

1 Title: Ontogenetic changes in the spatial learning capability of jack mackerel *Trachurus*

2 *japonicus*

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12 Running head: ONTOGENY OF LEARNING IN JACK MACKEREL

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14 ABSTRACT

15 Ontogenetic changes in learning capability were studied in jack mackerel *Trachurus*
16 *japonicus* (Temminck & Schlegel) juveniles ranging from 20 to 95 mm standard length (L_S)
17 collected from either pelagic or coastal habitats. Simple spatial and reversal learning tasks
18 were used to estimate learning capability. There was no size dependence in the scores of
19 simple reward conditioning using a Y-maze, whereas the scores of reversal learning tasks
20 showed a clear sigmoidal curve of increase with an inflexion point at 51.7 mm L_S . The
21 increase of this learning capability coincided with the size at which juveniles recruit from
22 offshore pelagic to coastal rocky habitats.

23 Key words: behavioural ontogeny; cognitive ecology; habitat shift; life history strategy;
24 *Trachurus japonicus*

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26

INTRODUCTION

27 Learning in animals plays an important role in adaptation to changes in environmental
28 conditions and thus enhances survival potential. Fish have been reported to learn survival
29 skills in various life history contexts, such as predator avoidance (Brown, 2003; Kelley &
30 Magurran, 2003), homing (Dodson, 1988; Odling-Smee & Braithwaite, 2003), and food
31 search and handling (Ehlinger, 1989; Warburton, 2003).

32 Although the study of learning is well established in freshwater fishes (Coble et al.,
33 1985), relatively few studies have focused on the learning of marine fishes, presumably due
34 to the difficulty of sampling and maintaining them in the laboratory. Previous studies have
35 revealed ontogenetic changes in learning capability through the juvenile stage for some
36 marine fishes such as striped jack *Pseudocaranx dentex* (Bloch & Schneider) (Tsukamoto et
37 al., 1995), Pacific threadfin *Polydactylus sexfilis* (Valenciennes) (Masuda & Ziemann, 2000)
38 and striped knifejaw *Oplegnathus fasciatus* (Temminck & Schlegel) (Makino et al., 2006).
39 Masuda & Ziemann (2000) proposed that changes in learning capability coincide with
40 ontogenetic shifts in habitat. Indeed most marine fishes experience a major habitat shift and
41 thus face different cognitive challenges during their life history.

42 All of the above-mentioned studies have examined only hatchery-reared fishes which
43 have never experienced natural environmental conditions. Some of the roles of learning
44 capability (e.g., in relation to predator avoidance, foraging and homing etc.) would better be

45 evaluated by using wild individuals because hatchery-reared fish may show behavioural
46 inferiority in survival capability such as feeding and anti-predator performance as well as
47 having developmental constraints on learning such as a smaller brain size compared with
48 natural fish (Huntingford, 2004; James et al., 2009). Additionally, the investigation of skills
49 among fish from different life history stages in the natural environment can help us reveal
50 the relationship between learning capability and habitat shift.

51 Jack mackerel, *Trachurus japonicus* (Temminck & Schlegel), one of the most important
52 fisheries resources in Japan, forms large schools and spawns in offshore areas (Sassa et al.,
53 2008). After hatching, larvae drift offshore either independently or associated with floating
54 objects such as seaweed or jellyfish (Sassa et al., 2006). As they reach a standard length of
55 ca. 50 mm, juveniles recruit to rocky coastal reefs (Masuda et al., 2008; Kanaji et al., 2009).
56 In this study, spatial learning capability, including simple spatial learning and its reversal
57 learning tasks, was evaluated in pre and post recruiting stage wild juveniles using a Y-maze.
58 We hypothesized that a shift in learning capability would be associated with recruitment to
59 the spatially complex rocky shore.

60

61 **MATERIALS AND METHODS**

62 Ontogenetic changes in learning capability by reward conditioning were examined in
63 single fish ranging from 20 to 95 mm L_S (standard length). Fish were captured by three
64 different methods: (1) pelagic fish: collecting individuals associated with drifting objects
65 such as the giant jellyfish *Nemopilema nomurai* (Kishinouye) (14, 23 Oct and 26 Nov 2007)
66 or drifting algae (18 July 2007) with a hand net while snorkeling in ca. 10 km offshore area
67 of Maizuru, Kyoto (35°68' N, 135°44' E), (2) migrating fish: sampled from a set net located
68 ca. 2 km offshore of Maizuru (35°59' N; 135°49' E; 31 July 2007), and (3) coastal fish:
69 captured by artificial fly angling from a pontoon of Maizuru Fisheries Research Station
70 (MFRS) (35°49' N, 135°36' E, 13 July and 21 Sep 2007). These fish were introduced into
71 separate 500 L black tanks provided with filtered sea water at an exchange rate of 4 L per
72 min. They were fed commercial dry pellets (Otohime S2, Syoki-siryou Kyowa N700,
73 Kyowa Hakko Bio Co., Ltd. Tokyo, Japan) and defrosted krill *Euphausia* sp. from July to
74 December. When fish were confirmed to forage actively on pellets near the water surface,
75 one fish was transferred to an experimental tank and the experiment was started. A total of
76 40 juveniles ($L_S 57.7 \pm 20.5$ mm, mean \pm SD) were used to conduct the experiment: 21
77 pelagic fish ($L_S 42.8 \pm 14.7$ mm), 11 migrating fish ($L_S 74.4 \pm 6.0$ mm) and 8 coastal fish
78 ($L_S 73.9 \pm 16.4$ mm).

79 Five identical glass tanks (L \times W \times H: 60 \times 30 \times 36 cm, 25 cm in water depth) were

80 prepared as Y-maze experimental tanks for fish < 90 mm L_S . A larger tank ($L \times W \times H$: $90 \times$
81 30×36 cm, 25 cm in water depth) was used for fish ≥ 90 mm L_S ($n = 3$), as these individuals
82 did not acclimatize well in the small tank. Each tank was separated into left and right
83 sections by a 20×30 ($L \times H$) cm (30×30 cm in the large tank) PVC board set at the center
84 of one of the ends. These two separated zones were designated as the conditioning area (Fig.
85 1). A removable PVC board ($W \times H$: 30×30 cm) was set as the gate at a distance of 20 cm
86 (30 cm in the large tank) from the opposite end to the conditioning area, defined as the
87 acclimatization area. Filtered sea water was delivered to the experimental tanks in the
88 conditioning area and drained out from the acclimatization area. Each tank was covered on
89 all sides with a grey sheet to minimize the effects of the observer.

90 An individual was introduced into the acclimatization area on the day previous to the
91 training and left to acclimatize overnight. A few pellets were provided immediately before a
92 training trial, and if the fish foraged on the pellets, the experiment was started. If not, the
93 experiment was postponed for another day or two. Fish that did not feed after 2 days of
94 acclimatization or did not swim to the conditioning area within 5 min from the time of gate
95 opening were not used in further experiments and regarded as aborting fish. Aborting fish
96 were measured in L_S . During the experimental period, fish ≤ 40 mm L_S were provided with
97 3-6 small pellets (ca. 0.7 mm in diameter, Syoki-siryou Kyowa N700) and fish > 40 mm L_S
98 were provided with 1-5 large pellets (ca. 1.4 mm in diameter, Otohime S2). The amount of

99 reward was established by preliminary survey so that fish never satiated during the training.
100 Feeding was conducted by remote control feeding device, which allowed pellets to drop by
101 pulling a string.

102 The behaviour of fish was observed after gently opening the gate. Fish were first trained
103 to enter the left side of the branch of a Y maze (original learning task); when the fish swam
104 to the left side, pellets were dropped as the reward into the left side. After feeding on the
105 pellets, the fish was returned gently to the acclimatization area. When the fish swam to the
106 right side, the fish was returned to the acclimatization area without being provided with
107 pellets. The process from opening the gate to returning the fish to the acclimatization area
108 was defined as one trial, and the interval of each trial was about 1 min. Ten trials comprised
109 one session and two consecutive sessions were conducted four times a day at intervals of 30
110 min or longer. The percentage of choosing the correct side in one session was calculated as
111 the criteria of learning. Once a fish chose the correct side 70 % or more times in three
112 consecutive sessions, it was considered to have learnt the task (Makino et al., 2006). After
113 being conditioned to the original learning task, the fish was conditioned to the reversal
114 learning task where the position of feeding was changed from left to right. When a fish
115 chose the right side 70 % or more times in three consecutive sessions on the reversed task
116 the fish was then again conditioned to an additional reversed task, thus returning the reward
117 side back to the left. Eight sessions a day were carried out for three consecutive days.

118 Therefore each test fish was conditioned in a total of 24 sessions or 240 trials including the
119 original learning task and all the reversal learning tasks. The reversal learning task was
120 repeated (“right to left” and “left to right”) depending on the achievement of the learning
121 task until the end of 240 trainings. The average percentage of the correct choice of side until
122 the accomplishment for each learning task was calculated as a score of each task, and these
123 values were summed to give the total score for each individual. Each fish was anesthetized
124 and measured for L_S after the experiment.

125 Overall, of all fish indicated a pattern of the total scores increase around 50 mm L_S . Over
126 50 mm L_S , the scores plateaued and remained constant. Therefore, the relation between L_S
127 and the total score of learning was fitted with a nonlinear least squares model; $y = c + (d - c)$
128 $/ [1 + \exp \{-(a + b * x)\}]$. Fish were divided and compared as two size groups based upon
129 their differing performance patterns. Total scores were also compared between different
130 habitat groups (i.e. pelagic, migrating or coastal fish) by the Kruskal-Wallis test followed by
131 the Steel-Dwass method.

132 Personality (bold or shy) of fish may affect learning performance (Sneddon, 2003).
133 Aborting rate was used as a criterion of shyness and was compared in each size and habitat
134 group. Similarly, laterality may also influence learning in spatial tasks (Brown & Braithwate,
135 2005; Brown et al., 2004). All the fish were conditioned to the left area on the original
136 learning task, so if there was a difference in laterality with body size, learning score could be

137 affected by the fish's laterality (Miklosi & Andrew, 1999; Bisazza et al., 1998). Laterality of
138 individual fish was estimated by the side (left or right) of the first selection on the original
139 learning. Laterality was then compared with the body size. There was a possibility that
140 learning performance was affected by the rearing period because tested fish were kept in
141 captivity for various durations ranging from 5 and 92 days. As plasticity of fish is affected
142 by rearing environment (Berjikian et al., 2001), overly long conventional rearing might have
143 had some effect on the behavioural performance of fish. The effect of rearing period on
144 learning performance was also evaluated by the correlation between rearing period and
145 learning capability.

146 **ETHICAL NOTES**

147 All fish used in experiments were subsequently released into the sea off the MFRS.
148 Small juveniles were kept until they reached 40 mm L_S , because the size range of *T.*
149 *japonicus* found in this area was between 40 and 120 mm L_S (Masuda et al., 2008).

150

RESULTS

151

152 The mean L_S of pelagic fish was smaller than those of other groups (Steel-Dwass method,
153 $P < 0.05$). There was no correlation between body size and acclimatization time (Spearman
154 rank method, $r = 0.09$, $P = 0.57$), nor between the habitats and acclimatization time
155 (Kruskal-Wallis test, $P = 0.50$).

156 Total learning score followed a logistic curve as follows (Fig. 2): $y = c + (d - c) / [1 +$
157 $\exp \{-(a + b * x)\}]$; $a = -47.6745$ ($P = 0.34$), $b = 0.9222$ ($P = 0.34$), $c = 132.3460$ ($P < 0.001$),
158 $d = 225.2855$ ($P < 0.001$). The curve had an inflexion point at 51.7 mm L_S with a score of
159 178.8. Total score of smaller fish was significantly lower than those of larger size
160 (Mann-Whitney U test, $n = 16 + 24$, $P < 0.001$). To investigate the relationship between
161 body size and score, the data were divided into two groups with L_S of over and below 51.7
162 mm. Then there was no correlation between body size and total learning score within each
163 size group (Spearman rank method; ≤ 51.7 mm: $r = 0.12$, $P = 0.65$; > 51.7 mm: $r = 0.34$, P
164 $= 0.10$). The relation between learning capability and body size was further analysed for
165 each learning task (Fig.3). Reversal learning was repeated for a maximum of four times
166 during the whole trials depending on the achievement of learning criteria. The average score
167 of the original learning task was 80.3 ± 9.4 points, which was achieved on average in $4.3 \pm$
168 0.8 sessions. There was no size dependence in the score of original learning task (R_0) and
169 the fourth reversal learning task (R_4) (Spearman rank method, R_0 : $r = 0.24$, $P = 0.13$, R_4 : $r =$

170 0.16, $P = 0.32$), whereas there was a positive correlation between L_S and score in the first to
171 third reversal learning tasks (R_1 : $r = 0.36$, R_2 : $r = 0.65$, R_3 : $r = 0.61$, $P < 0.05$). The score
172 showed a clear increase from around 50 mm in the second and third reversal learning task.

173 Observation of fish behaviour suggested that smaller fish tended to go directly to the
174 learned area once original learning was established and had difficulty achieving reversal
175 learning. In contrast, although larger fish also went to the original learning area at the
176 beginning of reversal learning, they tended to stop in front of the conditioning area after
177 several mistakes. Then they started to enter the correct (reversed) side.

178 The median score of pelagic, migrating and coastal fish were 146.3 (median, IQR (inter
179 quartile range): 123.0 - 180.7), 231.0 (IQR: 221.1 - 244.2) and 215.5 (IQR: 186.0 - 227.3),
180 respectively (Fig. 4a). The score of pelagic fish was significantly lower than those of the
181 other two groups (Kruskal-Wallis test followed by Steel-Dwass method, $P < 0.05$). When
182 the scores of fish > 51.7 mm L_S were compared to eliminate the size bias, medians in pelagic
183 ($n = 5$), migrating ($n = 11$) and coastal ($n = 8$) fish were 217.3 (IQR: 205.4 – 236.9), 231.0
184 (IQR: 221.1 - 244.2) and 215.5 (IQR: 186.0 - 227.3), respectively, and did not differ
185 significantly (Kruskal-Wallis test, $P = 0.36$; Fig.4b).

186 A total of 50 fish aborted the experiment: 25 pelagic fish ($L_S 42.8 \pm 14.7$ mm), 16
187 migrating fish ($L_S 74.4 \pm 6.0$ mm) and 9 coastal fish ($L_S 73.9 \pm 16.4$ mm). There was no
188 significant difference in aborting rate between fish over and below 51.7 mm (Fisher's exact

189 test, $P = 0.83$) and among habitats (Fisher's exact test, $P = 0.92$). A total of 25 fish selected
190 the left side and 15 fish selected the right side on the first original learning task. There was
191 no significance difference of the first selection on the original learning task between fish
192 over and below 51.7 mm (Fisher's exact test, $P = 1.00$). There was no correlation between
193 the rearing duration and learning score in each size group (Spearman rank method, ≤ 51.7
194 mm: $r = -0.12$ $P = 0.67$, > 51.7 mm: $r = 0.07$, $P = 0.76$). These findings suggest that these
195 factors do not affect the difference of learning score by size and habitat.

196

197

DISCUSSION

198 There was no size-dependence in the original learning score and even the smallest
199 individuals learned the task. Early juveniles of *T. japonicus* (size range of ca. 10-50 mm)
200 often associate with jellyfish and feed on foods collected by jellyfish (Masuda et al. 2008).
201 The basic spatial learning capabilities represented by the original learning task indicate that
202 early juveniles may be able to quickly learn the edible parts of jellyfish. Relatively simple
203 spatial learning skills are likely to be advantageous for survival even in this poor spatial
204 environment.

205 On the other hand, there was size dependence in the total score including original and all
206 reversal learning scores, bigger fish having a higher score than smaller ones within the size
207 range studied. This was due to differences in reversal learning capability. In particular in the
208 second and third reversal learning task, fish above 51 mm showed a higher score than
209 smaller fish. The total time of reversals indicated a similar tendency, suggesting that reversal
210 learning capability increases with a flexion point at about 50 mm L_S . This result may imply
211 that the development of reversal learning capability is related to ontogenetic habitat shift in *T.*
212 *japonicus*, because at about 50 mm L_S *T. japonicus* recruit from offshore pelagic to coastal
213 rocky reefs area (Masuda et al., 2008; Kanaji et al., 2009). Our study considers reversal
214 learning capability as the ability to quickly learn a novel feeding area in a spatially complex
215 environment. Such a learning capability may not be as important in pelagic environments

216 which lack spatial complexity. Therefore, these results suggest that an increase in reversal
217 learning capability coincides with the recruitment period from the pelagic zone to the rocky
218 reef.

219 Makino et al. (2006) showed that the learning capability of *O. fasciatus* increases during
220 the transition from offshore to coastal habitat. In this study, *T. japonicas* showed a similar
221 improvement of learning capability during the habitat shift. However, the improvement of
222 learning capability was different in terms of the developmental processes between these
223 species. Learning capability of *O. fasciatus* improved gradually as they grow from 20 to 70
224 mm Ls. In contrast, learning performance of *T. japonicas* increased suddenly at a threshold
225 size of 51.7 mm. It is tempting to compare the development of brain morphology, which
226 may possibly explain the difference in the improvement trajectories of learning capability in
227 these two species.

228 In the reversal training, smaller fish tended to continue going directly to the original
229 feeding area. Although larger fish also went to the area of original learning at the beginning
230 of reversal learning, their choice changed after several trials without rewards. These
231 observations suggested that smaller fish learned only the cue, such as a position of feeding,
232 whereas larger fish learned the spatial information of overall feeding area. Small, and thus
233 pelagic, stages of fish may require relatively simple cues for learning feeding areas, whereas
234 cognition of spatial complexity is likely to be necessary for larger coastal fish. Our

235 speculation coincides with Odling-Smee et al. (2008) who found that in sympatric species of
236 the stickleback *Gasterosteus aculeatus* L. species complex, fish from a benthic population in
237 the littoral zone had superior spatial learning abilities to those from a limnetic population in
238 the pelagic zone. The development of learning capability revealed in our study may reflect
239 the behavioural strategy of *T. japonicas* during its life history as it migrates from pelagic to
240 coastal environments. Hawkins et al. (2008) suggested that in hatchery reared Atlantic
241 salmon *Salmo salar* L. predator recognition developed at ecologically appropriate periods
242 during ontogeny; three-week-old juveniles showed only an innate response, and 16- to
243 20-week-old fish showed acquired response to predator odour. Thus, there may be
244 ontogenetic, species specific changes in learning ability in fish.

245 Comparison of learning scores among habitats showed that coastal and migrating fish
246 had a higher learning capability than pelagic fish. This trend supports the hypothesis that
247 the development of learning ability coincides with a habitat shift from offshore pelagic to
248 coastal reefs. However, the result may be biased by the size variation of individuals from
249 each habitat; indeed there was no difference of learning capability among habitats in fish >
250 51.7 mm L_S . On the other hand, there is a possibility that larger fish sampled from drifting
251 objects were at the last stage of recruitment from pelagic to rocky reef. This was observed
252 during sampling; small juveniles tended to hide inside or behind a floating object, whereas
253 large individuals tended to swim away from the object and headed to the bottom

254 (Takahashi and Masuda, pers. obs. 2007; Masuda, 2009). It is thus suggested that larger
255 pelagic juveniles are those ready for the transition to rocky reef. The developments of
256 sensory or kinematic organs are often considered as requirements for recruitment (Poling
257 and Fuiman, 1998; Kingsford et al., 2002; Fisher, 2005). The present study suggests that
258 the development of learning capability may also be an important factor for the recruitment
259 to coastal rocky reef. The improvement of learning ability, and thus an increase in
260 adaptability for life in a variable environment, is thus suggested as the factor which enables
261 juveniles to recruit a complex habitat such as coastal rocky shore.

262 Fish often experience multiple, drastic environmental changes during their early life
263 history (Yousan, 1988). Present study investigated the ontogeny of learning capability in *T.*
264 *japonicus* and suggested that these fish were equipped with the appropriate capability in
265 accordance with such changes. Studying the ontogeny of learning capability in fish
266 provides an understanding of the role of learning capability during life history. Further
267 studies should focus on combining environmental factors with learning capability using
268 both wild and hatchery-reared fish. Research on learning capability with various
269 conditioning stimuli may also be required to further investigate learning performance in the
270 context of life history strategies.

271

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277

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350

Figure Caption

Fig.1. Schematic drawing of the experimental tank. A fish was kept in the acclimatization area until the gate was opened. In the original learning task, the fish was rewarded by pellets when it went into the left side. In the reversal learning task, the correct side was reversed from left to right.

Fig.2. Total score including original and all reversal learnings in 240 trials for fish captured from the drifting objects (\circ), set net (\bullet) and angling (\blacksquare). Each marker represents one fish. Solid line represents nonlinear least square model fitted to the data. Model equation is $y = 929395 / \{1 + e^{-56.37 - 1.15x}\} + 126.85$. Dotted line represents the inflexion point of the model.

Fig.3. Score of original and each reversal learning task. (a) original learning, (b) first, (c) second, (d) third and (e) fourth reversal learning. Each line indicates a linear regression line. Individuals that could not accomplish a learning stage were treated as zero score, and black plots indicate such individuals.

Fig. 4. (a) The median of the total score of all fish captured under each sampling method. Bars indicate inter quartile range (drifting objects: $n = 21$, set net: $n = 11$, angling: $n = 8$). Scores with different letters were significantly different (Steel-Dwass method, $P < 0.05$). (b) The median of the total score of fish > 51.7 mm L_S captured under each sampling method. Bars indicate interquartile range (drifting objects: $n = 5$, set net: $n = 11$, angling: $n = 8$).

Figure

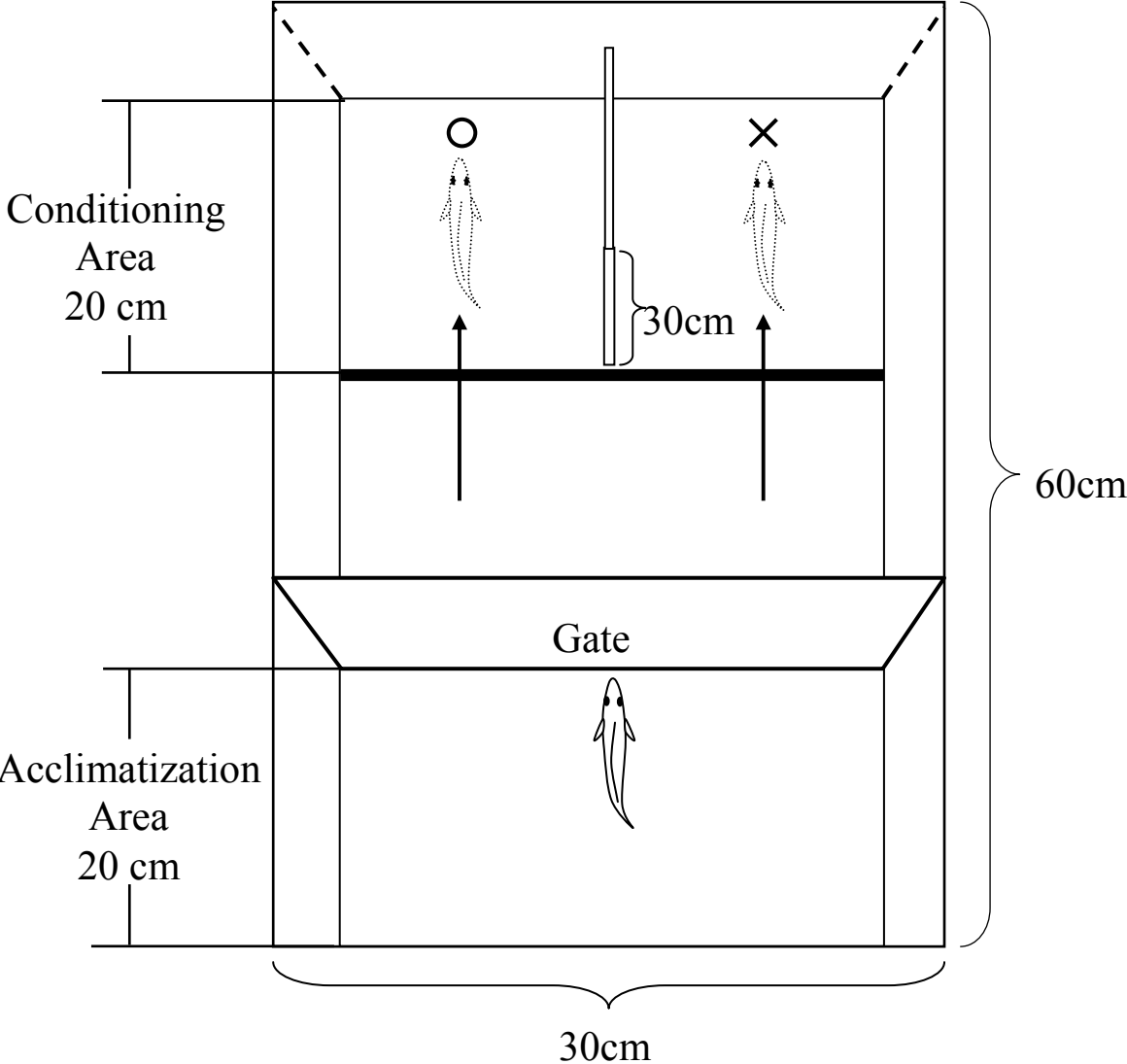


Fig.1

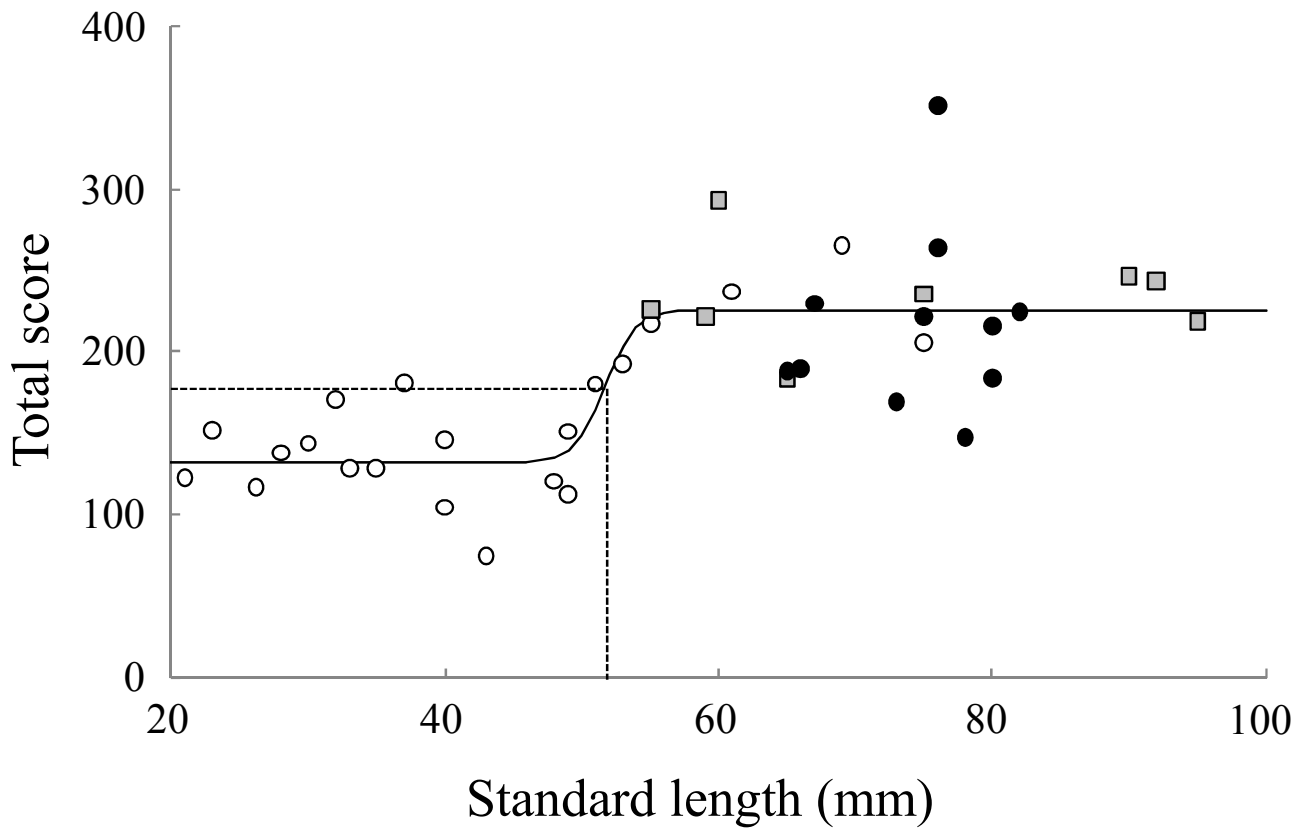


Fig.2

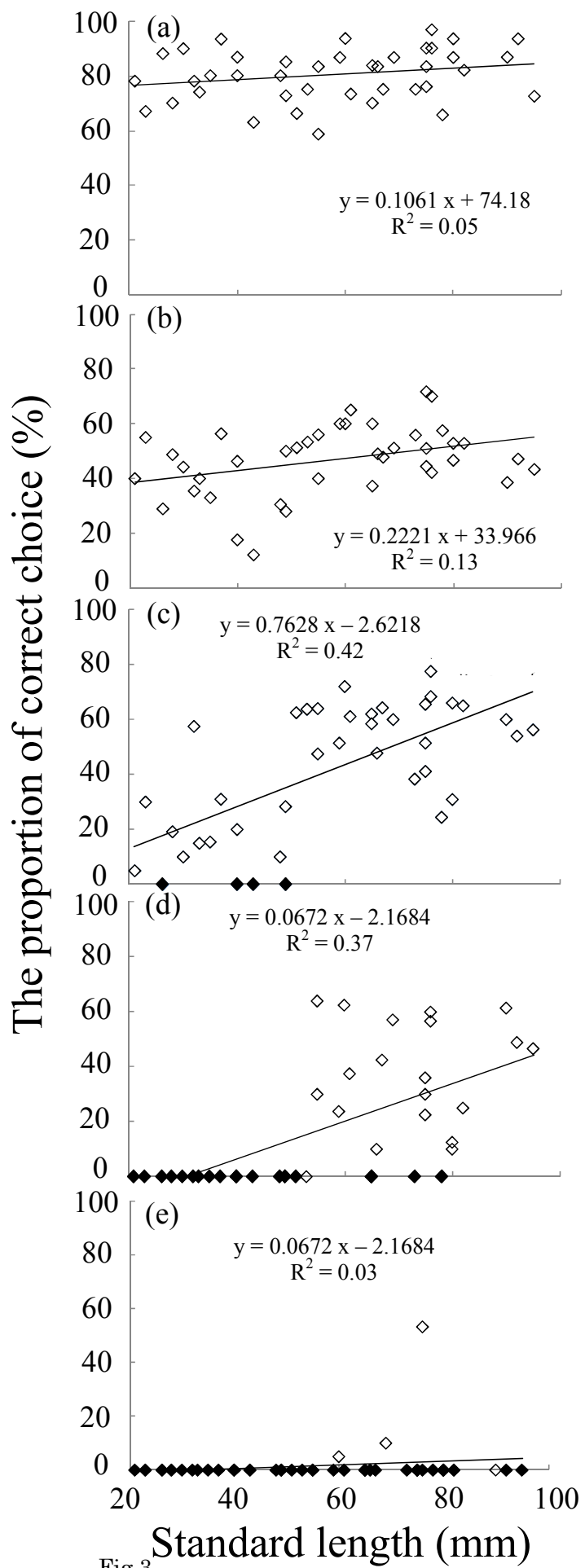


Fig.3

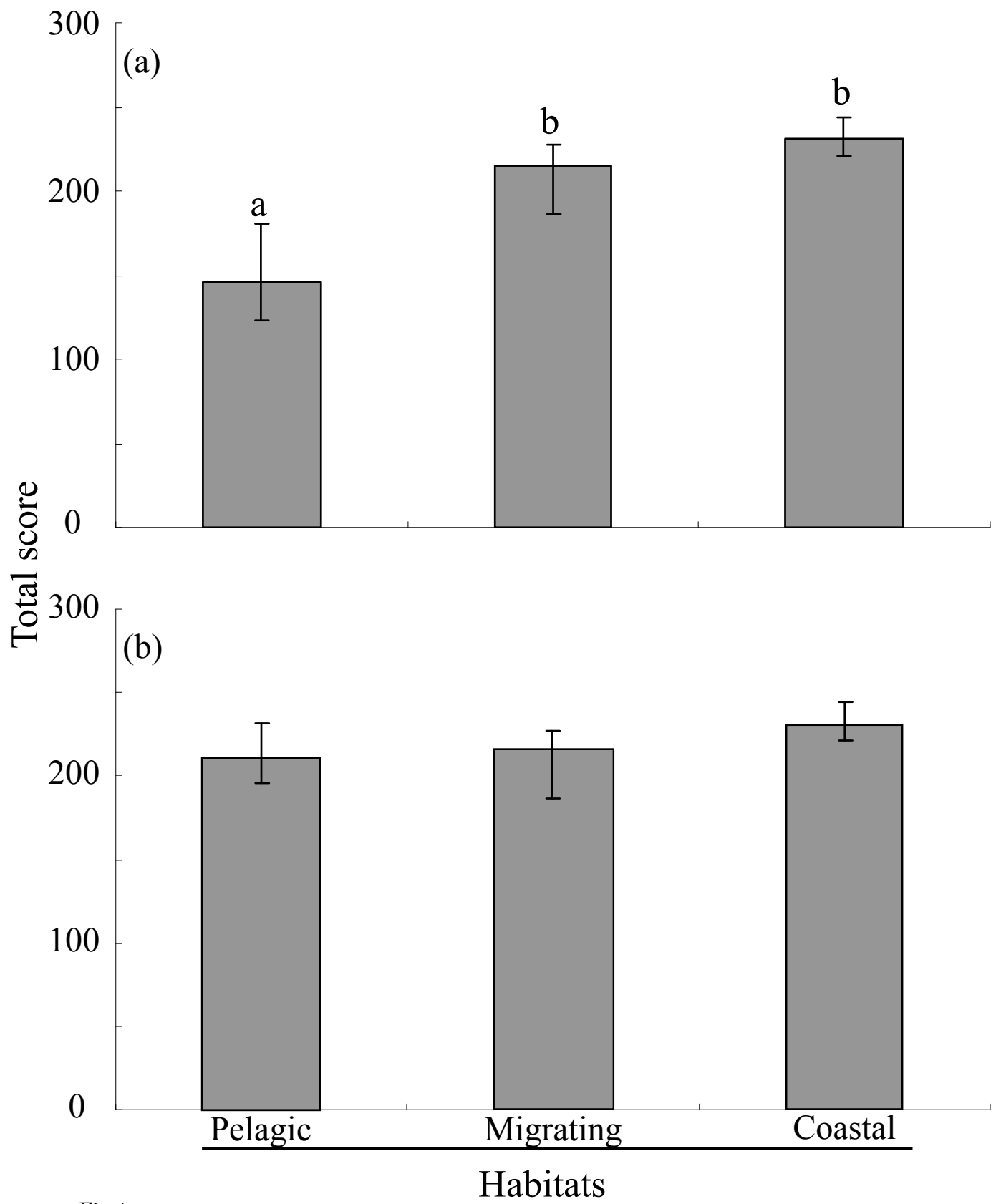


Fig.4