Life-history traits and intra-cohort divergence of clearhead icefish (*Protosalanx chinensis*), indicating cannibalism increased fitness

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Cannibalism is considered one of the causes of intra-cohort size divergence in fish and is usually believed to result in increased fitness in terms of survival and reproduction, but direct evidence of this is lacking. Population demographics of the clearhead icefish (*Protosalanx chinensis*) from Lake Xingkai (Khanka) were investigated for one year. Size-frequencies exhibited a bimodal distribution from July through January, where the population diverged into an upper and a lower modal group based on size. Stomach content analysis confirmed the occurrence of cannibalism, where fish belonging to the larger, upper modal group preyed upon those of the smaller, lower modal group. We found *P. chinensis* does not spawn until all of the oocytes have reached maturity and then a single spawning event occurs although the oocytes may develop asynchronously in the ovary. Upper modal group females matured slightly earlier than those of the lower modal group, and reproductive investment was considerably greater in the upper modal group than the lower modal group. The lower modal males made up the majority of the population after the spawning period, which meant they may have few opportunities to participate in reproduction. Therefore, piscivory and cannibalism of *P. chinensis* appears to have increased fitness of the fish belonging to the upper modal group and reduced the fitness of those belonging to the lower modal group greatly.

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23 **Abstract**

24 Cannibalism is considered one of the causes of intra-cohort size divergence in fish and is usually

25 believed to result in increased fitness in terms of survival and reproduction, but direct evidence

26 of this is lacking. Population demographics of the clearhead icefish (*Protosalanx chinensis*) from

27 Lake Xingkai (Khanka) were investigated for one year. Size-frequencies exhibited a bimodal

28 distribution from July through January, where the population diverged into an upper and a lower

29 modal group based on size. Stomach content analysis confirmed the occurrence of cannibalism,

30 where fish belonging to the larger, upper modal group preyed upon those of the smaller, lower

31 modal group. We found *P. chinensis* does not spawn until all of the oocytes have reached

32 maturity and then a single spawning event occurs although the oocytes may develope

33 asynchronously in the ovary. Upper modal group females matured slightly earlier than those of

34 the lower modal group, and reproductive investment was considerably greater in the upper modal

35 group than the lower modal group. The lower modal males made up the majority of the

36 population after the spawning period, which meant they may have few opportunities to

37 participate in reproduction. Therefore, piscivory and cannibalism of *P. chinensis* appears to have

38 increased fitness of the fish belonging to the upper modal group and reduced the fitness of those

39 belonging to the lower modal group greatly.

40

41

Introduction

43

44   Many piscivorous fishes exhibit an ontogenetic dietary shift, transitioning from non-fish

45   prey to piscivory over time. An early transition to piscivory is thought to result in increased

46   growth and reproductive fitness, decreased mortality, and therefore enhanced lifetime fitness

47   (Werner and Gilliam 1984; Post et al. 1988). In some piscivorous fishes, young-of-the-year

48   (YOY) intra-cohort individuals exhibited differential timing to the onset of piscivory, driving

49   bimodal size frequency distributions and cannibalism in the age-0 group. In these cases, the

50   larger, upper modal group (cannibals) increased their growth rate and decreased survival rate of

51   the smaller, lower modal group (prey) (Buijse and Houthuijzen 1992; Frankiewicz et al. 1996;

52   Post 2003; Huss et al. 2010; Heermann et al. 2013). However, direct evidence of increased

53   reproductive fitness with the transition to piscivory is absent, although Post (2003) suggested that

54   an early transition to piscivory may result in higher lifetime fecundity since these fish have a

55   larger relative size and potentially more spawning opportunities in a lifetime.

56   The clearhead icefish, *Protosalanx chinensis* (Abbott 1901), is a small, pelagic, euryhaline

57   fish species of the family Salangidae that occurs in eastern Asia (Xie and Xie 1997; Saruwatari et

58   al. 2002). It is a short-lived semelparous fish, completing its lifecycle in about 1 year (Tang et al.

59   2012). Early-stage juveniles feed mainly on zooplankton, while larger individuals in young and

60   adult-stage could switch to fish and shrimp and feed primarily on conspecifics (Tang et al. 2013).

61   The size-frequency of the population becomes bimodal from Month to Month (Zhu 1985).

62   Considering the unique biological characteristics of *P. chinensis*, we present evidence of within-

63   population size divergence, and the advantage of larger individuals over smaller individuals in

64   survival and reproduction. These findings provide direct evidence of cannibalism, and its effects

65   on reproductive fitness of both females and males.

66

67   **Methods**

68   Study area

69   Lake Xingkai (Khanka) is a large shallow lake,located between China and Russia, serving

70   as a boundary. It is connected to the Ussuri River through the Sungacha River. The northern part

71   of the lake (28% of the total area) is located in China and the southern part (72% of the total

72   area) is located in Russia. The water level area in Khanka is variable and varies from 3940 to

73   5010 km^2. The long-term average water level area is 4070 km^2 with an average depth of 4.5 m.

74   Since 2010, there has been an increase in the water level in the lake. Lake Khanka/Xingkai is one

75   of the most important international wetlands in the world. Specimens were sampled from the

76   northwestern part of Khanka Lake near the locality of Dangbi in China(N 45°15′49.12″ -

77   45°15′8.62″, E 132°02′35.22″ - 132°01′7.73″, Fig.1).

78

79   Sampling procedure

80   Clearhead icefish (*P. chinensis*) were sampled monthly from March 2010 through March

81   2011 except for April 2010. Different sampling gear was used in winter and ice-free seasons to

82   sample fish effectively. A cone trawler net (length, 3 m; diameter, 1 m; mesh size, 1 x 1 mm)

83   was used for sampling fish in May, while a seine net (length, 200 m; height, 8 m; mesh size, 2 x

84   2 mm) was used for sampling from June through November 2010. For each sample, the seine net

85   was drawn parallel to the shore where the water depth was less than 1.5 m, for about 50 m.

86   Further, four gill nets (length, 30 m; height, 1 m; mesh size, 10 mm, 15 mm, 20 mm, and 23 mm

87   between opposite knots) positioned randomly were deployed in gangs, tied end to end

88   perpendicular to the shore for 24 h per month during the freeze-up period (March 2010 and

89   December 2010 to March 2011). For the reproductive biology and cannibalism experiments, we

90   used two extra gill nets (length, 100 m; height, 1 m; mesh sizes, 20 and 23 mm between opposite

91   knots) in the freeze-up period to obtain adequate samples.

92

93   Life history traits analysis

94   The clearhead icefish died immediately after they were captured in nets. Over 100 specimens

95   were caught in each monthly sample and were measured for standard length (SL; to the nearest 1

96   mm) and weight (WB; to the nearest 0.01 g). A row of scales typically appears at the base of the

97   anal fin of maturing males and the anal fin also becomes larger and wave-shaped in mid-October,

98   but no sexual dimorphism appears before that point, so the sex of each fish was determined by

99   examining dissected gonads. Females have a larger ovary on the left of the ventral cavity and a

100   smaller ovary on the right side, while males have a single testis on the right of the cavity. Sex

101   ratios were determined, and their difference from parity was tested using a binomial test. Chi-

102   square tests were performed to assess differences in sex ratios among months.

103   The gonads of females sampled in November, December, and January were used to

104   determine the gonadosomatic index (GSI) and maturity stage, and more than 50 specimens were

105   dissected for reproductive biology studies each month. In *P. chinensis*, the left ovary is usually

106   larger than the right one. The middle portion of the left ovary was selected for histological

107   examination. Stages of maturity were classified into six phases according to Sun (1985). Both

108   ovaries were removed and weighed to the nearest 0.0001 g (W_G), and the GSI was calculated as

109   follows:

110    $GSI=100W_G/(W_B - W_G)$.

111   The number of oocytes(both pre-vitellogenic and vitellogenic oocytes)from dissected

112   ovaries was counted in December and January. Two sub-samples of tissue weighing

113   approximately 0.1 g were taken from the middle section of each ovary and preserved in 5%

114   formalin. The oocyte counts in these two sub-samples were determined using a dissecting

115   microscope and were used to estimate fecundity if the coefficient of variation of N per unit ovary

116   weight was below 5% for the two sub-samples. The total fecundity (F_A) and relative fecundity

117   (F_R) were calculated in January as follows:

118    $F_A = \Sigma Cn\ W_O n\ /W_S n$ and $F_R = 100\ F_A/W_B$,

119   where Cn is the counted number of eggs in sub-sample n, $W_O n$ is the corresponding ovary

120   weight, $W_S n$ is the sub-sample weight and n is the number of subsamples.

121   To reveal the proportion of pre-vitellogenic oocyte change with overall gonad development,

122   the most advanced oocyte diameters were determined by measuring the 10 largest oocytes under

123   a dissecting microscope to represent the advancement of gonad development (West 1990). The

124   proportion of pre-vitellogenic oocytes (P_p) can be described as:

125                                    $P_p = 100(Np \times N-1)$

126   The Mann-Whitney U test was used to compare the developmental stages of gonads between the

127   upper and lower modal groups in the same cohort within the maturing season. The difference in

128   GSI between November, December, and January, as well as the difference in fecundity between

129   December and January, was tested using analysis of covariance (ANCOVA) with WB as the

130   covariate. Differences in GSI, fecundity, and relative fecundity between the upper and lower

131   modal groups in January were examined using one-way analysis of variance (ANOVA). The

132   difference of Pp between December and January was compared using Mann-whitney U test. The

133   relationship between Pp and the most advanced oocyte diameters was analyzed with general

134   linear models. All statistical analyses were conducted using STATISTICA 12.0 (StatSoft, Tulsa,

135   OK, USA). $P < 0.05$ was considered significant.

136

137   Analysis of cannibalism

138   *P. chinensis* are translucent, allowing for gross examination of gut contents and visual

139   identification of cannibalism in individuals. We chose to dissect cannibals with visible prey in

140   their guts. Cannibals and prey were examined for SL (to the nearest 1 mm). The prey to cannibal

141   size ratios in about 20 cases were calculated for each month from July through December.

142

143   **Results**

144   Growth and intra-cohort size divergence

145   Two cohorts of *P. chinensis* were identified during the sampling period. Individuals

146   collected in March 2010 belonged to the 2009 cohort and the individuals sampled after March

147   2010 belonged to the 2010 cohort. Samples collected in March 2010 ranged in SL from 81 to 225

148   mm and consisted of reproductive females and males from the 2009 cohort. *P. chinensis*

149   juveniles belonging to the 2010 cohort were sampled from May 2010 onwards, and the SL

150   distribution pattern was unimodal until early July, when a bimodal length distribution began to

151   emerge and lasted through January 2011. From November to January, the reproductive

152   population could be divided into the lower modal group (SL < 120 mm) and upper modal group

153   (SL>120 mm) on the basis of size (Fig. 2). The population sampled in February and March did

154   not exhibit a bimodal distribution because the fish died after spawning.

155

156   Characteristics of cannibals and prey

157   Cannibalism was first observed in July. The SL of cannibals sampled during this month

158   ranged from 65 to 91 mm, while those of prey ranged from 38 to 52 mm. Both cannibals and

159   prey grew larger over time. The cannibals generally reached a SL of >120 mm by November,

160   and the prey were usually smaller than 120 mm (Table 1). Given that the reproductive population

161   in November could be divided into two size groups by SL with 120 mm as the cutoff (Fig. 2), it

162   is apparent that the upper modal group was comprised of cannibals and the lower modal group

163   was comprised of the prey. The prey to cannibal size ratio ranged from 0.47 to 0.67 (Table 1).

164

165   Examination of sex ratio

166   The sex of all sampled individuals was determined from early October 2010 to early March

167   2011. Monthly observations of sex ratios (male to female) did not differ from parity (1:1) from

168   October through January (P = 0.808, 0.410, 0.563, 0.621, respectively) or vary significantly

169   among months (x^2 = 1.499, df = 3, P = 0.683). However, the sex ratios in February and March

170   were 13.4 and 18.1, respectively, due to natural mortality of females after spawning (Fig. 3). The

171   remaining population mainly consisted of males in the lower modal group (Fig. 2). From October

172   through January, sex ratios did not differ from parity in the upper modal group (P = 0.453, 0.450,

173   0.475, 0.527, respectively) or the lower modal group (P = 0.462, 0.409, 0.428, 0.635,

174   respectively).

175

176   Gonad development and the differences between the two groups

177   Oocytes developed asynchronously in ovaries of *P. chinensis*; pre-vitellogenic (Phase III

178   & II) oocytes and vitellogenic (Phase IV & V) oocytes existed in the same ovary. The gonads of

179   female *P. chinensis* did not develop to stage II until early October, after which they developed

180   quickly to stage III in the first half of October. In early November, individuals in stages III and

181   IV of gonadal development accounted for 61.5% and 38.5% of the female population,

182   respectively. A few oocytes developed to stage V at the beginning of December, but all the

183   oocytes in an ovary did not develop synchronously to the same stage. Most female gonads

184   developed to stage IV or V and the fish could spawn in early January, but only a few post-

185   spawning individuals were sampled in February and March (Fig. 4). The oocytes developed

186   asynchronously, and oocytes of different developing phases may commonly occur in the same

187   ovary of maturing females (Fig.5).

188   The Pre-vitellogenic oocytes occurred in samples from December and January (100%, n=50

189   and 22%, n=59, respectively). The proportion of pre-vitellogenic oocytes (Pp) in gonads sampled

190   in January became significantly lower compared to those sampled in December (Z=-15.99,

191   P<0.001, see Fig. 6). Linear regression indicated that the proportion of pre-vitellogenic oocytes

192   declined significantly ($F1,107 = 6.18$, P=0.014, see Fig. 6), as indicated by the observation of

193   increased oocyte diameters in the developing gonads. This indicates that *P. chinensis* will spawn

194   as many eggs as possible in a single spawning event occurs.

195   Most female gonads developed to stage III or IV in early November, and females in the

196   upper modal group seemed to mature faster than those in the lower modal group, although this

197   difference was not significant (Z = -1.117, P = 0.239). In early December, females in maturity

198   stage IV accounted for the largest proportion both in the upper (88.5%) and lower modal groups

199   (81.5%), and the maturity stage distribution was not significantly different between the groups (Z

200   = -1.401, P = 0.161). In early January, almost all of the female gonads developed to stage IV or

201   V, and no significant differences were observed in the developmental rates between the groups

202   (Z = -1.934, P = 0.053) (Fig. 7).

203

204   Differences in reproductive investment between the groups

205   The GSI increased dramatically from November to January, ranging from 1.8 to 10.2% in

206   November, 2.9 to 44.1% in December, and 7.6 to 76.4% in January (Fig. 8). Results of the

207   ANCOVA (BW as the covariate) indicated that the differences in GSI among the three months

208   were all significant ($F2,161 = 185.3$, P <0.001). The GSI of fish in the upper modal group was

209   significantly higher than that of fish in the lower modal group in November (ANOVA, $F1,50 =$

210 56.3, P <0.001), December (ANOVA, F1,51 = 50.0, P <0.001), and January (ANOVA, F1,57 =

211 95.1, P <0.001) (Fig. 8).

212 Results of the ANCOVA (BW as the covariate) also revealed no significant difference in

213 fecundity between early December and early January (F2,110 = 3.4, P = 0.067). In other words,

214 there was no down-regulation of fecundity during gonad development or indeterminate

215 spawning. Samples from January were used to analyze intra-population divergence of fecundity.

216 Fecundity ranged from 1,592 to 36,705 eggs, and relative fecundity ranged from 500 to 1,646

217 eggs per gram BW. The relative and absolute fecundity were significantly higher in females from

218 the upper modal group than those in the lower modal group (ANOVA, F1,57 = 121.5, P <0.001

219 and ANOVA, F1,57 = 21.94, P <0.001, respectively) (Fig. 9).

220

221 **Discussion**

222 Piscivorous, cannibalism and size divergence

223 Size variation among clearhead icefish populations has been previously reported (Zhu 1985;

224 Wang and Jiang 1992; Tang et al. 2003). Xie et al. (2001) noted two peaks within the size

225 frequency distribution of a reproductive population. However, this is the first report of within-

226 cohort bimodal size distribution in *P. chinensis*. Bimodal size distribution is well documented in

227 iteroparous fishes (Huss et al. 2010; Alejo-Plata et al. 2011), and studies on Percidae species

228 revealed diet shift contributing to the size divergences in YOY fish, and that the extreme growth

229 of the upper modal group was induced by piscivory (cannibalism) (Frankiewicz et al. 1996; Post

230 2003; Urbatzka et al. 2008). The synchronous investigation on diet composition showed that a

231 few bigger individuals of *P. chinensis* began to feed on fish and cannibalism also occured in

232 early July, and then piscivory and cannibalism accompanied the size bimodal pattern forming

233 (Tang et al. 2013). And the victims of cannibalism accounted for the majority of the diet of

234 cannibals in December and January (Tang et al. 2013).

235

236 Fitness of the cannibals

237   The absolute and relative fecundity reported in the present study for a population of *P.*

238 *chinensis* in Lake Khanka shows wider range (1,592 - 36,705 eggs, and 500 - 1,646 eggs/gram-

239 BW) than populations from other locations (3,295 to 34,520 eggs, and 340 to 1,290 eggs/gram-

240 BW) (Zhang et al. 1981; Xie et al. 2001). While there is no published information illustrating the

241 difference in reproductive investment between the two modal groups of clearhead icefish, this

242 investigation demonstrates that the reproductive investment of females belonging to the upper

243 modal group(cannibals) was significantly higher than that of females from the lower modal

244 group(victims) in terms of GSI, absolute fecundity and relative fecundity. In common, larger fish

245 has higher absolute fecundity and lower relative fecundity than the smaller conspecifics. *P.*

246 *chinensis* cannibals have both higher absolute fecundity and relative fecundity than the victims,

247 which means piscivory and cannibalism increased reproductive potential greatly. In addition, the

248 cannibals grow faster and become bigger than the potential victims, which will increase their

249 survival rate undoubtedly.

250

251 Gonad development and spawning pattern

252   Researchers have offered multiple theories to describe the reproductive strategy of *P.*

253   *chinensis*. Sun (1985) reasoned that *P. chinensis* spawn twice during their lifetime upon

254   examination of their gonad histology, but Xu et al. (2000) determined that this species spawns

255   once before death. Xie et al. (2001) theorized that *P. chinensis* can spawn once or multiple times.

256   Our research supports the theory that *P. chinensis* exhibits a semelparous reproductive strategy,

257   although oocytes developed asynchronously in the same gonad. This is different from other

258   semelparous species such as chum salmon *Oncoryhchus keta* (Crozier et al. 2008). The

259   asynchronous development of oocytes should be attributed to the relatively rather high fecundity

260   and the nutrition may not be enough to develop all the oocytes at the same time, which is a

261   mechanism to produce as many eggs as possible in a spawning event in a life time.

262

263   Sex ratio and mate selectivity

264   Sex ratios did not differ from parity before spawning (October through December) or during

265   spawning (primarily early to mid-January) in both the upper modal and lower modal groups.

266   This is similar to reports for this species from other locations (Zhang et al. 1981; Sun and Zhou

267   1989; Xu et al. 2000; Xie et al. 2001). However, we found that the reproductive population was

268   mainly composed of males in the lower modal group after January. We hypothesize that males in

269   the lower modal group have a reduced opportunity to participate in spawning. The intra-cohort

270   sex selectivity of *P. chinensis* may influence evolution towards early birth and faster growth,

271   although this theory requires further study.

272

273   Life history strategy

274   The *P. chinensis* is a small fish that matures early with a short life span and relatively high

275   fecundity. This makes it an exception from the three-point life-history continuum model

276   proposed by Winemiller and Rose (1992). Larger individuals (upper modal group) tend to exhibit

277   an opportunistic life-history strategy, but characterized by relatively higher fecundity. An

278   opportunistic colonization strategy facilitates range expansion of an invading species through

279   early maturity in frequently changing or stochastic environments (Fox et al. 2007; Ribeiro et al.

280   2009). Exceptional higher fecundity would undoubtedly contribute to rapid increase in

281   population size and spread of the opportunistic fish, *P. chinensis*.

282   **Conclusion**

283   Transition to feed on fish increased the investment of the female *P. chinensis* and may also

284   increase the fitness of male in reproductive competing. This research provided a direct evidence

285   that transition to be carnivorous is positively significant in evolution, although further study on

286   increasing the fitness of male *P. chinensis* need to be conducted.

287

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356

357

358

359

Figure 1

Location of Lake Khanka (China/Russia) and sampling site.

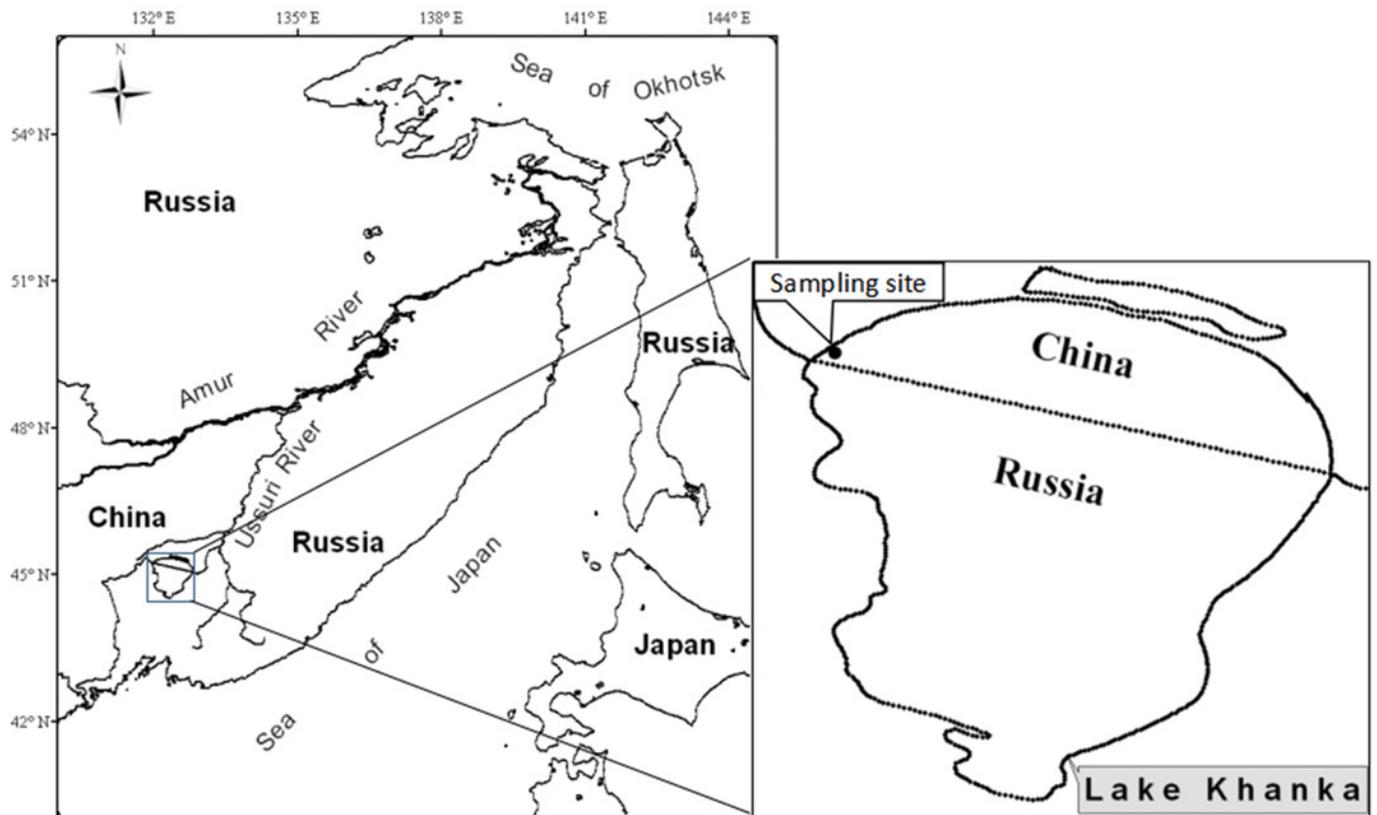



Figure 2

. Standard length frequency distribution of *P. chinesis* in Lake Khanka from March 2010 through March 2011. The solid line connects lower modal groups and the dashed line connects upper modal groups.

A, Cohort born in 2009; B-L, Cohort born in 2010. Jan, January; Feb, February; Mar, March; Jun, June; Jul, July; Aug, August; Sep, September; Oct, October; Nov, November; Dec, December.

(A) 4 Mar 2010 n = 104

(B) 15 May 2010 n = 126

(C) 17 Jun 2010 n = 149

(D) 4 Jul 2010 n = 105

(E) 7 Aug 2010 n = 137

(F) 4 Sep 2010 n = 104

(G) 4 Oct 2010 n = 152

(H) 1 Nov 2010 n = 147

(I) 6 Dec 2010 n = 242

(J) 5 Jan 2011 n = 221

(K) 1 Feb 2011 n = 144

(L) 4 Mar 2011 n = 115

Number of fish

Standard Length (mm)

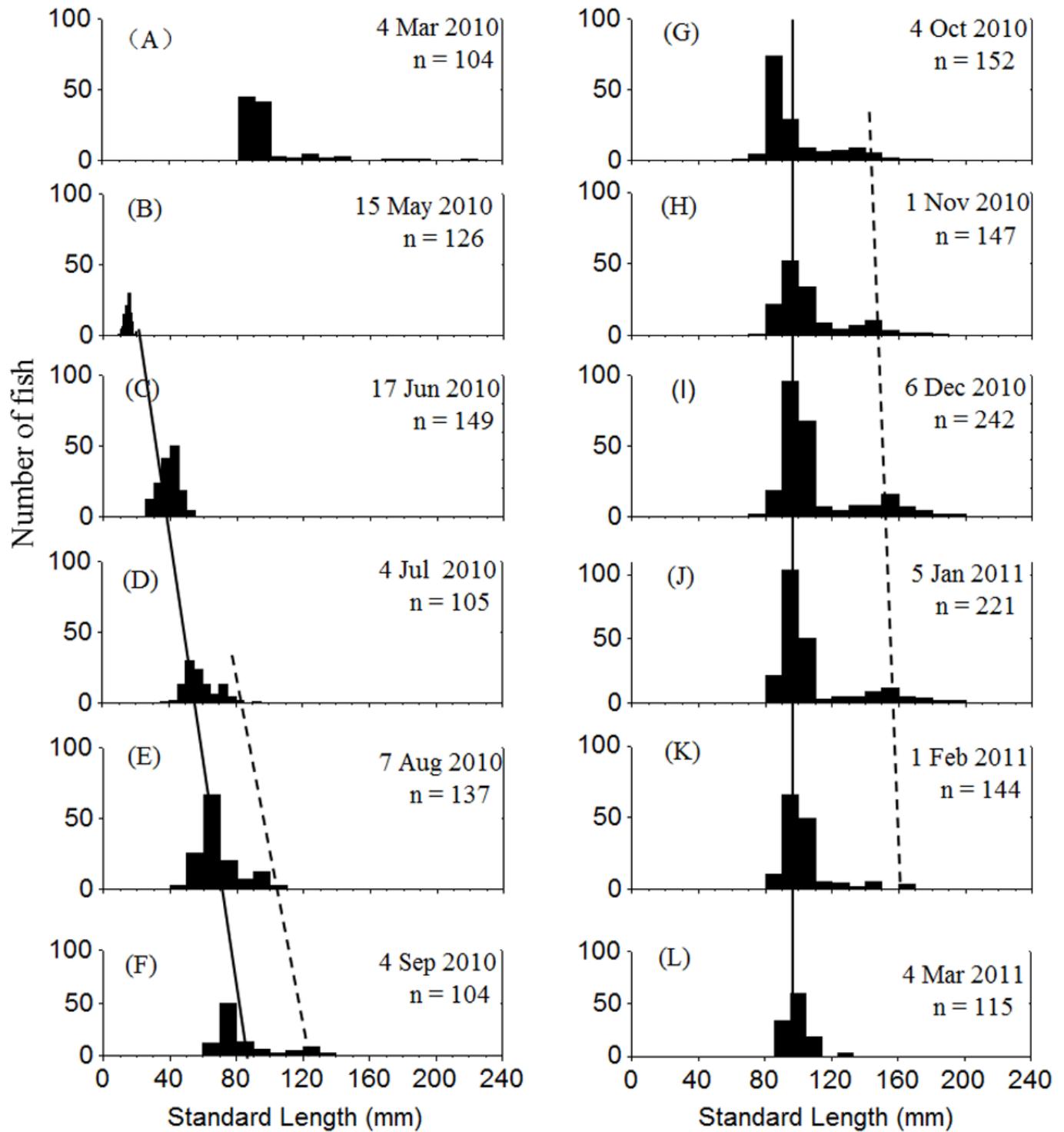



Figure 3

Monthly sex ratio variation from 4 October 2010 through 4 March 2011.

Oct, October; Nov, November; Dec, December; Jan, January; Feb, February; Mar, March.

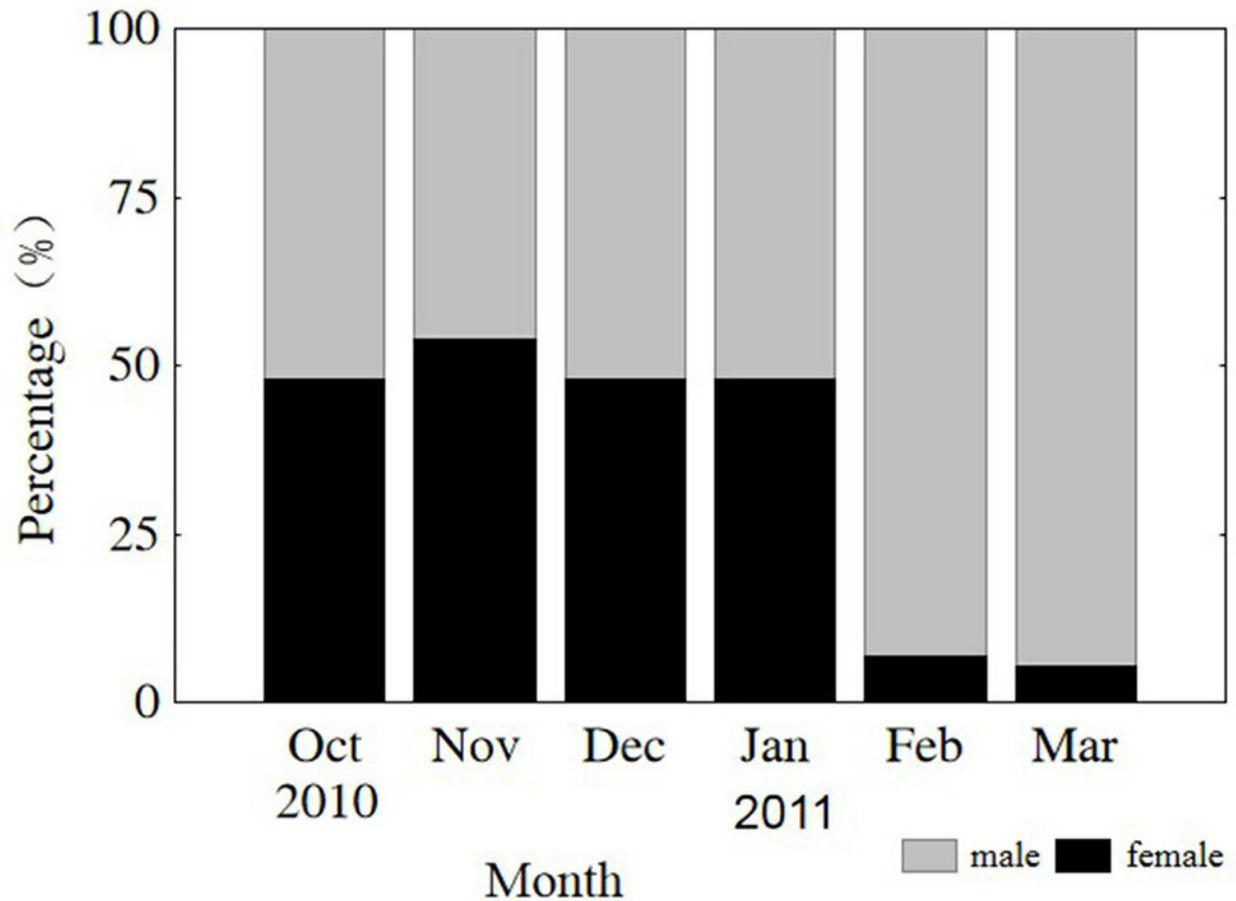



Figure 4

Percentage of *P. chinesis* at different ovarian maturity stages from early October through early March.

Gonad maturity stage: *white*, I; *crossed*, II; *vertical lines,* III; *horizontal lines,* IV; *diagonal lines,* V; *black*, VI. S, September; O, October; N, November; D, December; J, January; F, February; M, March.

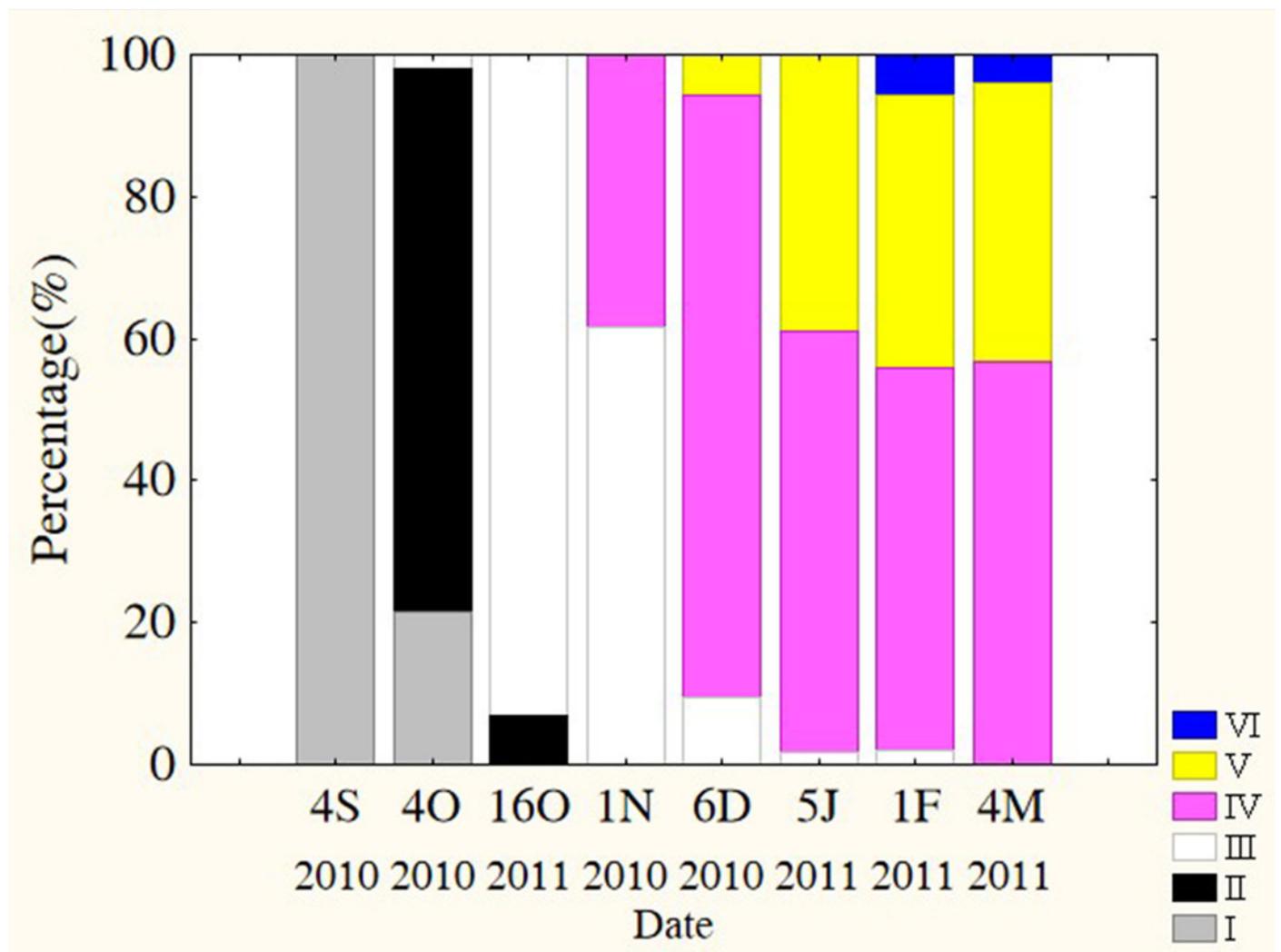



Figure 5

The asynchrony of oocytes development of *P.* chinensis.

Cross-section of ovary (a) and egg micrograph (b) of a fish in November (SL,145mm; BW,16.64g); cross-section of ovary (c) and egg micrograph (d) of a fish in January (SL,180mm; BW, 26.15g): (←) Phase II (Perinucleolar) oocyte; (↘) Phase III (Yolk vesicle) oocyte; (➡) Phase IV (Yolk) oocyte; (↑) Pre-vitellogenic (Phase II&III) oocyte; (↓) Phase V (migratory nucleus) oocyte. Scale bar = 1mm.

Figure 6

Proportion of pre-vitellogenic oocytes variation in relation to gonad development in December and January.

December (▲) and January (▢)

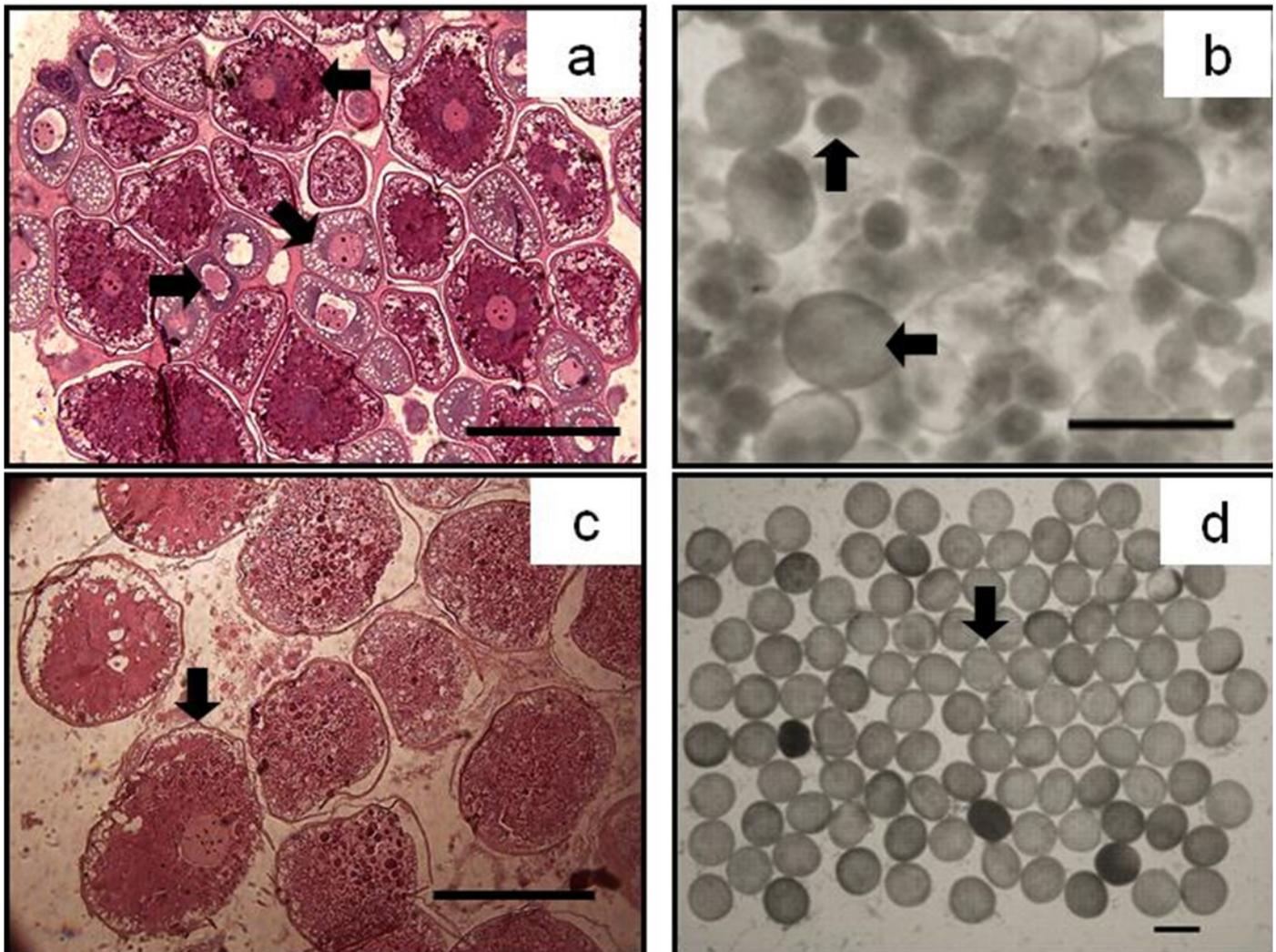



Figure 7

Percentage of *P. chinesis* females with different ovarian maturity stages in early November, December 2010 and January 2011 from the lower modal group (a, SL < 120 mm) and upper modal group (b, SL > 120 mm).

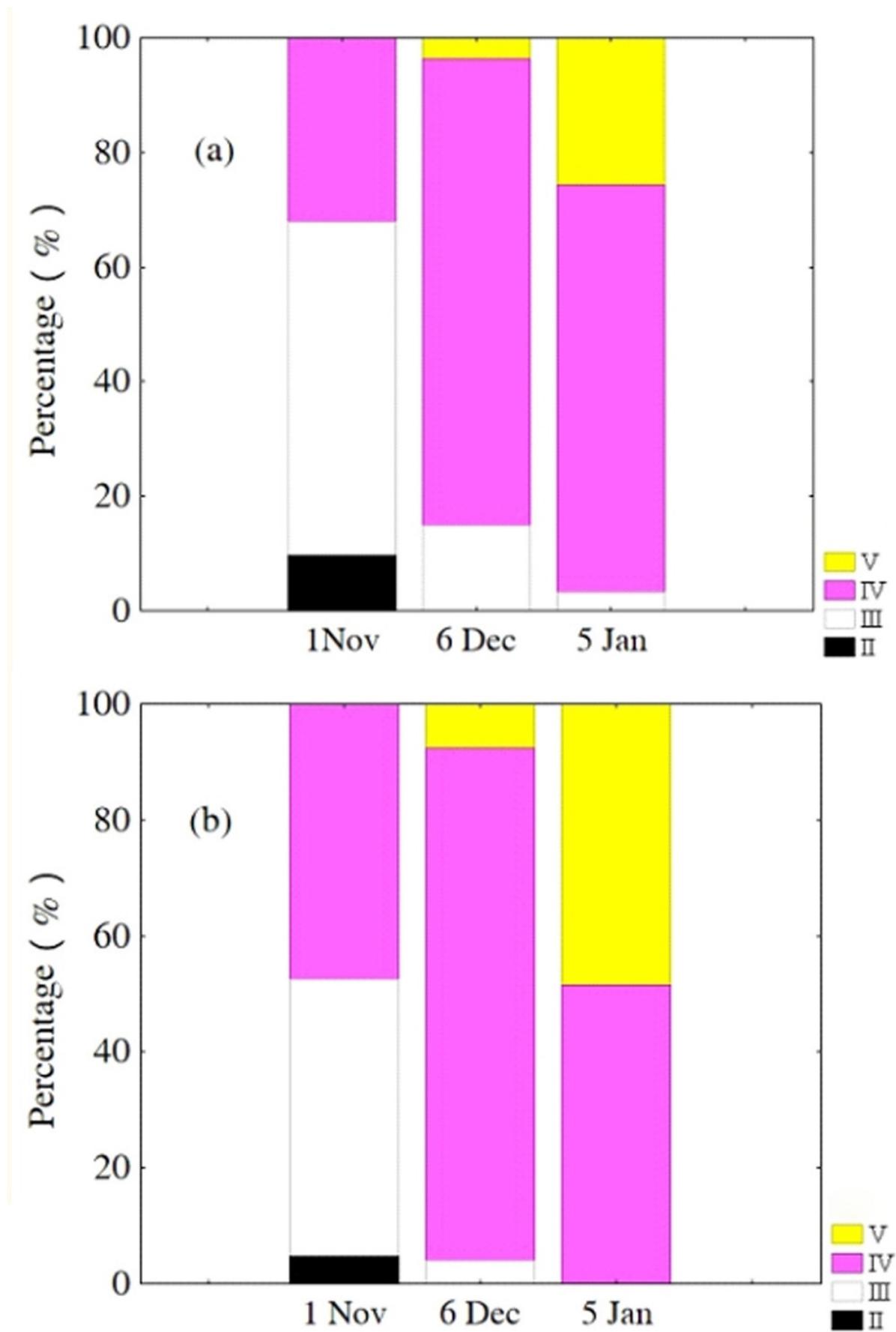



Figure 8

Intra-population variation in gonadosomatic index (GSI) in November 2010(a), December 2010(b) and January 2011(c).

SL = standard length.

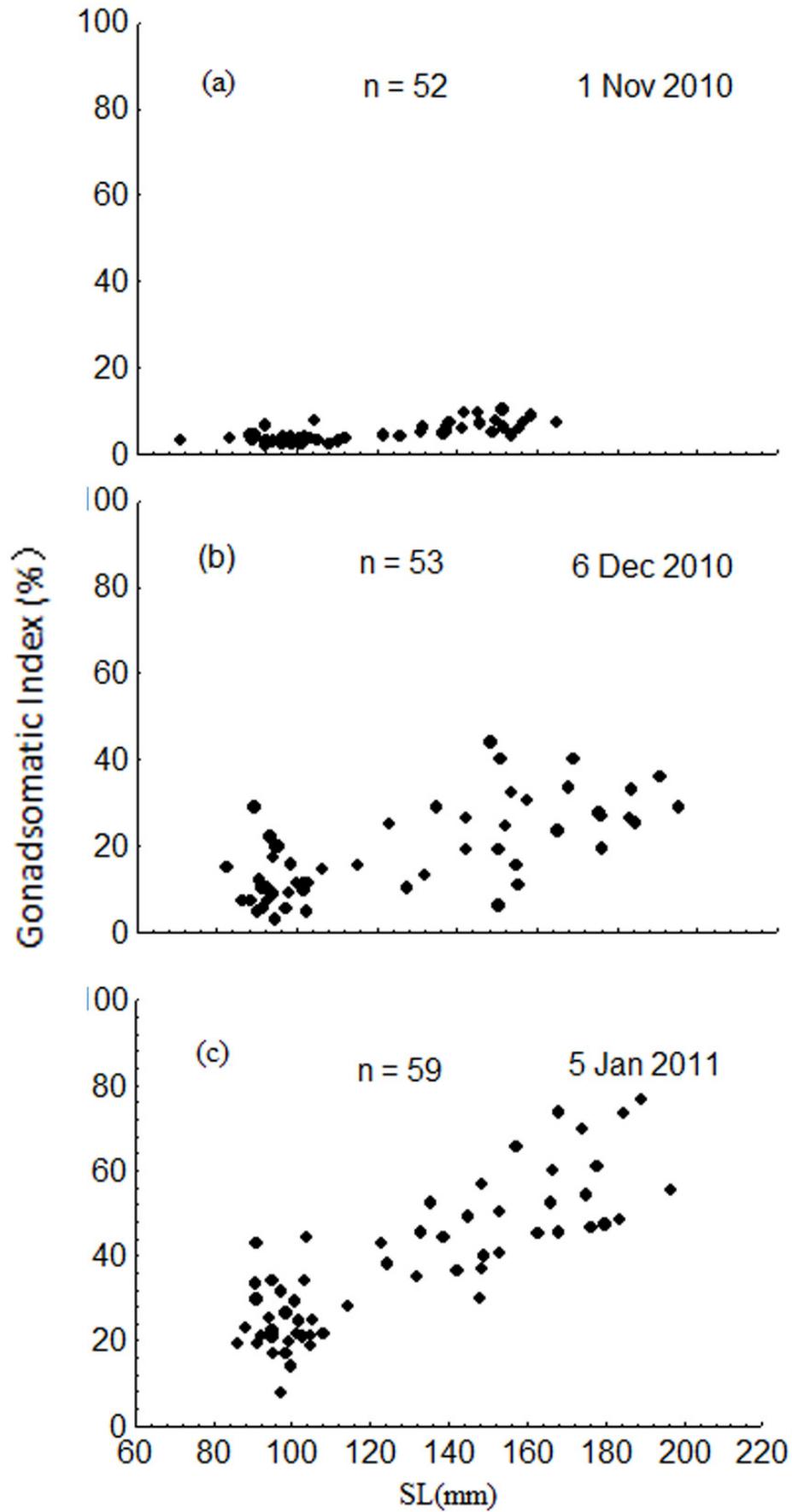
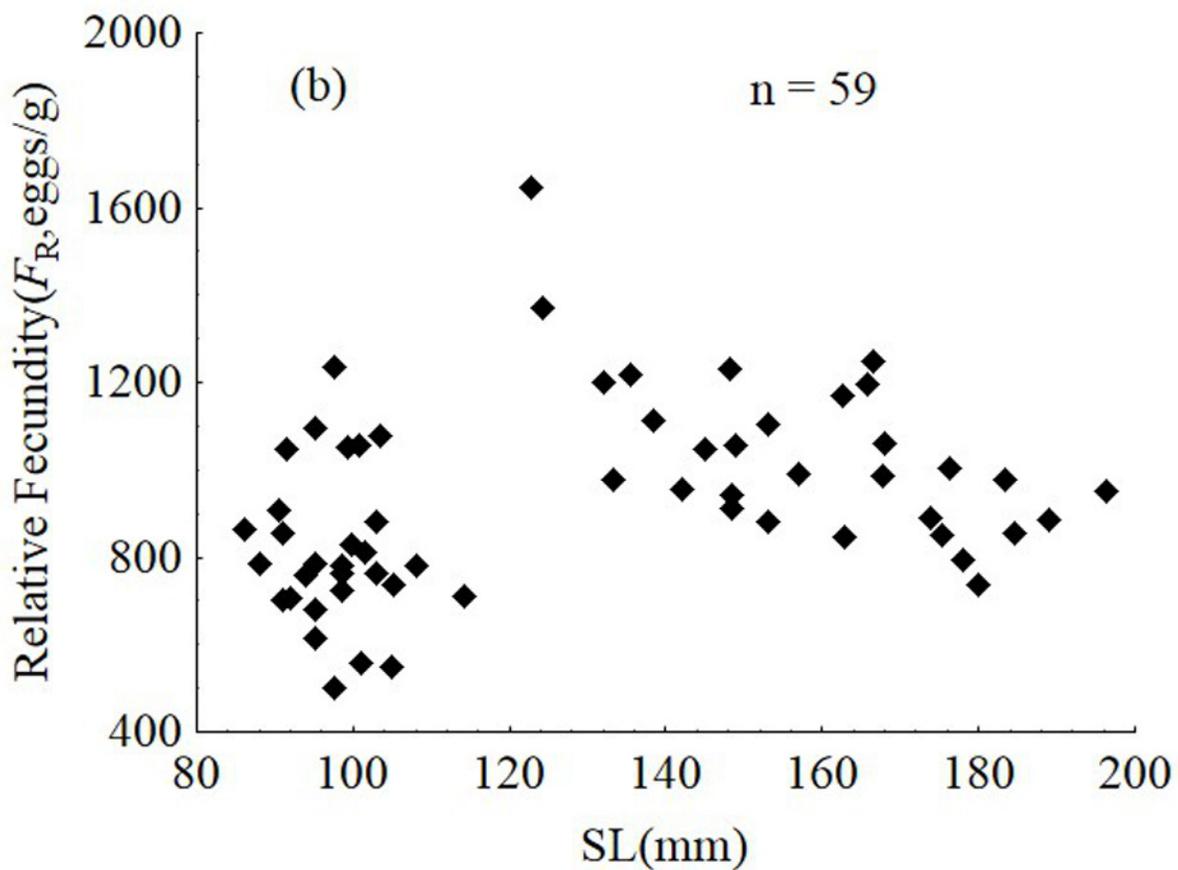
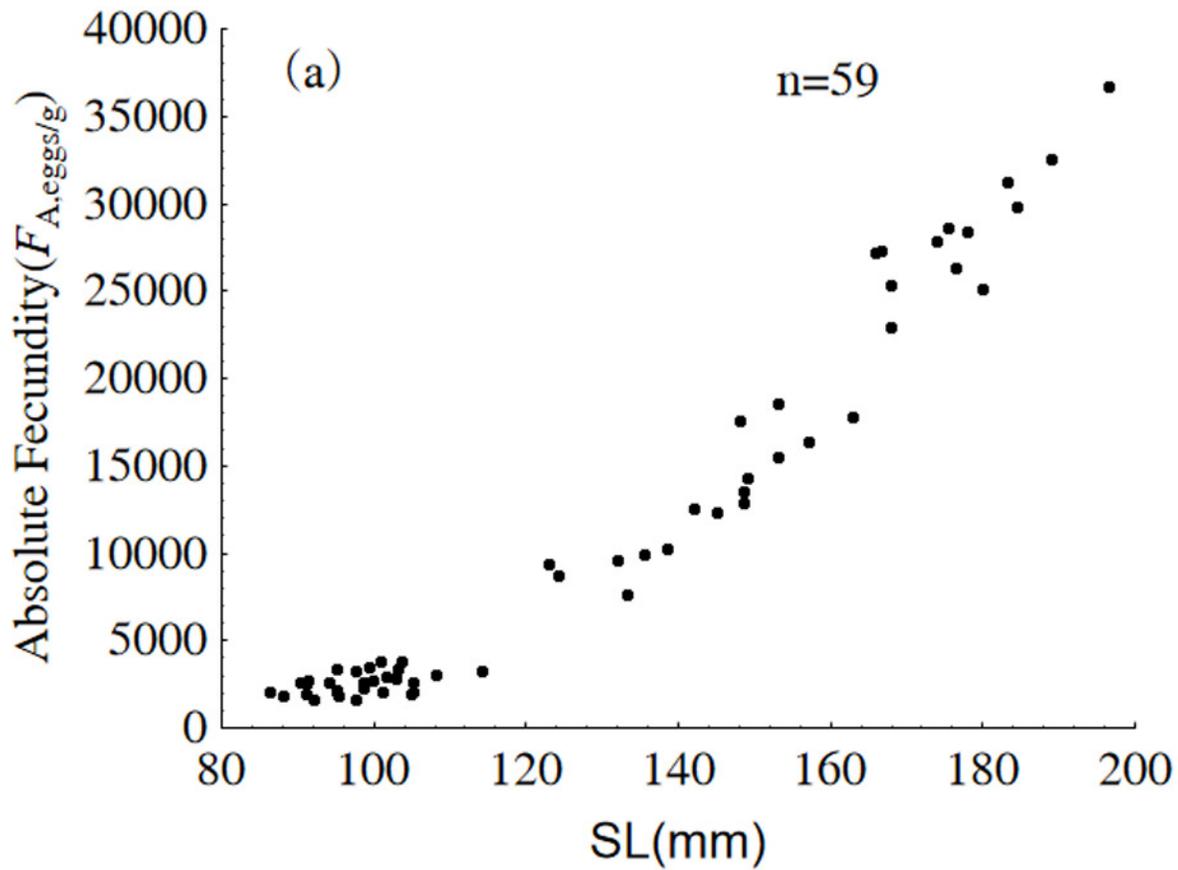



Figure 9

Absolute fecundity(a) and relative fecundity (b) of *P. chinesis* females sampled in January.

SL = standard length

Differences in mean standard lengths (SL) ± standard deviation (SD) between *P. chinensis* cannibals and prey.

Jul, July; Aug, August; Sep, September; Oct, October; Nov, November; Dec, December.

1   Placement of Table 1: Page 9

Month	N	SL of cannibals (mm)		SL of the prey (mm)		SL of the prey / SL of cannibals	
		Range	Mean (S.D.)	Range	Mean (S.D.)	Range	Mean (S.D.)
Jul	24	65-91	76±7.2	38-52	48±6.2	0.54-0.65	0.63±0.02
Aug	25	72-110	89±13.5	46-59	51±4.9	0.47-0.64	0.57±0.05
Sep	29	108-146	128±9.5	55-75	65±5.5	0.48-0.54	0.51±0.02
Oct	31	119-177	139±16.1	72-102	83±8.6	0.49-0.67	0.60±0.05[a]
Nov	27	122-189	147±15.7	71-115	88±10.2	0.51-0.65	0.60±0.03
Dec	35	123-196	153±16.7	82-117	93±9.6	0.50-0.70	0.61±0.04