Biological Conservation 214 (2017) 213–222

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Assessment of impacts and potential mitigation for icebreaking vessels transiting pupping areas of an ice-breeding seal

Susan C. Wilson[a,*], Irina Trukhanova[b], Lilia Dmitrieva[c], Evgeniya Dolgova[d], Imogen Crawford[a], Mirgaliy Baimukanov[e], Timur Baimukanov[e], Bekzat Ismagambetov[e], Meirambek Pazylbekov[f], Mart Jüssi[g], Simon J. Goodman[c,*]

[a] Tara Seal Research, Killyleagh, Co. Down, N. Ireland, UK
[b] Polar Science Center, Applied Physics Laboratory, University of Washington, Seattle, USA
[c] School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, UK
[d] Lomonosov Moscow State University, Russian Federation
[e] Institute of Hydrobiology & Ecology, Karasaysky Raion, Almaty, Kazakhstan
[f] Institute of Fisheries, Almaty, Kazakhstan
[g] Pro Mare MTÜ, Saula, Kose, Harjumaa EE 75101, Estonia

ARTICLE INFO

Keywords:
Caspian Sea
Pinniped
Marine mammal
Ship strikes
Aerial survey
Conservation

ABSTRACT

Icebreaker operations in the Arctic and other areas are increasing rapidly to support new industrial activities and shipping routes, but the impact on pinnipeds in these habitats is poorly explored. We present the first quantitative study of icebreakers transiting ice-breeding habitat of a phocid seal and recommendations for mitigation. Impacts were recorded from the vessel bridge during seven ice seasons 2006–2013, for Caspian seals (*Pusa caspica*) breeding on the winter ice-field of the Caspian Sea. Impacts included displacement and separation of mothers and pups, breakage of birth or nursery sites and vessel-seal collisions. The flight distance of mothers with pups ahead was < 100 m, but measurable disturbance occurred at distances exceeding 200 m. Separation distances of pups from mothers were greatest for seals < 10 m to the side of the vessel, and declined with increasing distance from the vessel. The relative risk of separation by ≥ 20 m was greatest for distances < 50 m from the vessel path. Seals on flat ice were more likely to be separated or displaced by ≥ 20 m than seals in an ice rubble field. The relative risk of vessel collisions with mothers or pups was significantly greater at night when breaking new channels (12.6 times), with vessel speeds ≥ 4 kn (7.8 times). A mitigation hierarchy is recommended for the Caspian Sea which could be applied to Arctic pinnipeds, including reducing icebreaker transits during critical periods, and using data from aerial surveys to plan routes to minimise encounters with seals. Where pre-emptive avoidance is not possible, recommendations include maintaining a safe separation from breeding seals at least 50 m beyond the distance at which measurable disturbance occurs, speed limits, use of thermal imaging at night, dedicated on-board Seal Observers, and training of vessel officers to take effective reactive measures.

1. Introduction

Shipping in Arctic waters is developing rapidly due to increased activity for oil, gas and mineral extraction. Polar tourism is also growing, and reduced sea ice cover has allowed the opening up of new transpolar cargo routes. The potential for impacts from oil and gas (O & G) exploration and increased shipping on marine mammals in Arctic ice habitat was identified in the early 1980s, with the suggestion that icebreakers could have lethal impacts on nursing pups via vessel collisions, crushing, or displaced ice (Davis, 1981; Stirling and Calvert, 1983), but since then the focus has been on oil spills, pollution, and physical injury or behavioural disturbance due to noise (Engelhardt, 1983; Weilgart, 2007). The escalation of arctic shipping is predicted to lead to increased interactions with marine mammals (Laidre et al., 2015). Collision between vessels and marine mammals is recognised as a potentially significant impact for cetaceans in open waters (Laist et al., 2001; Vanderlaan and Taggart, 2007) and in the Arctic (Reeves et al., 2014) and a programme has been established in eastern US

Abbreviations: MP, seal mother-pup pair; LP, lone pup; P, pup; M, mother; kn, knot (nautical mile); SoV, side of vessel path

* Corresponding authors at: School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK.
E-mail addresses: suewilson@sealresearch.org (S.C. Wilson), irina_trukhanova@yahoo.com (I. Trukhanova), sealilia@gmail.com (L. Dmitrieva), e.dolgova@mail.ru (E. Dolgova), imogencrawford@hotmail.com (I. Crawford), institute_he@mail.ru (M. Baimukanov), t.baimukanov@mail.ru (T. Baimukanov), bekza88@mail.ru (B. Ismagambetov), make_1984@mail.ru (M. Pazylbekov), mart.jussi@gmail.com (M. Jüssi), s.j.goodman@leeds.ac.uk (S.J. Goodman).

http://dx.doi.org/10.1016/j.biocon.2017.05.028

coastal waters to understand and mitigate the threat of ship strikes to right whales (Vanderlaan et al., 2009; Laist et al., 2014). Ice-breeding pinnipeds are likely to be most sensitive to vessel impacts during birthing and lactation (hereafter referred to as 'pupping'), and the first description of icebreaker impacts on seal mothers and pups was for Caspian seals (Härkönen et al., 2008). Vessel impacts have also been inferred for breeding harp seals (*Phoca groenlandica*) in the White Sea (Vorontsova et al., 2008), and a programme to avoid breeding colonies detected by an aerial survey in the White Sea was trialled in 2009 (Gershenzon et al., 2009). Huntington (2009) suggested that regulation of shipping, with clear operational guidelines to mitigate impact on marine mammals, should be developed in advance of a shipping boom rather than retrospectively, and also that conservation measures developed elsewhere may have application within the Arctic.

The Caspian seal is endemic to the land-locked Caspian Sea. Although still relatively numerous, with a population estimated at 104,000–168,000 animals in the years 2005–12 (Härkönen et al., 2008; Dmitrieva et al., 2015; Goodman and Dmitrieva, 2016), numbers have declined by 90% over the past century primarily due to over-hunting (Härkönen et al., 2012), and the species is now listed as Endangered by IUCN. A range of ongoing threats include continued hunting, fisheries-related mortality, habitat loss and ecosystem changes (Härkönen et al., 2012; Dmitrieva et al., 2013; Goodman and Dmitrieva, 2016).

Caspian seals pup and mate on the winter ice field which forms in the shallow northern Caspian Sea in January—March (Wilson et al., 2017). This area overlaps with several major oil fields, including Kashagan in the Kazakh sector, which was discovered in 2000 and entered production in October 2016 (Gizitdinov, 2016). The offshore installations are supported by vessels transporting supplies and waste (primarily sewage) along a 300 km route between artificial islands and Bautino port (Fig. A1). During the ice season the ships traverse areas of ice forming the breeding habitat of the Caspian seal (Härkönen et al., 2008; Wilson et al., 2017). In this study we quantify impacts of icebreakers transiting through the seal pupping areas and examine implications for mitigation strategies. We discuss how results of this study might be applied to seal species breeding in other frozen seas.

2. Materials and methods

2.1. Study area and vessels

Observations were made between late January and mid-March 2006–2013 from four icebreakers operated by the company Agip KCO and their contractors. The vessels use a navigation corridor extending north and north-east from Bautino approximately 300 km to the Kashagan field (Fig. A1). The corridor crosses a shallow shelf known as the 'Saddle' which has high densities of breeding seals in most years. The water depth along the shipping corridor is approximately 3–5 m, with average ice thickness up to about 50 cm. A total of 39 icebreaker transits on the Bautino-Kashagan-Bautino route were surveyed during the ice seasons 2006–2013 (Table B1). At least one icebreaker transit was observed in each year except for 2007, ranging from 1 transit in 2006 to 23 in 2012. Access to vessels was opportunistic, and determined by operational constraints.

2.2. Annual records of the vessel transit corridor overlap with seal pup distribution

Data delineating the vessel transit corridor were obtained from Agip KCO records of vessel GPS locations, and from GPS locations recorded by survey teams during observation transits. These GPS locations were used to generate a minimum convex polygon delimiting the extent of icebreaker distributions in each year using ArcGIS software (ESRI, New York). Delineation of the breeding areas in each year and areas with > 5 pups/km^2 were extracted from the results of aerial surveys carried out during the peak pupping period from mid–late February 2005–2012 (Fig. 1; Dmitrieva et al., 2015).

An estimate of overall shipping activity during the core pupping season (25th January–7th March; Wilson et al., 2017) was made using Automatic Identification System (AIS) data purchased from www.marinetraffic.com. AIS data was not available or sparse for 2006–2012, so only 2013 was taken as having representative coverage. A minimum of 102 distinct transits from 18 vessels (mean 2.4 transits per day; range 0–11) were estimated through an area around the 'Saddle', defined by the points 45.85N 49.8E, 45.85N 51.15E, 45.22N 51.15E, 45.22N 49.8E. At least 1 vessel was present in the area for 39 days of the 41 day period.

2.3. Recording of vessel-seal encounters

Observations using binoculars were made from the vessel bridge which was ~15 m above ice level for all vessels, with 1–2 observers on each side. Vessel-seal encounters and transit through ice habitat were documented using digital photograph sequences, digital voice recorders, check-sheets and notebooks. Distance of seals from the bridge was recorded using laser rangefinders (Nikon 800 and 1000) or estimated visually for seals < 30 m from the ship or during darkness. When available, hand-held GPS units were used to record vessel-seal encounter waypoints, vessel tracks, vessel speed and heading. All data were compiled in spreadsheets, together with photograph references. Altogether a total of 674 vessel-seal encounters (Encounter List) were collated for analysis. For each vessel-seal encounter the following data were recorded when available: date; time; whether it was light or dark (hours of darkness approximately 19:00–09:00 in February); type of icebreaker (A–D) in terms of vessel dimensions, deadweight and draught (Table B1; vessels A & C were run by one shipping company, B and D were run by two separate companies); GPS location; focal seal(s) type (Mothers (M), Pups (P), lone pups (LP) without mother in attendance); developmental stage of pup from 1 (new-born) to 4 (fully moulted; Wilson et al., 2017); whether the vessel was breaking a new channel or travelling in an existing channel; ice habitat type (deformed ice structures, smooth ice pans surrounded by ice ridges, or flat ice); distance or distance band from the vessel side (Distance SoV; < 10 m, 10–49 m, 50–99 m, 100–199 m); vessel speeds immediately prior to and during each vessel-seal encounter (cruising and response speeds, respectively); and a verbal description of the encounter context.

The following outcomes of encounters were recorded: collision (strike, run over or drag an animal beneath the vessel); pup wetting (lanugal pups forced into water or covered by brash ice); maximum separation distance between Mother (M) and Pup (P), and whether MP pairs were separated by ≥ 20 m; displacement of seals (any shifting of position, movement away from vessel, including M entering the water – treated as binary Yes/No outcome) and maximum displacement distance.

Displacement and MP separation distances were estimated in most cases from photographic records. For MP separations distances were estimated on the basis of adult body lengths (ABL) between Mother and Pup (1ABL = ~1 m). Displacement distances could only be estimated in a minority of cases either where physical reference points (ice features) were visible or where the observer was able to assess visually the approximate distance.

Not all data were recorded for all vessel-seal encounters owing to varying levels of training and experience of observers.

2.4. Statistical analysis

Statistical analyses and data visualisations were performed in the *R* statistical package (*R* core team 2016). Binary logistic regression, implemented in the rms *R* package (Harrell, 2016), was used to evaluate the association of predictor variables with binary encounter outcomes. Predictor variables included vessel speed; distance from side of vessel (SoV) category; seal type (MP or LP); habitat type (featured ice, or flat ice); vessel type, year, channel type (new or old), daylight status (light,

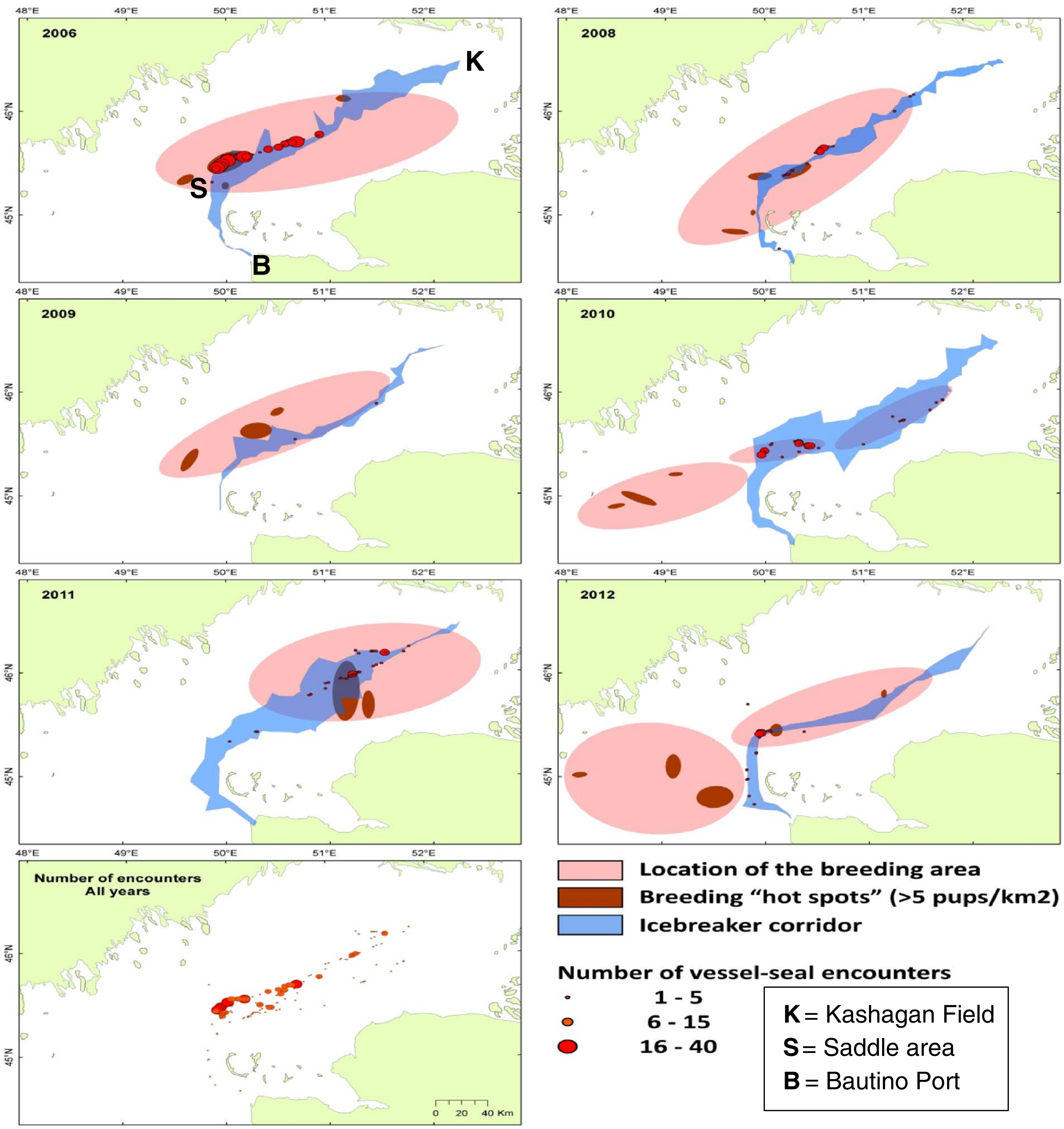

Fig. 1. Maps showing the overlap between icebreaker positions recorded during surveys and seal pup density distribution in different years of the icebreaker study. Pup distribution data from aerial survey data (Härkönen et al., 2008; Dmitrieva, 2013); icebreaker corridor data from GPS data recorded on board icebreakers.

dark). Binary encounter outcomes included seal displacement, MP separation ≥ 20 m and vessel collision. Distance from side of vessel categories were treated as continuous variable, with values 1, 2, 3, 4, for bands of increasing distance. Speed was also treated as continuous variable, while all others were treated as categorical. In the case of collisions the analysis was restricted to seal encounters < 10 m from the vessel side. Model comparison was evaluated using Akaike Information Criterion (AIC) values and Likelihood Ratio tests (LRT).

3. Results

3.1. Overlap of icebreaker navigation corridor with seal breeding areas

The location and extent of the overlap between the vessel corridor and the seal pup distribution differed in each of the study seasons (Fig. 1). Years with more extensive ice cover were observed to have a more westerly distribution of pups and less overlap with the vessel corridor (Dmitrieva, 2013; authors' unpublished data). Vessel-seal encounters primarily occurred in the area between Kalamkas and the ice edge, and particularly in the Saddle area, where seal densities were highest in most years (Figs. 1; A1). The vessel corridor remained relatively constant, although varying in breadth among seasons. The main pupping areas were outside the vessel corridor in 2009, 2010 and 2012, but were bisected by the corridor in 2006, 2008 and 2011 (Fig. 1).

3.2. Impact of icebreaker transit on breeding habitat

Caspian seal breeding habitat comprised networks of birth sites, typically indicated by birthing blood and fluids, pup shelters in the form of ice ridges or piles of ice slabs, water access holes and adjacent small polynyas (Wilson et al., 2017; Fig. A2a, b). Depending on ice conditions, vessels would either break new routes, or follow existing channels and leads.

Breaking new ice resulted in a vessel-wide channel of brash (churned, broken) ice (Fig. A2, c, d), partially frozen water (Fig. A3) or open water, depending on ambient temperature and ice conditions. Lanugal pups had difficulty in negotiating brash ice due to the uneven surface and patches of water. Vessel encounters < 10 m from pups while creating new channels were always considered to be breaking pupping habitat (Fig. A4a, b) and a total of 81 such encounters were recorded.

Pre-existing shipping channels were often colonised by seals using them as leads into the interior of the ice field, and pregnant females and mothers with new-born pups were seen hauled out at, or close to, the edge of shipping channels (Figs. A3, A4c). A total of 228 vessel encounters with pups < 10 m SoV along a pre-existing channel were recorded.

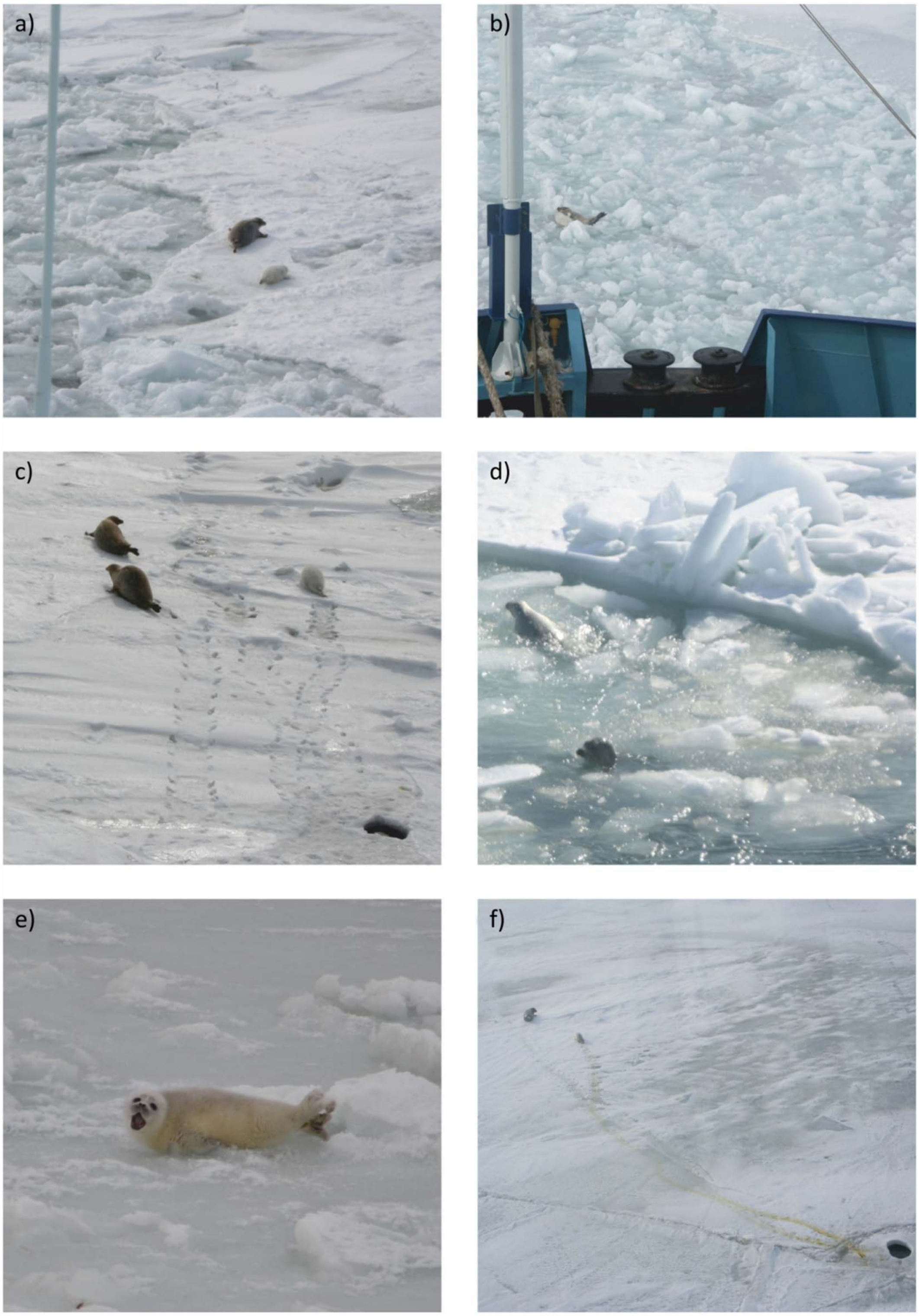

Fig. 2. Mother and pup response to vessel approach. a) Mother-pup pair at old channel edge move away from vessel as pair, pupping habitat converted to brash ice; b) mother-pup pair move into the channel in front of the ship instead of moving away; c) chaperoning mother turns to pup (pup defecates), d) Lanugal pup has fallen into ice crack as vessel passed, e) lone pup giving distress call as vessel passes; f) Mother and pup displaced from position beside water access hole. Both mother and pup leave trail of urine and faeces, indicating stress response.

Table 1
Coefficients and significance values for terms in best fit binary logistic regression models evaluating probability of seal displacement, mother-pup separation by > 20 m, and vessel-seal collisions.

Displacement (Daylight observations)					
Model call: *Displaced ~ Distance SoV + Seal type + Habitat + Year*, family = binomial					
Parameter	Coefficient	Std Error	Wald Z	P (> |Z|)	Model significance
Distance SoV	− 1.0781	0.1892	− 5.697	1.22E-08	Null deviance: 336.2, d.f. 305
Seal type MP	0.8075	0.4816	1.677	0.0936	Residual deviance: 222.4, d.f. 298
Habitat1 flat	1.3869	0.4501	3.081	0.0021	AIC: 238.43
Year 2008	17.0224	898.7655	0.019	0.9849	Model LRT: χ^2 113.8
Year 2010	− 0.1841	0.4087	− 0.45	0.6524	d.f. 7, P = 1.48E-21
Year 2011	1.2057	0.6648	1.814	0.0697	
Year 2012	1.9398	1.1136	1.742	0.0815	
Mother-pup Separation ≥ 20 m (Daylight observations)					
Model call: *Displaced* ≥ 20 m ~ *Distance SoV + Habitat type + Vessel*, family = binomial					
	Coefficient	Std Error	Wald Z	P (> |Z|)	Model significance
Distance SoV	− 0.6637	0.3188	− 2.082	0.0374	Null deviance: 180.04, d.f. 236
Habitat1 flat	2.0502	0.6297	3.256	0.0011	Residual deviance: 146.91, d.f. 231
Vessel B	2.7895	0.8578	3.252	0.0011	AIC: 158.91
Vessel C	2.4797	0.7925	3.129	0.0018	Model LRT: χ^2 33.1, d.f. 5, P = 3.54E-6
Vessel D	19.1621	966.1936	0.020	0.9842	
Collisions (for seals < 10 m from side of vessel)					
Model call: *Collision ~ Prior speed + Seal type*, family = binomial					
	Coefficient	Std. error	Wald Z	P (> |Z|)	Model significance
Prior speed	0.497	0.193	2.575	0.0100	Null deviance: 73.05, d.f. 85
Seal type: MP	− 1.082	0.658	− 1.643	0.1004	Residual deviance: 60.49, d.f. 83 AIC: 66.49 Model LRT: χ^2 12.56, d.f. 4, P = 0.0019

3.3. Behavioural response of seals to icebreaker passage

When the vessel approached a mother-pup pair, the usual response was for the mother to move away from the vessel and for the pup to attempt to follow (Fig. 2a, b). Thus mothers and pups were displaced from their nursery site. Typically pairs moved to the side of the vessel or, less frequently, ahead along the vessel path (Fig. A4c). Mothers usually moved slowly, chaperoning the pup by frequently turning to check and pausing to wait (Fig. 2c), so the separation distance would not exceed a few metres (Wilson et al., 2017). However, mothers occasionally moved away rapidly without chaperoning the pup, resulting in the pup being left behind and some degree of separation of mother and pup. Ice slabs and ridges provided shelter to LPs attempting to avoid the vessel (Fig. A5). Mothers sometimes slipped into the water via a breathing hole or adjacent polynya, while the pup remained on the ice. White-coat pups never entered the water voluntarily until well-grown in late season (Wilson et al., 2017), but lanugal pups close to the vessel were occasionally observed to be wetted as a result of vessel passage (6/312 total encounters < 10 m SoV; Fig. 2d).

LPs sometimes failed to move away from the vessel or moved more slowly than pups following their mothers, although LPs were observed to follow neighbouring MPs (Wilson et al., 2017). LPs were sometimes encountered in pairs or small groups following one another for short distances (Fig. A6). Typically around a third of pups may be observed as LPs (Dmitrieva et al., 2015; Wilson et al., 2017), but larger aggregations of LPs, were sometimes recorded along the shipping channel edge in 2006, 2010 and 2012 (Fig. A6a). Dead pups were also occasionally seen close to the channel edge, either intact or partially eaten by eagles. Whether the latter were killed by the eagles or scavenged post-mortem is unknown.

Overt stress indicators in response to vessel passage were observed in the form of distress calls from pups close to the vessel or when separated from their mothers (Fig. 2e), or when mother or pup left a urine or faecal trail (Fig. 2f) as they moved away.

3.4. Flight distance

The flight distance ahead of the ship's bow at which MPs and LPs at the edge of pre-existing channels started to move was measured during daylight during the 2006 transit and ranged from 0 to 90 m (average 41.7 m, n = 42, SD = 30.8) for MPs, and 0 to 85 m (average 31.3 m, n = 10, SD = 32.8) for LPs (P > 0.05 Mann-Whitney *U* test). For a vessel moving at a typical cruising speed of 6 kn, this flight distance allows a MP or LP at 90 m, 42 m and 31 m ahead about 29 s, 13 s and 10 s respectively to leave the channel edge before the vessel would reach them.

3.5. Seal displacement

The proportion of seals displaced (any distance) from their resting position by the vessel passage was greatest for seals < 10 m SoV (98% of MPs and 95% of LPs) and least for seals 100–199 m SoV (50% MPs and 29% LPs) (Table B2). Using the full dataset (Encounter List), Distance SoV, Habitat, Light, Vessel type, and Year all explained significant variation in Displacement when fitted as single predictors in binary logistic regressions (Table C1). Multi-predictor models were fitted using daylight observations only to

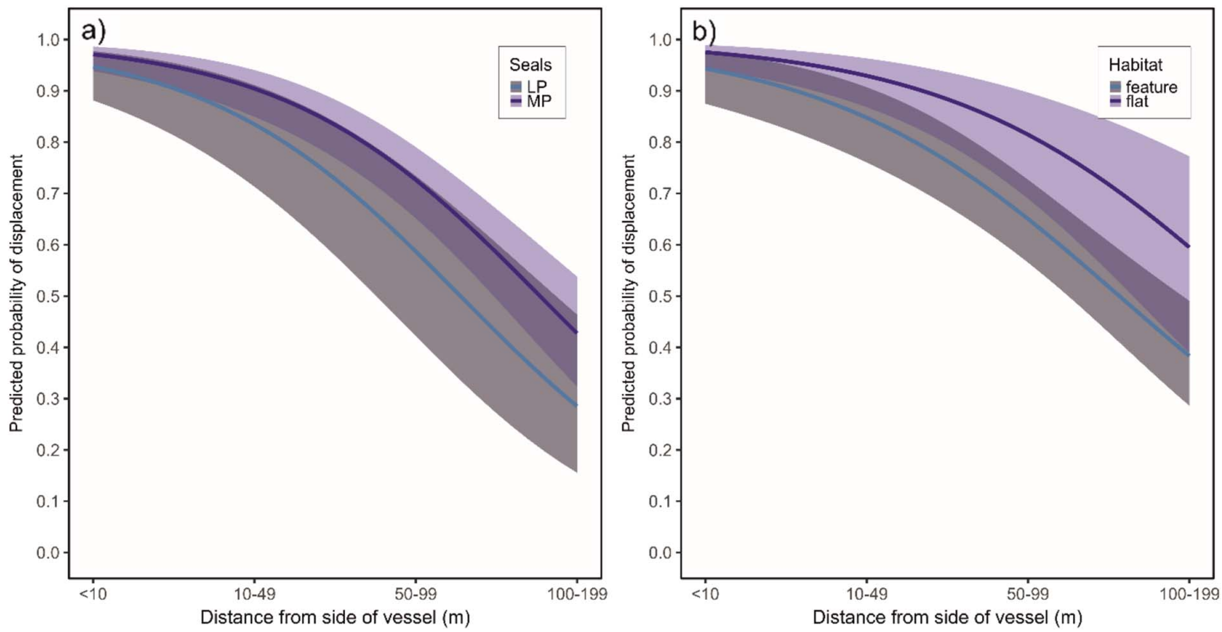

Fig. 3. a) Predicted probability, from binary logistic regression, of (a) seal displacement relative to distance from side of vessel, for Lone Pups (LP) and Mother-Pup pairs (MP) – derived from Model 9, Table C3; and b) seal displacement relative to distance from side of vessel, for on featured ice versus flat ice – derived from Model 14, Table C2. Solid lines indicated fitted values, and shaded areas 95% confidence intervals.

avoid potential bias due to inability to observe seal movements in darkness at distances > 50 m, and using records with complete data for Distance SoV, Habitat, and Channel. In the best fit model (*Displaced* ~ *Distance SoV* + *Seal type* + *Habitat* + *Year*; AIC 238.4; Tables 1; C2, C3), the log odds of displacement decreased by − 1.08 with each distance band, increased by 0.81 for MP pairs relative to LPs and increased by 1.39 for flat ice relative to featured ice. The difference in log odds between MP and LP (Seal type) displacement was not significant at the 0.05 level, and the model only provided a significantly better fit than the fifth ranked model (*Displaced* ~ *Distance SoV* + *Seal type* + *Habitat* + *Channel* + *Year* + *Vessel*; AIC 242.19); d.f. − 1, Deviance − 6.34, P (χ^2) = 0.012. However, Seal type was significant in the best fit model when dropping Habitat to allow use of 230 observations previously excluded due to missing Habitat data (Tables C4, C5). While Year appears as significant term, this probably reflects differences in encounter context between years and potentially other factors such as differences between observers in recording seal movement. At < 10 m from vessels, the displacement probability was around 0.95 for both seal types, decreasing to 0.4 for MPs at 100–199 m and 0.30 for LPs, and to 0.6 and 0.4 on flat and featured ice respectively (Fig. 3).

3.6. Mother-pup separation

Separation of mother and pup was a consequence of displacement when the mother moved too rapidly for the pup to keep up. Since displacement could only rarely be measured due to lack of reference points, separation distance is primarily used in the following analysis.

In total there were 417 MP encounters for which both separation distance and SoV distance bands (at the start of the encounter) were available. Mean separation ranged from 10.13 m (SD = 10.92, range = 0–60 m, n = 184) for seals < 10 m SoV, to 3.56 m (SD = 7.07, range = 0–40 m, n = 88) for seals 100–199 m SoV (Fig. 4a), and decreased significantly across the SoV distance bands (Kruskal-Wallis χ^2 62.383, d.f. 3, P < 0.0001). The frequency of MP separations of ≥ 20 m was highest (24.5%) at < 10 m to the SoV, falling to (4.5%) at 100–199 m to the SoV (Fig. 4b). Overall, 85% of 69 ≥ 20 m separation events for which distance SoV was recorded occurred at distances of < 50 m SoV.

There were eight records of mothers with new-born pups at distances < 100 m SoV. All moved some distance from their pups (Fig. A7), one mother giving birth as the vessel passed, fleeing from the new-born pup for at least 50 m (Encounter List, index #607).

MP separation of ≥ 20 m was adopted as a criterion for increased risk of complete loss of communication between M and P. A total of 73 instances of separation ≥ 20 m were recorded. In only one case was the mother seen to return to the pup, and in a further 9 cases the mother was observed eventually to wait. The final outcome of most separations could not be determined from the moving vessel, but at least two separations may have been irreversible. In one instance (Encounter List, index #228) the pup climbed out of the wrong side of the channel and fled across a non-pupping ice area. On another occasion (Encounter List, index #553), the mother fled for 500 m while the pup turned away from her track in a different direction, resulting in a separation of at least 200 m in a rubble field (Fig. A8).

Using the full dataset, each variable except Vessel prior speed and Channel explained significant variation in Separation when fitted as single predictors in binary logistic regressions (Table C6). Multi-predictor models were again fitted using daylight observations only and with complete data for Distance SoV, Habitat, and Channel. In the best fit model (*Separation* ≥ 20 m ~ *Distance SoV* + *Habitat type* + *Vessel*; AIC 146.9; Tables 1; C7, C8), the log odds of Separation ≥ 20 m decreased by − 0.664 with each distance band and increased by 2.05 for flat ice relative to featured ice. The top ranked model did not provide a significantly better fit compared to the top 5 models, but was a significantly better fit than models removing either Habitat or Vessel (AIC 168.06; d.f. − 1, Deviance − 11.15, P (χ^2) = 0.0008; AIC 170.94, d.f. − 3, Deviance − 24.032, P (χ^2) = 2.46e^{-05}, respectively). Differences among vessels should be interpreted with caution due to variation in encounter context (e.g. vessel types B and C had 14% of their encounters in flat ice, compared to 66% and 42% for vessel types A and D respectively), and potentially other factors such as differences in engine noise or observers. The predicted probability of separation by ≥ 20 m was 0.226 at < 10 m for flat ice, declining to 0.124 in the 100–199 m band, and 0.109 at < 10 m declining to 0.056 for ice features (Fig. 4c).

3.7. Vessel-seal collisions

A total of 20 collisions were recorded, but were rare in comparison

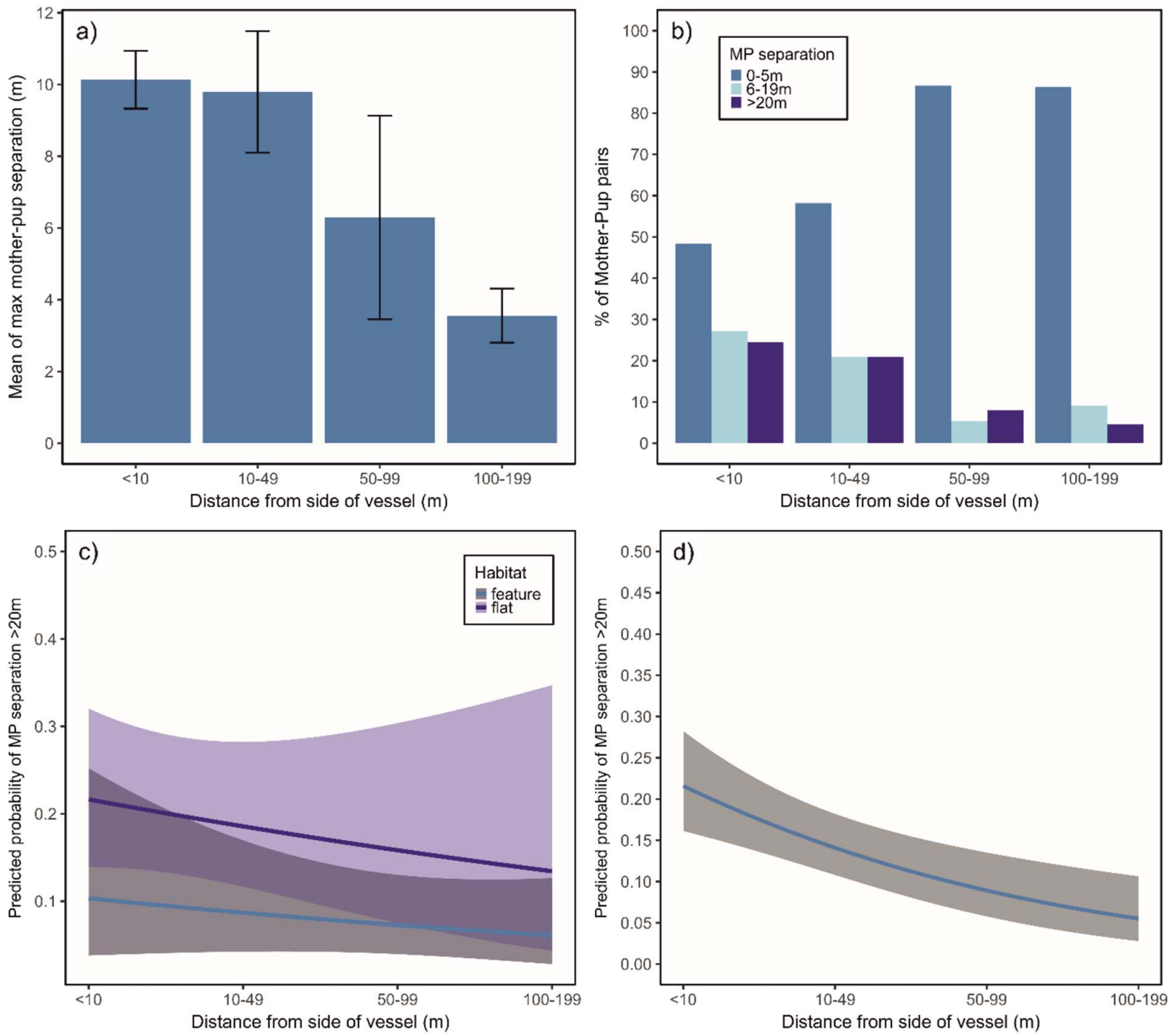

Fig. 4. a) Mean maximum separation for Mother-Pup (MP) pairs with standard error relative to distance from side of vessel; b) percentage of events with maximum separation of 0–5 m, 6–19 m and > 20 m for MP pairs relative to distance from side of vessel (data from all years); c) predicted probability, from binary logistic regression, of MP separation > 20 m relative to distance from side of vessel on featured versus flat ice – derived from Model 14, Table C7; d) predicted probability, from binary logistic regression, of MP separation > 20 m relative to distance from side of vessel – derived from Model 15, Table C7. For c) and d) solid lines indicated fitted values, and shaded areas 95% confidence intervals.

to the total of 312 encounters < 10 m from the vessel path. Of the 20 collisions, 13 involved LPs. Of the seven collisions with MPs, two were with the mother, four with the pup and one with both mother and pup. Data on vessel prior speed were available for 86 encounters < 10 m SoV, including for 13 collisions. Of these 13 collisions, all except 1 occurred with vessel prior speeds exceeding 4 kn.

Fitting predictors singly in binary logistic regression suggested each accounted for significant variation in collision risk (Table C9). However, evaluating the effects of Light and Channel independently is difficult since 16 of 20 collisions occurred under darkness when breaking new channels. Only multi-predictor models containing Prior speed were considered further, since speed was hypothesised as a key risk factor. *Collision ~ Prior speed + Seal type* (AIC 66.491) was the top ranked model (Tables C10, C11), with the log odds of collision increasing by 0.497 per unit speed, and decreasing by 1.082 for MP pairs relative to LPs (Table 1). However, this model did not provide a significantly better fit compared to the second ranked model containing Prior speed alone (AIC 67.265; d.f. −1, Deviance −2.773, P (χ^2) = 0.0957). The reduction in sample size due to considering only records with speed data is likely to decrease power to resolve different models. The probability of collision ranged from < 0.05 for MPs below 4 kn to around 0.75 for LPs at 10 kn (Fig. 5).

From all data with SoV < 10 m, the relative risk of collision was 7.85 (95% CI 1.07–57.61; odds ratio = 9.9, 95% CI 1.22–80.16, P < 0.0001; Fisher test) for vessel speeds exceeding 4 kn; and 12.6 (95% CI = 4.77–33.31; odds ratio = 16.47, 95% CI = 5.70–47.57, P < 0.0001; Fisher test) for breaking new channels at night compared to new channels during daylight.

3.8. *Attempted avoidance of seals by vessels*

When breaking new channels, vessel captains encountering seals in or close to the vessel path were sometimes able to take action to avoid collision either by slowly manoeuvring the vessel around the seals, or by stopping and waiting for the seals to move out of the vessel path.

Criteria for avoidance manoeuvring were either reversing or changing direction by at least 20 degrees. A total of 26 encounters with seals ≤ 10 m to SoV in new channels for which manoeuvring was recorded resulted in no collisions, although there were 8 instances of separation or displacement by ≥ 20 m. In 17 of 21 manoeuvre encounters with speed data, the prior speed was < 4 kn and for 20 occasions in which the subsequent encounter speed was measured, 15 had slowed to < 1 kn and a further five to ≤ 2.2 kn.

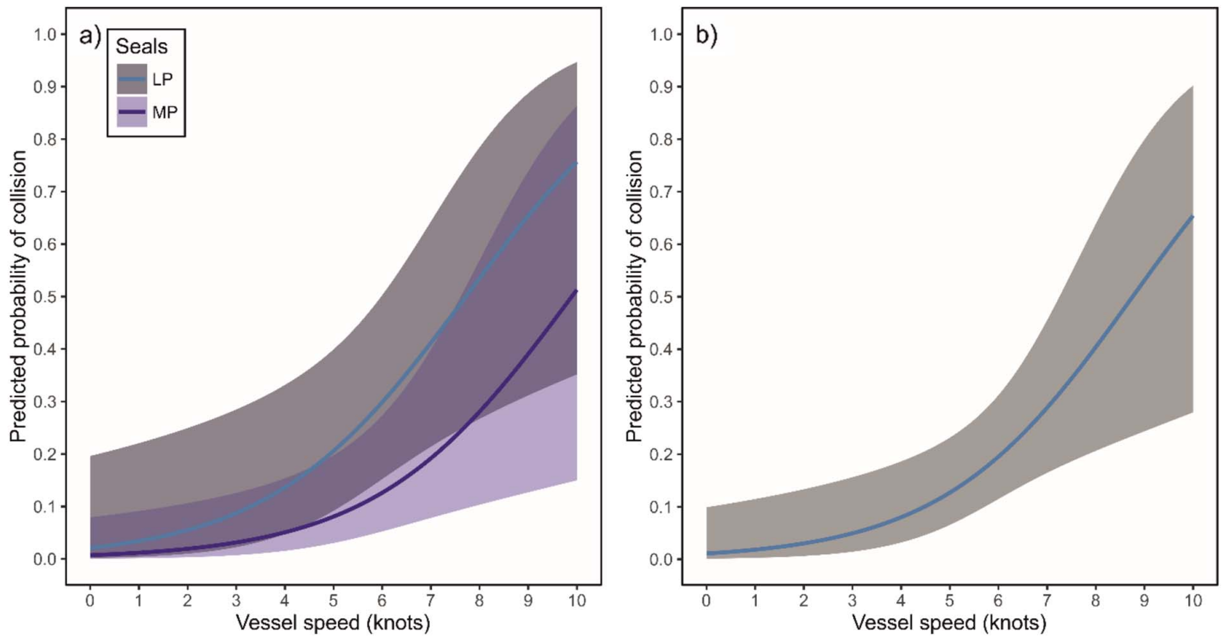

Fig. 5. Predicted probability, from binary logistic regression, of a) vessel-seal collision relative to vessel prior encounter speed, for Lone Pups (LP) and Mother-Pairs (MP) – derived from Model 1, Table C10 and b) vessel-seal collision relative to vessel prior encounter speed – derived from Model 2, Table C10. Solid lines indicated fitted values, and shaded areas 95% confidence intervals.

3.9. Differences among vessel types in management of seal encounters

The average speed prior to seal encounters < 10 m SoV (i.e. the vessel's cruising speed; Table B3) for vessels type A & C was higher (5.8 and 6.0 kn respectively) than for vessels type B & D (3.8 and 3.7 kn respectively; 2-tailed $P < 0.0001$, Mann-Whitney *U* test). The average response speed for encounters < 10 m SoV occurred was also higher, at 3.9 & 5.8 kn respectively, for A & C than for types B & D (2.1 and 1.8 kn respectively; 2-tailed $P = 0.005$, Mann-Whitney *U* test, comparing A & C with B & D). For encounters 10–49 m SoV, average prior and response speeds were again significantly higher for vessels type A & C compared to B & D (Table B3, 2-tailed $P < 0.0001$, Mann-Whitney *U* test, in each case). Vessel types B & D therefore appeared to show better management of encounters by maintaining speeds < 4 kn in high risk areas and by dropping to speeds below 2.2 kn during encounters to facilitate effective manoeuvring.

4. Discussion

Anthropogenic disturbance of animals may be defined as any human activity that causes a deviation from the animal's normal behaviour in response to that activity (Blanc et al., 2006). This definition applies at the scale of individuals, but may ultimately extend to demographic consequences at a population level. There is an increasing recognition of indirect effects (such as through stress and increased energetic burdens) on mortality or impaired reproduction, which need to be considered in addition to direct effects when evaluating impacts on seal populations arising from human activities (Jansen et al., 2010; Karpovich et al., 2015). In this study we documented vessel passage creating circumstances likely to cause stress and energy expenditure as well as occasional collisions with individuals. Our study could not attempt to determine the properties of the approaching vessel to which the seals were responding, i.e. whether visual, acoustic or both, but the mothers' flight response and the lone pups' tendency to seek shelter in ice features (Fig. A5) suggest anti-predator behaviour.

4.1. Impact of vessel passage on pupping sites

Pupping sites are usually situated on ice at least 20 cm thick, which would be expected to remain intact under natural conditions until the end of the lactation period. Pups, mothers and other adults will learn the topography of their site and use it until the final ice melt in the spring.

Vessel passage may destroy birth sites, water access holes, seal tracks and pup shelters and these features are replaced by brash ice or open water, often causing pups to be marooned on fragments of intact ice (Fig. A2) and wetted in brash ice created by vessels. Fragmented habitats may present pups with hazards causing disorientation, stress, increased energetic demands, and for lanugal Caspian seal pups, which are known to strictly avoid water, risk of hypothermia (Wilson et al., 2017). Since pups are usually quiescent when their mothers leave them temporarily to make foraging trips (Wilson et al., 2017), it is likely that groups of wandering or emaciated pups (Fig. A6) may include some which have lost their mother permanently.

Vessel channels could theoretically benefit seals by creating leads into the ice field, and expanding access to pupping habitat. However, seals pupping on the edge of such artificial leads (Fig. A4c) are vulnerable to vessel collisions, ice breakage and repeated disturbance. Ships could avoid channels after they have been colonised by seals and create fresh channels elsewhere, but the effectiveness of such a measure remains to be evaluated.

4.2. Seals' flight distance

The flight distance of Caspian seal mother-pup pairs or lone pups ahead of the vessel in daylight was < 90 m and averaged < 50 m. This short flight distance allows only a very limited time for seals in an approaching vessel's path to escape unless the vessel is able to stop or take avoidance action. At night the seals immediately ahead of the vessel barely moved until the ship had reached them, possibly dazzled by the ship's headlights. Mariners can therefore not assume that the seals will move out of the way of the vessel and the onus of avoidance manoeuvring falls to the vessel captain (see Appendix D).

4.3. Probability of seal displacement with respect to distance from vessel

The overall probability of displacement declined with distance to the side of the vessel path, but was still > 0.50 at the limit of the observation strip at 200 m. Thus the maximum range of vessel disturbance extends beyond the range that can be accurately quantified by observers on vessel bridges. This means that the 'safe distance' for vessels to pass Caspian seals mothers and pups without causing significant disturbance should be considered to be ~250 m.

4.4. Mother-pup separation and displacement

We found a significant association between the probability of mother-pup separation > 20 m, proximity to the side of vessel and ice type. The apparent effect of ice type on reducing the probability of separation may arise partly because mothers and pups treat the ice ridge as cover from disturbance or predators (Fig. A5).

Separation of mother and pup at any time during the pup's dependency period has the potential to compromise pup survival. Separation in the immediate neonatal period (Fig. A7) could disrupt postnatal bonding between mother and pup (Lawson and Renouf, 1985). Even with older pups, separation has the potential to become permanent if mother and pup are displaced beyond their familiar nursery area and are sufficiently far apart to lose communication (Fig. A7). Caspian seal mothers are probably similar to harp seal mothers in using spatial information to return to the location where they left the pup (Kovacs, 1995) and therefore lone pups following mother-pup pairs away from the natal site may be at risk of not being found by their mother upon her return from a foraging trip.

Additional consequences to mother and pup from displacement due to vessel disturbance could arise from induced stress responses (e.g. Atkinson et al., 2015). Release of adrenalin due to the immediate effect of a disturbance, may inhibit oxytocin-mediated mammary blood flow and milk ejection in the mother (Gorewit and Aromando, 1985). Karpovich et al. (2015) demonstrated an increase in heart rate in harbour seals, *Phoca vitulina*, subjected to vessel disturbance, occurring in seals remaining on the ice and also persisting in subsequent haul-out. These authors concluded that repeated vessel disturbance could have a prolonged influence on seals' energetic balance. It is likely that in undisturbed conditions, Caspian seal pup movement is limited to short distances around the nursery site (Wilson et al., 2017). Flight by mother and pup from the vessel, coupled with return to their original site with water access holes and familiar shelter or topography, could therefore result in additional energy costs, although we are unable to quantify these costs at present.

4.5. Vessel-seal collisions

Only seals in the direct path of the vessel (< 10 m from the side of the vessel) are in immediate danger of collision with a vessel. An animal in the water within one vessel beam about the centreline of the vessel track may come under the vessel's drawing forces and be dragged laterally towards the hull and propellers (Silber et al., 2010). Therefore any seal in the water < 10 m to the side of these vessels (beam width range 16–21 m; Table A1) would be in the danger zone.

Although most (98%) mothers with pups at < 10 m responded by attempting to move away, 23% of lone pups at < 10 m did not show any flight response. This is the undoubtedly why the majority (65%) of the vessel-seal collisions witnessed were with lone pups. Our finding that the probability of vessel-seal collisions on the ice increases substantially at cruising speeds of ≥ 4 kn, and that successful manoeuvring around seals always occurred at speeds ≤ 2.2 kn, provides an evidence base for recommending a speed limit of < 4 kn for icebreaker transits through Caspian seal pupping areas. Given that collisions were 12.5 times more likely to happen at night, this would suggest that use of thermal imaging equipment should be mandatory for unavoidable night-time transits through seal breeding areas.

4.6. Population level consequences of icebreaker impacts on Caspian seals

AIS data indicate a minimum of approximately 100 vessel transits through the core breeding area per season during our study period (mean 2.4 per day). The 674 vessel-seal encounters over 39 transits (range 0–357 per transit) observed in this study suggest a few 100 s to 1000 s of mothers and pups could potentially be exposed along this route each season (depending on ice conditions and vessel routing), out of an estimated total ~34,000 breeding females (Dmitrieva et al., 2015). There is significant annual variation in the degree of overlap of the navigation corridor with breeding hotspots, while ice drift can change whether vessel paths intersect with breeding colonies over short time periods. In years with stable ice-sheets, such as 2006 and 2012, vessels tend to reuse channels, potentially repeatedly disturbing the same animals. In other years, greater drift of seal-bearing ice and a wider vessel corridor, e.g. 2011, could mean exposure occurs over a wider area, but with individuals exposed less frequently.

Evaluating the consequences of icebreaker impacts for population demography is not possible at present. However, we can consider icebreaker impacts in the context of other sources of mortality for the population. Since the decline of hunting from the late 1990s, by-catch in illegal fisheries has become the single biggest cause of anthropogenic mortality, and may often exceed the safe Biological Removal (PBR) of ~3200 annually (Dmitrieva et al., 2013). Although the total direct mortality associated with shipping is likely to be less than from by-catch, it may nevertheless be important since it impacts directly on breeding females and their young. In addition to direct mortality, degraded pupping habitat and repeated vessel disturbance have the potential to create energetic costs and stress. While these cannot be quantified fully at this time, cumulatively they may represent an additional avoidable pressure for a population faced with other multiple stressors. Expansion of oil and gas operations in the NE Caspian Sea in future is likely to bring more vessels and shipping routes across the seal breeding area with a proportional increase in impact. Future work could aim to evaluate total cumulative impacts of icebreaker passage using PCoD (Population consequences of disturbance) models, currently being developed in the context of other offshore energy developments (Harwood et al., 2014).

4.7. Mitigation of icebreaker impact on ice-breeding seals in the Caspian

To minimise continuing or future impact on breeding Caspian seals, we recommend a hierarchical approach to mitigation (Appendix D), as is generally accepted to be best practice in industrial settings, comprising: 1) remove exposure of seals to vessel traffic by reducing the need for icebreaker operations during the sensitive breeding season – this may be achieved by planning logistics so supplies are in place prior to the seal breeding season and developing alternative strategies for waste management; 2) seal-avoidance route-planning and pre-emptive mitigation - This may be informed by historical seal pupping location data from previous years (Fig. 1), but also requires current knowledge of the location and approximate densities of seal colonies in the vessel corridor area, which may be obtained by aerial surveys. Vessel transits can then be routed to avoid high density seal aggregations within the navigational constraints of the north Caspian; 3) reactive measures - The difference our study recorded between vessels operated by different shipping companies in reducing speed in high risk areas suggests that attitude and awareness of vessel officers and crew can potentially have a highly significant effect on mitigating impact. However, reactive mitigation should be viewed as a solution only when pre-emptive measures have failed and contact with breeding seals is unavoidable.

Our quantitative impact assessment is currently being used to develop an evidence-based Seal Observer (SO) monitoring and reporting system for vessels traversing Caspian seal breeding ice (Appendix D). Marine Mammal Observers (MMO) monitoring and reporting procedures have become standard best practice world-wide for seismic surveying and drilling for the oil and gas industry (Nowacek et al., 2013). The role of MMOs (SOs) on icebreaking vessels traversing seal habitat should be to advise vessel crews on reactive measures and to document encounters, impacts and avoidance of impact, so that the success of measures such as route planning can be assessed quantitatively. Impact avoidance should be assessed in relation to specific measurable indicators (e.g. number of seal encounters within different distance bands SoV, number of collisions and MP separations ≥ 20 m), as is standard practice for industrial Health-Safety-Environment (HSE) monitoring frameworks.

4.8. Application to other Arctic ice-breeding pinniped species

There is increasing potential for industrial impacts on Arctic marine mammals as economic pressures and climate change push human activity into previously remote and inaccessible areas (Laidre et al., 2015). The present study highlights the need to consider physical impacts on ice-breeding seals and habitats from icebreakers transiting through breeding grounds. Our findings on seal response and types of impact seen in the Caspian will apply broadly to polar ice-breeding seal species. Impacts are likely to vary between species depending on the stability of the ice habitat and site tenacity, flight distance, pup body size and ability to withstand water immersion, mother response to vessel approach, strength of mother pup following behaviour, length of lactation and pup development rates. Arctic icebreakers are much larger, more powerful, and can negotiate thicker ice at higher speeds than Caspian vessels, with concomitant implications for seal visibility, collision avoidance and manoeuvring thresholds. Nevertheless, the general principles underlying the mitigation measures recommended for the Caspian seal can still apply with adaptations to circumstances in the ranges of other ice-breeding pinnipeds.

Acknowledgments

This work was funded by Agip KCO and NCPOC through a contract "Quantitative assessment & impacts on seal population" (2008-397) with the University of Leeds, under the North Caspian Sea Production Sharing Agreement (NCSPSA) Venture. We thank past Company colleagues for support which made this work possible, particularly Walter Rizzi, Gulsim Mutysheva, Igor Lukashov, Vladimir Terentyev and Olivier Pauwels. Davide Speranza and Indira Kenzhegulova also contributed data and photographs. We are also grateful to international team members Brian Black, Brian McNamara and Chris McKnight for invaluable field support. Onboard dedicated observers in different years, including Yesbol Kasimbekov, Nurgul Mukanova, Salauat Kaldebaev, Sergey Ukhov, Damir Zharkenov, Fedor Sarayev, Aidyn Kydyrmanov and Kobey Karamendin, contributed additional data and photographs. Also, we thank the Captain and crews of the survey vessels for their hospitality and cooperation with the study. Finally, we thank Randall Reeves and two other reviewers for their constructive comments on the original manuscript.

Supplementary data

Appendix A – Supplementary Figures A1–A8
Appendix B – Supplementary Tables B1–B3
Appendix C – Supplementary Model Tables C1–C11
Appendix D – Framework for mitigation of icebreaker impacts on Caspian seals

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.05.028.

References

Atkinson, S., Crocker, D., Houser, D., Mashburn, K., 2015. Stress physiology in marine mammals: how well do they fit the terrestrial model? J. Comp. Physiol. B. 185, 463–486. http://dx.doi.org/10.1007/s00360-015-0901-0.

Blanc, R., Guillemain, M., Mouronval, J., Desmonts, D., Fritz, H., 2006. Effects of non-consumptive leisure disturbance to wildlife. Rev. Ecol. (Terre Vie) 61, 117–133.

Davis, R.A., 1981. Report of a workshop on arctic marine mammals. Can. Tech. Rep. Fish. Aquat. Sci. 1005 (iv + 13 pp.).

Dmitrieva, L., 2013. The Abundance, Habitat use and Conservation of Caspian Seals (*Pusa caspica*). (PhD thesis) University of Leeds.

Dmitrieva, L., Kondakov, A.A., Oleynikov, E., Kydyrmanov, A., Karamendin, K., Kasimbekov, Y., Baimukanov, M., Wilson, S., Goodman, S.J., 2013. Assessment of Caspian seal by-catch in an illegal fishery using an interview-based approach. PLoS ONE 8 (6), e67074. http://dx.doi.org/10.1371/journal.pone.0067074.

Dmitrieva, L., Härkönen, T., Baimukanov, M., Bignert, A., Jüssi, I., Jüssi, M., Kasimbekov, Y., Verevkin, M., Vysotskiy, V., Wilson, S., Goodman, S.J., 2015. Inter-year variation in pup production of Caspian seals (*Pusa caspica*) 2005–2012 determined from aerial surveys. Endanger. Species Res. 28, 209–223. http://dx.doi.org/10.3354/esr00689.

Engelhardt, F.R., 1983. Petroleum effects on marine mammals. Aquat. Toxicol. 4, 199–217.

Gershenzon, O.N., Filippova, A.V., Skripnik, E.N., Velikanov, A.S., 2009. Space Technology for the White Sea Greenland Seal Population Protection. Vector Razvitiya V 1. pp. 54–59.

Gizitdinov, N., 2016. Bloomberg news. https://www.bloomberg.com/news/articles/2016-10-14/oil-from-50-billion-kashagan-field-starts-flowing-for-export.

Goodman, S., Dmitrieva, L., 2016. *Pusa caspica*. The IUCN Red List of Threatened Species 2016: e.T41669A45230700. http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T41669A45230700.en. (Downloaded on 03 April 2017).

Gorewit, R.C., Aromando, M.C., 1985. Mechanisms involved in the adrenalin-induced blockade of milk ejection in dairy cattle. Exp. Biol. Med. 180 (2), 340–347. http://dx.doi.org/10.3181/003797-180-42186.

Härkönen, T., Jüssi, M., Baimukanov, M., Bignert, A., Dmitrieva, L., Kasimbekov, Y., Verevkin, M., Wilson, S., Goodman, S.J., 2008. Pup production and breeding distribution of the Caspian seal (*Phoca caspica*) in relation to human impacts. Ambio 37, 356–361.

Härkönen, T., Harding, K., Wilson, S., Baimukanov, M., Dmitrieva, L., Svensson, C.J., Goodman, S.J., 2012. Collapse of a marine mammal species driven by human impacts. PLoS ONE 7 (9), e43130. http://dx.doi.org/10.1371/journal.pone.0043130.

Harrell Jr., F.E., 2016. RMS: Regression Modeling Strategies. R package version 4.5-0. https://CRAN.R-project.org/package=rms.

Harwood, J., King, S., Schick, R., Donovan, C., Booth, C., 2014. A protocol for implementing the interim Population Consequences of Disturbance (PCoD) approach: quantifying and assessing the effects of UK offshore renewable energy developments on marine mammal populations. Report number SMRUL-TCE-2013-014. Scot. Mar. Fresh. Sci. 5 (2).

Huntington, H.P., 2009. A preliminary assessment of threats to arctic marine mammals and their conservation in the coming decades. Mar. Policy 33, 77–82.

Jansen, J.K., Boveng, P.L., Dahle, S.P., Bengston, J.L., 2010. Reaction of harbour seals to cruise ships. J. Wildl. Manag. 74 (6), 1186–1194.

Karpovich, S.A., Skinner, J.P., Mondragon, J.E., Blundell, G.M., 2015. Combined physiological and behavioural observations to assess the influence of vessel encounters on harbour seals in glacial fjords of southeast Alaska. J. Exp. Mar. Biol. Ecol. 473, 110–120.

Kovacs, K.M., 1995. Mother-pup reunions in harp seals, *Phoca groenlandica*: cues for the relocation of pups. Can. J. Zool. 73 (5), 843–849.

Laidre, K.L., Stern, H., Kovacs, K.M., Lowry, L., Moore, S.E., Regehr, E.V., Ferguson, S.H., Wiig, Ø., Boveng, P., Angliss, R.P., Born, E.W., Litovka, D., Quakenbush, L., Lydersen, C., Vongraven, D., Ugarte, F., 2015. Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. Conserv. Biol. 29, 724–737. http://dx.doi.org/10.1111/cobi.12474.

Laist, D.W., Knowlton, A.R., Mead, J.G., Collet, A.S., Podesta, M., 2001. Collisions between ships and whales. Mar. Mamm. Sci. 17, 35–75.

Laist, D.W., Knowlton, A.R., Pendleton, D., 2014. Effectiveness of mandatory speed limits for protecting North Atlantic right whales. Endanger. Species Res. 23, 133–147. http://dx.doi.org/10.3354/esr00586.

Lawson, J.W., Renouf, D., 1985. Parturition in the Atlantic harbor seal *Phoca vitulina concolor*. J. Mammal. 66, 395–398.

Nowacek, D.P., Bröker, K., Donovan, G., Gailey, G., Racca, R., Reeves, R.R., Vedenev, A.I., Weller, D.W., Southall, B.L., 2013. Responsible practices for minimizing and monitoring environmental impacts of marine seismic surveys with an emphasis on marine mammals. Aquat. Mamm. 39, 356–377. http://dx.doi.org/10.1578/AM.39.4.2013.356.

Reeves, R.R., Ewins, P.J., Agbayani, S., Heide-Jörgensen, M.P., Kovacs, K.M., Lydersen, C., Suydam, R., Elliott, W., Polet, G., van Dijk, Y., Blijleven, R., 2014. Distribution of endemic cetaceans in relation to hydrocarbon development and commercial shipping in a warming Arctic. Mar. Policy 44, 375–389.

Silber, G.K., Slutsky, J., Bettridge, S., 2010. Hydrodynamics of a ship/whale collision. J. Exp. Mar. Biol. Ecol. 391 (1–2), 10–19.

Stirling, I., Calvert, W., 1983. Environmental threats to marine mammals in the Canadian Arctic. Polar Rec. 21 (134), 443–449.

Vanderlaan, A.S.M., Taggart, C.T., 2007. Vessel collisions with whales: the probability of lethal injury based on vessel speed. Mar. Mamm. Sci. 23 (1), 144–156.

Vanderlaan, A.S., Corbett, J.J., Green, S.L., Callahan, J.A., Wang, C., Kenney, R.D., Taggart, C.J., Firestone, J., 2009. Probability and mitigation of vessel encounters with North Atlantic right whales. Endanger. Species Res. 6, 273–285.

Vorontsova, M.N., Chernook, V.I., Glazov, D.M., Filippova, A.V., 2008. Current threats to the survival of the harp seal (*Phoca groenlandica*) White Sea population. In: Marine Mammals of the Holarctic, 14–18 October 2008, Odessa, Ukraine, pp. 586–592.

Weilgart, L.S., 2007. A brief review of known effects of noise on marine mammals. Int. J. Comp. Psychol. 20, 159–168.

Wilson, S.C., Dolgova, E., Trukhanova, I., Dmitrieva, L., Crawford, I., Baimukanov, M., Goodman, S.J., 2017. Breeding behavior and pup development of the Caspian seal, *Pusa caspica*. J. Mammal. 98 (1), 143–153. http://dx.doi.org/10.1093/jmammal/gyw176.