Options for modulating intra-specific competition in colonial pinnipeds: the case of harbour seals (*Phoca vitulina*) in the Wadden Sea

Rory P Wilson, Nikolai Liebsch, Agustina Gomez-Laich, William P. Kay, Andrew Bone, Victoria J Hobson, Ursula Siebert

Colonial pinnipeds may be subject to substantial consumptive competition because they are large, slow-moving central place foragers. We examined possible mechanisms for reducing this competition by examining the diving behaviour of harbour seals (*Phoca vitulina*) after equipping 34 seals (11 females, 23 males) foraging from three locations; Rømø, Denmark and Lorenzenplate and Helgoland, Germany, in the Wadden Sea area with time-depth recorders. Analysis of 319,021 dives revealed little between-colony variation but appreciable inter-sex differences, with males diving deeper than females, but for shorter periods. Males also had higher vertical descent rates. This result suggests that males may have higher overall swim speeds, which would increase higher oxygen consumption, and may explain the shorter dive durations compared to females. Intersex variation in swim speed alone is predicted to lead to fundamental differences in the time use of three-dimensional space, which may help reduce consumptive competition in harbour seals and other colonial pinnipeds.

Options for modulating intra-specific competition in colonial pinnipeds: the case of harbour seals (*Phoca vitulina*) in the Wadden Sea

Rory P. Wilson[1,2], Nikolai Liebsch[3], Agustina Gómez-Laich[4], William P. Kay[1], Andrew Bone[1], Victoria J. Hobson[1], Ursula Siebert[5*]

[1]Swansea Laboratory for Animal Movement, Biosciences, College of Science, Swansea University, Singleton Park, Swansea, SA2 8PP, Wales, UK

[2]IFM-GEOMAR, Düsternbrooker , Weg 20, 24105 Kiel, Germany

[3]Customized Animal Tracking Solutions, 7 Marlua Ave, Moffat Beach, QLD 4551, Australia

[4]Centro Nacional Patagonico-CONICET, Boulevard Brown 2915, Puerto Madryn (U9120ACD), Chubut, Argentina

[5]Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine Hannover, Werftstr. 6, 25761 Büsum, Germany (corresponding author: ursula.siebert@tiho-hannover.de)

Abstract

Colonial pinnipeds may be subject to substantial consumptive competition because they are large, slow-moving central place foragers. We examined possible mechanisms for reducing this competition by examining the diving behaviour of harbour seals (*Phoca vitulina*) after equipping 34 seals (11 females, 23 males) foraging from three locations; Rømø, Denmark and Lorenzenplate and Helgoland, Germany, in the Wadden Sea area with time-depth recorders. Analysis of 319,021 dives revealed little between-colony variation but appreciable inter-sex differences, with males diving deeper than females,

25 but for shorter periods. Males also had higher vertical descent rates. This result suggests that males

26 may have higher overall swim speeds, which would increase higher oxygen consumption, and may

27 explain the shorter dive durations compared to females. Intersex variation in swim speed alone is

28 predicted to lead to fundamental differences in the time use of three-dimensional space, which may

29 help reduce consumptive competition in harbour seals and other colonial pinnipeds.

30

31 **Keywords**: dive behaviour, sexual segregation, pinniped, dive duration, swim speed, harbour seal

32

33 **Highlights**

34 ● Harbour seals foraging in the Wadden Sea area dived to mean maximum depths of less than 20 m.

35 ● Both sexes increased dive duration with depth but females dived proportionately longer.

36 ● Males had higher descent and ascent rates than females.

37 ● It is suggested that apparently higher swim speed in males may constrain dive duration.

38

1. Introduction

Competition is a major driver explaining patterns of space use in animals (MacArthur 1958, Pianka 2011) and it is considered particularly severe in central-place foraging (*sensu* Orians and Pearson 1979) and colonial breeders, such as seabirds or pinnipeds, because the density of animals around the breeding site leads to correspondingly high local pressure on resources (e.g. see Birt et al. 1987, Lewis et al. 2006, Gaston et al. 2007, Breed et al. 2013). There are a number of mechanisms proposed to reduce consumptive pressure in central-place foraging marine vertebrates. These relate primarily to different individuals taking either different types of prey (Forero et al. 2002, Ishikawa and Watanuki 2002, Garthe et al. 2007) or the same prey in different spaces (e.g. Wilson 2010). Both of these are fostered by differences in area use (Thompson et al. 1998), depths (Ishikawa and Watanuki 2002, Laich et al. 2012) and even the timing of foraging bouts (Harris et al. 2013). It has been noted though, that spatial and temporal segregation in resource use does not necessarily guarantee a reduction in competition (Wilson 2010).

Competition should be most apparent intra-specifically because individuals of many species are essentially morphologically and behaviourally identical. In addition, while inter-specific competition can theoretically lead to species extinction (Bengtsson 1989, Andersen et al. 2007), intra-specific (and particularly inter-gender) competition cannot. It is partly for this reason, therefore, that there is presumably strong selection pressure for central-place foraging, colonial species to exhibit sexual differences in foraging behaviour. In many marine, air-breathing, diving vertebrates these differences in foraging behaviour can be driven by size, because allometric effects modulate mass-specific metabolic rate (Kleiber 1932, Schmidt-Nielsen 1997), body oxygen stores (Halsey et al. 2006, Brischoux et al. 2008), fasting capacity (Lindstedt and Boyce 1985) and a suite of other performance-

63 related parameters (see Peters 1983). Unsurprisingly,, it is specifically the gender-related differences in

64 body mass that have been linked to sex-dependent differences in depth use in both seabirds, such as

65 Imperial cormorants (*Phalacrocorax atriceps*; Laich et al. 2012) and Galapagos cormorants

66 (*Phalacrocorax harrisi*; Wilson et al. 2008), and pinnipeds, such as Northern elephant seals (*Mirounga*

67 *angustirostris*: Le Boeuf et al. 2000) and New Zealand fur seals (*Arctocephalus forsteri*; Page et al.

68 2005). Indeed, sex-dependent difference in foraging is considered to be a major contribution to

69 minimizing the effects of competition, not least because bottom-foraging species distributing

70 themselves according to depth, also do so with regard to foraging area (e.g. Quintana et al. 2011).

71 However, not all colonial, central-place foraging diving vertebrates are sexually dimorphic, which

72 should mean, in terms of foraging at least, that there are no differential capacities with regard to depth

73 use, for example. How then, might niche partitioning be achieved?

74

75 We studied the foraging behaviour of the harbour seal (*Phoca vitulina*). This species is a ubiquitous,

76 slightly dimorphic species, with the male body mass being some 20% greater than the female

77 (Riedman 1990, Lindenfors et al. 2002), which forms large stable colonies in the Northern Hemisphere

78 (Ross et al. 2004). Specifically, we used animal-borne multiple channel loggers to determine if there

79 were any obvious gender-dependent differences. Given the very modest dimorphism between sexes

80 compared to many pinnipeds (Lindenfors et al. 2002), we hypothesized that there would be no inter-sex

81 difference in depth use but expected that there may be some evidence of differential foraging

82 behaviour.

83

84

85 **2. Materials and methods**

86

2.1 Location and devices

Between June 2004 and December 2006, 73 seals were equipped with tags at three well-established haul-out sites within the Wadden Sea and adjacent offshore areas; the Lorenzenplate (54.38°N, 8.53°E – hereafter 'LP'), Rømø (55.21°N, 8.50°E – hereafter 'DK') and Helgoland (54.19°N, 7.92°E – hereafter 'HE') (Fig. 1). The tags (140 g, 90 x 65 x 28 mm) were multiple channel loggers (Driesen and Kern GmbH, Bad Bramsted, Germany) recording dive depth, heading, body orientation, temperature and light, and capable of storing up to 32 megabytes of data in a flash RAM with 16 bit resolution at sampling intervals between 1 second and 24 hours (Liebsch 2006). We used a sampling interval of 5 seconds which nominally allowed a recording period of up to 94 days. The loggers were deployed in tandem with a quartz crystal-controlled timers (60 g, 75 x 37 x 20 mm), able to release the tags from the backs of the animals by burning through a nylon filament that held the main package, which consisted of the timer and the logger within a specially moulded, hydro-dynamically shaped flotation package (280 g, 210 x 90 x 65 mm) made of a 70:30 mix of resin and hollow beads (for details see Liebsch 2006), from a neoprene pocket stuck to the seal's back.

2.2 Seal capture

Helgoland seals, which are well accustomed to tourists, were approached and caught by hand, while animals on Lorenzenplate and Rømø were captured using seine netting techniques (Jeffries et al. 1993). The tagging did not cover any periods of lactation or breeding. Many more seals were captured than were tagged, and all animals, whether tagged or not, were given a veterinary examination to ensure that only healthy animals judged to be adults were tagged (permit number for animal experiments V312-72241.121-19 (70-6/07); Ministry of Energy, Agriculture, the Environment and Rural Areas

111 Schleswig-Holstein, Germany). Target seals were then strapped to a specifically designed bench to

112 assist with device attachment and to reduce handling stress. First, the device attachment site, which

113 was on the posterior two thirds of the dorsal midline (cf. Bannasch et al. 1994), was cleaned with

114 seawater to remove excess sand, and then cleaned and dried with acetone. The legs of the neoprene

115 pocket containing the tags (see above) were then glued to the animal using Devcon epoxy (Danvers,

116 USA). After release, the packages were either released from the seal by the timer or were shed during

117 the moult. Following device separation, most drifted ashore, intended for pick up by beach walkers,

118 who would return the package to the specified address.

119

120 2.3 Statistical analysis

121

122 All submersions deeper than 1 m were considered as dives. Dives were divided into two categories; 'U-

123 dives' or foraging dives, in which the bottom phase lasted more than 5 s (Schreer and Testa 1996), and

124 all other dives, which included 'V-dives' and 'parabolic' dives (see Le Boeuf et al. 1992, Sala et al.

125 2011 for definitions). Since, however, more than 94% of the dives were classified as U-dives, statistical

126 analyses were only performed on these submersions. For each U-dive, the following parameters were

127 calculated: maximum depth, total duration, bottom duration and the vertical velocity of each dive phase

128 (i.e. descent, bottom and ascent). Differences in these parameters between sites and sexes were tested

129 using linear mixed effects models (LMM) fitted by restricted maximum likelihood (REML). In these

130 models, diving characteristics were set as response variables and individual as a random effect. All

131 models were run using the R package nlme (Pinheiro et al. 2011). Differences in the vertical velocity

132 between diving phases were also tested using a mixed effect model. In this case, the vertical velocity

133 was set as a response variable, the dive phase as the predictor and the individual as a random factor.

134 Mixed effect models were also used to test the effect of maximum dive depth, sex and site on dive

duration. Finally, the effect of body parameters (i.e. weight and length) on the diving behaviour was analyzed using linear models whereby sex and site were also included as explanatory variables. All statistical analyses were performed using the open source statistical package R version 2.13.0 (R Development Core Team 2011). For those parameters with several measurements from individuals, mean values were obtained by calculating a mean over the means from each individual. These values are shown with their standard deviation.

3. Results

Of the 73 devices deployed, 55 were recovered (75%) of which 34 registered at least one complete foraging trip (the only results presented herein; Table 1) comprising a total of 301,778 U-dives (Supplementary Data 1). Males appeared to return more often without a full data set than females (Table 1), for reasons that are unclear.

3.1 Sexual segregation of foraging behaviour

3.1.1 *Depth utilisation*

During their U-dives, males went significantly deeper than females (LMM, Sex effect $F_{1,31}=4.4$, p=0.04) (Fig. 2a), with no differences in these depths between the three studied sites (LMM, Site effect $F_{1,31}=0.01$, p=0.9). Mean maximum dive depths were 17.5±2.5, 13.4±3.6 and 19±9 m for males, compared with 12.6, 13.4±3.4 and 8.8±3.5 m for females, from DK, LP and HE, respectively.

3.1.2 *Dive durations*

159   During dives, both sexes spent a similar amount of time underwater (LMM, Sex effect $F_{1,31}=2.4$,

160   p=0.1) (Fig. 2b) with no differences observed between the three locations (LMM, Site effect $F_{1,31}=0.07$,

161   p=0.8). Mean maximum dive durations were 174±34.6, 199±31 and 185±51 s for males and 213,

162   211±36.3 and 198±9.8 s for females, from DK, LP and HE, respectively. Deeper dives were

163   accompanied by longer durations, although the relationship between these parameters differed between

164   sexes (Fig. 3). During shallow dives, males and females spent a similar amount of time underwater,

165   however, as dives became deeper, females tended to remain longer underwater than males (LMM,

166   Depth effect $F_{1,301742}=65328$, p<0.001; Sex effect $F_{1,32}=9$, p=0.006; Sex*Depth effect $F_{1,301742}=1018$,

167   p<0.001)(y=3.3x+131 and y=4.5x+153 for males and females, respectively).

168

169   3.1.3 *Vertical velocities*

170   There was a significant difference in the rate of change of depth between dive phases as a whole

171   (LMM, Phase effect $F_{1,905298}=1664062$, p=0.006), with the general mean value for the bottom phase

172   being 0.005±0.003 m/s compared with 0.5±0.2 and 0.6±0.2 m/s for the descent and ascent rates,

173   respectively. Males descended and ascended the water column at higher rates than females (Sex effect

174   $F_{1,31}=8.0$, p=0.008; Sex effect $F_{1,31}=8.4$, p=0.006; for the descent and ascent phase, respectively) and

175   the same pattern was observed in the three studied sites (Site effect $F_{1,31}=0.7$, p=0.4; Site effect

176   $F_{1,31}=2.9$, p=0.09; for the descent and ascent phase, respectively). Mean male descent rates were

177   0.7±0.1, 0.6±0.1 and 0.7±0.2 m/s compared with 0.5, 0.6±0.1 and 0.4±0.1 m/s for the females, for DK,

178   LP and HE, respectively. The rate of change of depth during the bottom phase was similar between

179   sites (Site effect $F_{1,31}=0.1$, p=0.7) with values of 0.007±0.002, 0.003±0.003 and 0.007±0.003 m/s for

180   the males and 0.004, 0.003±0.003 and 0.003±0.001 for the females, for DK, LP and HE, respectively.

181

182   3.1.4 *Body weight and diving behaviour*

183   Mean masses of tagged males and females from the three different colonies were (males) 69.4±22

184   (n=5), 74.6±22.8 (n=8) and 70.2±13.1 (n=8) kg *vs* (females) 82.0 (n=1), 77.7±14.2 (n=6) and 99.5±2.1

185   (n=2) kg for animals from DK, LP and HE, respectively. Overall, there was no significant difference

186   between male and female body weight in our tagged animals (t = 1.8, df = 19, p = 0.091), males having

187   a mean weight of 71.7±18.5 kg compared to 83±14.7 kg for females. This result was in stark contrast to

188   patterns shown by all seals captured (most were not tagged) during the study. Here, of 377 animals

189   caught, males were significantly heavier than females (means of 70.5±17.7 kg *vs* 62.0±15.7 kg,

190   respectively; Mann-Whitney W = 19461, p < 0.01) although there was no specific separation into adult

191   and sub-adult animals undertaken (Supplementary data 2). Of the tagged animals, neither females nor

192   males showed a significant relationship between body weight and mean maximum dive depth (r^2 =

193   0.02, p = 0.5; Weight effect $F_{1,29}$=0.4, p=0.5; Sex effect $F_{1,28}$=2.1, p=0.2) (Fig. 4a). However, body

194   weight was strongly and positively related with mean dive duration with the relationship between both

195   parameters, being similar for both sexes (y=1.3x+100.7; r^2 = 0.4, p <0.01; Weight effect $F_{1,29}$=16.2,

196   p<0.001; Sex effect $F_{1,28}$=0.7, p=0.4) (Fig. 4b). For both sexes, a similar positive relationship was also

197   observed between the mean bottom duration and body weight (y=1.3x+55.9; r^2 = 0.5, p <0.001; Weight

198   effect $F_{1,29}$=23.9, p<0.001; Sex effect $F_{1,28}$=0.9, p=0.4) (Fig. 4c). Neither the descent or the ascent rate

199   (change in depth) was affected by body weight (Weight effect $F_{1,29}$=0.3, p=0.6; Sex effect $F_{1,28}$=4.2,

200   p=0.05; Weight effect $F_{1,29}$=0.2, p=0.6; Sex effect $F_{1,28}$=4.3, p=0.05; for the descent and ascent phases

201   respectively). The rate of change of depth during the bottom phase decreased with increasing body

202   weight but this relationship was only significant for males (y=-8.9.10^{-5}x+1.2.10^{-2}, r^2 = 0.3, p=0.03;

203   Weight effect $F_{1,28}$=5.1, p=0.03; Sex effect $F_{1,29}$=8.8, p=0.006) (Fig . 4d)

204

205   3.1.5 *Body length*

206 Mean length of tagged males and females from the three different colonies were (males) 161.2±19.4

207 (n=5), 166±21.4 (n=8) and 158±9.5 (n=8) kg *vs* (females) 156 (n=1), 160±11.7 (n=6) and 166±16.3

208 (n=2) kg for animals from DK, LP and HE, respectively. As with weight, there was no significant

209 difference between male and female body length in the tagged animals (t = -0.2, df = 22, p = 0.9),

210 males having a mean body length of 1.62±0.17 m compared to 1.61±0.11 m for females. Again, this

211 contrasted with the full capture data (377 animals) where males were significantly longer than females

212 (1.62±0.13 m *vs* 1.56±0.11 m; Mann-Whitney W = 20369, p < 0.01). As with body weight, there was

213 no relationship between body length and mean maximum dive depth for either of the sexes in the

214 tagged animals (r^2 <0.01, p = 0.9; Length effect $F_{1,29}$=0.03, p=0.8; Sex effect $F_{1,28}$=2.5, p=0.1) (Fig.

215 5a). However, a positive relationship was observed between body length and mean dive duration for

216 both sexes (y=1.3x-6.1, r^2=0.3, p=0.005; Length effect $F_{1,29}$=9.3, p=0.005; Sex effect $F_{1,28}$=3.9, p=0.06)

217 (Fig. 5b). A strong positive relationship between mean bottom duration and body length was only

218 found for the males (y=1.5x-93.4, r^2=0.5, p<0.001; Length effect $F_{1,29}$=13.2, p=0.001; Sex effect

219 $F_{1,28}$=5.4, p=0.03) (Fig. 5c). Neither sex showed a relationship between body length and the rate of

220 change in depth during the descent phase (Length effect $F_{1,28}$=0, p=0.9; Sex effect $F_{1,29}$=4.1, p=0.05),

221 the bottom phase (Length effect $F_{1,28}$=3.2, p=0.08; Sex effect $F_{1,29}$=8.8, p=0.006) or the ascent phase

222 (Length effect $F_{1,28}$=0.01, p=0.9; Sex effect $F_{1,29}$=4.3, p=0.05).

223

224

225   **4.   Discussion**

226

227 This study seemed to have a systematic bias in the age distributions of the captured animals that may

228 serve to confound patterns. It is well documented that mature male harbour seals are somewhat longer

229 and heavier than mature females (Lindenfors et al. 2002) and our larger sample of captured animals

230   showed this trend clearly, even though the animals that we selected for tagging showed no significant

231   differences. We suggest that this result was due to the limited sample size with high variation and

232   likely some unintended bias in selection of animals for tagging. As reported earlier, we ensured that

233   only healthy animals were tagged following an extensive veterinary examination so the bias may have

234   come from this too, especially if smaller males were in better condition than larger males. Regardless

235   of how this bias arose, tagged males were likely to have been younger animals than the tagged females,

236   and thus any differences in diving behaviour are unlikely to be driven by allometry effects (Schreer and

237   Kovacs 1997, Thompson et al. 1998). Non-equivalence in age groupings of the two genders makes our

238   intersex comparison less than ideal, particularly if some of our animals were, unintentionally, sub-

239   adults. We have no objective way of assessing this *post-hoc*. However, given the fact that all

240   individuals within one area have the potential to compete, any differences between males and females

241   in our findings might, nonetheless, point to mechanisms that reduce competition. In this regard, it is

242   interesting to note that grey seals (*Halichoerus grypus*) begin to exhibit sex-related differences in

243   diving even when young and essentially monomorphic, even though the sexes are dimorphic as adults

244   (Breed et al. 2011, cf. Breed et al. 2013).

245

246   Our hypothesis, that there would be no intersex differences in depth use in harbour seals, was not borne

247   out by the data because, despite there being no significant differences between the tagged sexes in

248   either body length or mass, males dived deeper than females (Fig. 2a). The generally accepted

249   phenomenon that larger species can dive deeper (Schreer and Kovacs 1997, Thompson et al. 1998)

250   stems from the observation that larger species can also stay submerged for longer (Schreer and Kovacs

251   1997, Irvine et al. 2000), and thus have more time to reach greater depths (Halsey et al. 2006). These

252   depth- and duration-linked allometric trends have been explained by decreasing mass-specific

253   metabolic rate with increasing mass (Butler and Jones 1982, Halsey et al. 2006) coupled with linearly

254 increasing body oxygen stores with mass (Brischoux et al. 2008). In short, while the mass-specific

255 amount of oxygen available for dives remains the same, smaller species use it faster, and so cannot

256 remain underwater as long (Halsey et al. 2006). But here too, our results seem at odds with convention

257 because there were significant differences in dive durations between male and female harbour seals,

258 with females staying longer underwater (Fig. 2b), despite the fact that they reached shallower depths

259 (Fig. 2a). Interestingly, all these patterns were apparent even though both male and female animals

260 adhered to conventional allometric theory (see above) by generally diving longer if they were more

261 massive (Figs 4 & 5).

262

263 All other things being equal, the explanation for the intersex differences could, however, stem from a

264 differential rate of energy expenditure underwater linked to differing activities so that oxygen stores

265 were used at differential rates. In fact, the rate of change of depth data indicate a mechanism by which

266 this mechanism could have occurred. Although absolute swim speed was not measured, the vertical

267 velocities during the descent and ascent phases of the dive (which were derived from adjacent depth

268 readings divided by the sampling interval) were significantly higher, by some 34%, in male than in

269 female seals. If dive angles were the same, this finding implies that the males were actually swimming

270 faster, and having to use more power to do so.

271

272 In order to speculate on the potential effect of this explanation, we assume, in a first iteration, that both

273 sexes have an approximate 'normal swim speed' of about 1.4 m/s (Williams and Kooyman 1985). By

274 then using an approximate gender-common descent rate of 0.585 m/s (the mean of all values across

275 sites and sexes), we can derive a descent angle of approximately 24.7˚. These values allow us to

276 compute the proper sex-specific descent rates to re-assess putative sex-specific swim speeds as 1.60

277 and 1.20 m/s for males and females, respectively (noting that this process simply translates a difference

in vertical descent rate of 34% into an absolute swim speed difference of 34%). Williams and

Kooyman (1985) calculated that the drag force of harbour seals was related to swim speed via the

following equation:

Drag = 6.49 Speed$^{1.79}$ (Equation 1)

where drag is given in Newtons and speed in metres per second. Thus, males and females would

experience drags of 15.05 and 8.99 N, respectively, at their calculated swim speeds. Gas respirometric

studies examining the relationship between swim speed and power in harbour seals, give this as:

Rate of oxygen consumption = 4.6 + 3.1 Speed$^{1.42}$ (Equation 2)

where the rate of oxygen consumption is given in ml/kg/min (Davies et al. 1985). Thus, these gender-

specific derived speeds translate into metabolic powers of about 3.56 and 2.89 W/kg for males and

females, respectively (assuming that 1 ml oxygen equates to 20.1 J; Schmidt-Nielsen 1997). These

calculations give a difference of some 23% between the sexes, which equates well with the 36%

difference in the best-fit gradients in the relationship between dive duration and dive depth for the two

sexes (Fig. 3 – see results or regression equations). If our calculations are approximately correct, they

are unsurprising because maximum dive depth modulates energy expenditure by integrating both time

(and therefore energy) for the commuting period between the water surface and the preferred foraging

depth as well as increasing bottom time (and therefore energy) with increasing depth. Critically,

increases in both commuting (vertical) distance during the transition phases between surface and

foraging depth and bottom distance with increasing depth (see Mori 2002 and references therein) will

301 implicate higher energy expenditure at higher speeds (see above), leading to an overall reduction in

302 dive duration, as we observed in our data.

303

304 The observations made above assume that both males and females dive at approximately the same

305 angle, and that swimming speeds calculated for the descent are also applied during the extensive

306 bottom phase. Variation in either of these two parameters will alter predictions accordingly.

307 Irrespective of the extent to which swim speed genuinely varies between male and female harbour

308 seals, it is clear that speed is an important variable needed in discussions of niche partitioning, both

309 inter- and intra-specifically, most particularly because the power required to swim underwater

310 increases approximately as a cube of the swim speed (e.g. Boyd et al. 1995, Culik et al. 1996, Bethge et

311 al. 1997). Higher swim speeds may take one gender away from minimum costs of transport, reducing

312 dive duration, as observed here. At the same time, higher speeds would tend to take the faster gender

313 (males) rapidly into more distant regions which should help to mitigate competition. Certainly,

314 consideration of swim speed alone may help explain why, irrespective of body mass, in some cases it is

315 the males that dive deeper and longer (Baechler et al. 2002, Staniland and Robinson 2010), while in

316 other cases it is the females that do this (Beck et al. 2003a, b, c). This suggestion may also explain

317 inter-gender differences in foraging location (e.g. Breed et al. 2006). Thus, if our assumptions

318 regarding our harbour seal data are correct, we would predict that males from our study colonies range

319 farther than the females and that, given the gentle increase in depth with distance from the colonies,

320 which may help explain inter-sex differential depth use and dive durations, and ultimately be a

321 mechanism by which this species minimizes consumptive competition.

322

323   **4.   Conclusions**

324   Although harbour seal populations in northern Europe are not currently so large that severe

325   consumptive competition might be expected, the habit of forming colonies, along with historically

326   large population as baselines, implies that selection pressure should play some role in selecting for

327   inter-gender behavioural or morphological differences to reduce competition. Our results showing

328   increasing dive duration with dive depth are in line with many other pinniped studies but our

329   observation that females have higher depth-specific dive durations than males requires an explanation.

330   Although there were differences between males and females in our untagged population, our animals

331   sampled for tagging had no gender-linked differences in body mass or length, both factors which are

332   often linked to dive capacity. Interestingly, we noted higher vertical speeds in our tagged males which,

333   if representative of swimming speeds overall, should equate to higher metabolic rates and consequently

334   shortened dive durations. Differential travel speeds should affect a suite of features, such as ability to

335   detect prey and changing dive:pause ratios, which translate into differential foraging ecology. Although

336   speculative, we suggest that this phenomenon requires further investigation since it could prove an

337   important mechanism for minimizing competition in harbour seals and other colonial pinnipeds

338

339

References

Andersen SM, Teilmann J, Harders PB, Hansen EH, Hjøllund D (2007) Diet of harbour seals and great cormorants in Limfjord, Denmark: interspecific competition and interaction with fishery. ICES Journal of Marine Science: Journal du Conseil 64:1235-1245.

Baechler J, Beck CA, Bowen WD (2002) Dive shapes reveal temporal changes in the foraging behaviour of different age and sex classes of harbour seals (*Phoca vitulina*). Fisheries Bethesda 1577:1569-1577.

Bannasch R, Wilson RP, Culik B (1994) Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. Journal of Experimental Biology 194:83-96

Beck CA, Bowen WD, Iverson SJ (2003a) Sex differences in the seasonal patterns of energy storage and expenditure in a phocid seal. Journal of Animal Ecology 72:280-291

Beck CA, Bowen WD, McMillan JI, Iverson SJ (2003b) Sex differences in diving at multiple temporal scales in a size-dimorphic capital breeder. Journal of Animal Ecology 72:979-993

Beck CA, Bowen WD, Mcmillan JI, Iverson SJ (2003c) Sex differences in the diving behaviour of a size-dimorphic capital breeder: the grey seal. Animal Behaviour 66:777-789

366   Bengtsson J (1989) Interspecific competition increases local extinction rate in a metapopulation
367   system. Nature 340:713-715

368   Bethge P, Nicol S, Culik BM, Wilson RP (1997) Diving behaviour and energetics in breeding little
369   penguins (*Eudyptula minor*). Journal of Zoology London 242:483-502

370   Birt VL, Birt TP, Goulet D, Cairns DK, Montevecchi WA (1987) Ashmole's halo: Direct evidence for
371   prey depletion by a seabird. Marine Ecology Progress Series 40:205-208

372   Boyd IL, Woakes AJ, Butler PJ, Davis RW, Williams TM (1995) Validation of heart rate and doubly
373   labelled water as measures of metabolic arte during swimming in Californian Sea Lions.
374   Functional Ecology 9:151-160.

375   Breed GA, Bowen WD, McMillan JI Leonard ML (2006) Sexual segregation of seasonal foraging
376   habitats in a non-migratory marine mammal. Proceedings of the Royal Society B 273:2319-2326

377   Breed GA, Bowen WD, Leonard ML (2011) Development of foraging strategies with age in a long-
378   lived marine predator. Marine Ecology Progress Series 431:267-279

379   Breed GA, Bowen WD, Leonard ML (2013) Behavioral signature of intraspecific competition and
380   density dependence in colony-breeding marine predators. Ecology and Evolution 3:3838-3854

381   Brischoux F, Bonnet X, Cook TR, Shine R (2008) Allometry of diving capacities: ectothermy vs.
382   endothermy. Journal of Evolutionary Biology 21:324-329

383   Butler PJ, Jones DR (1982) The comparative physiology of diving. Advances in Comparative
384   Physiology and Biochemistry 8:179-364

385   Culik BM, Pütz K, Wilson RP, Allers D, Lage J, Bost CA, Le Maho Y (1996) Diving energetics in
386   king penguins (*Aptenodytes patagonicus*). Journal of Experimental Biology 199:973-983.

387   Davis RW, Williams TM, Kooyman GL (1985) Swimming metabolism of yearling and adult harbor
388   seals *Phoca vitulina*. Physiological Zoology 58:590-596

389   Forero MG, Hobson KA, Bortolotti GR, Donázar JA, Bertellotti M, Blanco G (2002) Food resource
390   utilisation by Magellanic penguins evaluated through stable isotope analysis: segregation by sex
391   and age and influence of offspring quality. Marine Ecology Progress Series 234:289-299

392   Garthe S, Montevecchi WA, Chapdelaine G, Rail JF, Hedd A (2007) Contrasting foraging tactics by
393   northern gannets (*Sula bassana*) breeding in different oceanographic domains with different prey
394   fields. Marine Biology 151:687-694

395   Gaston AJ, Ydenberg RC, Smith GEJ (2007) Ashmole's halo and population regulation in seabirds.
396   Marine Ornithology 35:119-126

397   Halsey LG, Butler PJ, Blackburn TM (2006) A phylogenetic analysis of the allometry of diving. The
398   American Naturalist 167:276-287

399   Harris S, Rey AR, Phillips RA, Quintana F (2013) Sexual segregation in timing of foraging by imperial
400   shags (*Phalacrocorax atriceps*): is it always ladies first? Marine Biology 160:1249-1258

401   Irvine JG, Hindell MA, Hoff J, Burton HR (2000) The influence of body size on dive duration of
402   underyearling southern elephant seals (*Mirounga leonina)*. Journal of Zoology 251:463-471

403   Ishikawa K, Watanuki Y (2002) Sex and individual differences in foraging behavior of Japanese
404   cormorants in years of different prey availability. Journal of Ethology 20:49-54

405   Jeffries SJ, Brown RF, Harvey JT (1993) Techniques for capturing, handling and marking harbour
406   seals. Aquatic Mammals 19:21-25

407 Kleiber M (1932) Body size and metabolism. Hilgardia 6:315-353

408 Laich AG, Quintana F, Shepard ELC, Wilson RP (2012). Intersexual differences in the diving
409   behaviour of Imperial Cormorants. Journal of Ornithology 153:139-147

410 Le Boeuf BJ, Crocker DE, Costa DP, Blackwell CB, Webb PM, Houser DS (2000) Foraging Ecology
411   of Northern Elephant Seals. Ecological Monographs 70:353-382

412 Le Boeuf BJ, Naito Y, Asaga T, Crocker DE (1992) Swim speed in a female northern elephant seal:
413   metabolic rate and foraging implications. Canadian Journal of Zoology 70:786-795

414 Lewis R, O'Connell TC, Lewis M, Campagna C, Hoelzel AR (2006) Sex-specific foraging strategies
415   and resource partitioning in the southern elephant seal (*Mirounga leonina*). Proceedings of the
416   Royal Society B 273:2901-2907

417 Liebsch NS (2006) Hankering back to ancestral pasts: constraints on two pinnipeds, *Phoca vitulina* and
418   *Leptonychotes weddellii* foraging from a central place. PhD Thesis, Mathematisch-
419   Naturwissenschaftliche Fakultät der Christian-Albrechts-Universität zu Kiel 161 pp

420 Lindenfors PL, Tullberg BS, Biuw M (2002) Phylogenetic analyses of sexual selection and sexual size
421   dimorphism in pinnipeds. Behavioural Ecology and Sociobiology 52:188-193.

422 Lindstedt SL, Boyce MS (1985) Seasonality, fasting endurance, and body size in mammals. The
423   American Naturalist 125:873-878

424 MacArthur RH (1958) Population ecology of some warblers of northeastern coniferous forests.
425   Ecology 39:599-619

426 Mori Y (2002) Optimal diving behaviour for foraging in relation to body size. Journal of Evolutionary
427   Biology 15:269-276

428   Orians GH, Pearson, NE (1979) On the theory of central place foraging. Analysis of ecological

429   systems. Ohio State University Press, Columbus.

430   Page B, McKenzie J, Goldsworthy SD (2005) Inter-sexual differences in New Zealand fur seal diving

431   behaviour. Marine Ecology Progress Series 304:249-264

432   Peters RH (1983) The Ecological Implications of Body Size. Cambridge University Press, Cambridge.

433   Pianka ER (2011) Evolutionary Ecology. eBook.

434   Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2011) nlme: Linear   and

435   Nonlinear Mixed Effects Models. R package, version 2.13.0.

436   Quintana F, Wilson RP, Dell'Arciprete P, Shepard ELC, Gomez-Laich A (2011) Women from Venus,

437   men from Mars: Intersex foraging differences in the Imperial Cormorant *Phalacrocorax atriceps*

438   a colonial seabird. Oikos 120: 350-358.

439   R Development Core Team (2011). R: A language and environment for statistical computing.   R

440   Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL

441   http://www.R-project.org/.

442   Riedman M (1990) The Pinnipeds: Seals, Sea Lions and Walruses, University of California Press.

443   Ross PS, Jeffries SJ, Yunker MB, Addison RF, Ikonomou MG, Calambokidis JC (2004) Harbor seals

444   (*Phoca vitulina*) in British Columbia, Canada, and Washington State, USA, reveal a combination

445   of local and global polychlorinated biphenyl, dioxin, and furan signals. Environmental

446   Toxicology and Chemistry 23:157-165

447   Sala JE, Quintana F, Wilson RP, Dignani J, Lewis MN, Campagna C (2011) Pitching a new angle on

448   elephant seal dive patterns. Polar Biology 34:1197-1209

449   Schmidt-Nielsen K (1997) Animal physiology: adaptation and environment. Cambridge University

450   Press

451   Schreer JF and Kovacs KM (1997) Allometry of diving capacity in air-breathing vertebrates. Canadian

452   Journal of Zoology 75:339-358

453   Schreer JF, Testa JW (1996) Classification of weddell seal diving behaviour. Marine Mammal Science

454   12:227-250

455   Staniland IJ, Robinson SL (2010) Segregation between the sexes: Antarctic fur seals, *Arctocephalus*

456   *gazella*, foraging at South Georgia. Animal Behaviour 75:1581-1590

457   Thompson P, Mackay A, Tollit DJ, Enderby S, Hammond PS (1998) The influence of body size and

458   sex on the characteristics of harbour seal foraging trips. Canadian Journal of Zoology 76:1044-

459   1053

460   Williams TM, Kooyman GL (1985) Swimming performance and hydrodynamic characteristics of

461   harbour seals *Phoca vitulina*. Physiological Zoology 58:576-589

462   Wilson RP, Vargas FH, Steinfurth A, Riordan P, Ropert-Coudert Y, Macdonald DW (2008) What

463   grounds some birds for life? Movement and diving in the sexually dimorphic Galapagos

464   cormorant. Ecological Monographs 78:633-652

465   Wilson RP (2010) Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid

466   penguins. Functional Ecology 24:646-657

467

468   Figure captions.

469

470   Figure 1. Location of the three seal capture locations; Rømø (DK), Lorenzenplate (LP) and Helgoland

471   (HE). The shading of the sea area corresponds to 10 m depth intervals and the continuous black lines

472   show the boarder of the Wadden Sea National Parks of Schleswig-Holstein and Lower Saxony.

473   Figure 2. Frequency distribution of (a) the maximum depth (b) and dive duration of U-dives performed

474   by female (black bars) and male (grey bars) harbour seals.

475   Figure 3. Relationship between dive duration and maximum dive depth of female (black points) and

476   male (grey points) harbour seals. The lines (black for females and grey for males) represent the fitted

477   relationship. The points represent the mean dive duration for 2.5 m interval while the whiskers

478   represent the standard deviation.

479   Figure 4. Relationship between (a) mean maximum dive depth (b) mean dive duration (c) mean bottom

480   duration and (d) mean bottom speed as a function of body mass of female and male harbour seals. For

481   those cases where the relationship between sexes differed, female and male points and the fitted line

482   are shown in black and grey, respectively.

483   Figure 5. Relationship between (a) mean maximum dive depth (b) mean dive duration and (c) mean

484   bottom duration as a function of body length of female and male harbour seals. For those cases where

485   the relationship between sexes differed, female and male points and the fitted line are shown in black

486   and grey, respectively.

487

488

1

Location of seal captures

Location of the three seal capture locations; Rømø (DK), Lorenzenplate (LP) and Helgoland (HE). The shading of the sea area corresponds to 10 m depth intervals and the continuous black lines show the boarder of the Wadden Sea National Parks of Schleswig-Holstein and Lower Saxony.
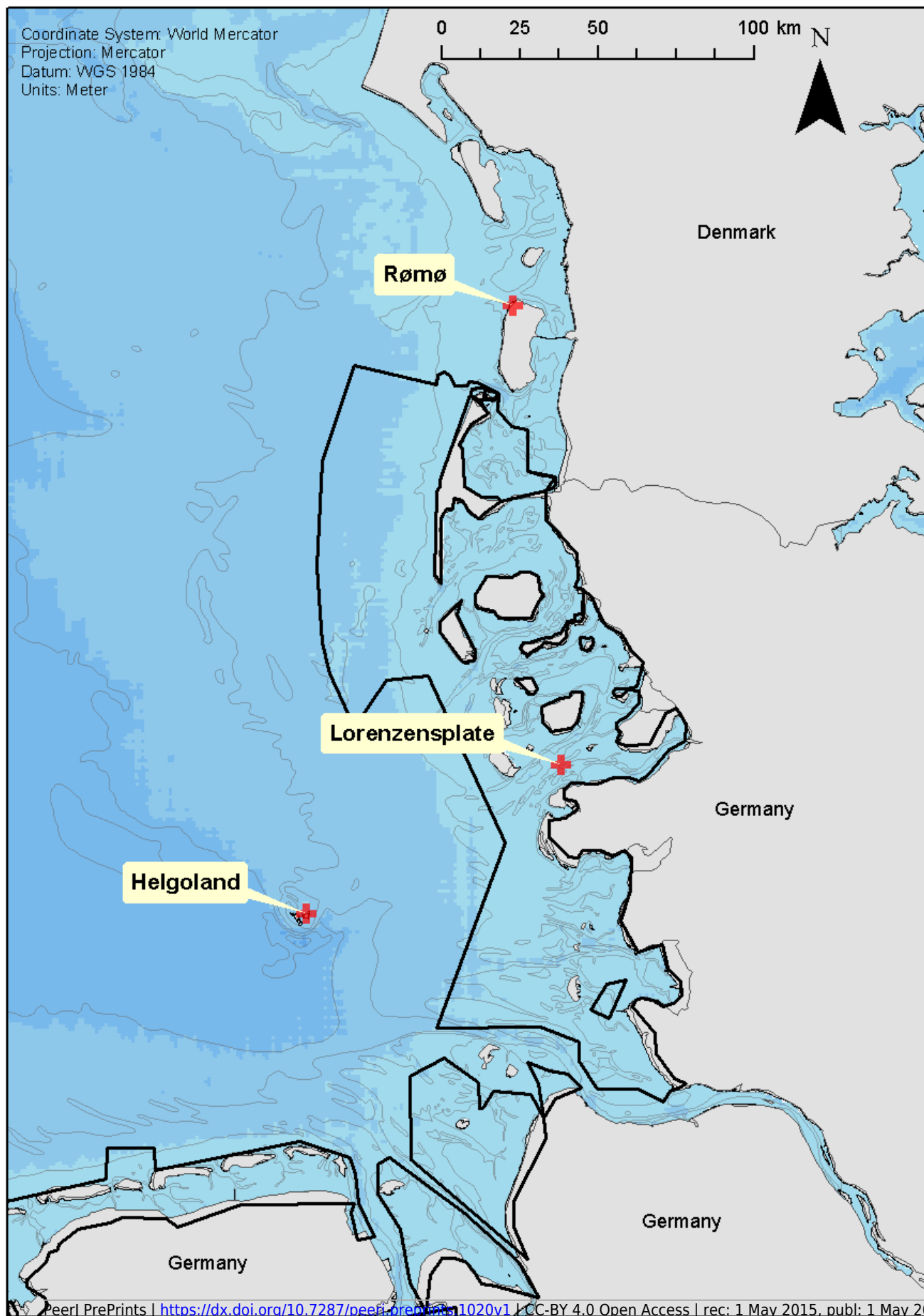
Table 1(on next page)

Number of devices deployed and recovered from harbour seals with usable data (containing data from at least one full foraging trip) from the three study sites

Table 1. Number of devices deployed and recovered from harbour seals with usable data (containing data from at least one full foraging trip) from the three study sites.

Location	Sex	No. equipped	No. recovered	No. with data
Lorenzenplatte	male	18	14	8
	female	12	9	7
Rømø	male	24	15	7
	female	1	1	1
Helgoland	male	15	13	8
	female	3	3	3
TOTAL		**73**	**55**	**34**

2

Frequency distribution of the maximum depth and dive duration of U-dives

Frequency distribution of (a) the maximum depth (b) and dive duration of U-dives performed by female (black bars) and male (grey bars) harbour seals

3
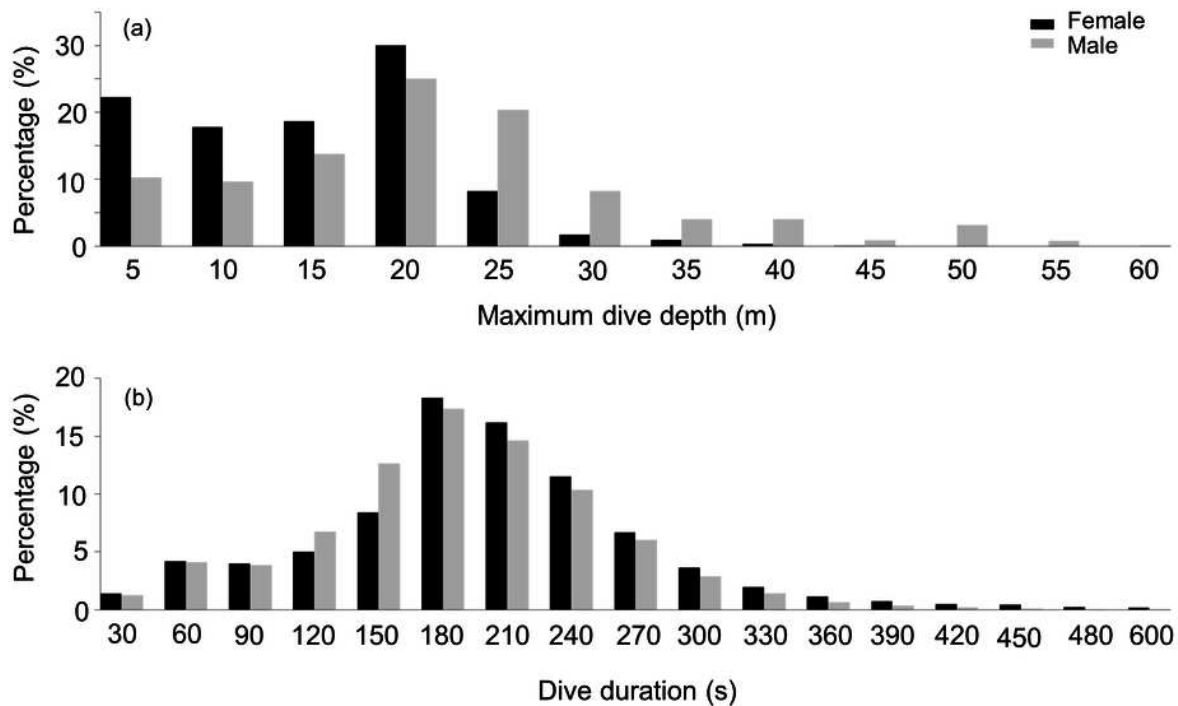
Relationship between dive duration and maximum dive depth of female and male harbour seals.
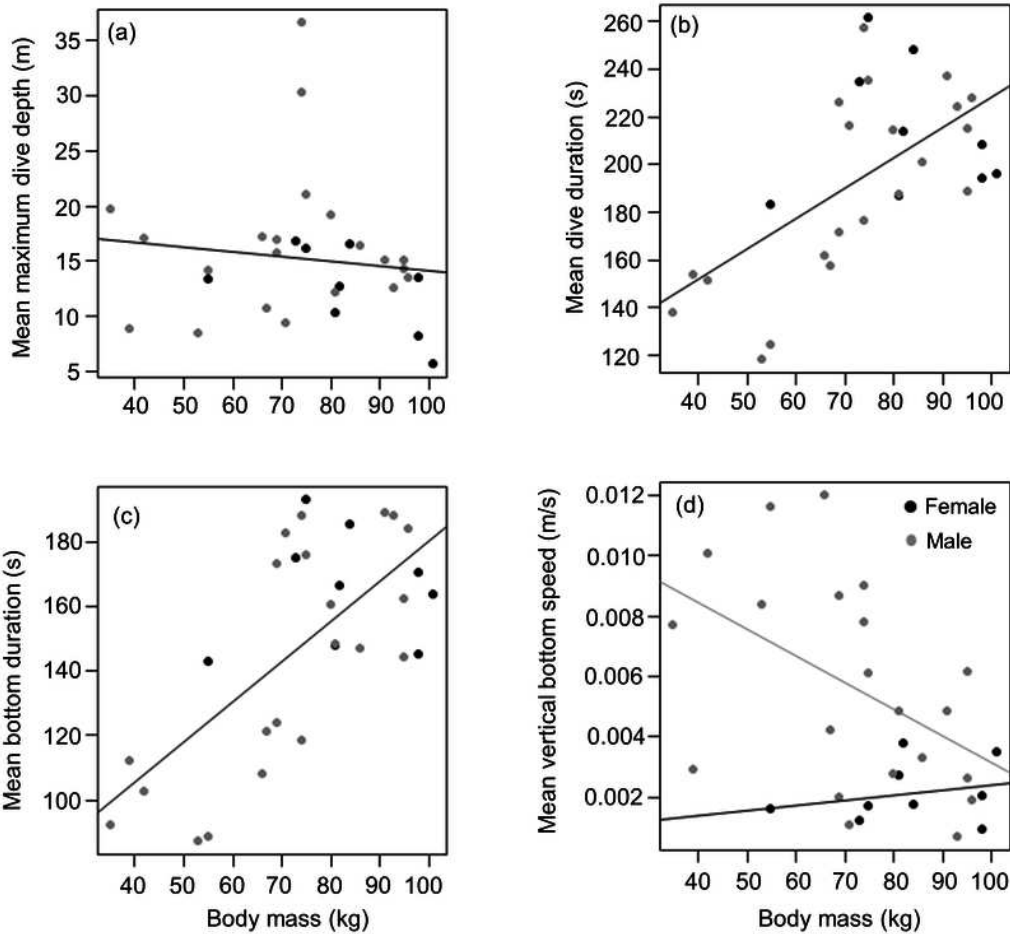
Relationship between dive duration and maximum dive depth of female (black points) and male (grey points) harbour seals. The lines (black for females and grey for males) represent the fitted relationship. The points represent the mean dive duration for 2.5 m interval while the whiskers represent the standard deviation.

4
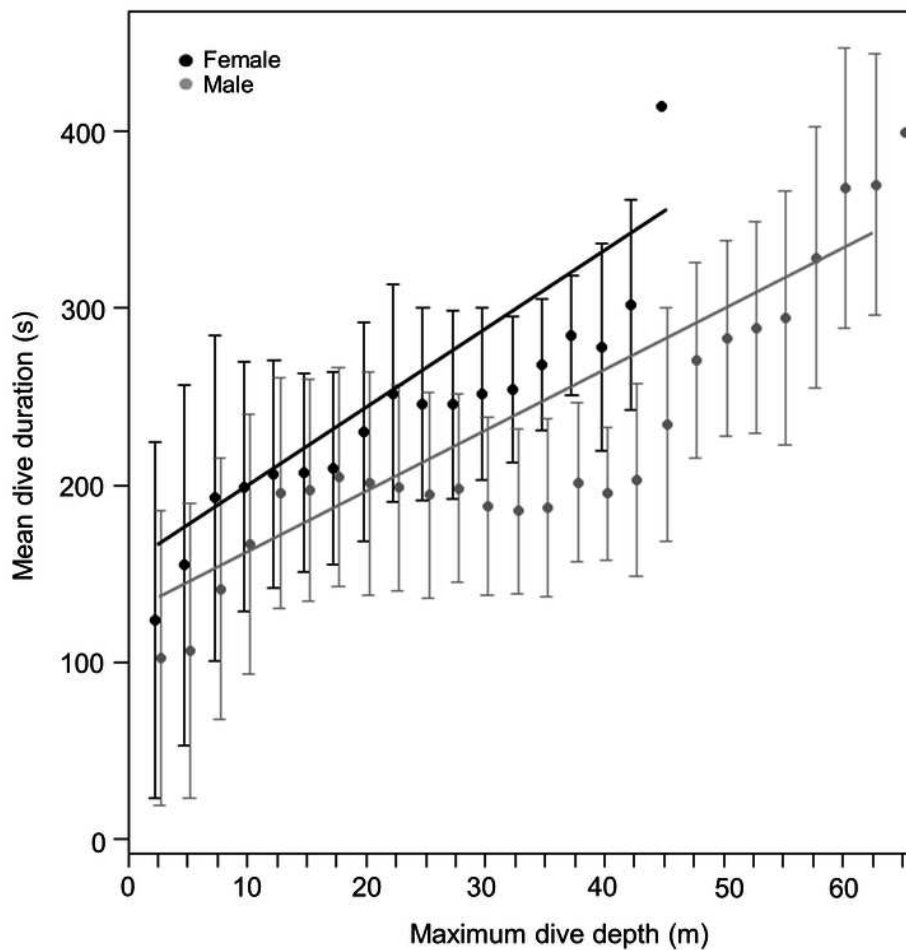
Relationship between mean maximum dive depth, mean dive duration, mean bottom duration and mean bottom speed as a function of body mass of female and male harbour seals.

Relationship between (a) mean maximum dive depth (b) mean dive duration (c) mean bottom duration and (d) mean bottom speed as a function of body mass of female and male harbour seals. For those cases where the relationship between sexes differed, female and male points and the fitted line are shown in black and grey, respectively

5

Relationship between mean maximum dive depth, mean dive duration and mean bottom duration as a function of body length of female and male harbour seals.

Relationship between (a) mean maximum dive depth (b) mean dive duration and (c) mean bottom duration as a function of body length of female and male harbour seals. For those cases where the relationship between sexes differed, female and male points and the fitted line are shown in black and grey, respectively