1   **The Effects of Sex-biased Fisheries on Crustacean Sex Ratios and Reproductive Output**

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Abstract

Crustacean fisheries often preferentially or exclusively harvest males, resulting in selection that alters sex ratios in fished populations. Sex-biased fisheries may occur when males are larger and fisheries are size-selective, or when regulations limit or prohibit harvest of females to protect sufficient spawning stock to maintain the population. This review explores the evidence for fishery-induced alterations in sex ratios in crustacean fisheries and the resulting effects on reproductive output at the level of the individual and population. Crustacean fisheries exhibit substantial spatial and temporal variation in exploitation, which could lead to hotspots of altered sex ratios. Experimental manipulations simulating the effects of selective harvest indicate that altered sex ratios can lead to sperm limitation and reduction in the reproductive output of individual females. The effects of altered sex ratios on reproduction at the population scale remain poorly understood. Future directions for improving our understanding of the effects of altered sex ratios on reproductive output include focused studies on sperm limitation at high fishery exploitation rates, model simulations of population scale reproductive output that account for individual variation in sperm quantity, and detailed studies of sperm storage and use during fertilization.

Keywords: Sex Ratio, Selective Harvest, Sperm Limitation, Reproduction, Crustacea

Introduction

The global catch of crustacean fisheries is increasing despite a leveling-off of wild capture of all fishery species, highlighting a critical need to improve our understanding of the effects of crustacean fisheries on fished populations, species, and ecosystems to inform the transition to Ecosystem-Based Management (Crowder et al. 2008; Anderson et al. 2011; FAO 2018). Compared to other taxa such as forage fish, fisheries targeting crustacean populations can deplete their biomass at lower rates of exploitation, while having equivalent ecosystem effects due to biomass removal (Eddy et al. 2017). When declines in crustacean fisheries occur, recruitment overfishing is commonly implicated as a cause of decline (Jamieson 1993; Orensanz et al. 1998; Armstrong et al 1998; Miller et al. 2011), but other mechanisms also affect population dynamics including disease (Meyers et al. 1987; Wilhelm and Mialhe 1996; Lee and Frischer 2004; Frischer et al. 2018; Groner et al. 2018) and environmental variability (Shanks and Roegner 2007; Parada et al. 2010; Caputi and Brown 2011; Ogburn et al. 2012; Sanz et al. 2017). However, crustacean fisheries can also alter fished populations through other mechanisms such as changes in sex ratios.

Sex-biased harvest occurs in many crustacean fisheries, which can have follow-on effects on mating and reproductive output. In some fisheries, large males are more valuable than other segments of the population and are targeted by fishers (Millikin and Williams 1984; Sato 2012). In others, fishery regulations limit or prohibit the capture of females to protect the spawning stock (Jamieson et al. 1998; Miller et al. 2011). In either case, sex-bias results in population sex ratios that are skewed towards females (Jamieson et al. 1998; Miller et al. 2011; Sato 2012). In

53 rare cases, fisheries may selectively harvest females if there is sexual-segregation during

54 spawning migrations (e.g. Van Engel 1958). Shifts in the ratio of reproductively-capable males

55 and females at the time of mating, the operational sex ratio, can result in reductions in the

56 quantity of sperm transferred to females during mating that potentially reduces their reproductive

57 output (Smith and Jamieson 1991; Stevens et al. 1993; Lovrich et al. 1995; Carver et al. 2005;

58 Sato 2011; Ogburn et al. 2014; Pardo et al. 2015, 2017). At extremely biased sex ratios or in

59 species for which females preferentially mate with large males, females may have reduced

60 reproductive success because they are unable to find mates (Rowe and Hutchings 2003; Rains et

61 al. 2018). Selective harvest of large males may also result in micro-evolution towards smaller

62 size at maturity (Fenberg and Roy 2008). Although altered sex ratios related to sex-biased

63 fisheries have been observed for a variety of crustacean fisheries, the impacts on population-level

64 reproductive output remain poorly understood for many species (e.g. Ogburn et al. 2014; Rains

65 et al. 2016, 2018).

66

67 Sperm limitation, a condition in which females obtain insufficient sperm to fertilize their lifetime

68 potential brood production (Pennington 1985; Pitnick 1993), is a primary mechanism by which

69 altered sex ratios reduce reproductive effort. The details of sperm limitation likely differ

70 depending on the life history of individual species (Sato 2012). It may have a greater impact for

71 species with internal fertilization compared to broadcast spawners, and for species with short

72 mating seasons due to life history, behavior, or seasonal timing compared to species with

73 extended mating seasons with more opportunities for mating events (Waddy and Aiken 1986;

74 Sainte-Marie 1993). Species with long-term sperm storage without additional mating events

75 could be highly impacted, especially if they have multiple broods from a single mating event

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76 (Austin et al. 1975; Morgan et al. 1983; Paul and Paul 1992). Some mating behaviors may also

77 exacerbate sperm limitation, such as limited female mate choice combined with recently-mated

78 males remaining dominant mate-competitors (Kendall and Wolcott 1999; Sato and Goshima

79 2007a; Pardo et al. 2016). The goals of this paper are to explore sources of temporal and spatial

80 variation in size-selective fisheries, review experimental evidence supporting effects of size-

81 selective fisheries on crustacean mating systems, evaluate potential effects on reproductive

82 output, and identify future research needs to improve our understanding of the impacts of sex-

83 selective fisheries on crustacean populations.

84

85 **Variation in Fishery Exploitation**

86

87 Fishery exploitation varies in space and time, and understanding that variation is critical to

88 identifying hotspots of selective harvest where altered sex ratios and sperm limitation are most

89 likely to be found in wild populations. Synthesis of fisheries catch and effort data reveal global

90 and regional patterns of variation in fishery exploitation (Halpern et al. 2008; Watson et al. 2013;

91 Kroodsma et al. 2018; Belhabib et al. 2018). Variation in exploitation by crustacean fisheries at

92 regional scales can be substantial (Mullowney and Dawe 2009; Brehme et al. 2013;

93 Vasilakopoulos and Maravelia 2016; Bueno-Pardo et al. 2017). In Northeast Atlantic and

94 Mediterranean crustacean fisheries for example, exploitation rates for 63 stocks of six species

95 were below maximum sustainable yield (MSY) in northern areas compared with 2-4 times MSY

96 in southern areas despite management of all stocks under the European Commission Common

97 Fisheries Policy (Vasilakopoulos and Maravelia 2016). Within individual fisheries, fishing effort

98   and exploitation rate can vary at scales of a few to tens of km (Bonine et al. 2008; Turner et al.

99   2015), including due to sector-specific spatial patterns (Semmler 2016; Corrick 2018).

100

101   Temporal variation in fishery exploitation is also common due to mechanisms including seasonal

102   and interannual environmental variability, fishery regulations, and socioeconomic factors.

103   Seasonal variation in fishery exploitation can be particularly common at mid-high latitudes,

104   where patterns in exploitation can be driven by seasonal shifts in species distributions or

105   behaviors (Van Engel 1958; George and Nayak 1961; MacDiarmid 1991; Groeneveld and

106   Melville-Smith 1995; Robichaud and Campbell 1999; Stone et al. 1992; Stone and O'Clair

107   2001). For example, Robichaud and Campbell (1999) observed the highest trap catch of mature

108   lobsters *Homarus americanus* during summer in shallow waters of the Bay of Fundy, Canada,

109   likely associated with movement from deep to shallow water in spring for egg extrusion and

110   mating and a return to deeper areas in fall. Seasonal harvest is often mandated by fishery

111   regulations, including in fisheries for crabs (Miller 1976; Bunnell et al. 2010; Rasmuson 2013;

112   Kincaid and Rose 2014), shrimps (Watson et al. 1993), and mixed species, (Samy-Kamal et al.

113   2015). Environmental factors such as unfavorable weather conditions (Pet-Soede et al. 2001;

114   Sbrana et al. 2003; Bastardie et al. 2013) and seasonal occurrence of hypoxia (Purcell et al.

115   2017) can drive seasonal spatial patterns of fishing fleets. Multi-year shifts in target species

116   distribution also occur under warm or cold conditions or long-term climate change (Armstrong et

117   al. 2010; Parada et al. 2010), as observed for red king crab *Paralithodes camtschaticus* in Bristol

118   Bay, Alaska (Zacher et al. 2018). Finally, seasonal timing of exploitation can vary due to

119   economic or social drivers (Stephenson et al. 2018), such as concentration of fishing effort

120   targeting male blue crabs *Callinectes sapidus* in summer that yields localized exploitation rates

121   >50% per month (Semmler 2016) that coincides with the minimum operational sex ratio and

122   sperm quantity transferred during mating (Ogburn et al. 2014).

123

124   **Experimental Manipulation of Sex Ratios**

125

126   Experimental manipulation of mating events provides strong evidence suggesting that sex-biased

127   fisheries can cause sperm-limitation. Males often require days to months to recover the quantity

128   of sperm used in a single mating event (MacDiarmid and Butler 1999; Kendall et al. 2001; Sato

129   et al. 2005, 2006, 2010). For example, male spiny king crab *Paralithodes brevipes* had

130   significantly lower sperm stores 28 days after mating compared to unmated males, indicating that

131   they are unable to recover sperm stores between mating events within a mating season (Sato et

132   al. 2006). Males that mate more frequently than the recovery time can deplete the sperm stores

133   and transfer fewer sperm in subsequent mating events (Kendall and Wolcott 1999; MacDiarmid

134   and Butler 1999; Kendall et al. 2001, 2002; Hines et al. 2003; Sato et al. 2005, 2006, 2010; Sato

135   and Goshima 2006; Rubolini et al. 2007). Depletion of sperm from successive mating events

136   may be a particularly important mechanism of sperm limitation in species like the blue crab *C.*

137   *sapidus*, in which males use a large fraction of their sperm quantity and females obtain their

138   entire lifetime supply of sperm during a single mating event (Jivoff 1997a, 1997b).

139

140   The amount of sperm transferred during mating can also be regulated by a variety of other

141   factors related to reproductive biology and behavior. The quantity of sperm transferred can be

142   related to male size, female size, or the relative sizes of a mating pair (MacDiarmid and Butler

143   1999; Gosselin et al. 2003; Sato and Goshima 2006; Sato et al. 2006, 2010), although size and

144 sperm quantity are unrelated in others (e.g. Kendall et al. 2002). Females of some species are

145 only receptive for brief periods of a few days or less (Sato and Goshima 2006; Moyano et al.

146 2015), which can combine with male mate guarding behaviors to limit the opportunity for sperm

147 transfer (Rondeau and Sainte-Marie 2001; Kendall et al. 2001, 2002; Jivoff 2003). Males may

148 also exhibit plasticity in sperm allocation, reducing the amount of sperm transferred during each

149 mating event (the sperm economy hypothesis) as observed in snow crab *Chionoecetes opilio*

150 (Rondeau and Sainte-Marie 2001) and crayfish *Austropotamobius italicus* (Rubolini et al. 2006).

151 Other species such as the stone crab *Hepalogaster dentata* and marmola crab *Metacarcinus*

152 *edwardsii* do not exhibit sperm economy, instead increasing sperm transfer with increased mate

153 competition (Sato and Goshima 2007b, 2007c; Pardo et al. 2018). Experiments simulating the

154 effects of selective harvest by manipulating sex ratios or removing large males resulted in

155 reduced female reproductive success (fertilization rate and/or individual reproductive output)

156 (MacDiarmid and Butler 1999; Rondeau and Sainte-Marie 2001; Sato and Goshima 2006),

157 although few experiments have had a sufficient duration to evaluate consequences for

158 reproductive output.

159

160 **Reproductive Output**

161

162 The critical question for fishery managers is whether the sperm limitation due to altered sex

163 ratios observed in experimental settings translates into reductions in the reproductive output of

164 wild populations. For some fished species including snow crabs (Rondeau and Sainte-Marie

165 2001), king crabs (Sato et al. 2005, 2006, 2007), coconut crabs (Sato 2011), and lobsters

166 (MacDiarmid and Butler 1999), there appears to be little debate that some females could be

167   sperm-limited and that reproductive output may be diminished as a result. In contrast, there has

168   been substantial debate about whether sperm limitation reduces reproductive output at the

169   population level in other fisheries (Ogburn et al. 2014; Rains et al. 2016, 2018).

170

171   The blue crab *C. sapidus* in Chesapeake Bay provides a case study highlighting the difficulty of

172   evaluating the potential for population-scale sperm limitation. Mature female blue crabs mate

173   within one to several days following the molt to maturity and are not thought to molt or mate

174   again (Van Engel 1958). Sperm from the single mating period are stored for up to several years

175   and are used to fertilize multiple broods of eggs (Hines et al. 2003; Dickinson et al. 2006;

176   Darnell et al. 2009). Although the average female only survives for one spawning season, an

177   estimated 15% survive to a second spawning season (Miller et al. 2011). Large-male biased

178   fisheries result in altered sex ratios resulting in substantial variation in the quantity of sperm in

179   males (Carver et al. 2005), and that females receive during mating (Kendall et al. 2002; Hines et

180   al. 2003; Ogburn et al. 2014; Rains et al. 2016). Ogburn et al (2014) found that the quantity of

181   sperm females received declined at low operational sex ratios (the ratio of mature males to pre-

182   pubertal females) suggesting sperm limitation occurs in wild crabs, however Rains et al. (2016)

183   failed to observe a similar pattern in response to the sex ratio of adult crabs (note that sex ratio

184   was calculated differently in the two studies).

185

186   Simulation studies of reproductive output of Chesapeake Bay blue crabs have arrived at opposite

187   conclusions regarding population-scale sperm limitation. Ogburn et al. (2014) simulated the

188   lifetime reproductive output of individual female blue crabs at different levels of initial sperm

189   stores obtained during mating, rates of sperm decline during long-term storage, and sperm:egg

190   ratios during fertilization, finding that some individuals are likely sperm limited if they survive

191   to reproduce in a second spawning season. In contrast, Rains et al. (2018) used an individual-

192   based model to evaluate the effects of different selective fishing scenarios on operational sex

193   ratio and sperm quantity and found that simulated populations were only sperm limited when sex

194   ratios became so extreme that females were unable to find mates. Because unmated female blue

195   crabs are extremely rare in Chesapeake Bay (Hines et al. 2003; Ogburn et al. 2014; Rains et al.

196   2016), Rains et al. (2018) concluded that the population is not sperm limited. However, they

197   evaluated sperm limitation using the average number of sperm per female for the population, a

198   metric that is unlikely to detect sperm limitation if a relatively small portion of a population is

199   sperm limited.

200

201   A simple scenario illustrates the potential consequence of evaluating sperm limitation using

202   population average sperm quantity rather than individual reproductive output. Consider a

203   population of 10 female crabs that must receive 0.9 of the maximum amount of sperm during

204   mating (assigned a value of 1.0) to produce their full lifetime potential reproductive output. At a

205   low operational sex ratio, 2 of 10 crabs receive only 0.5 of the maximum load of sperm and the

206   other 8 receive the maximum (1.0). Calculating the population average sperm quantity yields a

207   value of 0.9, suggesting that there is no sperm limitation. However, two females only have

208   sufficient sperm to produce 55.6% of their lifetime reproductive output, clear sperm limitation if

209   they reach their full lifetimes. For the population as a whole, the sum of the reproductive output

210   of the individual females is 92.3% of the reproductive output calculated using the population

211   average. Thus, the effect of sperm limitation on population reproductive output may be difficult

212   to detect if population average sperm quantity is selected as a metric rather than the sum of

10

213   individual reproductive output. For the blue crab, additional detailed biological data like the

214   pattern and rate of sperm decline after mating, the number of sperm per egg used during

215   fertilization, and the minimum sperm:egg ratio required for successful fertilization are required

216   to accurately estimate whether reduced sperm stores lead to reductions in reproductive output

217   (Ogburn et al. 2014).

218

219   **Future Directions**

220

221   This review explored patterns in crustacean fisheries likely to concentrate fishing effort and

222   effects on sex ratios in space and time, experiments exploring mechanisms by which altered sex

223   ratios affect reproduction, and evidence that selective harvest affects population scale

224   reproductive output. The observed effects of selective (male-biased) harvest suggest a pattern

225   that the impact of altered sex ratios increases as female reproductive opportunity decreases, from

226   external fertilization to internal fertilization with a single brief period of receptivity (Table 1).

227   Further evaluation of the effects of sex-selective harvest on crustacean populations is a high

228   priority to increase fishery sustainability. In a review of the impacts of selective fisheries on

229   decapod crustacean populations, Sato (2012) suggested that a combination of management

230   actions (marine reserves, slot size limits, and maintenance of large individuals in good condition

231   after capture and release) should reduce selectivity for large individuals that can have the most

232   detrimental effects on populations. Evidence from the American lobster *H. americanus* suggests

233   that strict enforcement of such regulations may mitigate the effects of selective harvest, perhaps

234   even enhancing fishery production through increased population reproductive output (Comeau

235   and Hanson 2018). In order to understand whether such outcomes are possible in other fisheries,

236 several critical data gaps should be addressed in future studies on species subjected to selective

237 harvest.

238

239 • Identify hotspots of intensive fishery exploitation that could increase the likelihood of

240 altered operational sex ratios and sperm limitation and conduct field studies to determine

241 if females are receiving reduced sperm quantities (e.g. Pardo et al. 2017)

242 • Develop models of selective harvest scenarios and evaluate model results by scaling up

243 individual reproductive output

244 • Conduct experiments testing the sperm economy hypothesis in species managed by sex-

245 biased or male-only harvest controls

246 • Conduct longer term experiments to determine whether reductions in the amount of

247 sperm females receive during mating result in diminished reproductive output (e.g. Sato

248 and Goshima 2006)

249 • Determine the pattern and rate of decline of stored sperm following mating for species

250 with long term sperm storage

251 • Determine the number of sperm per egg used for fertilization and the minimum

252 sperm:egg ratio required

253

254 **Summary**

255

256 Size and sex selective fisheries alter sex ratios in some crustacean populations. Fishery

257 exploitation varies in space and time, indicating that studies on the impacts of selective fisheries

258 on sex ratios, and the sperm limitation and reductions in reproductive output that can result,

259   should account for this spatiotemporal variation. Manipulative experiments suggest the sperm

260   limitation is likely to occur in wild populations, however there are still few examples with clear

261   links between altered sex ratios, sperm limitation, and reduction in population reproductive

262   output. Future studies focused on identifying sperm limitation in wild populations, evaluating

263   consequences for reproductive output at the individual level, and improving our understanding of

264   processes occurring during sperm storage and fertilization are needed to improve our

265   understanding of the population level impacts of selective harvest strategies that alter sex ratios.

266

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Declaration of interest statement

In accordance with Taylor & Francis policy and my ethical obligation as a researcher, I am

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