

1 Variation with depth in temperate seagrass associated fish assemblages in southern
2 Victoria, Australia

3
4 Neil Hutchinson^{1,2*}, Gregory P Jenkins^{1,3}, Andrew Brown¹ and Timothy M Smith^{1,4}

5 ¹ Fisheries Research Branch, Department of Primary Industries, DPI Queenscliff centre, P.O. Box
6 114, Queenscliff 3225, Victoria, Australia

7 ² JCU Singapore, TropWATER - Centre for Tropical Water and Aquatic Ecosystem Research,
8 James Cook University, 600 Upper Thomson Road, Singapore 574421

9 ³ Department of Zoology, University of Melbourne, Melbourne 3010, Victoria, Australia

10 ⁴ Centre for Integrative Ecology, Deakin University, Waurn Ponds, Victoria, Australia

11
12 * Corresponding author: Neil Hutchinson

13 Email: neil.hutchinson@jcu.edu.au Tel: +65 6422 4466 Fax: +65 6455 2833
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15 **Abstract** Variability in the abundance and distribution of seagrass-associated fish assemblages
16 was examined at different depths in a temperate bay in southern Australia. Depth differences in
17 seagrass-associated fish assemblages are poorly known but this information is critical given that
18 seagrass loss can occur at specific depths depending on the cause. Overall, 69 species of fish from
19 26 families were recorded, with higher species richness in shallow than deep beds, with 12 species
20 found only in deep beds and 22 species found only in shallow beds. While the total fish
21 abundance (i.e., abundance of all species recorded) varied between years and seasons, and to some
22 extent between sites, it was significantly higher in shallow than deep seagrass beds in the majority
23 of cases. Although there was some variation between sites, seagrass tended to be longer and have
24 a higher biomass in shallow than deep beds during both spring and autumn throughout the study.
25 A positive relationship between seagrass biomass/length and total fish abundance/species richness
26 was apparent. Assemblage structure tended to be distinct at each depth, with the largest species
27 recorded in shallow seagrass. Large numbers of small schooling fish, such as atherinids,
28 dominated in shallow seagrass but were not found in deep seagrass. Loss of seagrass could
29 therefore have varying implications for distinct assemblages found at different depths.

30
31 **Keywords** Seagrass habitats; *Zostera nigricaulis*; Port Phillip Bay; nursery
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INTRODUCTION

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35

36 Much has been written on the significance of seagrass beds (Larkum et al. 2006), including
37 their provision of important ecosystem services (Barbier et al. 2011; Lavery et al. 2013).
38 Costanza et al. (1998) proposed that, globally, seagrass beds provide ecosystem services
39 equivalent to over US\$28 000 ha⁻¹ year⁻¹ and estimates in South Australia (McArthur and Boland
40 2006) suggest that secondary production contributions from seagrass in the State's gulf waters
41 alone contribute over AU\$134,000,000 year⁻¹ to the economy (values quoted for these two studies
42 have been updated taking inflation up to 2012 into account). Seagrass is, however, disappearing
43 from coastal areas at an increasingly rapid rate (Waycott et al. 2009). This is of particular concern
44 given that seagrass beds provide important habitat and food resources for a wide and diverse range
45 of organisms in both temperate and tropical regions (Howard et al. 1989; Bologna and Heck 1999;
46 Jackson et al. 2006a).

47 Approximately one third of the world's seagrass is thought to have disappeared over the
48 last 130 years (Waycott et al. 2009). This is due to a wide range of natural and anthropogenic
49 impacts such as declining water quality and coastal development (Shepherd et al. 1989; Orth et al.
50 2006; Grech et al. 2012) and loss of seagrass beds is expected to be further exacerbated by climate
51 change (Connolly 2009).

52 It is important to understand how declines in seagrass at different depths will impact
53 associated assemblages, given their ecological and economic importance (Duarte 2002). A wide
54 range of fish species utilise seagrass beds, some residing in them throughout their life history, and
55 others only using them during specific life stages or as food patches in a mosaic of varied habitat
56 types (Pollard 1984). This results in seagrass ecosystems often supporting disproportionately
57 higher abundances and diversity of fish than adjacent coastal habitats (Travers and Potter 2002).

58 As concern grows about potential impacts of habitat loss on fish populations (Engel et al.
59 1999), more evidence is emerging on specific impacts of seagrass loss, indicating that in many
60 cases these fish are unable to adapt to such changes (Hughes et al. 2002; Nakamura 2010). In the

61 event of seagrass loss, it is likely that impacts on fish assemblages will be variable and dependent
62 on a range of factors including the depth of seagrass beds that they utilise and the extent to which
63 species are tied to only one habitat type (Jenkins and Wheatley 1998; Jenkins and Hamer 2001;
64 Deudero et al. 2008). Those studies that have examined variation in assemblage structure of
65 seagrass associated fish at different depths (e.g., Francour 1997; Travers and Potter 2002;
66 Heithaus 2004; Pogoreutz et al. 2012) have, however, tended to identify one of two contrasting
67 patterns. Either abundance, diversity and size are found to be higher in deep seagrass beds (Bell et
68 al. 1992; Heithaus 2004; Jackson et al. 2006b) or the opposite scenario is described where they are
69 higher in shallow seagrass beds (Francour 1997; Travers and Potter 2002). Information regarding
70 such depth differences in cool, temperate systems is sparse (Jackson et al. 2006b; Smith et al.
71 2011).

72 In the present study, we investigate patterns of spatial and temporal variation in fish
73 assemblages associated with beds of *Zostera nigricaulis* in Port Phillip Bay, south-eastern
74 Australia. The main aim of the work presented is to identify the extent to which these
75 assemblages vary with depth. Additional, limited analysis is also performed to identify potential
76 relationships between fish abundance/species richness and seagrass length/biomass.

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MATERIALS AND METHODS

79 **Study site.** Fish assemblages (finfish and elasmobranchs) were sampled around low tide,
80 slack water in shallow (< 1 m) and deep (2–8 m) seagrass beds at Blairgowrie (38°21'S,
81 144°46'E), Mud Islands (38°16'S, 144°44'E) and St Leonards (38°11'S, 144°42'E); three sites
82 situated in the south of Port Phillip Bay, a large embayment in Victoria, temperate southern
83 Australia (Fig. 1). The bay is characterised by mean annual surface seawater temperatures from
84 ~10-20°C, a tidal range of ~0.9-1.7 m and mean annual salinities of ~35.5 g.kg⁻¹ (King 1970;
85 Blake and Ball 2001; Lee et al. 2012). Patches of the seagrass *Zostera nigricaulis* grew as a dense
86 monoculture at these sites as is characteristic of the genus (Moore and Short 2006), with mean
87 canopy heights ranging from ~50-250 mm in deep beds to ~150-400 mm in shallow beds. Total

88 seagrass coverage varied, with ~6% cover at Blairgowrie, ~41% at Mud Islands and ~13% at St
89 Leonards (Ball et al. 2009). These beds are known to harbour a wide variety of fish species
90 (Jenkins et al. 1997; Hindell et al. 2001; Smith et al. 2010).

91 **Fish sampling.** Fish assemblages were sampled on a biannual basis in autumn (April-
92 May) and spring (November) from 2008–2010. Samples were collected at each site using a
93 bottom weighted, 15 × 3 m seine net, with wings of 3 mm mesh, a cod-end of 1 mm mesh, and 15
94 m ropes at each end. The net, stowed in a fish-bin, was carried 15 m from an anchored research
95 vessel to which one of the end ropes was attached, by either wading if in shallow seagrass beds or
96 from a small tender when in deep beds. After setting the net in a straight line perpendicular to the
97 boat, the second end rope was returned to the research vessel. At shallow sites the net was then
98 hauled in slowly with the bottom of the net dragging along the substrate and the floats at the
99 surface. A modified technique was used for deep beds, with additional weights attached to the net
100 bridles and tow ropes to allow the net to be hauled along the substrate prior to it reaching the
101 surface. It should be noted that when sampling deep beds, the floats at the top of the net were
102 initially in mid water rather than at the surface due to the height of the net. At both depths, the net
103 was hauled in such a way that the bridles were ~4 m apart until the mouth of the net was lifted
104 from the water surface. The sweep area of one trawl was estimated to be approximately 100m².
105 Four random, replicate hauls were taken at both depths at each site. Where possible, fish were
106 identified, measured (standard length) and released in the field. Unidentified individuals were
107 euthanized by over-anaesthesia in a seawater bath containing 200mg/L of isoeugenol (AQUI-
108 S™), and preserved in 95% ethanol for laboratory analysis. All atherinids, potentially including
109 *Atherinosoma microstoma*, *Kestratherina brevirostris*, *K. esox* and *Leptatherina presbyteroides*,
110 were grouped due to issues related to sorting and identification of large numbers in the field.

111 **Seagrass sampling.** Six, 0.25 m² quadrats were randomly placed in seagrass beds at both
112 depths at each site, by snorkel or SCUBA where appropriate, and all seagrass was cut at the
113 sediment surface and removed. Average stem/leaf length for each quadrat was determined by

114 randomly measuring the length of ten plants. Biomass was determined after drying seagrass for
115 two days at 60°C.

116 **Data analysis.** Spatial and temporal variation in total fish abundance (i.e., abundance of
117 all species recorded), abundance of individual fish species, fish species richness, seagrass length
118 and seagrass biomass were analysed with a 4-factor mixed-model ANOVA (Underwood 1997).
119 This analysis was used to examine variation with year (3 levels; fixed and orthogonal; i.e., 2008,
120 2009 and 2010), season (2 levels; fixed and orthogonal; i.e., autumn and spring), site (3 levels;
121 random and orthogonal; i.e. Blairgowrie, Mud Islands and St Leonards) and depth (2 levels; fixed
122 and orthogonal; i.e. shallow and deep). Data for all analyses were checked for homogeneity of
123 variances (Cochran's *C*-test) and log transformed where appropriate to satisfy assumptions of
124 homogeneity of variances. Significant differences for fixed factors were examined further, where
125 appropriate, using SNK multiple comparison tests (Zar 1996).

126 The same 4-factor model was applied to a mixed-model permutational multivariate
127 analysis of variance (PERMANOVA; Anderson 2001) to identify significant differences in fish
128 assemblage structure. This analysis was run with 9999 permutations per test, on data obtained
129 through Bray-Curtis measures of dissimilarity on square root transformed abundance data.
130 Pooling was conducted on terms where the model gave negative estimates for components of
131 variation. Our primary interests were differences in assemblage structure between depths and
132 between seasons and therefore only those pair-wise comparisons that specifically address these
133 factors are reported for the appropriate interactions.

134 Subsequent relationships were visualised with non-metric multidimensional scaling
135 (nMDS) ordinations, and while stress levels obtained through this analysis should ideally be < 0.1,
136 values < 0.2 are thought to still provide an adequate representation of relationships between
137 replicates (Clarke 1993). A SIMPER procedure was then used to identify the species that
138 contributed most to treatment differences (Clarke 1993). Further analysis was conducted on raw
139 data using Kolmogorov-Smirnov two sample tests to identify differences in the size frequencies of
140 finfish with depth and season.

141 To examine relationships between seagrass and fish, data from the whole study was pooled
142 and linear regression analysis was employed to assess any influence of seagrass length and
143 biomass on fish abundance, species richness and common species.

144

145 **RESULTS**

146 A rich and diverse fish assemblage was found in all seagrass beds that were sampled.
147 Sixty nine species from 26 families were recorded throughout the study, the majority from
148 multiple samples, with 12 found only in deep beds (e.g., the callionymids *Eoacallionymus papilio*
149 and *Foetorepus calauropomus*), 22 found only in shallow beds (e.g., the Gobiid *Afurcagobius*
150 *tamarensis* and the sillaginid *Sillaginodes punctatus*), and 35 found at both depths (e.g., the
151 monacanthid *Acanthaluteres spilomelanurus* and the sygnathid *Stigmatopora nigra*). While some
152 of species occurred at only one or two of the sites, the majority of common species were found at
153 all sites (see additional data in Online Resource).

154 **Fish abundance and species richness**

155

156 Total fish abundance was significantly higher in shallow than deep seagrass beds during
157 the majority of visits (except at St Leonards in autumn 2008 and spring 2009, Mud Islands in
158 spring 2008 and Blairgowrie in spring 2010; Table 1; Online Resource; $Y \times Se \times Si \times De$: $F_{4, 108} =$
159 3.9144 , $P < 0.001$). Seasonal differences in total fish abundance in shallow seagrass beds were
160 inconsistent, but in all cases where significant differences occurred (at Mud Islands in 2008, St
161 Leonards in 2009, and Blairgowrie in 2010) abundances were higher in autumn than in spring
162 (Table 1). Total fish abundance in deep seagrass beds did not vary seasonally except on rare
163 occasions (Table 1). Significant differences in abundance between years were infrequent, with no
164 consistent pattern, and are not discussed any further (Table 1).

165 Variation in abundance with depth could also be seen for individual species. The
166 commonly occurring sygnathid, *Stigmatopora nigra* ($Y \times Se \times Si \times De$: $F_{4, 108} = 2.79$, $P = 0.030$) was
167 significantly more abundant in shallow than deep beds at the majority of sites during autumn of

168 each year (except at Blairgowrie in 2010; Table 1) and less commonly during spring (only at
169 Blairgowrie in 2008 and 2010, and at Mud Islands in 2009). Abundances of *S. nigra* were
170 significantly higher in autumn than spring each year in the majority of shallow seagrass beds
171 (except at Blairgowrie in 2008 and 2010), but rarely in deep beds (only at Mud Islands in 2009).
172 Significant differences in abundance between years, where they occurred, were inconsistent with
173 no apparent pattern.

174 Abundances of the monacanthid, *Acanthaluteres spilomelanurus*, ($\text{Se} \times \text{Si} \times \text{De}$: $F_{2, 108} =$
175 8.63 , $P < 0.001$; Table 1) also varied significantly with depth and season but patterns were
176 inconsistent (Table 1). This species was more abundant in shallow than deep beds at Blairgowrie
177 during autumn and more abundant in deep than shallow beds in spring at Blairgowrie and Mud
178 Islands (Table 1). Abundances were significantly higher in autumn than spring in deep beds at
179 Blairgowrie (Table 1) and more abundant in spring than autumn in shallow beds at Blairgowrie
180 and Mud Islands (Table 1).

181 Species richness rarely showed any significant difference between depths, seasons or years
182 ($\text{Y} \times \text{Se} \times \text{Si} \times \text{De}$: $F_{4, 108} = 2.72$, $P = 0.033$; Table 1).

183 **Fish size frequencies**

184
185 Fish lengths were significantly different between shallow and deep seagrass beds during
186 all visits (Table 2). These differences were predominantly due to two observed patterns. Firstly,
187 the largest fish recorded tended to be caught by the seine nets in shallow seagrass (Fig. 2), and
188 included a range of species such as the monacanthid, *Meuschenia freycineti*, and the tetraodontids
189 *Contusus brevicaudus* and *Tetractenos glaber*. Other large species including platycephalids,
190 rhombosolids and several species of elasmobranch tended to be few in number and were recorded
191 infrequently at both depths. Secondly, certain species occurred at one depth only. For example,
192 during spring 2008 and 2009 large numbers of *Sillaginodes punctatus* recruited only to shallow
193 seagrass beds, as indicated by a peak of fish in the 20 – 40 mm size range while during the same

194 periods the gobioid, *Genus C sp. 1* (Gomon et al. 2008) generally recorded in the 0 – 20 mm
195 size class, was found only in deep seagrass beds.

196 Differences were also apparent for individual species. For example, *A. spilomelanurus* and
197 *S. nigra* showed significant differences between depths on the majority of visits (Table 2; Figs. 3-
198 4). In autumn each year, a higher proportion of larger *A. spilomelanurus* (over 40 mm) were
199 found in shallow than deep seagrass, whereas in spring the largest individuals (over 80 mm) were
200 recorded in deep seagrass, where a broader size range including new recruits (< 20 mm) were also
201 found. While *S. nigra*, did not show such distinct differences, in autumn each year a higher
202 proportion of larger individuals (80 mm and over) tended to be recorded in shallow than deep
203 seagrass. In spring each year, the highest proportion of individuals in shallow seagrass were in the
204 80 – 100 mm size range, while in deeper seagrass there was a higher proportion of individuals
205 over 100 mm.

206 **Assemblage structure**

207
208 Fish assemblage structure was significantly different between shallow and deep seagrass
209 beds in each season and year for the three sites (Table 3). Four-factor PERMANOVA revealed
210 significant interactions between year, season, site and depth, with pairwise comparisons indicating
211 that assemblage structure was significantly different between autumn and spring at both depths
212 during each year for the majority of sites (except in deep seagrass in 2010 at Mud Islands and in
213 2008 and 2010 at St Leonards; Table 3). nMDS ordinations for each individual sampling visit
214 also showed clear differences in the similarity of assemblage structure in deep and shallow
215 seagrass beds throughout the study, with differences between sites in some instances, e.g., autumn
216 2010 (Fig. 5). Further analysis with SIMPER indicated that the species which made the greatest
217 contributions to variation between depths varied between sampling visits and included: the gobiids
218 *Afurcagobius tamarensis* and *Nesogobius maccullochi*, atherinids, the sygnathids *Stigmatopora*
219 *argus* and *S. nigra*, the monacanthid *Acanthaluteres spilomelanurus*, the tetradontid *Contusus*

220 *brevicaudus*, the clinid *Heteroclinus perspicillatus*, and the sillaginid *Sillaginodes punctatus*
221 (Table 4).

222 **Seagrass bed dynamics and possible relationship with fish**

223

224 In most cases, seagrass was significantly longer in shallow than deep beds at each site
225 during autumn, but only occasionally during spring each year ($Y \times Se \times Si \times De$: $F_{4, 180} = 5.94$, $P <$
226 0.001 ; Fig. 6). In the majority of cases, there were no significant differences in seagrass length
227 between seasons or years at either depth (Fig. 6).

228 Seagrass biomass was also significantly higher in shallow than deep beds in the
229 majority of cases ($Y \times Si \times De$: $F_{4, 180} = 5.19$, $P < 0.001$; $Se \times Si \times De$: $F_{2, 180} = 6.66$, $P = 0.002$; Fig. 7).
230 There were few seasonal differences in biomass in shallow or deep beds, but where such
231 differences were recorded, biomass was higher in spring than autumn (Fig. 7). There were no
232 consistent differences in biomass between years.

233 Significant positive relationships between species richness and both seagrass length ($F_{1, 34}$
234 $= 7.770$, $P = 0.009$, $r^2 = 0.186$) and seagrass biomass ($F_{1, 34} = 6.978$, $P = 0.012$, $r^2 = 0.170$) were
235 identified using regression analysis on data pooled across depths. Analysis also indicated
236 significant positive relationships between total fish abundance and both seagrass length ($F_{1, 34} =$
237 11.100 , $P = 0.002$, $r^2 = 0.237$) and seagrass biomass ($F_{1, 34} = 13.290$, $P < 0.001$, $r^2 = 0.275$).

238

239 **DISCUSSION**

240 The range of fish species recorded during the present study is typical of seagrass beds in
241 the region (Edgar and Shaw 1995; Jenkins et al. 1997; Smith et al. 2008). Assemblages at both
242 depths included fish that can be considered resident in seagrass such as several species of
243 sygnathids, monacanthids and odacids (Jenkins and Wheatley 1998). The majority of the other
244 species recorded were also closely associated with seagrass and surrounding sand patches (Gomon
245 et al. 2008; Froese and Pauly 2012).

246 There were clear differences in seagrass associated fish assemblages with depth,
247 supporting the initial findings of a concurrent study that utilised underwater video technology at
248 Mud Islands (Smith et al. 2012). While we identified depth differences in the distribution patterns
249 of many species, these were more complex for species found at both depths and further work is
250 needed on individual species to examine why depth differences occur. Distinct differences in total
251 fish abundance and species richness could also be seen between depths at the surveyed sites, with
252 approximately half of the species recorded in either shallow or deep seagrass beds alone. Total
253 fish abundance and species richness both tended to be higher in shallow (< 1 m) than deep (2-8 m)
254 seagrass beds as previously indicated by Smith et al. (2012). While this pattern is similar to those
255 shown by Francour (1997) and Travers and Potter (2002), it contrasts with other studies (e.g.,
256 Heithaus 2004; Jackson et al. 2006b). As discussed by Smith et al. (2012), this may partly be due
257 to a lack of consistency in sampling strategy and habitat definition, and large scale studies using
258 standardised methods may be required to identify any general patterns.

259 Differences in the length frequency distributions of fish caught in shallow and deep
260 seagrass beds during the present study supported those found by Smith et al. (2012) and other
261 studies at similar depths (e.g., Blaber et al. 1992). The differences that we identified were
262 primarily driven by the presence of larger fish such as *Meuschenia freycineti*, *Arripis spp.* and
263 *Haletta semifasciata* exclusively in shallow seagrass beds. The presence of these species in
264 shallow seagrass emphasises that shallow seagrass functions not only as a nursery habitat but is
265 also important for adult species. In spring, recruitment processes resulted in smaller overall fish
266 lengths in shallow seagrass, for example with *Sillaginodes punctatus* recruiting in shallow
267 seagrass only (also see Jenkins and May (1994). This occurrence of small individuals in shallow
268 seagrass beds is widely reported in terms of nursery ground function in both temperate and
269 tropical systems (Jackson et al. 2001; Gullstrom et al. 2002; Ford et al. 2010) and in Port Phillip
270 Bay recruitment of *S. punctatus* to shallow seagrass beds is thought to be related to food
271 availability (Jenkins et al. 1996; Jenkins and Hamer 2001), larval dispersal patterns (e.g., Jenkins
272 et al. 1998) and the avoidance of predators (Smith et al. 2011).

273 Compared to the video results of Smith et al. (2012), we recorded a limited number of
274 large fish in deep seagrass, indicating that there were probable gear selectivity differences
275 between the two techniques, interacting with depth. It is likely that the net sweep area in our
276 study varied with depth and that the net was more efficient in shallow than deep areas. This may
277 partly explain why we only caught larger fish and some pelagics such as the atherinids and
278 *Enoplosus armatus* in shallow water. The seine nets were, however, more successful in capturing
279 the incidence of small individuals than the cameras used by Smith et al. (2012). For example
280 while they only found adult *Acanthaluteres spilomelanurus* in deep seagrass, our netting showed
281 that juveniles were present at both depths. Given that recorded depth differences were consistent
282 between the two studies, we are confident that such differences were real rather than an artefact of
283 sampling, but suggest that it would be appropriate to use an amalgamation of these techniques in
284 future studies (Murphy and Jenkins 2010).

285 While we have discussed our findings in terms of differences in fish assemblages with
286 depth, there is a widespread issue with this and similar studies in the literature, in that depth may
287 be confounded with seagrass structure. Given limited resources, we were unable to address this in
288 the present study but it could be resolved through the use of standardised artificial seagrass beds.
289 While the positive relationships we identified between seagrass length or biomass and fish
290 abundance or species richness should, therefore, be viewed with some caution given that data was
291 pooled across depths, the physical structure of seagrass beds is likely to be an important factor
292 governing the distribution pattern of fish at different depths in the present study. Numerous other
293 studies have shown that seagrass structure, including length and biomass, influence the
294 distribution of fish in seagrass (e.g., Orth et al. 1984; Bell and Westoby 1986; Jackson et al.
295 2006b) yet there is still some disparity between studies as to the impact of the physical structure of
296 seagrass beds on fish abundances (Bell and Westoby 1986; Bell et al. 1992). This most likely
297 depends on whether fish are using the seagrass as a food resource, or whether it serves
298 predominantly as a refuge, and at what spatial scale these factors are most important. For
299 example, a recent study on the parrotfish *Leptoscarus vaigiensis* in Tanzania found that seagrass

300 complexity and feeding mode were important at small spatial scales whereas at larger spatial
301 scales the distribution of predators was more important, with seagrass canopy height as the main
302 predictor explaining variability in the density and biomass of predators (Gullstrom et al. 2011).

303 As in our study, Kendrick and Hyndes (2003) found differences in the depth distribution of
304 sygnathids. They suggested that differences in abundances between depths were partly due to
305 changes in seagrass cover and seagrass species. While the seagrass beds examined at each depth
306 during the present study were monocultures of the same species, *Zostera nigricaulis*, differences
307 in seagrass cover may interact with a range of other factors that are known to play an important
308 role in governing the distribution of *Stigmatopora nigra* and other seagrass associated fish
309 including patch size, variation in the ratio of area to edge perimeter, and habitat fragmentation
310 (Smith et al. 2008; Macreadie et al. 2009, 2010a, b).

311 While impacts of climate change on seagrass beds are difficult to predict (Short and
312 Neckles 1999) they may result in seagrass being more susceptible to loss at different depths. For
313 example, newly inundated shallow water areas created by sea-level rise may lack suitable
314 substrate for seagrass growth, impacting the upper limits of seagrass distribution, while increased
315 turbidity may impact lower depth limits (e.g., Saunders et al. 2013). The limited work that has
316 been conducted examining the impact of seagrass loss on faunal assemblages at specific depths
317 has concentrated on changes that occur in adjacent intertidal and shallow subtidal seagrass
318 communities (Micheli et al. 2008) rather than shallow and deep subtidal seagrass-associated fish
319 assemblages. Yet the factors responsible for recovery or adaptation are likely to be similarly
320 complex. In a situation such as that described in the present study, where deep and shallow
321 seagrass habitat are distinct, it is likely that fish which utilise both depths of seagrass, such as
322 shoaling species that are able to move large distances, may be better able to adapt to loss at either
323 depth. However, those found at only one depth are less likely to be able to do so unless they are
324 able to adapt to different conditions or make use of alternative habitats and food sources.

325 Seagrass beds are known to provide a wide range of resources to fish in both temperate
326 and tropical systems (Boström et al. 2006). These can include cryptic habitat that offers shelter

327 from predators as well as food, in the form of the seagrass itself, epiphytes and an assorted range
328 of invertebrate and vertebrate prey that also inhabit these systems (Klumpp et al. 1989). As such,
329 loss of seagrass may have a dramatic impact on fisheries (Bell and Pollard 1989; Gillanders 2005;
330 Waycott et al. 2009) with a large percentage of seagrass dependant species either disappearing
331 completely (Vanderklift and Jacoby 2003; Nakamura 2010) or becoming much less abundant
332 (Hughes et al. 2002). Our results indicate that the fish species and assemblages impacted by
333 seagrass loss will depend on the depth range affected, which in turn depends on the cause of loss.
334 Further study is required on a species by species basis to fully appreciate whether fish populations
335 exhibit the behavioural plasticity that will allow them to utilise seagrass outside of their current
336 depth distribution.

337

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546 **Figure captions**

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548 **Fig. 1** Map of sampling sites for seagrass associated fish in Port Phillip Bay, Victoria, Southern
549 Australia.

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551 **Fig. 2** Total proportion of finfish arranged by size class (mm) in deep (dark) and shallow (gray)

552 seagrass beds from Autumn 2008 to Spring 2010. Stars indicate the largest size class.

553 **Fig. 3** Total proportion of *Stigmatopora nigra* arranged by size class (mm) in deep (dark) and

554 shallow (gray) seagrass beds from Autumn 2008 to Spring 2010. Stars indicate the largest size

555 class.

556 **Fig. 4** Total proportion of *Acanthaluteres spilomelanurus* arranged by size class (mm) in deep

557 (dark) and shallow (gray) seagrass beds from Autumn 2008 to Spring 2010. Stars indicate the

558 largest size class.

559 **Fig. 5** nMDS ordination comparing the similarity of fish assemblages in deep and shallow

560 seagrass beds at three sites. Increasing distance between points indicates decreasing similarity.

561 **Fig. 6** Average (+SE) stem/leaf length recorded in seagrass beds at each site from Autumn 2008

562 to Spring 2010.

563 **Fig. 7** Average (+SE) biomass of seagrass recorded in seagrass beds at each site from Autumn

564 2008 to Spring 2010.

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Table 1. Summary of mean values (\pm SE) of fish abundance and species richness by depth, site and sampling time.

Total fish abundance		Autumn 2008	Spring 2008	Autumn 2009	Spring 2009	Autumn 2010	Spring 2010
<u>Deep</u>	Blairgowrie	24.25 \pm 3.82	18 \pm 2.89	26.75 \pm 14.29	14.25 \pm 6.41	13.25 \pm 8.06	45.25 \pm 23.53
	Mud Islands	21.25 \pm 11.10	21.25 \pm 4.19	21 \pm 8.06	10 \pm 5.017	4.75 \pm 2.32	3.75 \pm 1.75
	St Leonards	21.25 \pm 7.92	12 \pm 3.34	12.25 \pm 1.89	60.25 \pm 21.42	5.5 \pm 1.85	3.25 \pm 0.63
<u>Shallow</u>	Blairgowrie	122 \pm 43.84	488.25 \pm 309.73	161.25 \pm 57.92	142 \pm 49.64	216.5 \pm 31.01	56.25 \pm 16.85
	Mud Islands	327 \pm 20.22	38.5 \pm 6.06	121.75 \pm 53.44	130.75 \pm 61.08	259.25 \pm 74.22	288.25 \pm 43.17
	St Leonards	53.5 \pm 16.14	75.25 \pm 44.63	580.75 \pm 140.24	21.75 \pm 6.38	169.25 \pm 53.51	51.25 \pm 11.46
<i>S. nigra</i> abundance		Autumn 2008	Spring 2008	Autumn 2009	Spring 2009	Autumn 2010	Spring 2010
<u>Deep</u>	Blairgowrie	6.25 \pm 2.016	3.5 \pm 0.65	4.75 \pm 3.15	0.75 \pm 0.48	7 \pm 6.014	1 \pm 0.71
	Mud Islands	4 \pm 1.35	0	5.75 \pm 1.89	0	2.25 \pm 1.11	0
	St Leonards	3 \pm 1.73	0.5 \pm 0.29	9.75 \pm 5.66	8.25 \pm 4.50	0.5 \pm 0.29	0.5 \pm 0.5
<u>Shallow</u>	Blairgowrie	55.75 \pm 31.55	20.5 \pm 8.01	53 \pm 13.20	4 \pm 2.45	5.5 \pm 2.40	17 \pm 7.63
	Mud Islands	119 \pm 62.97	3 \pm 1.58	92.5 \pm 31.34	35.75 \pm 24.06	76.75 \pm 26.19	1.25 \pm 0.48
	St Leonards	22.75 \pm 11.03	0.75 \pm 0.25	78.75 \pm 42.49	2.25 \pm 1.60	123 \pm 46.72	5.75 \pm 2.50
<i>A. spilomelanurus</i> abundance		Autumn 2008	Spring 2008	Autumn 2009	Spring 2009	Autumn 2010	Spring 2010
<u>Deep</u>	Blairgowrie	0.25 \pm 0.25	4 \pm 1.78	0	8.5 \pm 4.03	0	34 \pm 19.74
	Mud Islands	7.25 \pm 4.23	19.25 \pm 4.09	2 \pm 1.41	6.25 \pm 3.94	0	1.75 \pm 1.11
	St Leonards	4.75 \pm 2.75	0 \pm 0	0 \pm 0	1.25 \pm 1.25	1.25 \pm 0.95	0.5 \pm 0.5
<u>Shallow</u>	Blairgowrie	1 \pm 0.41	2.75 \pm 1.38	5.5 \pm 2.90	0	6.25 \pm 3.71	1.5 \pm 0.96
	Mud Islands	0.75 \pm 0.75	0	2.5 \pm 2.18	0.75 \pm 0.48	1 \pm 1	0
	St Leonards	0.25 \pm 0.25	0	0.25 \pm 0.25	0	1.25 \pm 0.75	0
Species richness		Autumn 2008	Spring 2008	Autumn 2009	Spring 2009	Autumn 2010	Spring 2010
<u>Deep</u>	Blairgowrie	7.25 \pm 0.85	8.25 \pm 0.95	3.5 \pm 1.26	4.25 \pm 0.489	3 \pm 1.08	4.75 \pm 1.38
	Mud Islands	6.25 \pm 1.65	2.25 \pm 0.25	6 \pm 1.58	3.25 \pm 0.48	2 \pm 0.91	2 \pm 0.71
	St Leonards	6.75 \pm 1.49	4.75 \pm 0.75	5.25 \pm 0.48	9.5 \pm 1.5	3.75 \pm 1.11	2.75 \pm 0.25
<u>Shallow</u>	Blairgowrie	10 \pm 1.47	11 \pm 1.83	8.5 \pm 1.19	10.5 \pm 1.32	13.25 \pm 2.06	10.25 \pm 1.31
	Mud Islands	7.25 \pm 0.85	5.5 \pm 0.87	10.5 \pm 1.85	13 \pm 2.04	13.75 \pm 1.11	7.5 \pm 0.5
	St Leonards	7 \pm 0	7.5 \pm 1.66	8 \pm 0.41	9 \pm 2.04	16 \pm 1.78	9.5 \pm 0.87

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Table 2. Comparison using Kolmogorov-Smirnov two sample tests of length frequency data between fish in shallow and deep seagrass beds during each visit. Significant differences ($p < 0.05$) are shown in **bold**.

	Total fish		<i>S. nigra</i>		<i>A. spilomelanurus</i>	
	D	P	D	P	D	P
Autumn 2008	0.804	<0.001	0.162	0.152	0.403	0.217
Spring 2008	0.786	<0.001	0.455	0.006	0.624	0.001
Autumn 2009	0.890	0.003	0.248	<0.001	0.667	0.004
Spring 2009	0.478	<0.001	0.292	0.014	0.438	0.719
Autumn 2010	0.967	<0.001	0.668	<0.001	0.682	0.022
Spring 2010	0.962	<0.001	0.323	0.574	0.571	0.045

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Table 3. Summary of 4-factor PERMANOVA results based on Bray-Curtis distances, comparing fish assemblage structure across years (Y), seasons (Se), sites (Si) and depths (De). Significant differences ($p < 0.05$) are shown in **bold**. Estimates of components of variation were greatest at the level of individual replicate samples (36.9%) followed by depth (28.9%).

Source	df	MS	Pseudo- <i>F</i>	p(perm)
Y	2	4840.3	0.9601	0.566
Se	1	22484	3.2990	0.108
Si	2	9889.9	7.2504	0.001
De	1	69307	7.4669	0.1
Y×Se	2	3341.8	1.0634	0.459
Y×Si	4	5041.6	3.6960	0.001
Ye×De	2	6793.1	1.7254	0.166
Se×Si	2	6815.4	4.9965	0.001
Se×De	1	14338	2.2328	0.209
Si×De	2	9281.8	6.8046	0.001
Y×Se×Si	4	3142.6	2.3039	0.001
Y×Si×De	4	3937.1	2.8863	0.001
Se×Si×De	2	6421.7	4.7079	0.001
Pooled	6	3685.9	2.7022	0.001
Res	108	1364		

580 **Table 4.** Summary of SIMPER analyses indicating the relative importance of individual species
 581 contributing most to 50% depth differences during each sampling time (1 = most important), pooled for all
 582 sites. Numbers in superscript indicate percentage contribution.

Species	Autumn 2008	Spring 2008	Autumn 2009	Spring 2009	Autumn 2010	Spring 2010
<i>Acanthaluteres spilomelanurus</i>	5 ^{5.23}	2 ^{7.79}	6 ^{4.34}	2 ^{7.02}	9 ^{3.48}	4 ^{6.96}
<i>Acanthaluteres vittiger</i>			20 ^{1.89}			
<i>Afurcagobius tamarensis</i>	3 ^{6.56}	8 ^{3.68}	18 ^{2.29}	8 ^{4.52}		
<i>Arenigobius frenatus</i>			23 ^{1.39}			
Atherinidae	1 ^{10.04}	1 ^{8.33}	1 ^{14.82}	6 ^{4.96}	1 ^{12.11}	1 ^{12.81}
<i>Brachaluteres jacksonianus</i>	7 ^{4.95}		11 ^{3.39}			
<i>Contusus brevicaudus</i>			4 ^{4.85}	7 ^{4.8}		6 ^{5.69}
<i>Enoplosus armatus</i>			10 ^{4.06}		6 ^{4.73}	
Genus C Sp. 1		9 ^{3.56}	19 ^{2.13}	9 ^{4.35}		
<i>Gymnapistes marmoratus</i>			12 ^{3.2}			
<i>Halletta semifasciata</i>					8 ^{3.58}	
<i>Heteroclinus adelaide</i>			13 ^{3.11}		4 ^{5.43}	
<i>Heteroclinus kuiteri</i>			22 ^{1.75}			
<i>Heteroclinus perspicillatus</i>		3 ^{7.27}	7 ^{4.29}	3 ^{6.04}		
<i>Meuschenia freycineti</i>			15 ^{2.81}			
<i>Neodax balteatus</i>	6 ^{5.03}	7 ^{3.75}	9 ^{4.11}		3 ^{6.29}	5 ^{6.37}
<i>Nesogobius greeni</i>			8 ^{4.28}			
<i>Nesogobius maccullochi</i>			3 ^{5.29}			
<i>Nesogobius pulchellus</i>			17 ^{2.3}			
<i>Nesogobius sp2</i>	4 ^{5.24}		5 ^{4.78}			
<i>Parablennius tasmanianus</i>			21 ^{1.87}			
<i>Sillaginodes punctatus</i>		4 ^{7.13}		1 ^{10.38}		
<i>Stigmatopora argus</i>	8 ^{4.77}	6 ^{5.36}	16 ^{2.33}	5 ^{5.98}	5 ^{4.75}	2 ^{9.49}
<i>Stigmatopora nigra</i>	2 ^{9.39}	5 ^{6.1}	2 ^{8.9}	4 ^{6.01}	2 ^{8.09}	3 ^{8.73}
<i>Vanacampus phillipi</i>			14 ^{2.88}		7 ^{4.51}	

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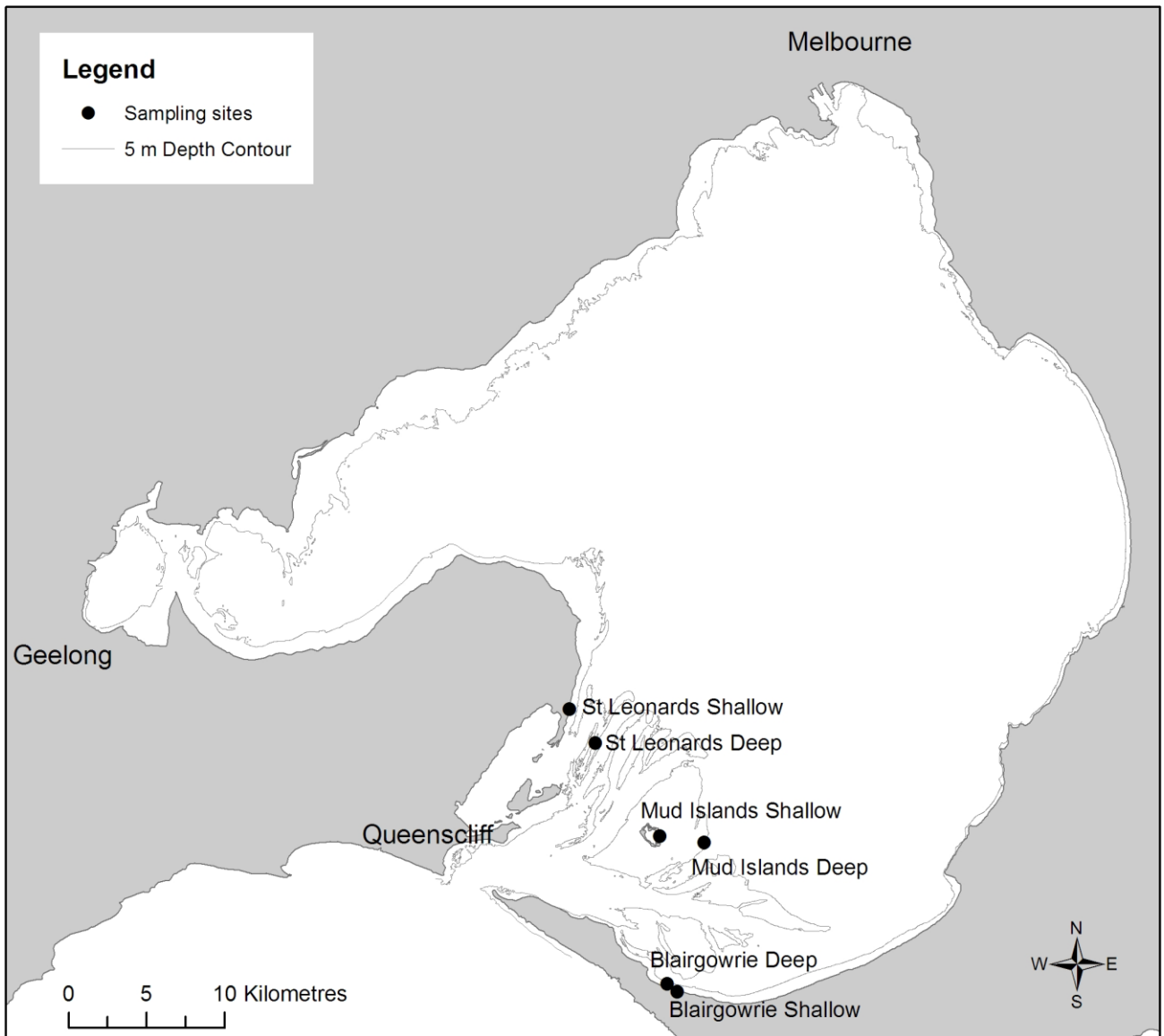
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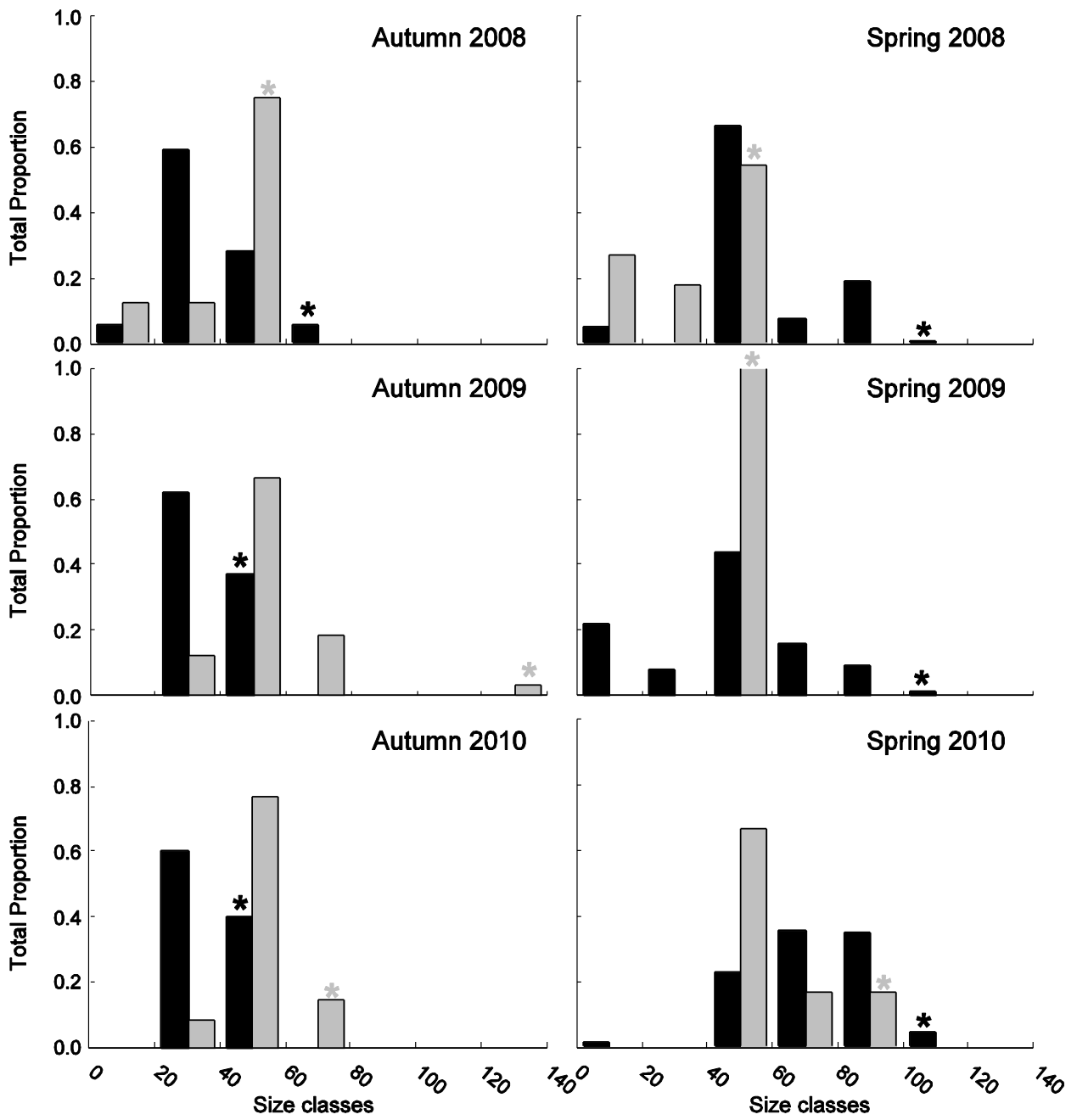
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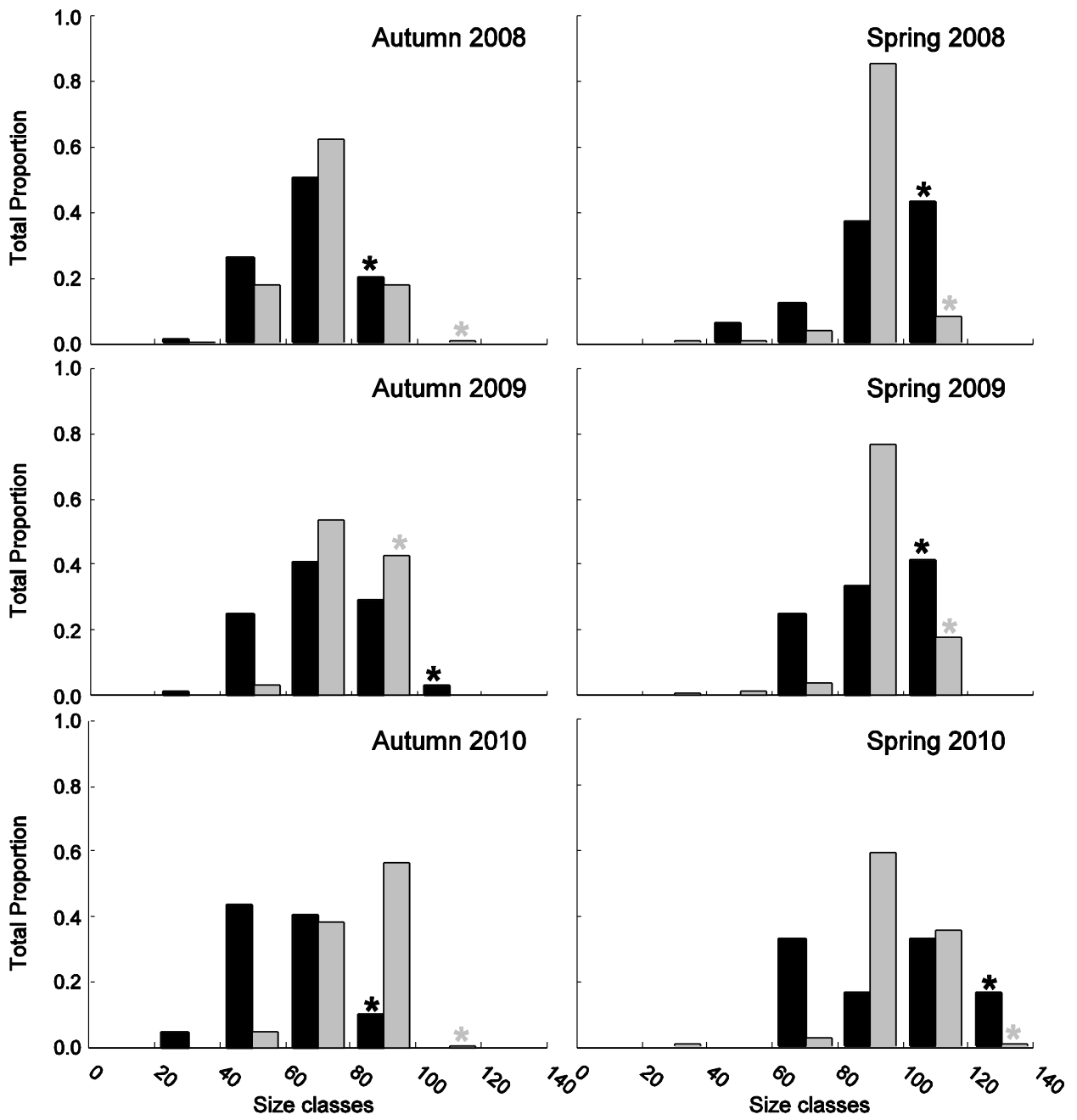
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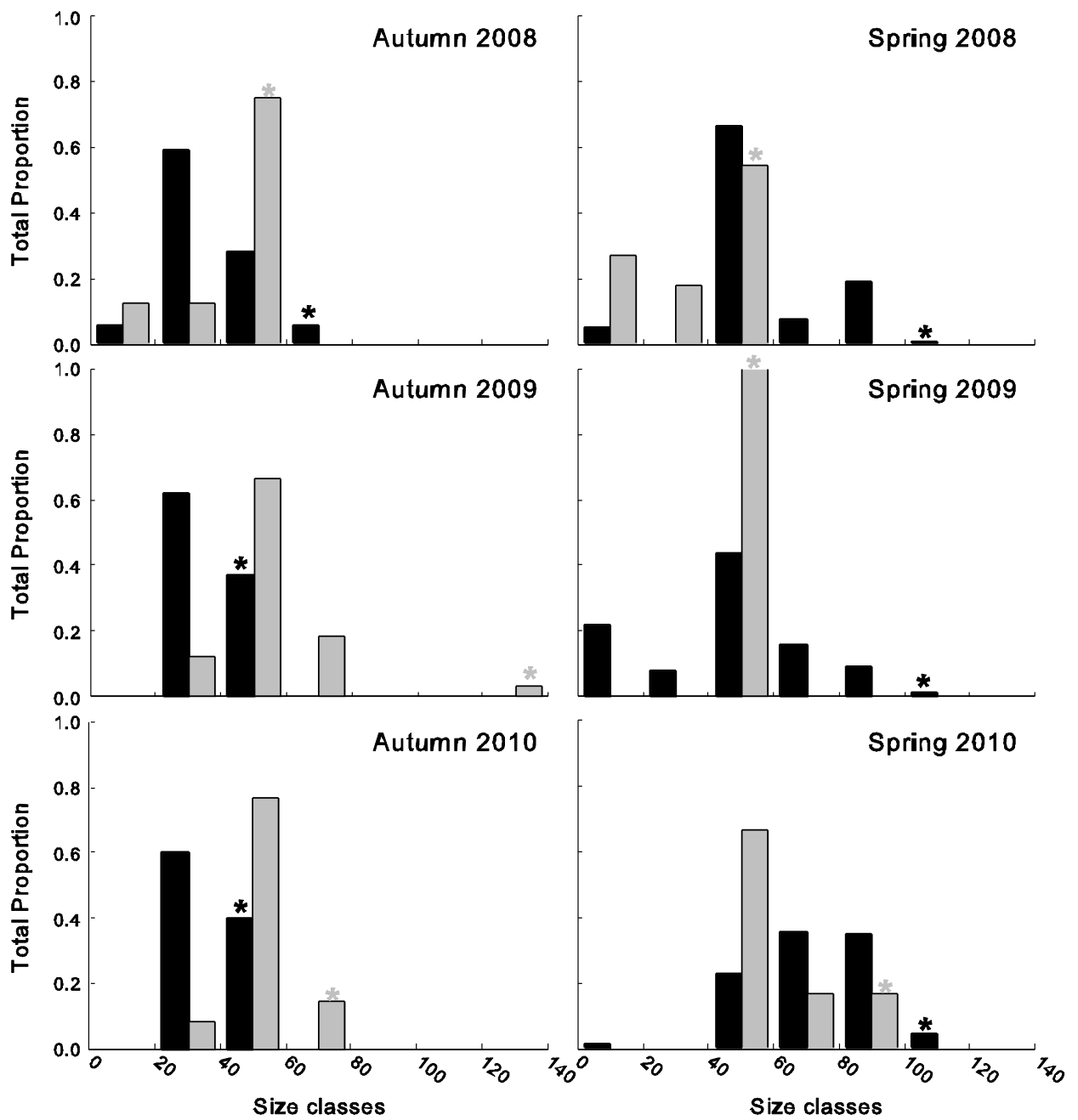


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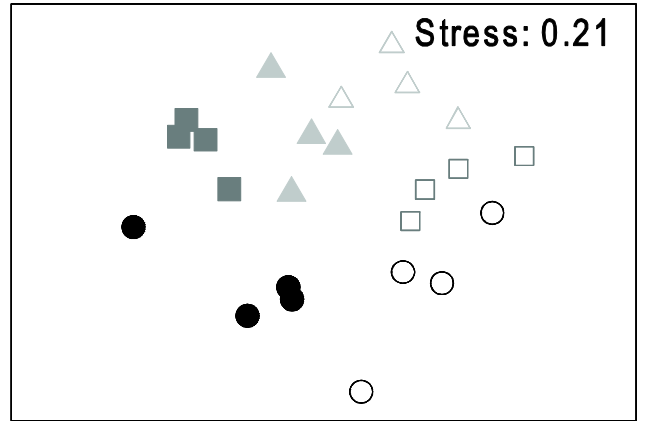
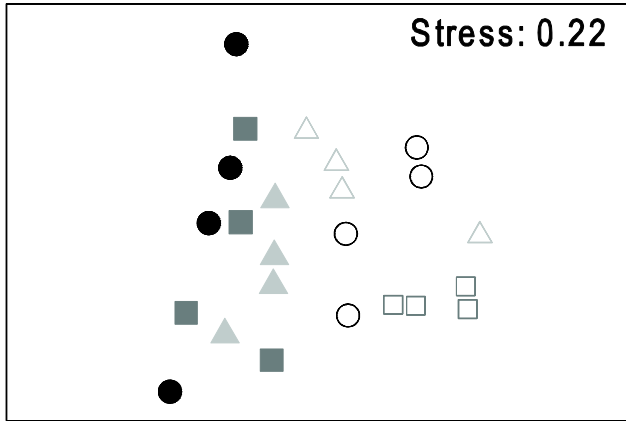




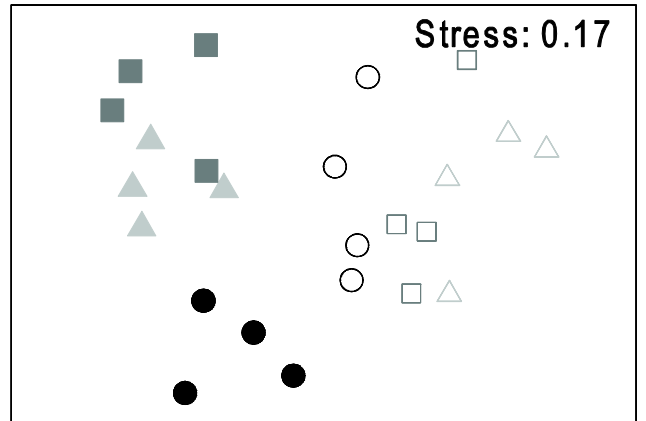
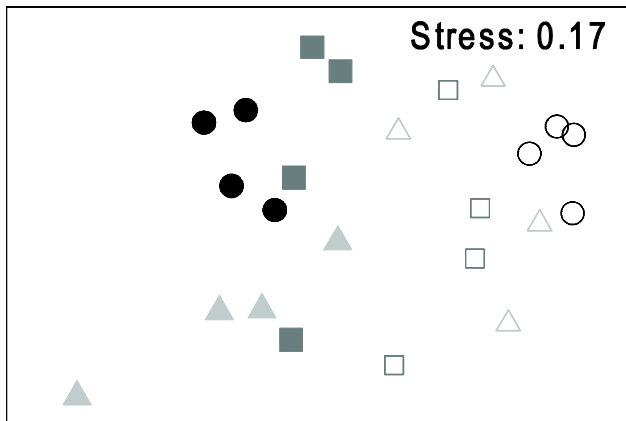
Autumn

Spring

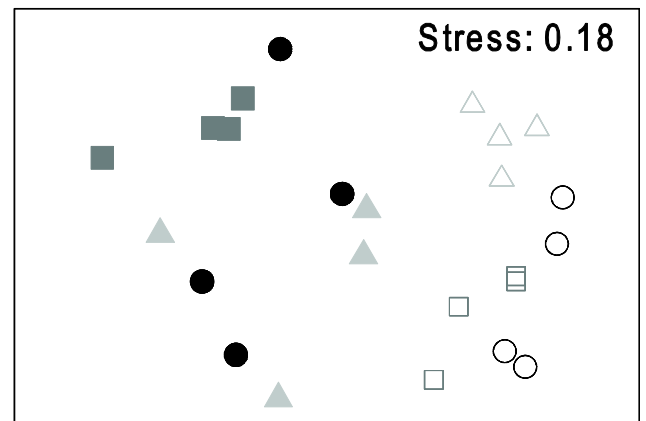
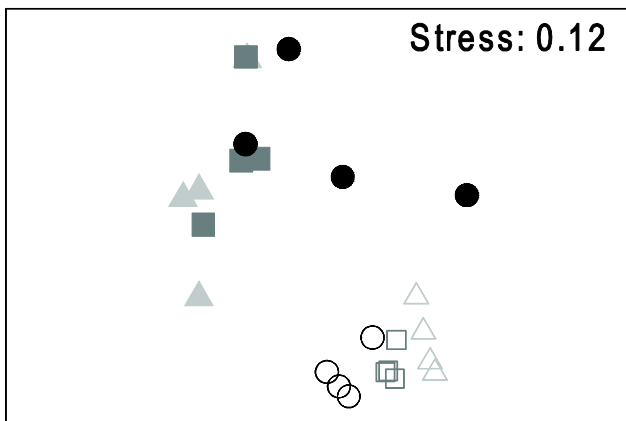
2008



2009



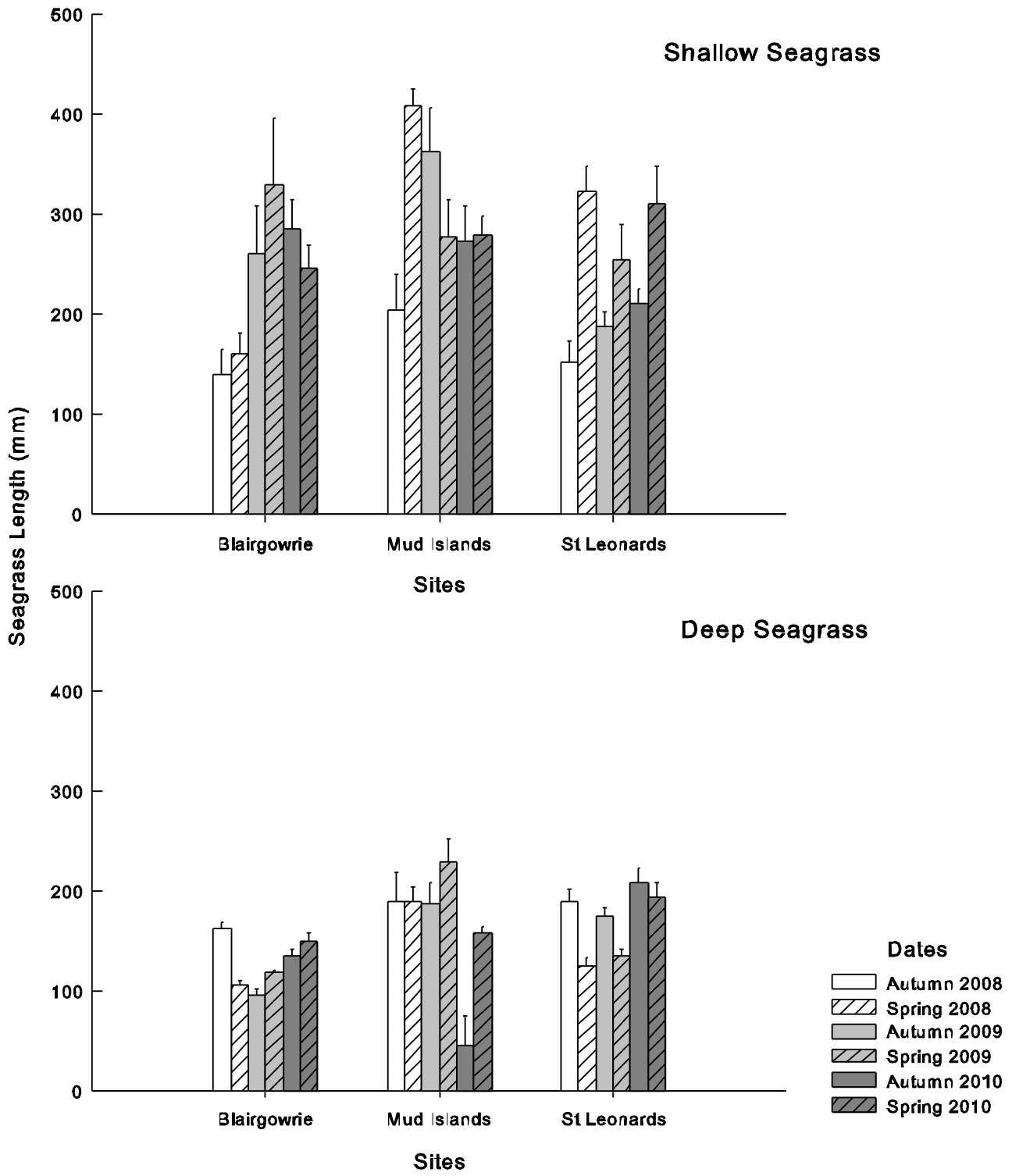
2010



- ▲ Blairgowrie Deep
- ▲ Blairgowrie Shallow
- Mud Islands Deep
- Mud Islands Shallow
- St Leonards Deep
- St Leonards Shallow

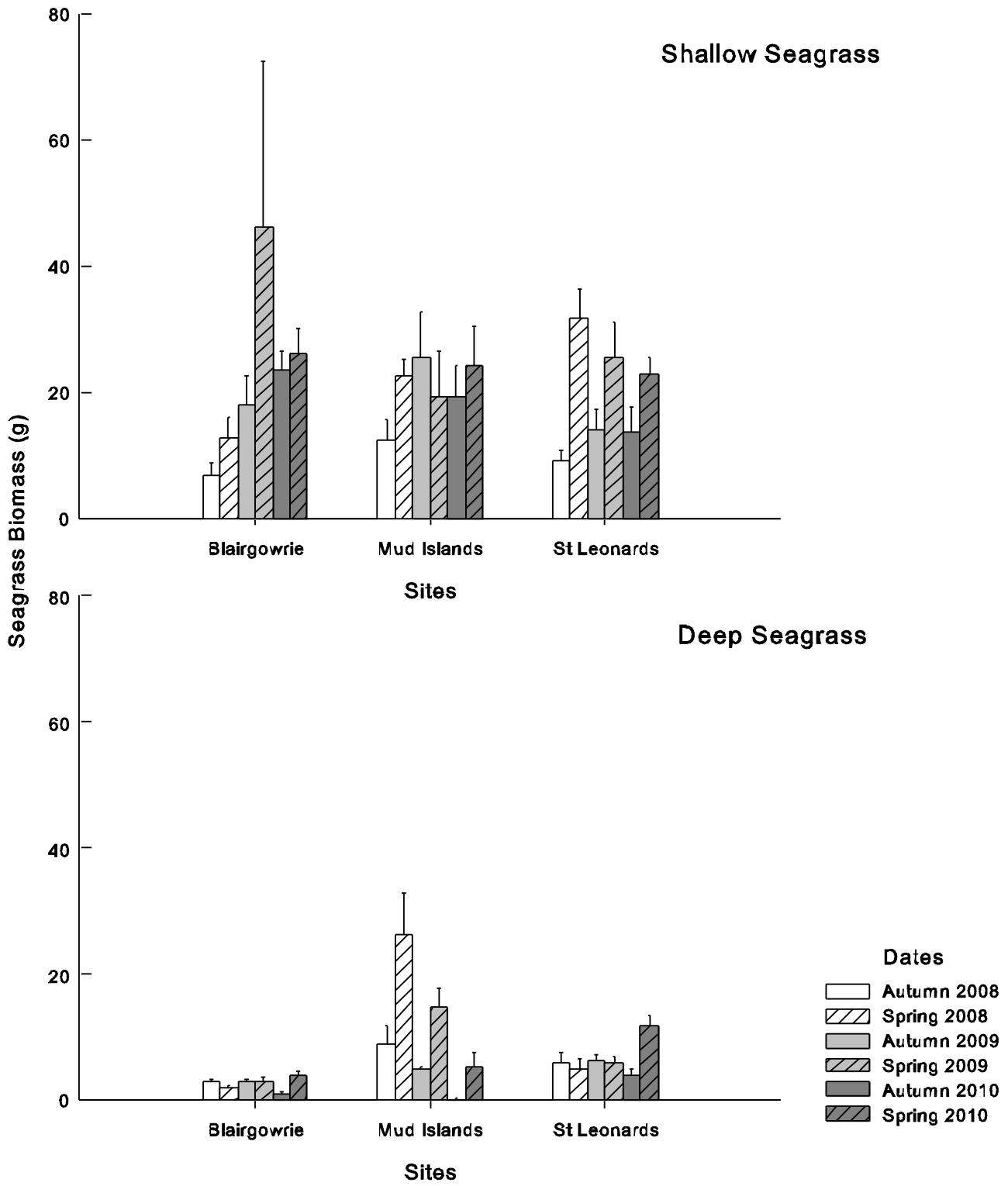
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Author/s:

Hutchinson, N; Jenkins, GP; Brown, A; Smith, TM

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