

1 Investigating photoreceptor densities, potential visual acuity, and cone mosaics of shallow water,
2 temperate fish species

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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 mm² for *S. flindersi* to 235 cones per 0.01 mm² for *P. melbournensis*. The rod densities ranged from 22 800 cells per 0.01 mm² for *L. mulhalli* to 76 634 cells per 0.01 mm² 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 adaptations 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

68 activities such as aquaculture and fisheries. The behaviour of fish in response to light is used for
69 sampling and ecological observations (Catalan, et al., 2014). Likewise, it has been hypothesised that
70 fish with higher potential visual acuity and/or sensitivity to light could be attracted to, or stimulated
71 to avoid, illuminated trawl fishing gear. However, it is critical to describe the visual function of
72 species that may interact with fishing gear, in order to interpret or predict their behavioural
73 response. Other studies have compared theoretical and behavioural visual acuity in fish (e.g.
74 Douglas & Hawryshyn, 1990; Temple et al., 2013). Theoretical visual acuity is generally an
75 overestimate of behavioural visual acuity, and the disparity is thought to be caused by neural
76 processing and muscle function (Douglas & Hawryshyn, 1990). However, in the absence of
77 behavioural measures an assessment of theoretical acuity is valuable in comparative studies as an
78 indicator of visually mediated responses.

79 A selection of shallow water teleost species in North-eastern Tasmanian coastal waters were chosen
80 to investigate eye and retinal morphology. These species are commonly taken as unwanted bycatch
81 in commercial fisheries (Knuckey, 2006). Lights on trawl gear offer the potential to reduce bycatch
82 since light increases the visual stimulus in front of the trawl allowing fish to perceive the gear.
83 However, additional characteristics of fish are likely to impact on escape response, for example
84 other sensory input (Bond 1996; Pankhurst, 1989), retinal convergence, and higher order neural
85 processing (Douglas & Hawryshyn, 1990). For all but one of the selected bycatch species,
86 *Trachurus declivis*, there is no literature that quantifies the photoreceptor cells and potential visual
87 acuity; provides the cone mosaic patterns; nor makes comparisons of the lens diameter, cone
88 diameter and total fish length. The eight teleost species were chosen because of their varying
89 morphologies. The aim of the study was to quantify the photoreceptor cell densities and potential
90 visual acuity as well as describe the cone mosaic and general eye dimensions. This information will
91 further enhance the interpretation of the response of fish to bycatch reduction devices, specifically
92 those using lights.

2. MATERIALS AND METHODS

93

2.1 EYE SAMPLE COLLECTION

94

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

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

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

2.2 HISTOLOGY AND RETINAL MORPHOLOGY

112

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

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:

$$124 \quad \text{Rods} = \text{PR nuclei} - \text{cone ellipsoids}$$

125 Cell counts were expressed as density: cells per 0.01 mm² (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 mm²) were used in the following equation:

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

139 Where, q is the mean distance between two cones in mm ($q = 0.1/\sqrt{p}$); where p is density of cones
140 per unit area 0.01 mm²), s is the shrinkage factor and F is focal length ($F = m \times r$; 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
$$\tan \beta = \frac{1 \text{ mm} (1 + s)}{F}$$

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 *mulhali*, *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 \pm 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 $2.1 \text{ mm} \pm 0.2$ (*L. gallus*) and $7.7 \text{ mm} \pm 0.4$ (*P. bassensis*) (
 166 Table I).

167

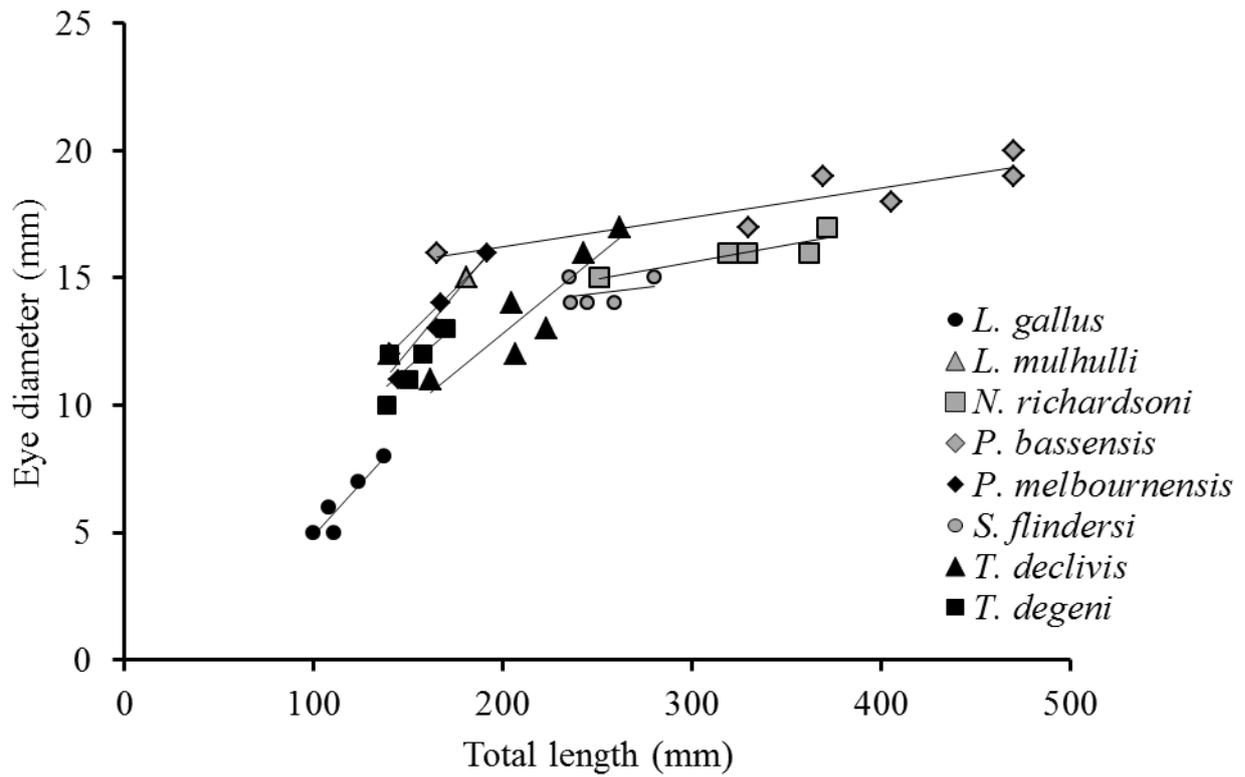
168 Table I: Fish size (length), eye and lens diameters, and cone photoreceptor diameter for the eight species studied from
 169 benthic trawls in North-East Tasmania. SC = single cones, DC = double cones.

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



176

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

179

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

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

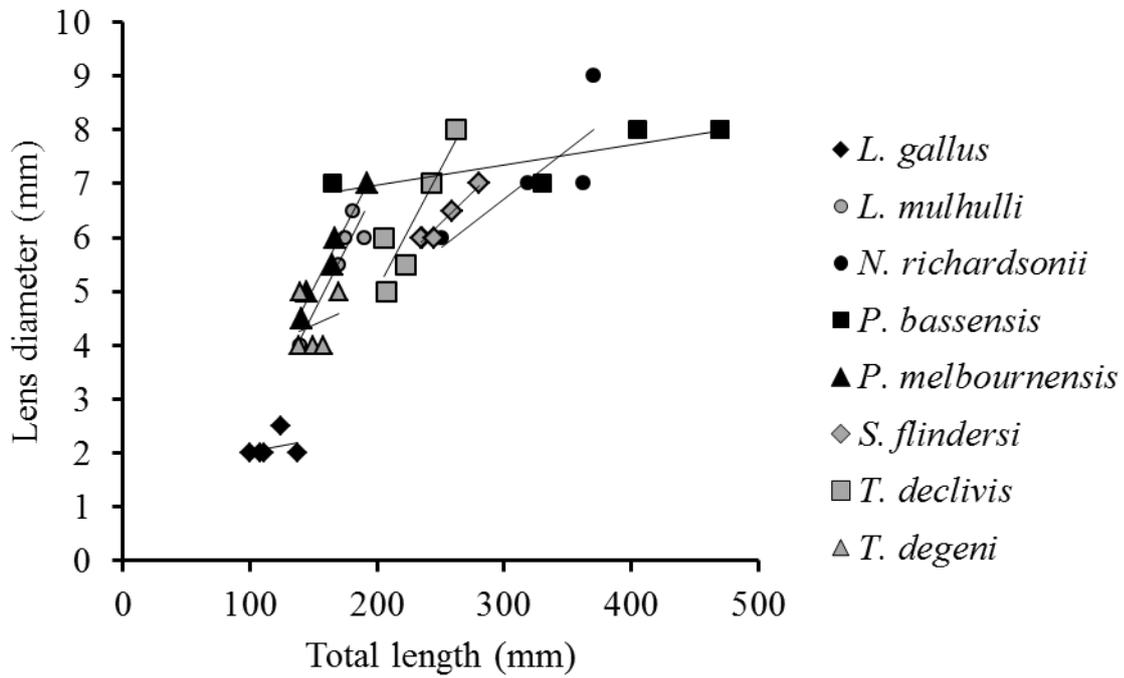
T. degeni 2.01 3 0.139 0.75

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. mulhulli*, 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.*

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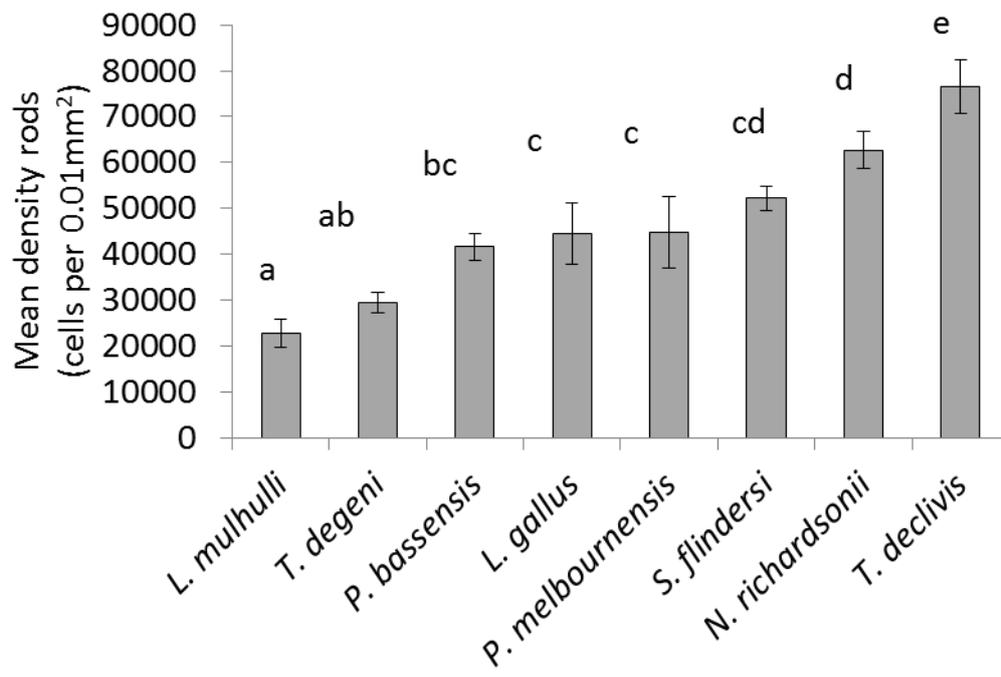
194 Table III: t-value, degrees of freedom (df), p-value and r^2 for Pearson's correlation between lens diameter (mm) and
 195 total fish length (mm) of eight species studied from benthic trawls in North-East Tasmania.

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

196

197 3.2 ROD DENSITY

198 The mean density of rods (cells per 0.01 mm²) 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 mm². 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 mm². The highest rod density of $76\,630 \pm 5\,876$ cells per 0.01 mm² was in *T.*
 203 *declivis*.



204

205 Figure 3: Mean number of rods (cells per 0.01 mm²) ± SE, in eight different teleost species studied from benthic trawls

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

207 *image.*

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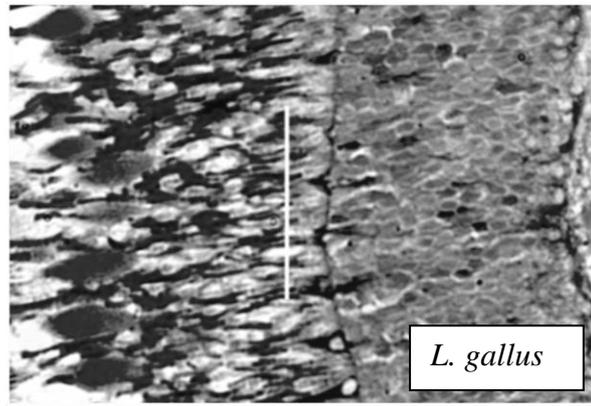
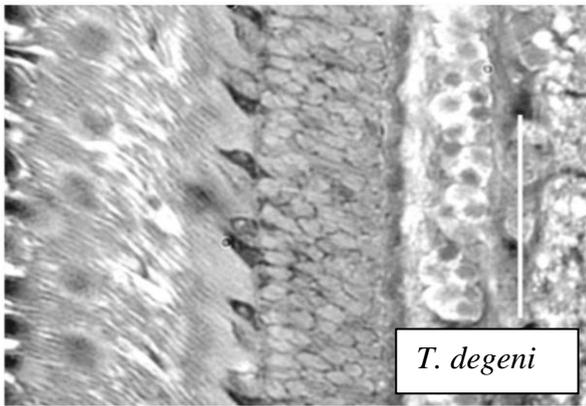
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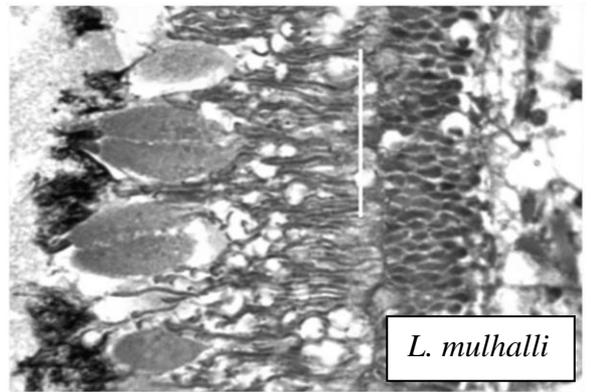
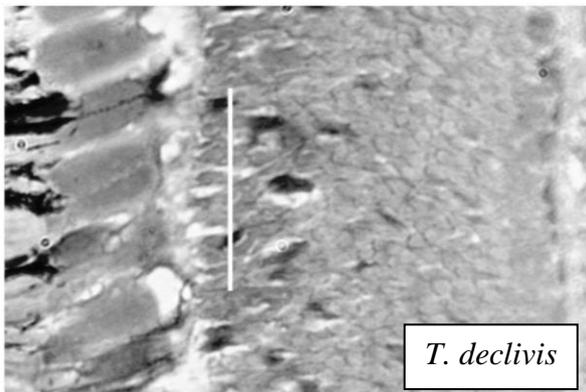
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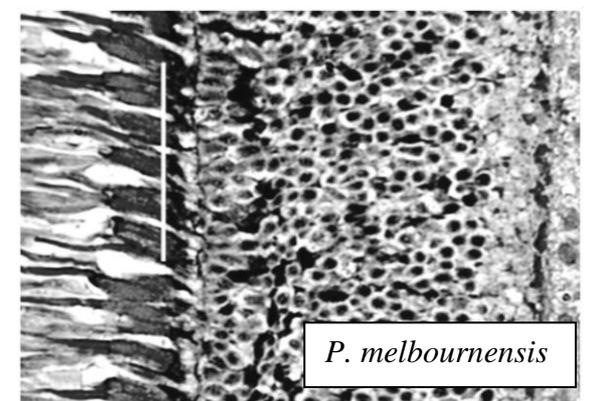
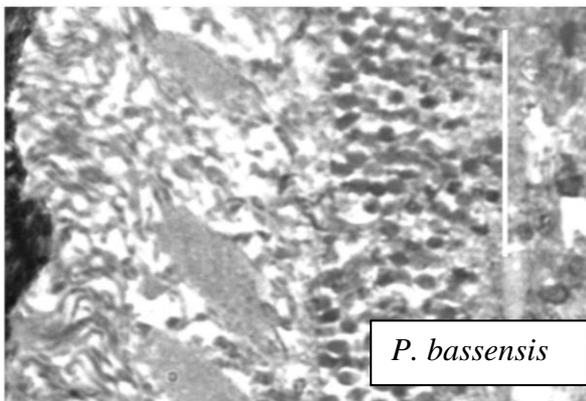
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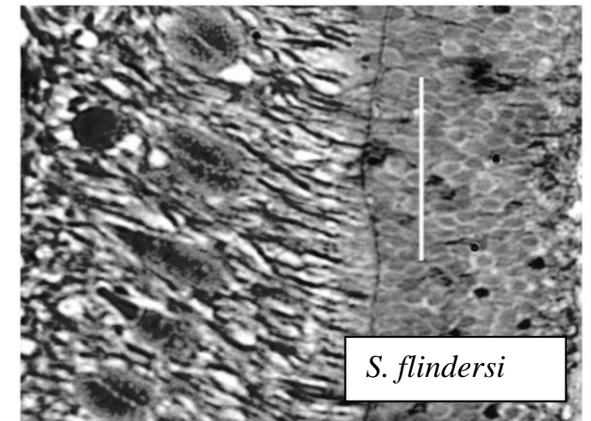
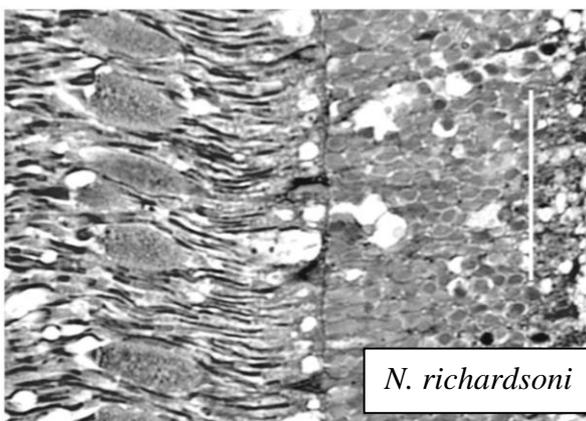
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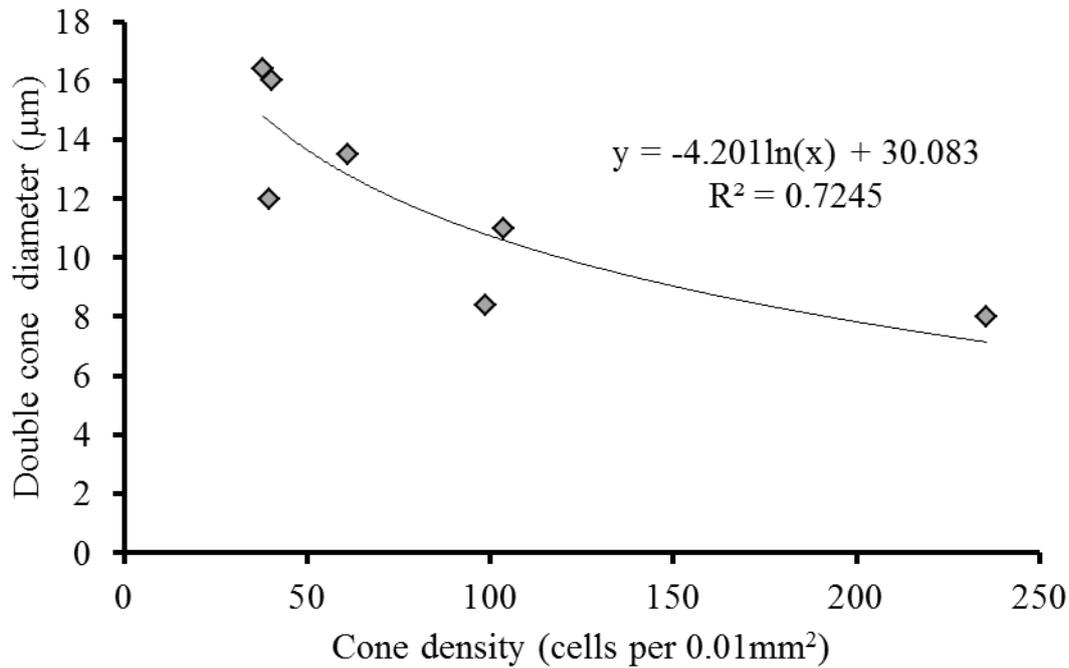
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Figure 4: Transverse section of the retinas, showing the photoreceptors, of eight different fish species studied from benthic trawls in North-East Tasmania. The scale bars are all 40 μm . *Double column fitting image.*

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.

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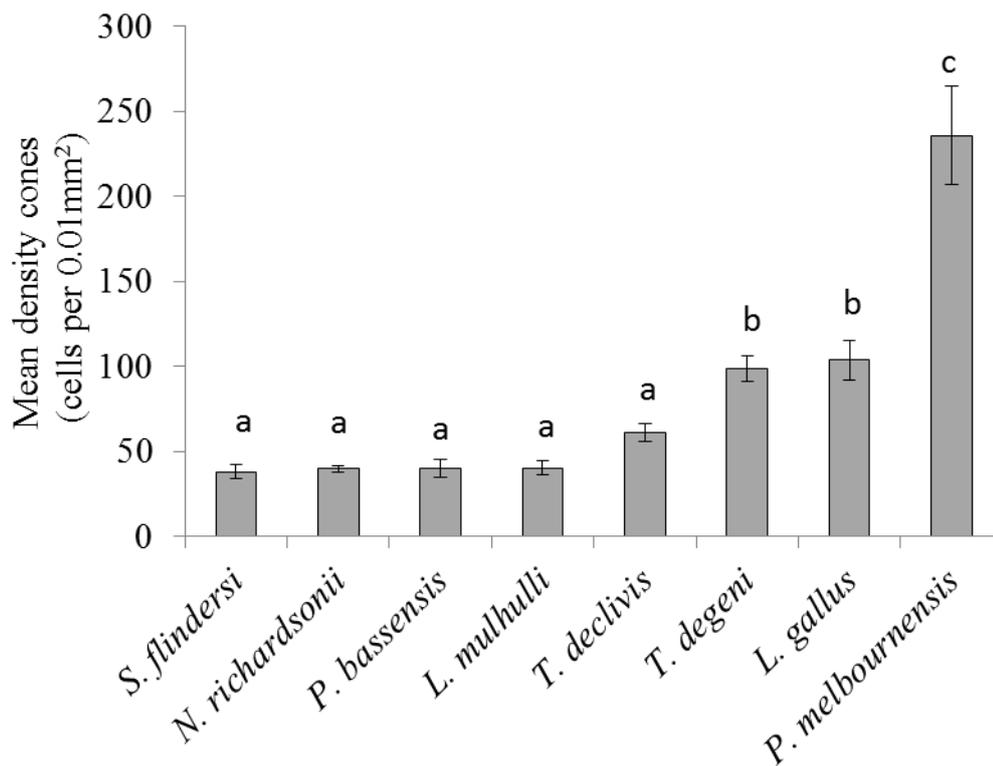


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231 Figure 5: Relationship between mean diameter (µm) of double cones and the cone density in each species studied from
232 benthic trawls in North-East Tasmania, with logarithmic equation. *Single column fitting image.*

233

234 The mean density of cones (cells per 0.01 mm²) 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 mm². *Thamnaconus degeni* and *L. gallus* had almost double this density, with
238 ~100 cones per 0.01 mm². *Parequula melbournensis* had over four times the density of the first
239 group with 235 ± 29 cones per 0.01 mm².



240

241 Figure 6: Mean density of cones (cells per 0.01 mm²) ± SE, in eight different teleost species studied from benthic
 242 trawls in North-East Tasmania. Common letters represent values that are not significantly different. *Double column*
 243 *fitting image.*

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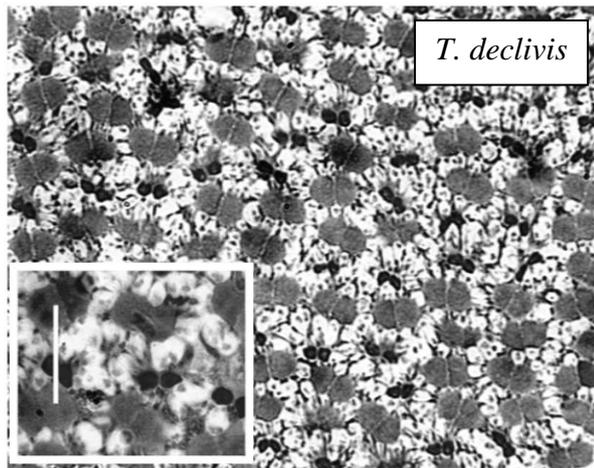
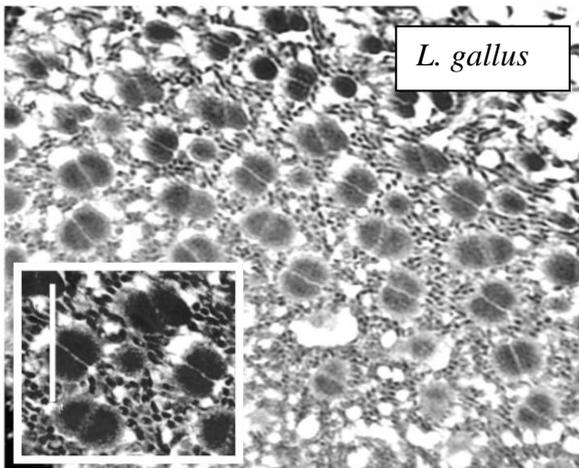
245 3.4 CONE MOSAICS

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

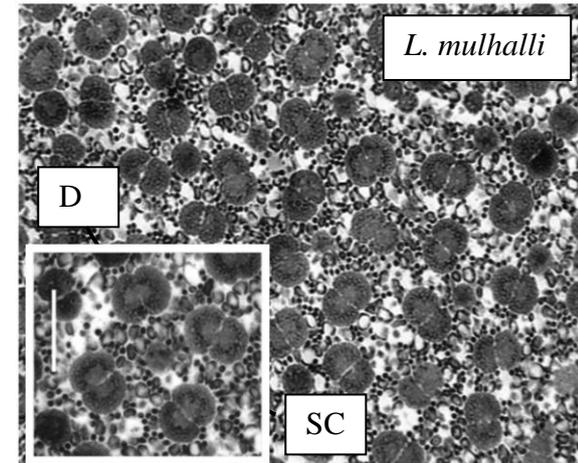
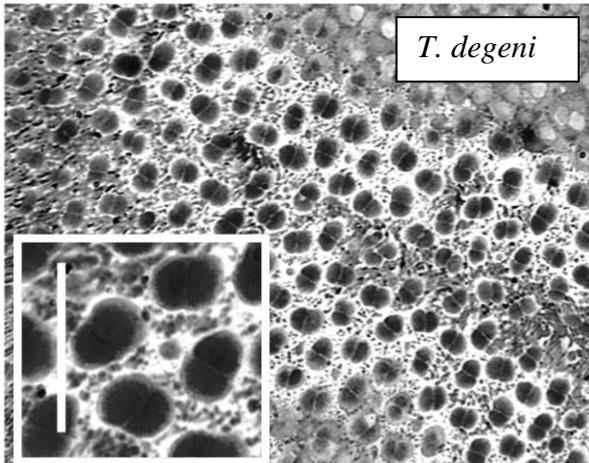
249 Table I). *Trachurus declivis* had only rows of double cones.

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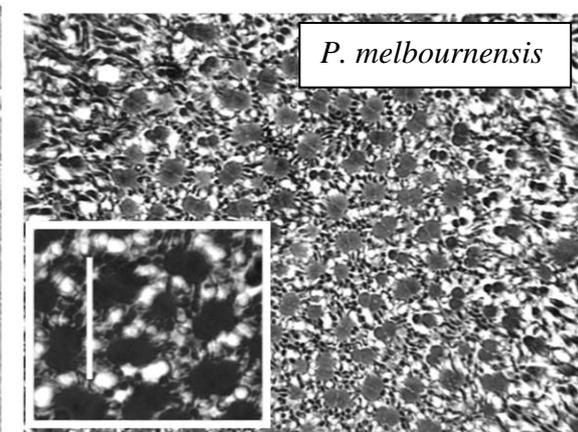
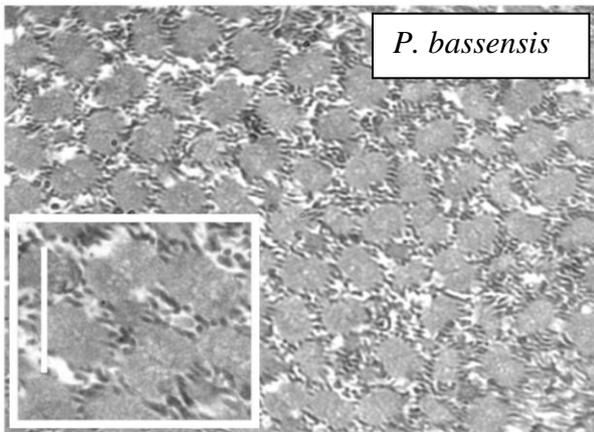
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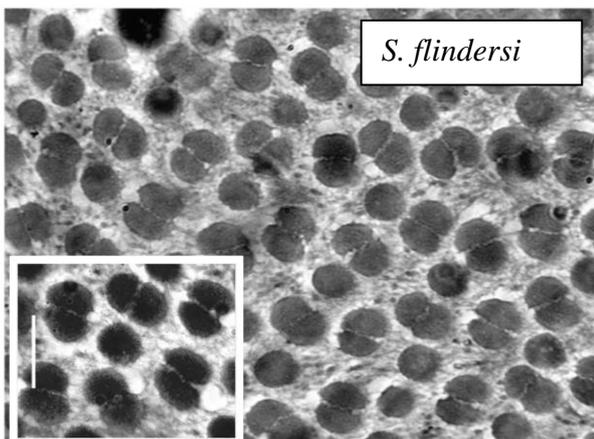
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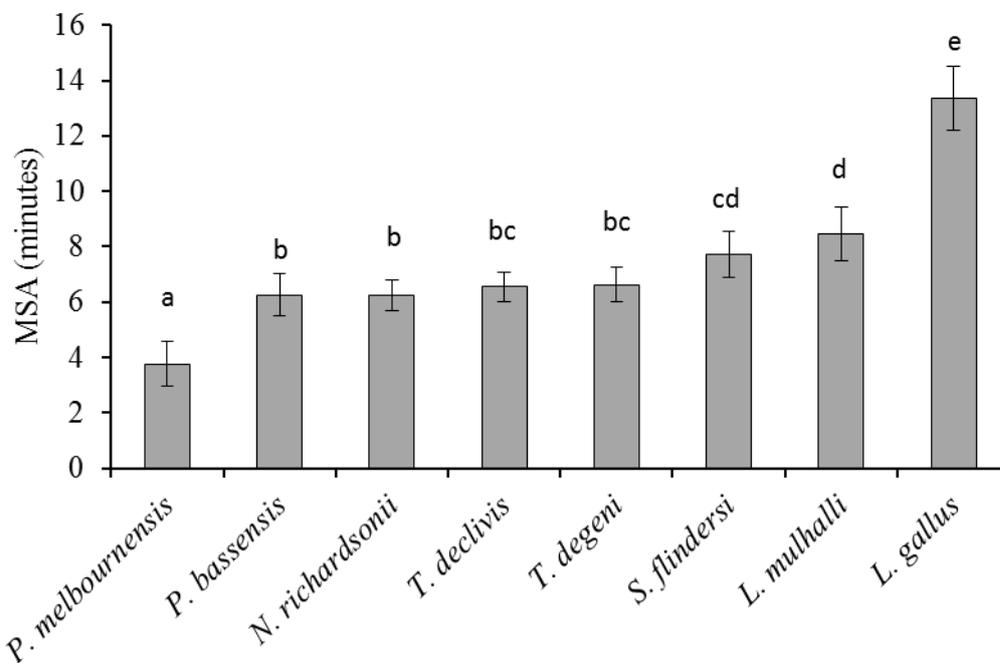


255 Figure 7: Tangential sections revealing the cone mosaic patterns in seven different fish species studied from
 256 benthic trawls in North-East Tasmania. The scale bars in insets are all 40 μm . DC = double cone; SC = single
 257 cone. *Double column fitting image.*

258

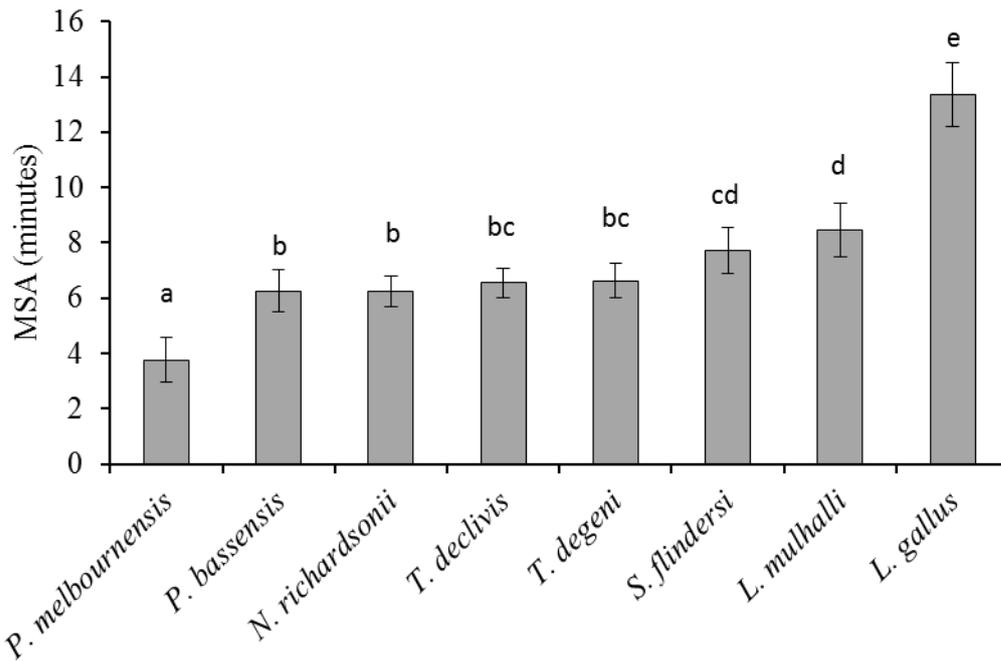
259 3.5 MINIMUM SEPARABLE ANGLE AND POTENTIAL VISUAL ACUITY

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. richardsonii* 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 (°)
<i>P. melbournensis</i>	a	0.3104	<i>L. gallus</i>	a	20.61
<i>P. bassensis</i>	b	0.1713	<i>T. degeni</i>	b	10.40
<i>N. richardsonii</i>	b	0.1658	<i>L. mulhalli</i>	c	8.49
<i>T. declivis</i>	b	0.1573	<i>P. melbournensis</i>	c	8.26
<i>T. degeni</i>	b	0.1576	<i>T. declivis</i>	c	8.15
<i>S. flindersi</i>	b	0.1359	<i>S. flindersi</i>	cd	7.31

<i>L. mulhalli</i>	bc	0.1248	<i>N. richardsonii</i>	d	6.32
<i>L. gallus</i>	c	0.0774	<i>P. bassensis</i>	d	5.93

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4. DISCUSSION

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*.

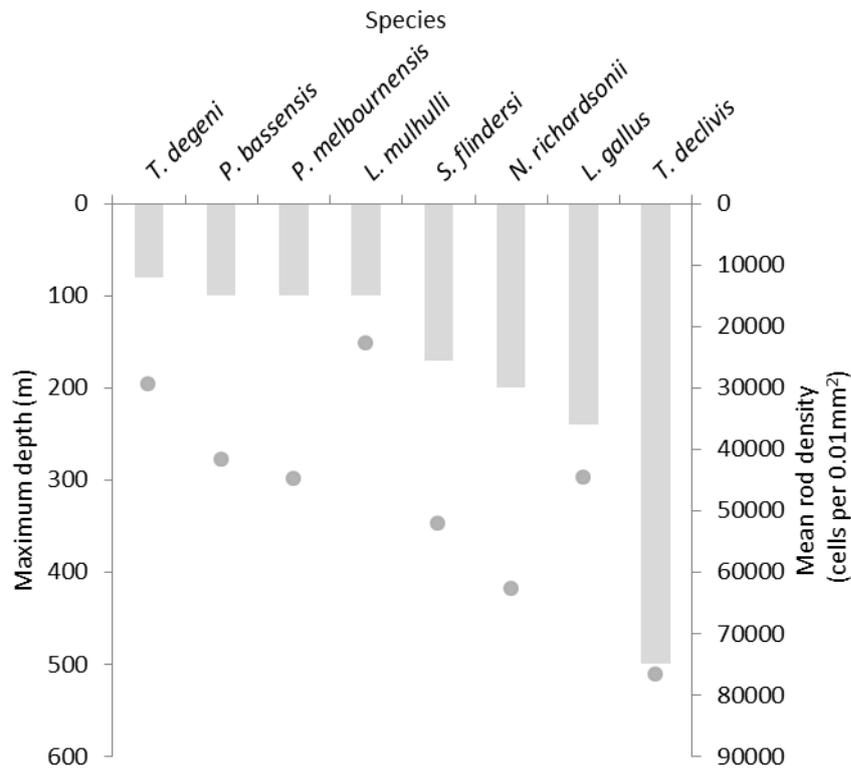
297 4.2 RODS

298 *Trachurus declivis* had only 7.6×10^6 rod cells per mm^2 of retina, which was similar to the
299 previously reported value of 1×10^7 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 mm²
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

322 Figure 9: Maximum habitat depth profile (m) (bars) of eight bycatch species with mean rod density (cells per
 323 0.01mm²) (dots). Depth data from Edgar (2012). *Double column fitting image.*

324

325 On the other end of the scale, *P. melbournensis*, *T. degeni*, and *P. bassensis* all had the lowest
 326 rod densities and inhabit waters up to 80-100 m deep. Even in closely related species this was
 327 the case, for example, *N. richardsonii* have more rods than *P. bassensis* probably because they
 328 are found up to 60 m deeper. This is because rods are adapted for detecting dim light, and
 329 therefore are more valuable for fish to perceive visual cues in low light intensity conditions
 330 associated with deep water (Fernald, 1988). For *T. declivis*, having the highest density of rods
 331 would likely result in this species responding quickly to lights, since rods are sensitive to the
 332 shift from dark to light (Bond, 1996). The only species that did not follow this trend was *L.*
 333 *mulhulli*. This species is usually located at depths up to 100 m but had the lowest estimate of
 334 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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430

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