) in the photoreceptors absorb

49   different light wavelengths and are stimulated at different light intensities (Fernald, 1988). This

50   means that fish can have both photopic vision (well-lit, colour) that is mediated by cones, and

51   scotopic vision (low-light) that is mediated by rods (Fernald, 1988). The arrangement of single,

52   double and sometimes triple cones in the retina is known as the mosaic, and is adapted to the

53   habitats and behaviour of a species (Evans & Browman, 2004, Lyall, 1957, Raymond, et al., 1995).

54   Likewise, the amount of rod and cone photoreceptor cell types in the retina is related to the habitat

55   and of the particular species. It has been well documented, for example, that those species living in

56   shallow waters often have a greater selection of cones than deep-water species that are

57   predominantly in the dark (Mas-Riera, 1991, Pankhurst, 1987).

58   In addition to the detection of certain wavelengths and light intensities, fish also need to be able to

59   resolve an image. The photoreceptor cells are also involved in potential visual acuity whereby the

60   resolving power of the eye is a function of photoreceptor cell spacing (in particular the cones) and

61   the lens size (Tamura, 1957). Lens size is important because the lens is not covered by the iris in

62   fish and the aperture is the lens diameter (Fernald and Wright, 1985). Potential visual acuity is used

63   to describe the fish's ability to detect fine detail and is important for shape discrimination (Douglas

64   & Hawryshyn, 1990). Some species require greater potential visual acuity to be able to discriminate

65   between a range of visual stimuli. This includes objects in the surrounding habitat and places to

66   hide or the shapes of other species that are considered predators (Lythgoe, 1968). Potential visual

67   acuity is a useful measure to compare the visual capabilities of fish, especially in response to human

activities such as aquaculture and fisheries. The behaviour of fish in response to light is used for

sampling and ecological observations (Catalan, et al., 2014). Likewise, it has been hypothesised that

fish with higher potential visual acuity and/or sensitivity to light could be attracted to, or stimulated

to avoid, illuminated trawl fishing gear. However, it is critical to describe the visual function of

species that may interact with fishing gear, in order to interpret or predict their behavioural

response. Other studies have compared theoretical and behavioural visual acuity in fish (e.g.

Douglas & Hawryshyn, 1990; Temple et al., 2013). Theoretical visual acuity is generally an

overestimate of behavioural visual acuity, and the disparity is thought to be caused by neural

processing and muscle function (Douglas & Hawryshyn, 1990). However, in the absence of

behavioural measures an assessment of theoretical acuity is valuable in comparative studies as an

indicator of visually mediated responses.

A selection of shallow water teleost species in North-eastern Tasmanian coastal waters were chosen

to investigate eye and retinal morphology. These species are commonly taken as unwanted bycatch

in commercial fisheries (Knuckey, 2006). Lights on trawl gear offer the potential to reduce bycatch

since light increases the visual stimulus in front of the trawl allowing fish to perceive the gear.

However, additional characteristics of fish are likely to impact on escape response, for example

other sensory input (Bond 1996; Pankhurst, 1989), retinal convergence, and higher order neural

processing (Douglas & Hawryshyn, 1990). For all but one of the selected bycatch species,

Trachurus declivis, there is no literature that quantifies the photoreceptor cells and potential visual

acuity; provides the cone mosaic patterns; nor makes comparisons of the lens diameter, cone

diameter and total fish length. The eight teleost species were chosen because of their varying

morphologies. The aim of the study was to quantify the photoreceptor cell densities and potential

visual acuity as well as describe the cone mosaic and general eye dimensions. This information will

further enhance the interpretation of the response of fish to bycatch reduction devices, specifically

those using lights.

2. MATERIALS AND METHODS

2.1 EYE SAMPLE COLLECTION

Fish samples were collected with a demersal fish trawl in North-East Tasmania. The trawl net measured 16 m in headline length and was designed to sweep an $11 - 13$ m wide strip of the seabed, was towed at 3 knots by a 35 m research vessel, the *FTV Bluefin*. The headline was 2.3 m above the seabed. Trawling was conducted during the night at 30 m depth starting at the following coordinates: 40°18"828'S and 148°32"646'E.

The left eyes of five fish were collected from each of eight species: roundsnout gurnard *Lepidotrigla mulhalli*; crested flounder *Lophonectes gallus*; sand flathead *Platycephalus bassensis*; eastern school whiting *Sillago flindersi*; tiger flathead *Neoplatycephalus richardsoni*; Degen's leatherjacket *Thamnaconus degeni*; silver biddy *Parequula melbournensis*; and jack mackerel *Trachurus declivis*. Work was carried out in accordance with the EU Directive of 2010/63/EU and the University of Tasmania Animal Ethics Committee approved the experimental procedures.

The fish length, eye and lens diameters were measured with callipers to the nearest 1 mm. Eyes were dissected and after inspection of eye quality (i.e. absence of corneal/lenticular opacity, pupil atrophy, and inflammation), a small incision was made to maximise infiltration of the fixative and to retain orientation. Samples were fixed for 24 h in 5% glutaraldehyde in a sucrose-phosphate buffer, then stored in 70% ethanol. The eye diameter was measured again post fixation, and the eyes were dissected to remove the retina prior to processing for histology.

2.2 HISTOLOGY AND RETINAL MORPHOLOGY

Retinal samples were manually dehydrated to 100% ethanol and embedded using a JB4 resin histology kit (JB4, Agar Scientific Ltd, UK). Retinas were halved to form dorsal and ventral areas. Ten random transverse sections (3 µm thickness) per retinal sample per area were cut with a Microm microtome (Heidelberg HM340) and placed in water drops on a glass slide, allowed to dry

5

117 and sections were stained with Lee's Methylene Blue-Basic Fuchsin and mounted in TBS®

118 SHUR/mount toluene-based mounting media with a coverslip. Three 100 µm transects from five

119 sections were randomly chosen and images taken under a light microscope at 400x magnification.

120 The number of photoreceptor (PR) nuclei and cone ellipsoids were counted in each transect. For the

121 purpose of this study, both double and single cones were counted as one (Hajar, et al., 2008). Cells

122 that overlapped the transect were only counted on the left side. The following formula was used to

123 find the number of rods:

124 $$Rods = PR\ nuclei - cone\ ellipsoids$$

125 Cell counts were expressed as density: cells per 0.01 mm^2 (squared counts from 100 µm transects).

126 The only differences between dorsal and ventral cell densities occurred in *L. mulhalli* (rods were 1.8

127 times higher in dorsal than ventral, t-test, df = 8, t = 2.86, *P* = 0.02; and cones were 1.6 times

128 greater in the dorsal than ventral, t-test, df = 8, t = 3.84, *P* = 0.004) and *P. bassensis* (cones were 2

129 times higher in dorsal than in ventral, t-test, df = 8, t-value = 4.39, *P* = 0.002). Consequently, the

130 cell counts were pooled by region for each of the eight species to enable further comparison based

131 on the average values for the whole eye.

132 Tangential sections (3 µm) per species were cut and stained in a similar fashion. From them, the

133 cone mosaic (the pattern of single and double cones) was observed. The tangential sections were

134 also used to measure the diameter of the single and double cones (treated as one unit) 'en face' at

135 the widest cross section using *Image J* (Version 1.46r, National Institute of Health, USA). To

136 calculate the minimum separable angle (MSA) (α), the lens diameter and highest density of cones

137 (per 0.01 mm^2) were used in the following equation:

138 $$tan\left(\frac{\alpha}{2}\right) = \frac{q(1+s)}{2F}$$

139 Where, *q* is the mean distance between two cones in mm (*q = 0.1/√p*); where *p* is density of cones

140 per unit area 0.01 mm^2), *s* is the shrinkage factor and *F* is focal length (*F = m* x *r*; where *m* is

141   Matthiessen's ratio (2.55) and *r* is lens radius in mm). Since no shrinkage was measured in the

142   majority of individuals (75%, *n*= 40) across all the species, the shrinkage factor was considered to

143   be zero and was omitted from the calculation of α. MSA (α) was used to find the potential visual

144   acuity (VA) according to (Tamura, 1957):

145
$$VA = \left(\alpha \times \frac{180}{\pi} \times 60 \right)^{-1}$$

146   Retinal magnification (β) was calculated using the following:

147
$$\tan \beta = \frac{1 \ mm \ (1 + s)}{F}$$

148   Whereby β is the angle subtended by a 1 mm projection on the retina.

149   2.3 DATA ANALYSIS

150   Pearson's correlation was used to measure the linear correlation between: eye diameter and total

151   fish length; and lens diameter and total fish length. A Student's t-test was used to compare cone and

152   rod densities in dorsal and ventral retinal areas within each species. An Analysis of Variance

153   (ANOVA) was used to detect statistical difference between species for the following: cone density,

154   rod density, minimum separable angle and potential visual acuity. Tukeys' post-hoc test was used to

155   find where the difference occurred. Data were accepted as significantly different when $P < 0.05$.

156   **3. RESULTS**

157   3.1 EYE AND RETINAL MORPHOLOGY

158   With the exception of the oval nature of the eyes of *P. bassensis* and *N. richardsoni*, all species had

159   round eyes. The species with laterally compressed body shape (including *T. degeni*, *T. declivis*, *L.*

160   *mulhalli*, *P. melbournensis* and *S. flindersi*) had eyes that are located on either side of the head

161   allowing for greater peripheral and binocular vision. In dorso-ventrally compressed fish, such as the

162   Platycephalus spp., eyes are orientated dorsally.

163 The fish eye sizes ranged from 6.2 ± 1.3 mm (mean ± SD, here and throughout) in the smallest
164 species (L. gallus) to 18.4 ± 1.5 mm in the largest (P. bassensis) and the mean lens diameter ranged
165 between 2.1 mm ± 0.2 (L. gallus) and 7.7 mm ± 0.4 (P. bassensis) (

166 Table I).

167

168 Table I: Fish size (length), eye and lens diameters, and cone photoreceptor diameter for the eight species studied from

169 benthic trawls in North-East Tasmania. SC = single cones, DC = double cones.

| Species | Total length (mm) | | | Eye diameter (mm) | Lens diameter (mm) | Cone diameter (µm) | |
	Mean (± SD)	min	max	Mean (± SD)	Mean (± SD)	Mean SC (± SD)	Mean DC (± SD)
L. gallus	116.0 (14.6)	100	137	6.2 (1.3)	2.1 (0.2)	6 (0)	11 (1.5)
L. mulhalli	171.2 (19.0)	140	190	13.2 (2.1)	5.6 (1.0)	6 (1.1)	16 (0.9)
N. richardsoni	326.4 (47.4)	251	371	16.6 (1.9)	7.2 (1.1)	N/A	N/A
P. bassensis	375.8 (125.6)	165	470	18.4 (1.5)	7.7 (0.4)	5 (0.6)	12 (1.2)
P. melbournensis	162.0 (20.4)	141	192	13.2 (1.9)	5.6 (1.0)	4 (0.5)	8 (0.6)
S. flindersi	251.0 (18.8)	235	280	14.4 (0.5)	6.3 (0.4)	11 (0.7)	16 (0.8)
T. declivis	211.8 (36.0)	162	262	13.4 (2.3)	5.9 (1.2)	N/A	14 (0.7)
T. degeni	131.4 (35.2)	139	170	11.6 (1.1)	4.4 (0.5)	2 (0.5)	8 (0.5)

170

171 The increase in eye diameter coincided with the increase in total fish length and was described with

172 linear trendlines (Figure 1). For five out of eight species there was a significant correlation between

173 the two variables (Table II). *Thamnaconus degeni* and *S. flindersi* had almost no correlation and *L.*

174 *mulhalli* could not be used as it only had two data points.

175
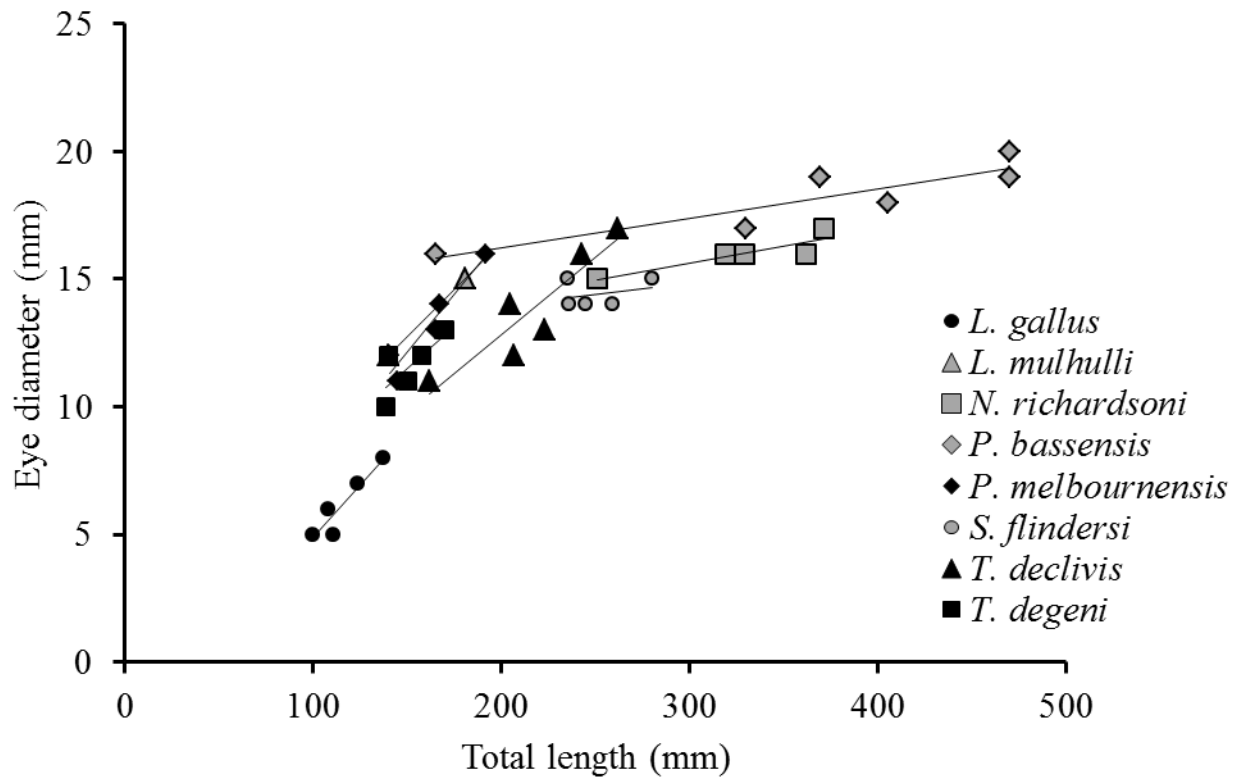
Figure 1: Eye diameter (mm) and total fish length (mm) of eight species studied from benthic trawls in North-East Tasmania. *Single column fitting image.*

Table II: t-value, degrees of freedom (df), p-value and r^2 for Pearson's correlation between eye diameter (mm) and total fish length (mm) of eight species studied from benthic trawls in North-East Tasmania.

Species	t-value	df	p-value	r^2
L. gallus	4.52	3	0.020	0.93
L. mulhalli	N/A	1	N/A	N/A
N. richardsoni	3.46	3	0.041	0.89
S. flindersi	0.57	3	0.606	0.31
P. bassensis	4.03	4	0.016	0.89
P. melbournensis	5.63	3	0.011	0.95
T. declivis	4.43	4	0.011	0.91

T. degeni	2.01	3	0.139	0.75	

182

183

184   Similarly, linear correlations show the trend between lens diameter and total length (Figure 2). Lens

185   diameter had a strong positive increase with increasing length of the fish for six out of eight species

186   (

187 Table III). Only half of the species, *P. bassensis , P. melbournensis , L. mulhalli, and S. flindersi,*

188 were found to have a significant correlation.
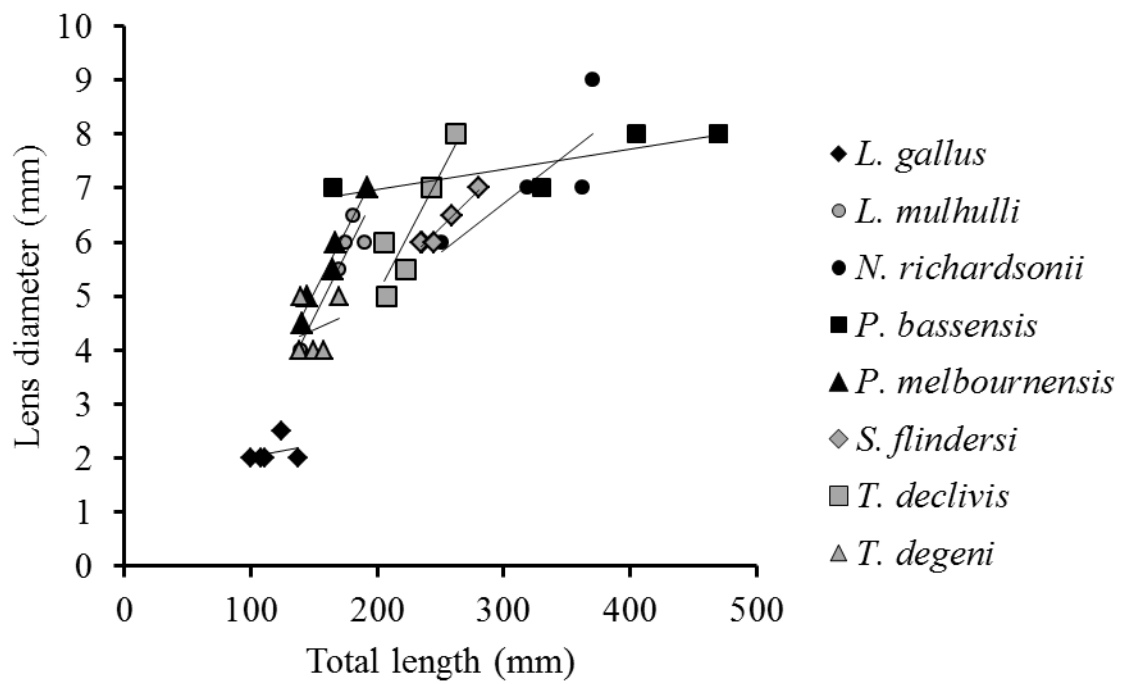
189

190 Figure 2: Lens diameter (mm) and total fish length (mm) of eight species studied from benthic trawls in North-East

191 Tasmania. *Single column fitting image.*

192

193

194 Table III: t-value, degrees of freedom (df), p-value and r^2 for Pearson's correlation between lens diameter (mm) and

195 total fish length (mm) of eight species studied from benthic trawls in North-East Tasmania.

Species	t-value	df	p-value	r^2
L. gallus	0.56	3	0.616	0.31
L. mulhalli	4.40	3	0.022	0.93
N. richardsoni	2.24	3	0.110	0.79
P. bassensis	3.38	4	0.027	0.86
P. melbournensis	8.84	3	0.003	0.98
S. flindersi	8.19	3	0.004	0.98
T. declivis	3.30	4	0.298	0.85
T. degeni	0.45	3	0.681	0.25

196

197 3.2 ROD DENSITY

198 The mean density of rods (cells per 0.01 mm^2) was significantly different across the eight different

199 species (ANOVA, $F_{7,72}= 12.72$, P<0.001) (Figure 3 and 4). *Lepidotrigla mulhalli* had the smallest

200 number of rods with 22 800 $\pm$ 2 980 per 0.01 mm^2. There was a central group, consisting of *P.*

201 *bassensis*, *L. gallus*, *P. melbournensis* and *S. flindersi*, with rod densities that ranged from 41 670 to

202 52 220 rods per 0.01 mm^2. The highest rod density of 76 630 $\pm$ 5 876 cells per 0.01 mm^2 was in *T.*

203 *declivis*.

204
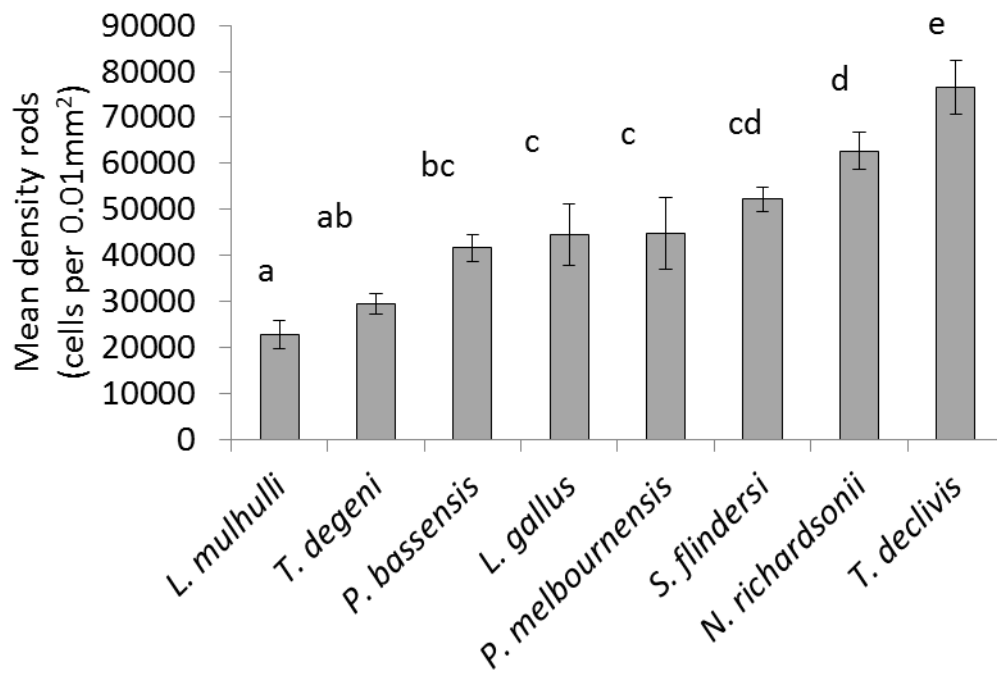
Figure 3: Mean number of rods (cells per 0.01 mm^2) ± SE, in eight different teleost species studied from benthic trawls
in North-East Tasmania. Common letters represent values that are not significantly different. *Double column fitting image.*

218 ## 3.3 CONE DENSITY AND DIAMETER
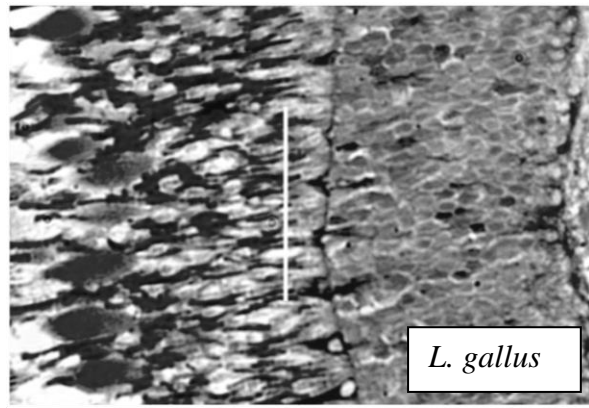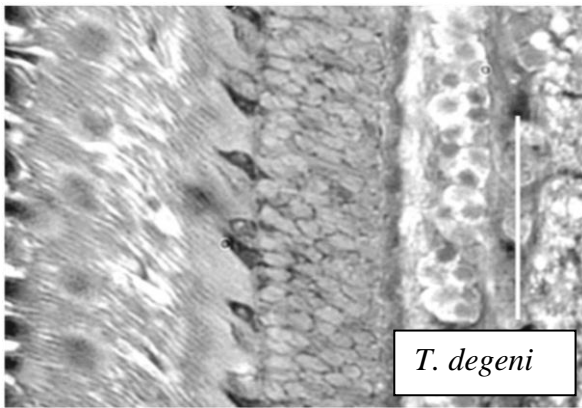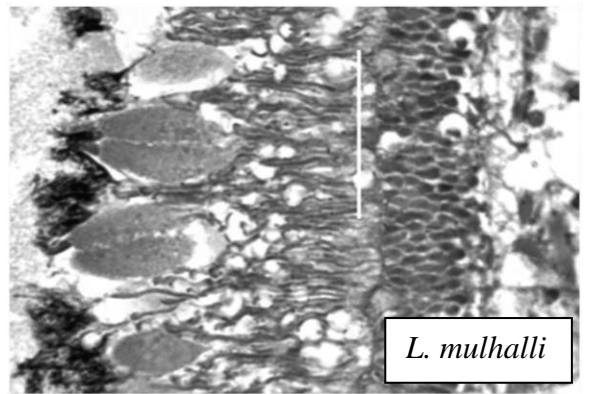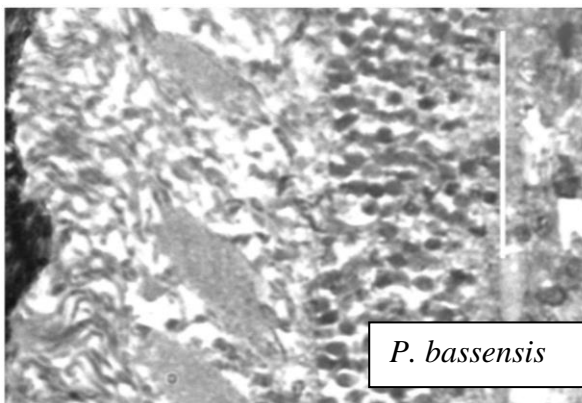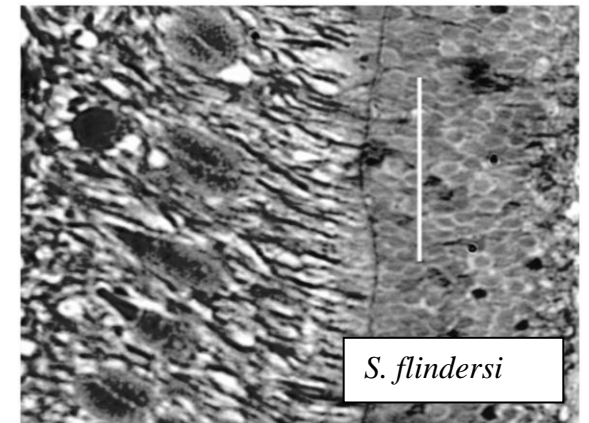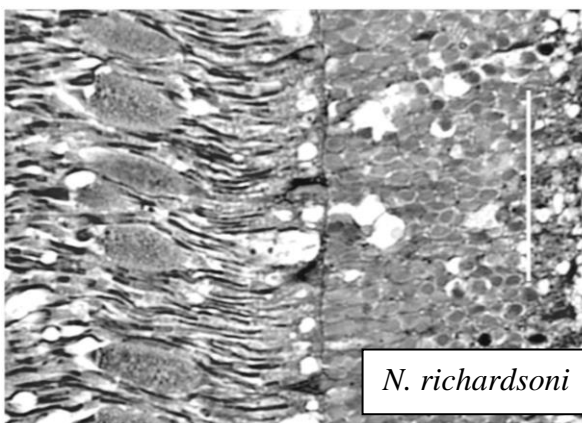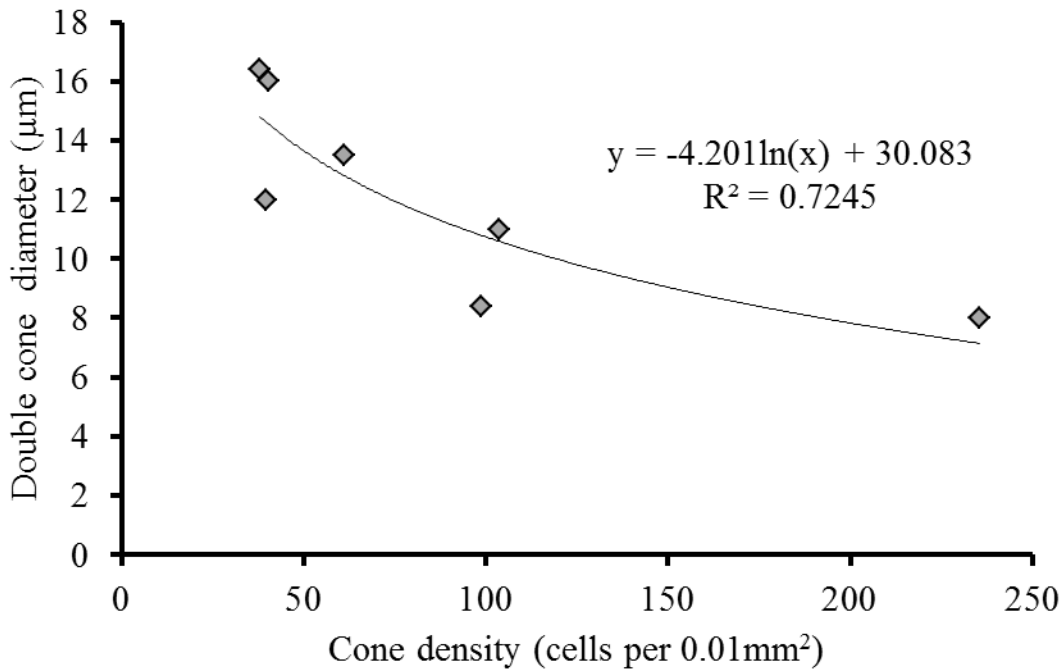
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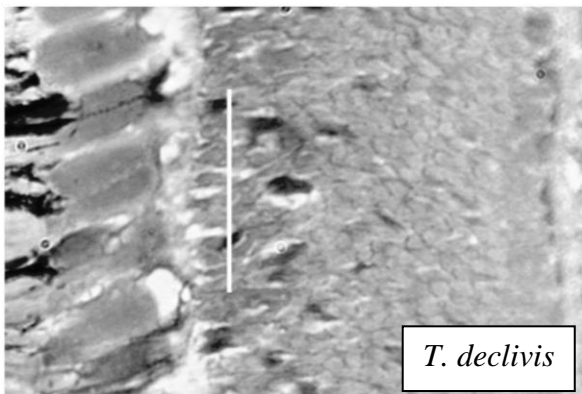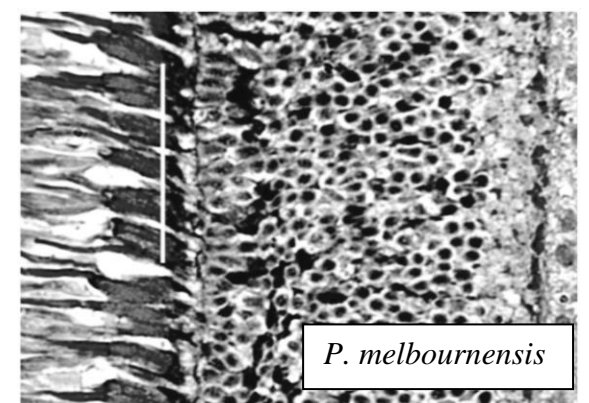
222
223 Figure 4: Transverse section of the retinas, showing the photoreceptors, of eight different fish species studied from

224 benthic trawls in North-East Tasmania. The scale bars are all 40 µm. *Double column fitting image.*

225

226   A logarithmic decay function described the relationship between double cone size, measured as

227   cone diameter, and cone density (Figure 5). 72% of the decrease in double cone size was predicted

228   to be a function of cone density.

229

The chart shows the relationship with equation:

$$y = -4.201\ln(x) + 30.083$$
$$R^2 = 0.7245$$

Y-axis: Double cone diameter (µm); X-axis: Cone density (cells per 0.01mm^2)

230

231   Figure 5: Relationship between mean diameter (µm) of double cones and the cone density in each species studied from

232   benthic trawls in North-East Tasmania, with logarithmic equation. *Single column fitting image.*

233

234   The mean density of cones (cells per 0.01 mm^2) was significantly different between species

235   (ANOVA, $F_{7,72}$= 32.564, P<0.001). Post-hoc analysis showed that species were in three main

236   groups (Figure 6). *Sillago flindersi*, *N. richardsoni*, *P. bassensis*, *L. mulhalli* and *T. declivis* all had

237   38-60 cones per 0.01 mm^2. *Thamnaconus degeni* and *L. gallus* had almost double this density, with

238   ~100 cones per 0.01 mm^2. *Parequula melbournensis* had over four times the density of the first

239   group with 235 ± 29 cones per 0.01 mm^2.

15

240
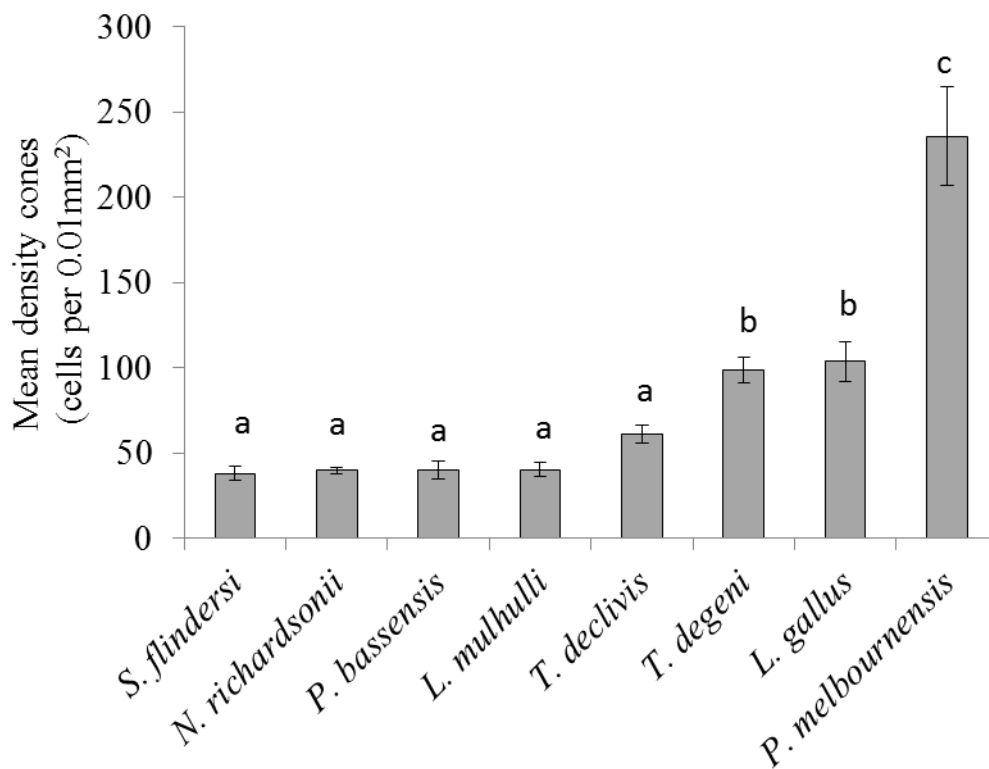
Figure 6: Mean density of cones (cells per 0.01 mm^2) ± SE, in eight different teleost species studied from benthic

trawls in North-East Tasmania. Common letters represent values that are not significantly different. *Double column*

fitting image.

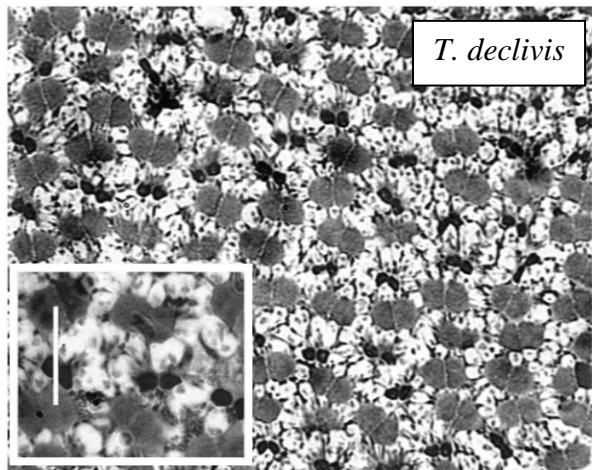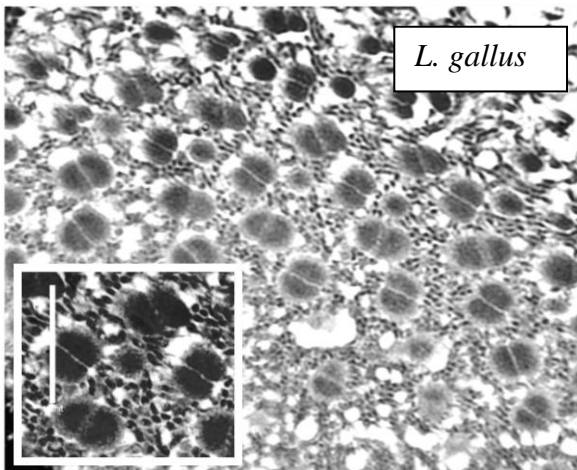## 3.4 CONE MOSAICS

Double cones were present in the mosaics of all species. With the exception of *T. declivis*, the
double cones were arranged as a set of four around a single cone (Figure 7). This arrangement
varied slightly for each species with respect to the size of the cone cells (
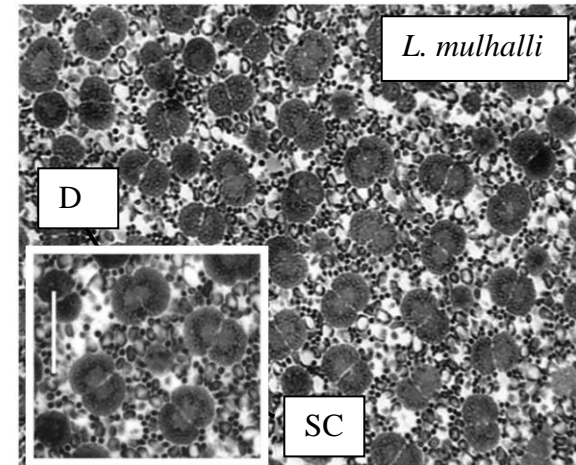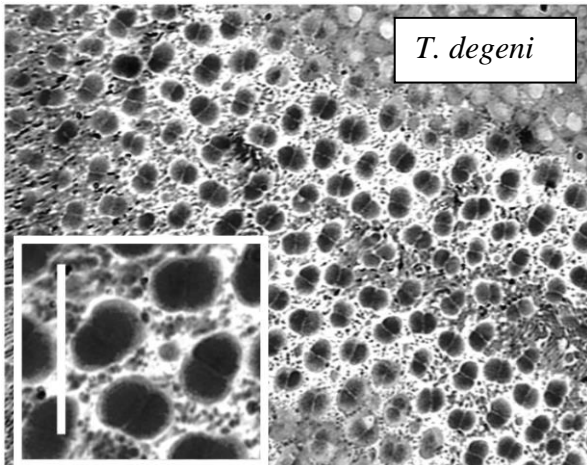
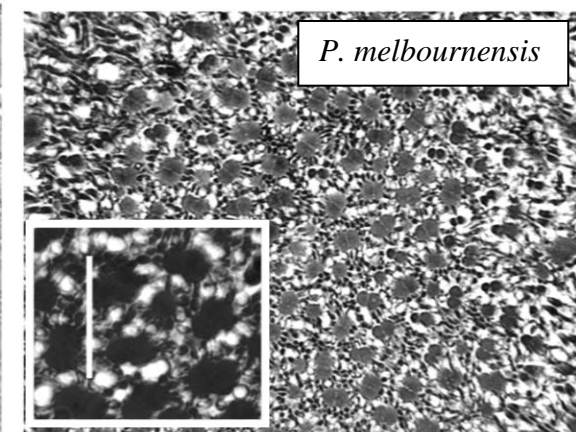Table **I**). *Trachurus declivis* had only rows of double cones.

250

251

L. gallus

T. declivis

252

T. degeni

L. mulhalli
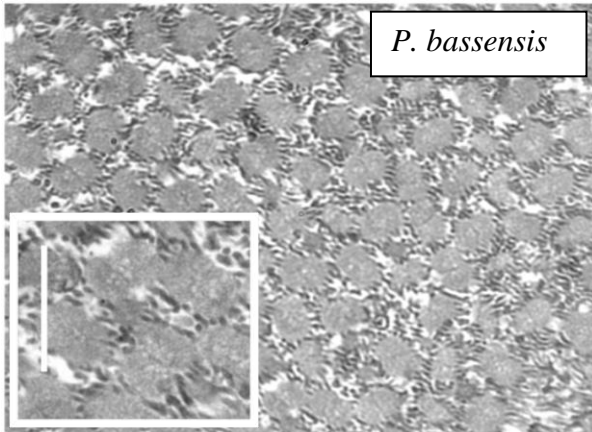
D

SC

253

P. bassensis

P. melbournensis

254

S. flindersi
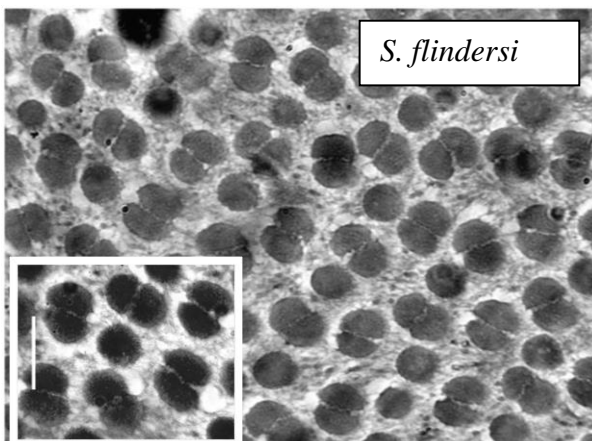
255 Figure 7: Tangential sections revealing the cone mosaic patterns in seven different fish species studied from

256 benthic trawls in North-East Tasmania. The scale bars in insets are all 40 µm. DC = double cone; SC = single

257 cone. *Double column fitting image*.

258

259 3.5 MINIMUM SEPARABLE ANGLE AND POTENTIAL VISUAL ACUITY

260 Mean MSA and VA were significantly different between the eight species studied (ANOVA,

261 $F_{7,32}$= 28.93, P<0.001, and $F_{7,32}$=15.15, P<0.001, respectively) (
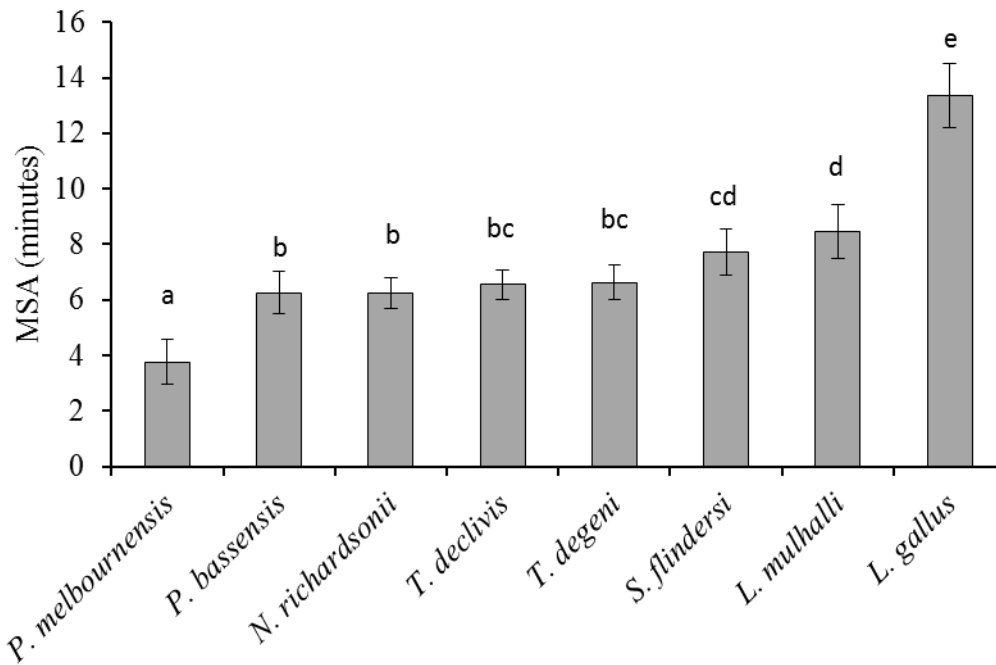
262

263 Figure 8, Table IV). *Lophonectes gallus* had the lowest value of VA, 0.078, while *L. mulhalli*,

264 *S. flindersi*, *T. degeni*, *T. declivis*, *N. richardsoni* and *P. bassensis* had from 0.125 to 0.171.

265 *Parequula melbournensis* had the highest value of 0.310. Retinal magnification (RM) was

266 also significantly different between the eight species (ANOVA, $F_{7,32}$= 65.37, P<0.001), Table

267 IV).
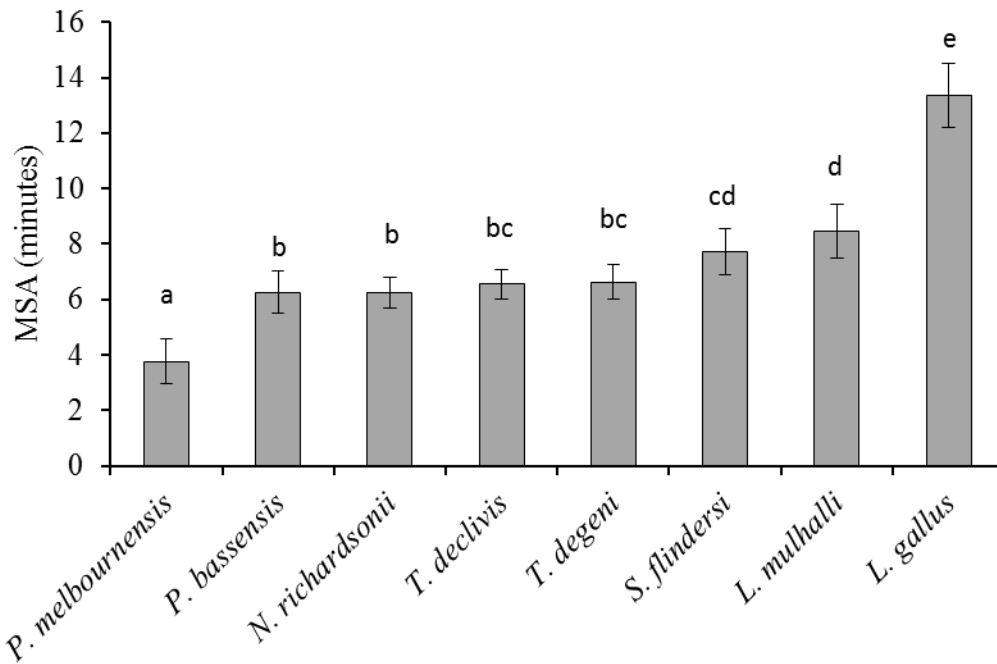
268

269   Figure 8: Mean MSA ± SE (points), in eight different temperate fish species studied from benthic trawls in

270   North-East Tasmania. Common letters represent values that are not significantly different. *Double column fitting*

271   *image.*

272   Table IV: Visual acuity (VA) and retinal magnification (degrees) in eight different temperate fish species

273   indicating the subsets from post-hoc analyses. Common letters represent values that are not significantly

274   different. Note: species are listed in order of highest to lowest VA and retinal magnification for ease of

275   interpreting subsets.

Species	Subset	VA	Species	Subset	Retinal magnification (°)
P. melbournensis	a	0.3104	*L. gallus*	a	20.61
P. bassensis	b	0.1713	*T. degeni*	b	10.40
N. richardsonii	b	0.1658	*L. mulhalli*	c	8.49
T. declivis	b	0.1573	*P. melbournensis*	c	8.26
T. degeni	b	0.1576	*T. declivis*	c	8.15
S. flindersi	b	0.1359	*S. flindersi*	cd	7.31

L. mulhalli	bc	0.1248	*N. richardsonii*	d	6.32
L. gallus	c	0.0774	*P. bassensis*	d	5.93

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277

278

4. DISCUSSION

279

280   4.1 DIMENSIONS OF THE EYE

281   An increase in both eye diameter and lens diameter occurred with an increase in total fish

282   length in five of the species assessed, based on a linear relationship. This increase was in

283   agreement with other studies (Fishelson, et al., 2004, Hajar, et al., 2008, Miyazaki, et al.,

284   2000). For those species that did not show a strong correlation in this study, this was likely

285   due to the limited range of lengths of the specimens collected. In contrast, the correlation

286   does not apply to deeper water species, where it is hypothesized that there is a limit on the

287   space in the retina for accommodating photoreceptor cells, and in this environment larger

288   eyes are observed relative to fish size (Kirschfeld, 1976). This study found that with

289   increasing cone densities there was a decrease in the diameter of each double cone which

290   agrees with the findings of Boehlert (1978). It is also recognised that, relative to fish size, eye

291   size is generally larger in carnivores than herbivores (Pankhurst, 1989). This was not the case

292   in this study as it was found that the two species with the largest eyes, *P. bassensis* and *N.*

293   *richardsonii*, had the smallest eye diameter to total length ratios. These two carnivorous

294   flathead species had the smallest ratios, followed by *T. degeni* which was the only herbivore

295   of the eight species. The largest eye sizes in relation to fish length were *L. muhulli* and *P.*

296   *melbournensis*.

297   4.2 RODS

298   *Trachurus declivis* had only 7.6 x 10^6 rod cells per mm^2 of retina, which was similar to the

299   previously reported value of 1 x 10^7 rods per mm^2 in a closely related species, yellowtail

300   horse mackerel (*Trachurus novaezealandiae*), from shallow waters of North-eastern New

301   Zealand (Pankhurst, 1989). Normally, the slight difference seen between the *Trachurus*

302   species could be attributed to the species inhabiting different ranges of depths (Edgar, 2008),

303   however in this case the maximum depth of both species is 500m (Gomon, et al., 2008).

304   Alternatively, it could be due to environmental conditions during larval development

305   (Fishelson, et al., 2012, Shand, 1997). *T. declivis* are more commonly found in deeper waters

306   and the juveniles are more likely to be found offshore than *T. novaezealandiae.* As such, it

307   would be expected that *T. declivis* have greater rod density but this is not the case here. Thus,

308   the difference seen could be due to natural interspecies variation. This could be tested by

309   estimating the rod densities of other *Trachurus* species for further comparison. No other

310   studies on photoreceptor cell densities exist for *L. mulhalli, S. flindersi, N. richardsoni, P.*

311   *melbournensis, P.bassensis, L. gallus and T degeni* or other closely related species.

312   A high density of rods is normally attributed to deeper habitat ranges (Eastman, 1988, Mas-

313   Riera, 1991). In this case, *T. declivis* is known to inhabit a maximum range of 500 m

314   (Gomon, et al., 2008), which is much deeper than the seven other species examined in this

315   paper, all with lower rod densities. It is evident that the mean number of rods per mm^2

316   increases with the expected maximum habitat depth of the species, see Figure 9. While *T.*

317   *declivis* had the greatest number of rods, *N. richardsoni*, *S. flindersi* and *L. gallus* had the

318   highest rod densities relative to the other estimates. The maximum habitat range of *N.*

319   *richardsoni, S. flindersi* and *L. gallus* extends to 160-240 m depth (Gomon, et al., 2008).

320

321
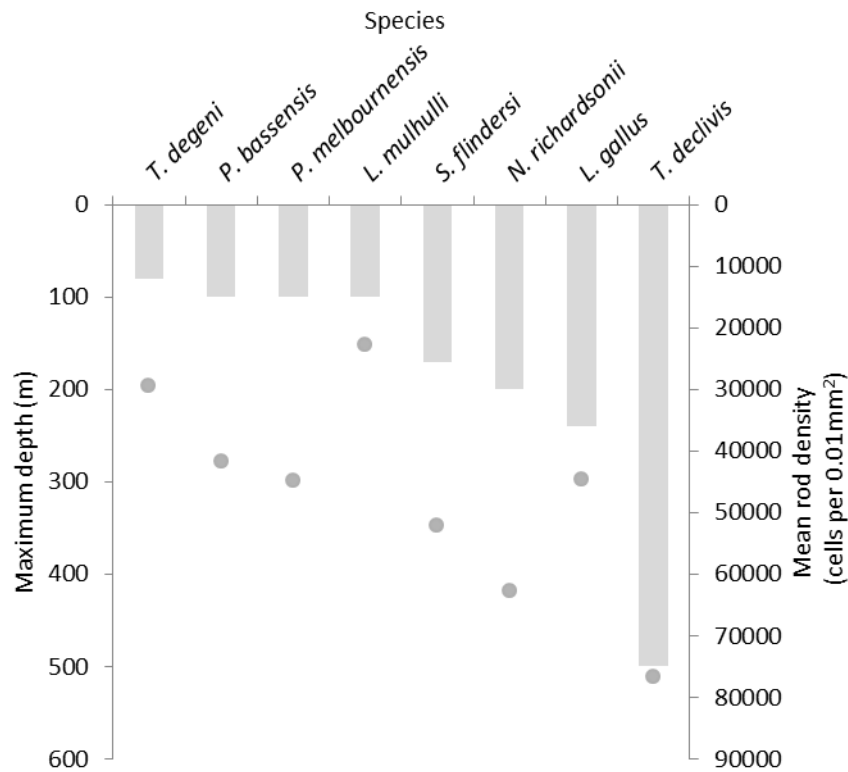
Figure 9: Maximum habitat depth profile (m) (bars) of eight bycatch species with mean rod density (cells per 0.01mm^2) (dots). Depth data from Edgar (2012). *Double column fitting image.*

On the other end of the scale, *P. melbournensis, T. degeni*, and *P. bassensis* all had the lowest rod densities and inhabit waters up to 80-100 m deep. Even in closely related species this was the case, for example, *N. richardsoni* have more rods than *P. bassensis* probably because they are found up to 60 m deeper. This is because rods are adapted for detecting dim light, and therefore are more valuable for fish to perceive visual cues in low light intensity conditions associated with deep water (Fernald, 1988). For *T. declivis*, having the highest density of rods would likely result in this species responding quickly to lights, since rods are sensitive to the shift from dark to light (Bond, 1996). The only species that did not follow this trend was *L. mulhalli*. This species is usually located at depths up to 100 m but had the lowest estimate of rod density. However, of the eight species, this species has the largest eye diameter to total

335 length ratio, and an intermediate retinal magnification. This could be an adaption that allows

336 for increased light capture and a larger depth range of the species. Alternatively, it could

337 simply be a reflection of the time actually spent at its maximum range.

338 4.3 CONES

339 The densities of cones were found to be less variable among species in this study than rod

340 densities. While foveae, specialized regions of high cone density, do occur in some fish

341 species (Wagner, 1990; Douglas & Hawryshyn, 1990), this feature was not assessed in this

342 study and average cone densities in dorsal and ventral regions were used for ease of species

343 comparisons. Foveae may contribute to differences in functional visual ability among species.

344 *Parequula melbournensis* had the greatest density of cones which suggests that they are

345 adapted to shallow habitats, but they are found in depths of greater than 100 m (Fishelson, et

346 al., 2012). This species is apparently diurnal (mostly active during the day), as are most of the

347 other species' in this study (Edgar, 2008), suggesting they would be less reliant on rods. The

348 high cone density of *P. melbournensis* could be due to the fact that this is a schooling species

349 (Edgar, 2008), requiring visual cues to maintain orientation in a group. However, *T. declivis*

350 also exhibits schooling (Gomon, et al., 2008), and had a much lower cone density. While it

351 has been shown that certain species have vision dependent schooling behaviours (Kowalko,

352 et al., 2013), most fish use the lateral line as the dominant mechanism for schooling (Larsson,

353 2012).

354 Conversely, *S. flindersi*, *N. richardsoni*, *P. bassensis*, *L. mulhalli* and *T. declivis*, all had the

355 lowest density of cones. It could be assumed that in the relatively shallow depth that light can

356 penetrate (to ~100 m), the absolute densities of cones are not as important as the types of

357 cones available. It has been demonstrated that single cones and double cones (and perhaps

358 also triple cones, that were not observed in this study) are sensitive to different wavelengths

359 of light (Loew & Lythgoe, 1978, Marc & Sperling, 1976, Tamura, 1957, Ullmann, et al.,

360 2011). The eyes of certain species may be adapted to their underwater visual environment

361 niche, for specific light intensities, light spectra, plankton colours, and dissolved and

362 particulate materials (McFarland & Munz, 1975).

363 4.4 CONE MOSAICS

364 The cone mosaic for six of the eight species had a similar arrangement of four double cones

365 around a center single cone, which is a common arrangement, especially in shallow water

366 species (Boehlert, 1978, Mas-Riera, 1991, Wagner, 1990). *Trachurus declivis* was different,

367 with rows of double cones, which is a known pattern for species in deeper water habitats and

368 shoaling species (Boehlert, 1978). This is contrary to a similar species, *Trachurus*

369 *mediterraneus ponticus*, which has a regular structural organization of four double cones

370 around a single cone (Podugolnikova, 1985). This difference is unexpected since both species

371 are deeper-water shoaling species. There are no studies in species similar to *L. mulhalli, S.*

372 *flindersi, P. melbournensis, P.bassensis, L. gallus and T degeni.* The shallow water species

373 would have increased visual capacity via colour sensitivity compared to the deeper water

374 species, since this is conferred by the complex cone mosaic that can allow for detection of

375 different light spectra (Boehlert, 1978, Losey, et al., 1999).

376 4.5 MINIMUM SEPARABLE ANGLE AND POTENTIAL VISUAL ACUITY

377 The MSA for *T. degeni* (6.6 minutes) was very similar to that of another Monocanthidae

378 species, *Cantherines modestus* which had a value of 6.4 minutes (Tamura, 1957). However,

379 the MSA of *L. mulhalli* (8.5 minutes) was higher than a related species *Chelidonichthys kumu*

380 (6.8 minutes) (Tamura, 1957). This difference was most likely due to the larger size of the

381 specimens examined, for example *C. kumu* grows to around 500 mm (Gomon, et al., 2008)

382 while the mean size of the *L. mulhalli* in this study was 172 mm. *S. flindersi* and *T. declivis*

383   from this study were not similar to their Japanese counterparts of the same size; the MSA for

384   *S. flindersi* (7.7 minutes) was less than that of the *Sillago japonica* (10.0 minutes), while in *T.*

385   *declivis* (6.6 minutes) MSA was less than *Trachurus japonicus* (7.7 minutes) (Hajar, et al.,

386   2008). The two *Sillago* species have many similar characteristics such as habitat and

387   maximum length, however the difference in depth range (up to 170 m for *S. flindersi* and up

388   to 30 m for *S. japonicus*) may be the key factor to these differences in the values (Matsuura,

389   1985). Similarly, the maximum habitat depth of *T. declivis* (up to 500 m) is deeper than the

390   maximum depth for *T. japonicus* (275 m) (Matsuura, 1985). The Japanese species have

391   higher MSA (lower resolution) even though they occur in shallower water with higher light

392   intensity.

393   Potential visual acuity is dependent upon cone cell density in the calculation, and therefore

394   these results tended to reflect similar patterns among the eight species. For this reason, *P.*

395   *melbournensis* had the largest calculated potential visual acuity. However, lens size is also an

396   important factor to determine potential visual acuity, which contributed to *L. gallus*

397   possessing the lowest potential visual acuity of the eight species. The other six species (*P.*

398   *bassensis*, *N. richardsoni*, *T. declivis*, *T. degeni*, *S. flindersi* and *L. mulhalli*) were not

399   significantly different. Higher potential visual acuity and low retinal magnification are

400   beneficial to an individual as they allow better distinguishing of fine detail at a greater

401   distance. The benefits could range from finding food, to avoiding predation, or avoidance of

402   commercial fishing gear (Hajar, et al., 2008, Walsh & Hickey, 1993, Zhang & Arimoto,

403   1993)

404

405   **5. CONCLUSION**

406   By estimating the potential visual acuity of different bycatch species, calculating rod density,

407   and reviewing the implications of specific photoreceptor mosaic patterns, the potential

408 vulnerability of the species to fishing gear could be suggested. Importantly, visual ability

409 alone is not the only contributor to fish behaviour and other sensory input (mechanosensory

410 and chemosensory) may be critical especially for crepuscular or deep water species (Douglas

411 & Hawryshyn, 1990). Retinal convergence and higher order neural processing of visual

412 information will also impact available visual stimuli, and detection of a visual cue alone

413 cannot determine a fishes response to escape, swim towards or not respond to the stimulus.

414 However, for temperate shallow water species, including those in this study, the dominant

415 sensory modality is vision (Pankhurst, 1989; Douglas & Hawryshyn, 1990). In terms of the

416 commercial fishery, in particular trawling, where a mix of fish are caught but only a select

417 few species are kept, this retinal morphology data can inform mitigation techniques such as

418 the use of light to reduce fish bycatch. The use of light could aid in increasing the sensory

419 detection of fishing gear, resulting in a visual cue for fish to detect an oncoming trawl and

420 potentially elicit an escape response.

421

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