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

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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.

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

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16  
17 **Abstract**

18  
19 Colonial pinnipeds may be subject to substantial consumptive competition because they are large,  
20 slow-moving central place foragers. We examined possible mechanisms for reducing this competition  
21 by examining the diving behaviour of harbour seals (*Phoca vitulina*) after equipping 34 seals (11  
22 females, 23 males) foraging from three locations; Rømø, Denmark and Lorenzenplate and Helgoland,  
23 Germany, in the Wadden Sea area with time-depth recorders. Analysis of 319,021 dives revealed little  
24 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

39 **1. Introduction**

40

41 Competition is a major driver explaining patterns of space use in animals (MacArthur 1958, Pianka  
42 2011) and it is considered particularly severe in central-place foraging (*sensu* Orians and Pearson  
43 1979) and colonial breeders, such as seabirds or pinnipeds, because the density of animals around the  
44 breeding site leads to correspondingly high local pressure on resources (e.g. see Birt et al. 1987, Lewis  
45 et al. 2006, Gaston et al. 2007, Breed et al. 2013). There are a number of mechanisms proposed to  
46 reduce consumptive pressure in central-place foraging marine vertebrates. These relate primarily to  
47 different individuals taking either different types of prey (Forero et al. 2002, Ishikawa and Watanuki  
48 2002, Garthe et al. 2007) or the same prey in different spaces (e.g. Wilson 2010). Both of these are  
49 fostered by differences in area use (Thompson et al. 1998), depths (Ishikawa and Watanuki 2002,  
50 Laich et al. 2012) and even the timing of foraging bouts (Harris et al. 2013). It has been noted though,  
51 that spatial and temporal segregation in resource use does not necessarily guarantee a reduction in  
52 competition (Wilson 2010).

53

54 Competition should be most apparent intra-specifically because individuals of many species are  
55 essentially morphologically and behaviourally identical. In addition, while inter-specific competition  
56 can theoretically lead to species extinction (Bengtsson 1989, Andersen et al. 2007), intra-specific (and  
57 particularly inter-gender) competition cannot. It is partly for this reason, therefore, that there is  
58 presumably strong selection pressure for central-place foraging, colonial species to exhibit sexual  
59 differences in foraging behaviour. In many marine, air-breathing, diving vertebrates these differences  
60 in foraging behaviour can be driven by size, because allometric effects modulate mass-specific  
61 metabolic rate (Kleiber 1932, Schmidt-Nielson 1997), body oxygen stores (Halsey et al. 2006,  
62 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

## 87 2.1 Location and devices

88

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

102

## 103 2.2 Seal capture

104

105 Helgoland seals, which are well accustomed to tourists, were approached and caught by hand, while  
106 animals on Lorenzenplate and Rømø were captured using seine netting techniques (Jeffries et al. 1993).  
107 The tagging did not cover any periods of lactation or breeding. Many more seals were captured than  
108 were tagged, and all animals, whether tagged or not, were given a veterinary examination to ensure that  
109 only healthy animals judged to be adults were tagged (permit number for animal experiments V312-  
110 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.

### 120 2.3 Statistical analysis

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



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

### 143 3. Results

144  
145 Of the 73 devices deployed, 55 were recovered (75%) of which 34 registered at least one complete  
146 foraging trip (the only results presented herein; Table 1) comprising a total of 301,778 U-dives  
147 (Supplementary Data 1). Males appeared to return more often without a full data set than females  
148 (Table 1), for reasons that are unclear.

#### 150 3.1 Sexual segregation of foraging behaviour

##### 152 3.1.1 *Depth utilisation*

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

##### 158 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  $174\pm34.6$ ,  $199\pm31$  and  $185\pm51$  s for males and 213,  
162  $211\pm36.3$  and  $198\pm9.8$  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  $0.005\pm0.003$  m/s compared with  $0.5\pm0.2$  and  $0.6\pm0.2$  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  $0.7\pm0.1$ ,  $0.6\pm0.1$  and  $0.7\pm0.2$  m/s compared with  $0.5$ ,  $0.6\pm0.1$  and  $0.4\pm0.1$  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  $0.007\pm0.002$ ,  $0.003\pm0.003$  and  $0.007\pm0.003$  m/s for  
180 the males and  $0.004$ ,  $0.003\pm0.003$  and  $0.003\pm0.001$  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  $F_{1,29}=4.3$ ,  $p=0.05$ ).

#### 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

278 in vertical descent rate of 34% into an absolute swim speed difference of 34%). Williams and  
279 Kooyman (1985) calculated that the drag force of harbour seals was related to swim speed via the  
280 following equation:

281

$$282 \text{ Drag} = 6.49 \text{ Speed}^{1.79} \quad (\text{Equation 1})$$

283

284 where drag is given in Newtons and speed in metres per second. Thus, males and females would  
285 experience drags of 15.05 and 8.99 N, respectively, at their calculated swim speeds. Gas respirometric  
286 studies examining the relationship between swim speed and power in harbour seals, give this as:

287

$$288 \text{ Rate of oxygen consumption} = 4.6 + 3.1 \text{ Speed}^{1.42} \quad (\text{Equation 2})$$

289

290 where the rate of oxygen consumption is given in ml/kg/min (Davies et al. 1985). Thus, these gender-  
291 specific derived speeds translate into metabolic powers of about 3.56 and 2.89 W/kg for males and  
292 females, respectively (assuming that 1 ml oxygen equates to 20.1 J; Schmidt-Nielsen 1997). These  
293 calculations give a difference of some 23% between the sexes, which equates well with the 36%  
294 difference in the best-fit gradients in the relationship between dive duration and dive depth for the two  
295 sexes (Fig. 3 – see results or regression equations). If our calculations are approximately correct, they  
296 are unsurprising because maximum dive depth modulates energy expenditure by integrating both time  
297 (and therefore energy) for the commuting period between the water surface and the preferred foraging  
298 depth as well as increasing bottom time (and therefore energy) with increasing depth. Critically,  
299 increases in both commuting (vertical) distance during the transition phases between surface and  
300 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

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348

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- 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

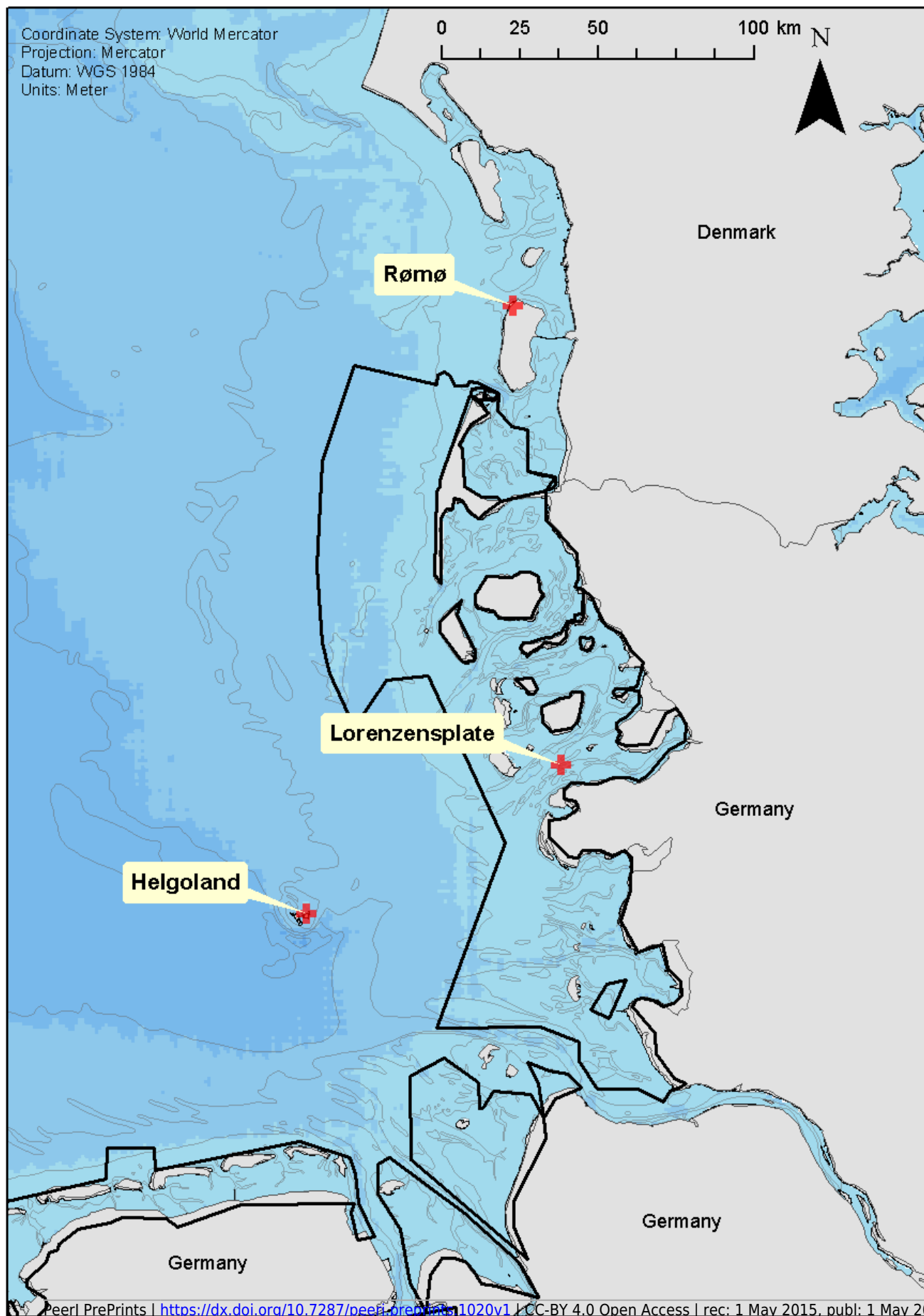
488



# 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

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

4

5 **Location**                      **Sex**    **No. equipped**    **No. recovered**    **No. with data**

6 Lorenzenplatte                      male                      18                      14                      8

7    female                      12                      9                      7

8 Rømø                                      male                      24                      15                      7

9    female                      1                      1                      1

10 Helgoland                              male                      15                      13                      8

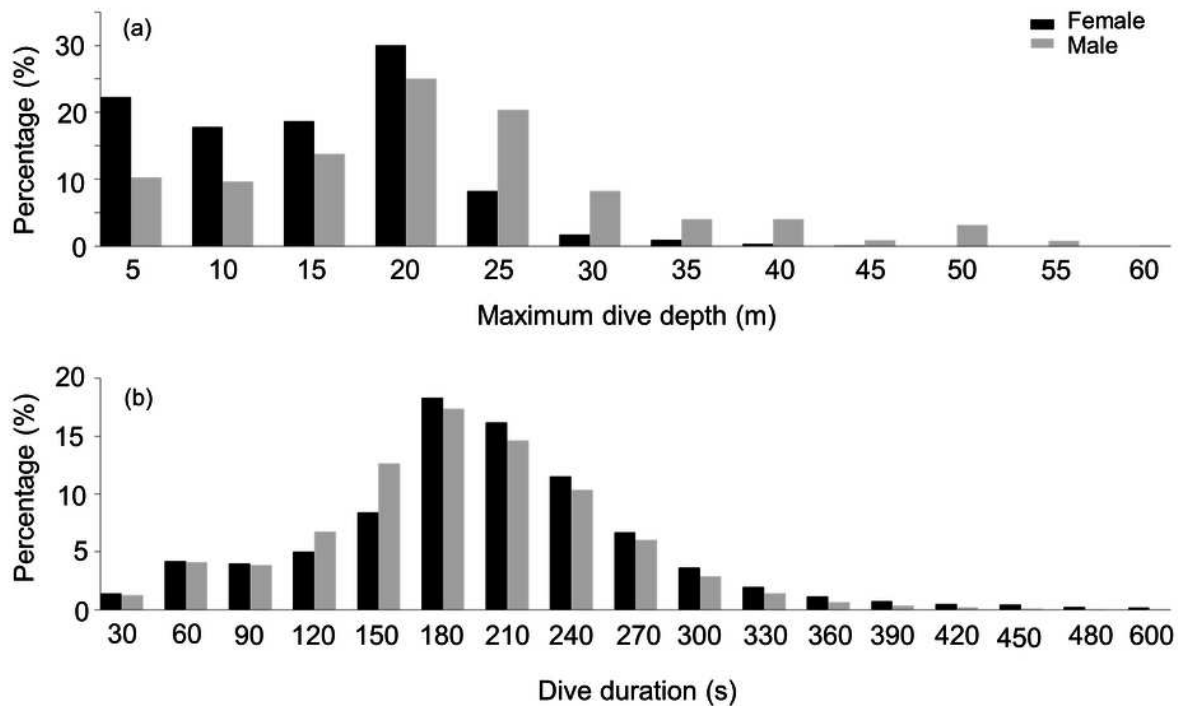
11    female                      3                      3                      3

12 **TOTAL**                                      **73**                      **55**                      **34**

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13

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

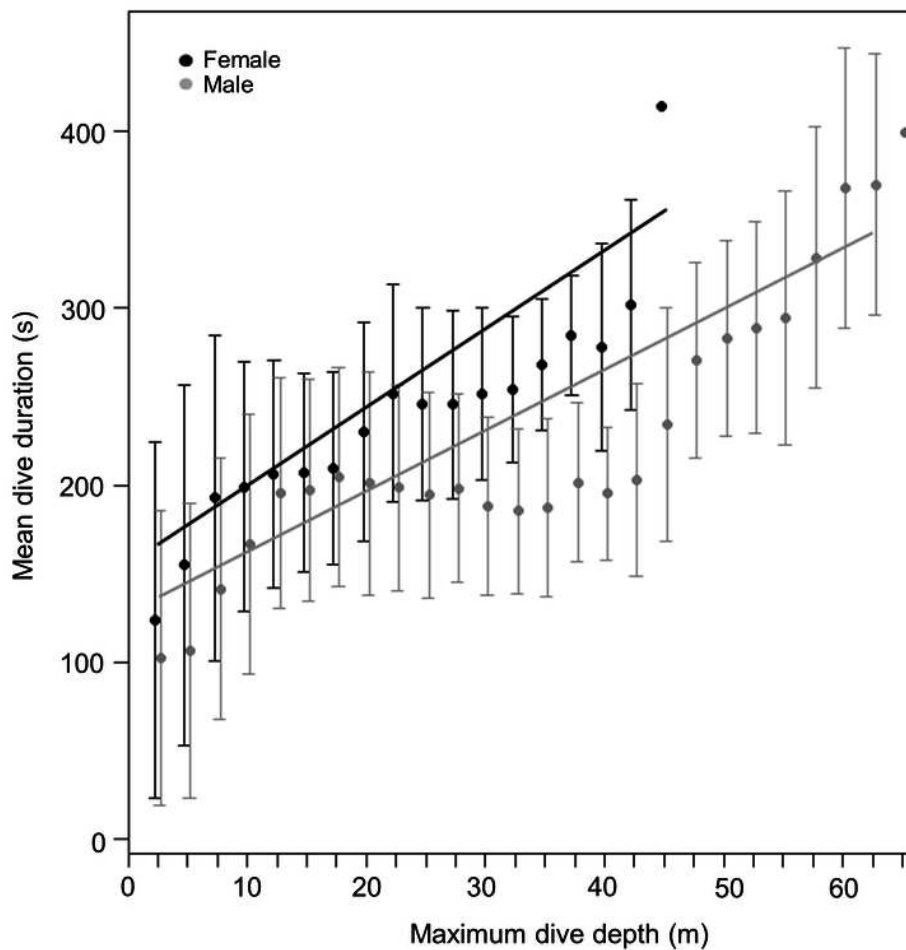
Frequency distribution of (a) the maximum depth (b) and dive duration of U-dives performed by female (black bars) and male (grey bars) harbour seals



# 3

Relationship between dive duration and maximum dive depth of female and male harbour seals.

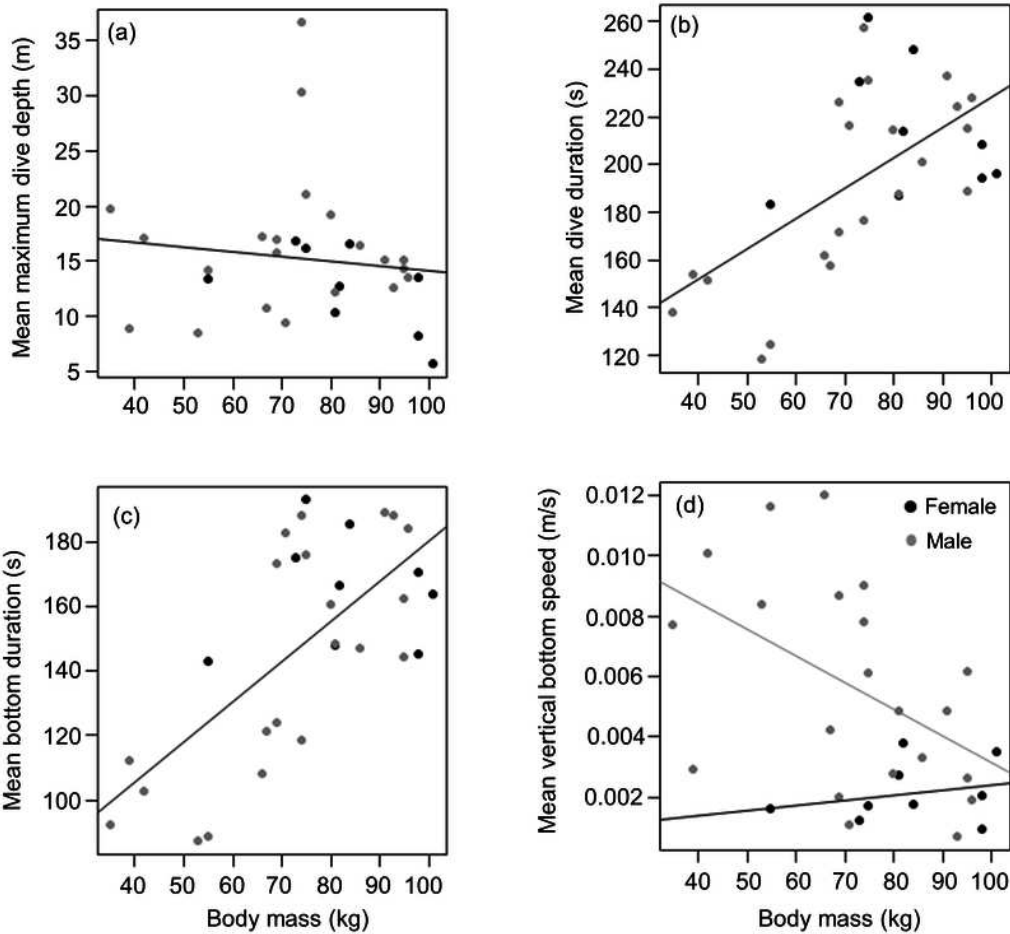
Relationship between dive duration and maximum dive depth of female (black points) and male (grey points) harbour seals. The lines (black for females and grey for males) represent the fitted relationship. The points represent the mean dive duration for 2.5 m interval while the whiskers represent the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



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

