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ORIGINAL PAPER

Distinct patterns of Arctic cod (*Boreogadus saida*) presence and absence in a shallow high Arctic embayment, revealed across open-water and ice-covered periods through acoustic telemetry

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Abstract With climate change resulting in unpredictable sea ice conditions between years, it is crucial to gain a more comprehensive understanding of the subsequent effects on Arctic marine ecosystems. Arctic cod (*Boreogadus saida*) play a key role in the Arctic marine food web, serving as a food source that is estimated to contribute up to 75 % of energy transfer to higher trophic levels. To investigate Arctic cod residency and distribution in Resolute Bay (74°44′N, 095°04′W), 85 individuals from four locations in the bay were captured, measured, weighed, implanted with acoustic tags and subsequently tracked on an acoustic array of 49 receivers. Two main periods of residence in the bay were identified, the first in open water and the second under ice cover, and both concluded with a collective mass departure of fish. A generalised linear mixed model was used to investigate the influence of variables on Arctic cod presence/absence in the bay, indicating that ingress and egress were influenced by environmental changes, particularly those associated with the transition from open-water to the ice-covered period. Timing and distribution, during the study period, appeared to be influenced by a combination of physiological acclimation, and a balance between resource availability and refuge from predators. Receiver site Residence Index (RI) analysis revealed strong site fidelity of fish towards the northern areas of the bay, and this behaviour was consistent between tagging groups and individuals, indicating that the majority of tagged cod were representative of a single school. This study represents the first employment of acoustic telemetry to monitor the movements of individual Arctic cod over 9 months, incorporating both open-water and ice-covered periods.

Keywords *Boreogadus saida* · Acoustic telemetry · GLMM · Residence Index · High Arctic

Introduction

Few places on Earth can be described as relatively uninfluenced by human activities. The high Arctic is one such region, where inhospitable conditions have historically limited anthropogenic activities that cause ecosystem disturbance (Ellis and Ramankutty 2008). Over the past few decades, however, sea ice extent in the high Arctic environment has been decreasing as a result of climate change (Stroeve et al. 2007). This has attracted large amounts of vessel traffic, including commercial transport, cruise ships, oil/gas exploration and commercial fishing during expanded open-water periods, particularly across the Northwest Passage (Stewart et al. 2007; Judson 2010; Reeves et al. 2012). As a result of dramatic regional ecosystem disturbance, in terms of both climate change and increasing anthropogenic activities, it is important to obtain baseline ecosystem information from which to predict and monitor changes over time.

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The Arctic marine ecosystem is typified by low biodiversity, relative to temperate and tropical regions (Costello et al. 2010). This ecosystem trait results in a relatively simplified food web based on a limited number of trophic interactions, but this can place increased importance/reliance on individual trophic links. Arctic cod (*Boreogadus saida*) represent a key species in this ecosystem, estimated to transfer up to 75 % of all energy from lower to upper trophic levels through their biomass alone (Bradstreet et al. 1986; Welch et al. 1992; Crawford and Jorgenson 1996). Arctic cod represent the primary food source of most mammalian predators in the high Arctic including beluga (*Delphinapterus leucas*), narwhal (*Monodon monoceros*) and ringed seals (*Pusa hispida*), all of which are important species for subsistence and traditional food sources (Welch et al. 1992; Crawford and Jorgenson 1996; Asselin et al. 2011). Additionally, Arctic cod commonly occur in the diets of many other species, including teleosts and sea birds (Crawford and Jorgenson 1996; Matley et al. 2012; Harter et al. 2013; Hop and Gjøsæter 2013). As such, baseline data on Arctic cod represent an essential prerequisite not only for the monitoring of the species, but also for the Arctic marine ecosystem as a whole.

Arctic cod, a member of the Gadidae family, feed predominately on copepod eggs and nauplii during the larval stage (Michaud et al. 1996). With increasing size, juveniles feed mainly on copepodites, switching to amphipods and calanoid copepods after maturity (Bain and Sekerak 1978; Benoit et al. 2010; Renaud et al. 2012; Bouchard et al. 2014). In addition, fish have also been found in the stomachs of mature individuals and cannibalism has been documented (Benoit et al. 2010; Matley et al. 2013). Arctic cod have a circumpolar distribution in the high Arctic, inhabiting various habitats along the continental shelf, including shallow coastal waters, epipelagic surface waters and deep-water areas (Geoffroy et al. 2011). They are strongly associated with sea ice, which is proposed to offer protection from predators, suitable spawning habitat and food resources derived from ice-associated primary production (Crawford and Jorgenson 1993; Bouchard and Fortier 2011; Crawford et al. 2012). In the Northwest Passage region, Arctic cod are thought to spawn under ice between November and March (Hop and Gjøsæter 2013), with eggs hatching between April and May (Bouchard and Fortier 2011).

The use of shallow coastal areas has been reported in the summer months by all sizes of Arctic cod, particularly in the Canadian Arctic Archipelago (CAA; Welch et al. 1993; Drost et al. 2014). Shallow embayments throughout the CAA are highly productive areas, particularly around river mouths where the seasonal mixing of fresh and salt water stimulates productivity (Hop and Gjøsæter 2013). Freshwater run-off in such embayments can also offer a thermal refuge (Bouchard and Fortier 2011; Parker-Stetter et al. 2011). Arctic cod may exhibit extended residence within these embayments to exploit seasonal resources, even during the open-water period when sea ice is absent. In turn, the use of shallow coastal embayments by Arctic cod offers important foraging opportunities to marine predators such as seals and whales (Crawford and Jorgenson 1993; Geoffroy et al. 2011); thus, the presence in these areas is particularly important for Inuit communities to support traditional practices, such as hunting.

The extent to which Arctic cod migrate horizontally throughout the Arctic region is unclear. It has been suggested that Arctic cod are unlikely to undertake long-distance migrations (Benoit et al. 2010); however, due to this species' small size, the ability to track the movements of individuals over time had not been possible. To date, the occurrence, residence and spatial use of Arctic cod have only been investigated through intermittent hydroacoustic surveys over relatively short timescales (Crawford and Jorgenson 1993; Benoit et al. 2008; Geoffroy et al. 2011; Crawford et al. 2012; Benoit et al. 2014; Geoffroy et al. submitted). The use of acoustic telemetry in this study provided the first opportunity to continuously document the presence/absence and distribution of individual Arctic cod in this location, providing important baseline data on the fine-scale movement of this species in the high Arctic. The specific aims of this study were to: (1) describe the spatial distribution of Arctic cod in Resolute Bay, Barrow Strait, in both open-water and ice-covered periods, and determine whether cod in the bay represent discrete schools or one large school; and (2) examine the presence and absence of Arctic cod in Resolute Bay, in relation to environmental conditions and toothed whale presence.

Materials and methods

Study site

Resolute Bay is located on the southern coast of Cornwallis Island, Nunavut, Canada (74°41N, 94°52W; Fig. 1), where the presence of Arctic cod was first documented in 1972 (Green and Steele 1975). The bay is ~3.7-km wide at the mouth and ~3-km long from north to south. Depths within the bay are variable (Fig. 1), with a pinnacle extending up to ~2-m depth at the centre of the mouth of the bay, which restricts the entry of pack ice in the winter. At the north of the bay, a deep-water area extends down to ~30 m. The substrate is comprised of rock and soft sediments, with patches of kelp throughout. There are three freshwater run-off inputs, Resolute Stream on the west shore, the Mecham River and an unnamed stream on the east shore. Tidal range averages ~1.5 m, with minimal tidal flow within the

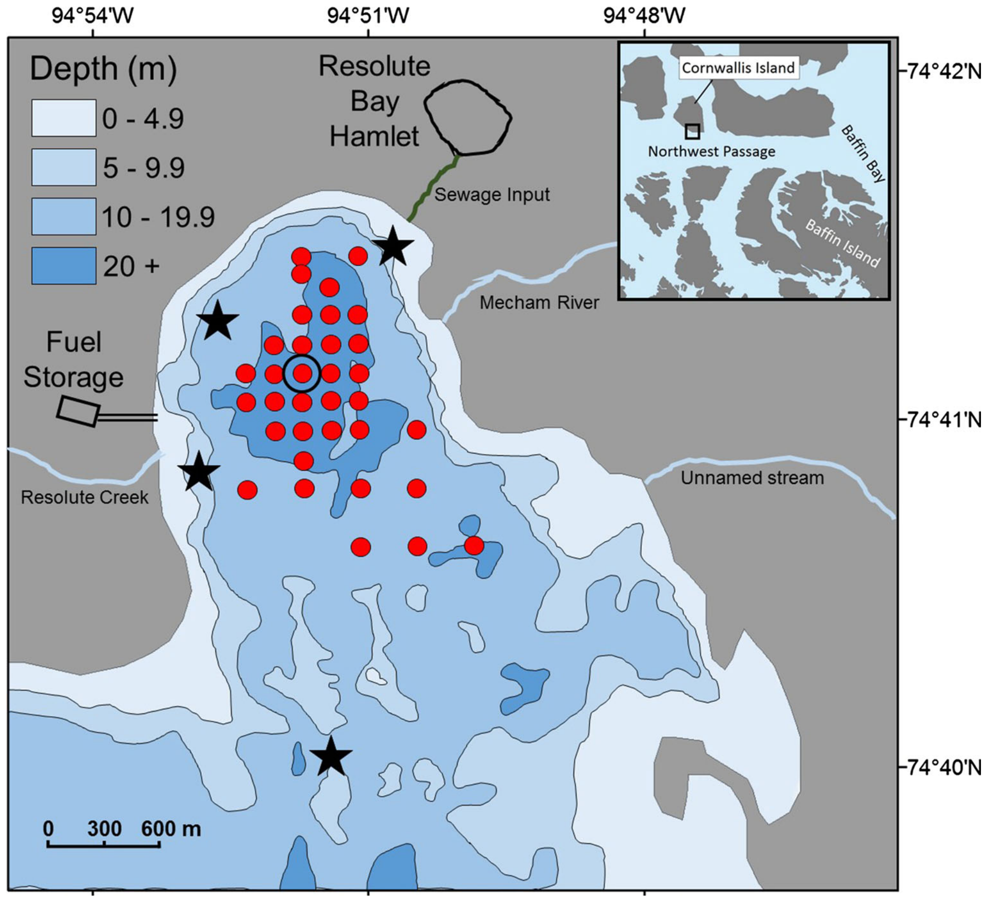

Fig. 1 Resolute Bay study site, located on Cornwallis Island, Nunavut, Canada (74°41N, 94°52W). *Inset* shows location of study (*black box*) relative to the broader Canadian Arctic Archipelago (CAA). *Red dots* represent receiver stations, the *black circle* indicates the location of the oceanographic station and CPOD echolocation recorder. *Stars* indicate capture locations for Arctic cod (*Boreogadus saida*). (Color figure online)

bay. At the north end of the bay and slightly offset to the east is the community of the Resolute Bay Hamlet, which has a population of ~250 people. Untreated sewage from the town is discharged directly into the northeast part of the bay through a pipe on the shore, and on the western shore, there is a fuel storage facility. Resolute Bay is one of seven shallow embayment habitats available along the 100-km coastline of south Cornwallis Island.

Fish capture and tagging

Arctic cod were located in the bay with a split-beam hydroacoustic system (BioSonics® DT-X; 200 kHz; 6° nominal beam width) coupled to a JRC® GPS to geo-reference data directly on a Panasonic® Toughbook CF-29 computer. Searching and fishing were conducted from a 5.5-m aluminium hulled boat with a 30-hp outboard motor. When a school was identified by the hydroacoustic system, the boat was held in place under power while rod and reel were used to capture Arctic cod by jigging with hook size #5 sabiki rigs, with the feather removed and bead retained. On capture, hooks were removed and the fish were placed into a holding tank on board. A tagging station was set up in a tent on the shore of the bay to minimise transport and holding time. Following a minimum holding period of 1 h to ensure no lasting effects of capture, each specimen was placed in an anaesthetic bath of MS222 (4 g:20 l of seawater). After 2–5 min, operculum movement became slow and irregular and the fish was considered sufficiently anaesthetised. A small piece of pectoral fin (~5 mm^2) was removed with surgical scissors for future genetic and stable isotope analysis. Fork [*FL*] and total [*TL*] lengths were measured to the nearest 1 mm and weight [*TW*] measured to the nearest 0.01 g. The fish were then placed into a sponge cradle their gills intermittently irrigated with seawater from a squeeze bottle. A small mid-ventral incision (~8 mm) was made anterior to the pelvic fins, and a Vemco® V6 transmitter (380 s nominal delay between transmissions) inserted into the body cavity, with a tag to body weight ratio <2 % for all specimens. The incision was closed with two independent coated Vicryl sutures (Ethicon® VCP423, 3-0 FS-2 cutting) tied with a double surgeon's knot. All surgical equipment, including the transmitter, was sterilised by soaking in a 10 % betadine solution prior to surgery, and the incision site was swabbed with the same solution. The duration of each procedure was 2–4 min. Fish were then placed in a recovery tank and monitored until they regained equilibrium. All fish were released together at the site of capture,

~1 h after the final surgery. Standard tagging procedures were reported following Thiem et al. (2011).

Acoustic telemetry

Acoustically tagged Arctic cod were tracked with an array of 49 Vemco VR2W 180-kHz receivers (Fig. 1). The array was designed as a grid to cover the bay as effectively as possible with receiver deployed at depths >15 m and spaced between 150 and 300 m apart. This deployment depth was selected based on the minimum depth that receivers would be safe from sea ice, based on sea floor scaring identified by the hydroacoustic unit. Moorings consisted of a ~2-m braided rope riser attached to a mesh-wrapped rock anchor of ~40 kg. The rope riser was separated by an ORE® Port ME acoustic release and held vertical by a hard lift float, with the receiver attached to a V-cup above the float. Seventeen V6-4x sync tags were deployed throughout the array to monitor system performance (*see below*). Receivers were deployed and maintained from July 2012 to August 2013, but receiver battery powers appeared to run out around May based on sync tag detections (*see below*). For this reason, data analysis was restricted to the period from 1 August 2012 to 30 April 2013.

Detection range testing

To assess receiver performance in the bay, a fixed detection range test was established for the duration of the project, located at the northern end of the bay where the depth to substrate was ~25 m. The detection range test consisted of a fixed acoustic tag and receiver mooring followed by six fixed receiver moorings in a linear design, together providing seven distance intervals for assessment: 0, 88, 150, 220, 300, 350 and 435 m (see Supplementary material Fig. S1). The acoustic tag used was a V6-4x (Vemco®), the same tag type as those surgically implanted in all study specimens, but with a nominal delay of 600 s. Following array retrieval and download, two periods were selected to assess the difference in receiver performance during open water and under full ice cover. The open-water period was assessed from 1 August to 30 September, 2012, while the ice-covered period was assessed was from 1 December 2012 to 31 January 2013. For both periods, the number of detections logged per day was calculated as a proportion of the expected number of daily transmissions. These proportions were plotted for each of the set distances intervals and a Weibull 5-parameter peak curve fitted to the data.

Environmental and marine mammal monitoring

Environmental parameters were monitored and obtained from an oceanographic station, moored at ~25 m and located in the central northern portion of the bay (Fig. 1). A Satlantic® STOR-X obtained and archived dissolved oxygen (DO), sampling for 30 s every hour at 5 s resolution. Water temperature and salinity were measured by a Sea-Bird Electronics® 37-SIP CTD, sampling for 30 s every hour at 1 s resolution, also archived on the STOR-X. Weekly, ice cover proportions within the bay were obtained from the Canadian Ice Service archives (ec.gc.ca/glaces-ice), with photoperiod and moon illumination obtained from the time and date online archives (timeanddate.com). Toothed whale presence and absence was monitored on a Chelonia Limited® C-POD echolocation recorder, also located in the central northern portion of the bay (Fig. 1). This device recorded the time and date of toothed whales presence by recording and logging the click vocalisations produced by beluga and narwhal.

Data analysis

To identify and remove false detections created by acoustic tag collisions (Heupel et al. 2006), the full detection database was filtered using the White-Mihoff Filtering Tool, which identifies false detections in two stages. Firstly, detections were considered false if isolated on the full array by an hour. Following this initial filtering step, for the remaining detections, swimming speeds between concurrent detections were assigned. Swimming speeds were assessed for feasibility based on maximum sustained swimming speed and an effective detection range of 150 m. Detection range values were based upon detection range test results (see "Results" section). Since no published data on Arctic cod maximum sustained swimming speeds currently exist, these were based on the published swimming speed for a similar species, Atlantic cod (*Gadus morhua*) (He 1991). Based on a maximum sustained swimming speed of 0.9–1 BL s^{-1} in cold water and a mean body length of tagged Arctic cod of 19.8 cm, this translated to an average swimming speed of 0.19 ms^{-1}. Detections isolated by a swimming speed in excess of this were considered false and deleted.

Detections on the complete array were plotted by unique tag ID code over time to provide a visual depiction of temporal presence and absence of tagged fish within the bay. Ice cover, salinity, dissolved oxygen, water temperature, photoperiod, moon illumination and toothed whale presence were then overlaid on the cod presence and absence data to assess patterns and associations. To ensure that cod presence/absence records represented a true biological pattern rather than a result of acoustic array functional dynamics, array performance was examined throughout the course of the study. The presence of sync tags allowed the temporal functional performance of the receivers to be tested, even when tagged cod were not present in the bay. Using the receiver event data, average daily transmission conversion rates could be calculated as the difference between the number of received pings divided by eight (the number of pings transmitted in a coded ID sequence), relative to the number of recorded detections.

A generalised linear mixed model (GLMM) with a binomial error structure and logit link function was used to test for Arctic cod presence/absence (binary response variable) each day in Resolute Bay, relative to environmental parameters and toothed whale presence. Fixed parameters included in the model were toothed whale presence/absence, salinity (PSU), dissolved oxygen (DO; %), water temperature (°C), sea ice coverage (%), photoperiod (day length; hours), moon phase (illumination scale from 0 to 1) and month. Arctic cod ID was included as a random effect. Analysis was performed using R version 3.1.1 (R Development Core Team 2014) where the GLMM was fit using the glmmPQL function in the MASS package with a first-order autoregressive function (AR1) to account for temporal autocorrelation. To assess model fit, we calculated a marginal r^2 (solely fixed effects) and conditional r^2 (both fixed and random effects) using the methods described by Nakagawa and Schielzeth (2013). Significance was defined by P values <0.05.

Arctic cod Residence Index (RI) was calculated as the number of days an individual fish was detected at each receiver station divided by the total number of days the fish was detected anywhere on the acoustic array. RI was used over raw number of detections as it reduces the potential bias of a large number of detections, at a given station, being generated by a low number of individuals. Results were plotted on the array map as graduated symbols in ArcMap® 10.2, to visually depict spatial preference within the bay area. Mean RI was calculated for all acoustically tagged cod for the entire monitoring period of 1 August 2012 to 30 April 2013. To investigate the influence of tagging location on spatial use, mean RI was calculated for all individuals grouped by tagging location. To investigate individual variability in spatial use, RI values were calculated for the four individual Arctic cod from the largest tagging group (c), with the highest number of days detected on the array. To investigate temporal trends in spatial use, mean RI was calculated for the open-water period 1 August to 30 September 2012 and the ice-covered period 10 November 2012 to 10 January 2013, for all cod present for >8 days in both periods ($n = 27$).

Results

Study specimens

A total of 85 Arctic cod were acoustically tagged (Table 1), and all individuals actively swam off following the tagging process. Total Length (*TL*) of tagged individuals ranged from 155 to 274 mm (mean = 198 ± 2.3 SE), while weight ranged from 27.8 to 122.3 g (mean = 53.2 ± 1.9 SE). Based on *TL*s, all tagged individuals were considered to be mature.

Detection range test

Effective detection range for this study was defined as the distance at which 60 % of transmissions were detected and logged based on the Weibull 5-parameter peak curve (Kessel et al. 2014). As expected, in this relatively shallow low ambient noise environment, both a minimum and maximum effective detection range were found (Kessel et al. 2015), and these values varied between open-water and ice-covered periods (Fig. 2). During the open-water period, the receivers had a minimum effective detection range of 10 m and a maximum of 130 m, while during the ice-covered periods, a minimum of 40 m and a maximum of 198 m were found. Due to the comprehensive array grid design, the bay experienced good coverage in both periods; consequently, it was unlikely a tagged fish could be present in the bay for very long before being detected.

Detection summary

Between the 1 August 2012 and the 30 April 2013, a total of 1,212,156 detections from 77 of the 85 tagged Arctic cod IDs were recorded on the acoustic array. Filtering, based on a 1-h isolation interval, identified 6210 false detections which were subsequently removed from the database. The second stage of filtering, assuming a swimming speed >0.19 ms^{-1}, identified an additional 65 false detections that were removed. The final filtered Arctic cod detection database contained a total of 1,205,881 detections, which were used for subsequent analysis.

Basic presence/absence pattern

Residence time in the bay varied between individuals from 30 to 259 days (mean = 96.6 ± 4.9 SE). After an initial 82-day period of extended residence in the bay area, all but three of the 77 individuals exhibited a collective departure on the 22 October 2012 (Fig. 3). Following a 15-day absence, 44 Arctic cod collectively returned to the bay array on 7 November 2012, with the rest of the fish not detected inside the bay again. After a 63-day-long second residence period inside the bay, again all but the same three individuals displayed a collective departure on the 9 January 2013 (Fig. 3). Presence in the bay was observed during both open-water and ice-covered periods (Fig. 3b). The initial absence occurred during ice formation and coincided with ice cover of 80–90 % (Fig. 3b). During the

Table 1 Summary of tagged Arctic cod characteristics for each tagging group (a to d) and total individuals tagged; TL is total length, SD is standard deviation, and RI is Residence Index, with the top five receivers in descending order of RI value from left to right

Tagging group	Number	Date tagged	Mean TL (cm)	TL range (cm)	TL SD	RI top 5 receivers
A	12	31-Jul-12	20.5	18.0–27.4	2.6	2, 1, R1, V1, 5
B	8	26-Jul-12	18.3	15.5–21.4	2.0	2, 1, R1, V1, 5
C	35	03-Aug-12	19.8	17.0–24.9	1.9	2, 1, R1, V1, 5
D	30	30-Jul-12	20.0	17.0–25.8	2.0	2, 1, R1, V1, 5
Total	85	Jul–Aug 2012	19.8	15.5–27.4	2.1	2, 1, R1, V1, 5

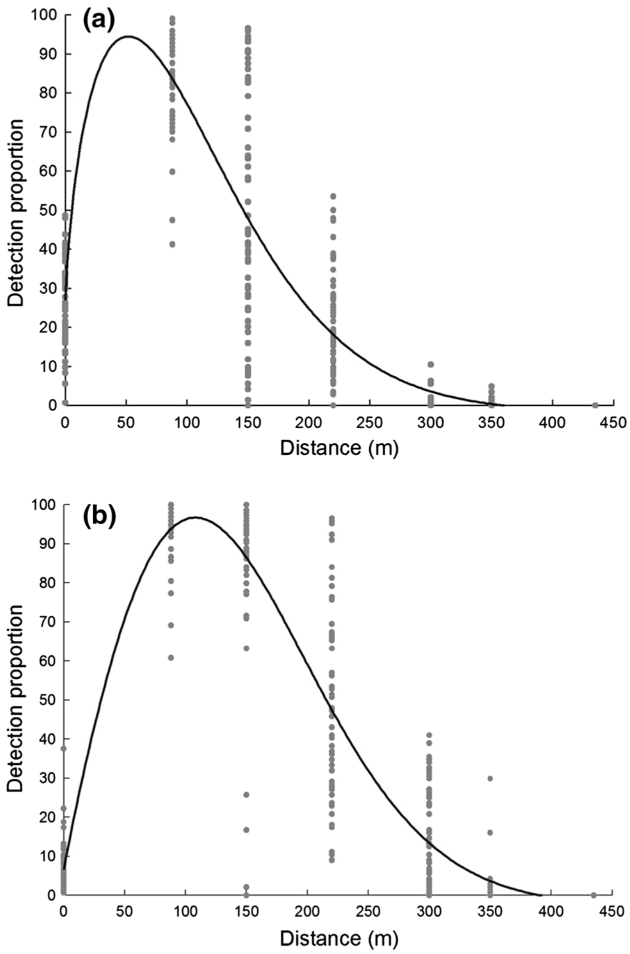

Fig. 2 Detection range profiles for **a** open-water period (1 August–30 September, 2012) and **b** ice-covered period (1 December 2012–31 January 2013). Effective detection range was defined by the distances at which 60 % of transmissions were recoded

time of initial absence (22 Oct–7 Nov), receiver performance was operating between 60 and 75 %, with received pings consistent with that expected from the sync tags (Fig. 3a). Following the second mass departure from the bay, receiver performance was operating between 60 and 85 %, and received pings were again consistent with that expected from the sync tags. Thus, functional receiver performance and consistent detection range test results throughout the monitoring period demonstrated that the observed presence/absence pattern represented true behaviour of the study species and was not an artefact of array functionality (Payne et al. 2010).

Factors driving presence and absence

The generalised linear mixed model estimated a significant negative relationship between Arctic cod presence/absence and salinity, sea ice concentration, moon phase and toothed whale presence (Table 2; Fig. 3). A significant positive relationship occurred between Arctic cod presence/absence and dissolved oxygen, photoperiod and month (January to December; Table 2). A non-significant negative relationship between Arctic cod presence/absence and water temperature occurred, and water temperature was highly correlated with salinity (0.77) and sea ice concentration (0.84).

Spatial distribution

Mean RI values of all Arctic cod ($n = 77$) indicated a preference for the deeper area towards the north of the bay (Fig. 4). The five receiver sites to the very north of the bay had the highest mean RI values, ranging between 0.67 and 0.86 (Table 1). These receiver sites were in closest proximity to the town residence, marina and sewage outlet. Tagging location did not influence spatial use within the bay, with all four groups exhibiting a near identical pattern of RI (Fig. 4; Table 1). The five receivers with the highest mean RI values were consistent, not only by receiver sites, but also by RI value ranking from high to low, for total tagged cod and each of the four tagging groups (locations A to D; Table 1; Fig. 4). The four individuals from capture group (c), with the highest number of days recorded on the acoustic array, were ID 862 ($n = 144$), ID 865 ($n = 144$), ID 870 ($n = 144$) and ID 867 ($n = 143$). All four individuals showed highest RI at the same five monitors to the very north of the bay. When comparing mean RI between open-water and ice-covered periods, for all individuals present in both periods for >8 days ($n = 27$), there was variation in spatial use between the two periods (Fig. 4). During the open-water period, the deep area to the very north of the bay

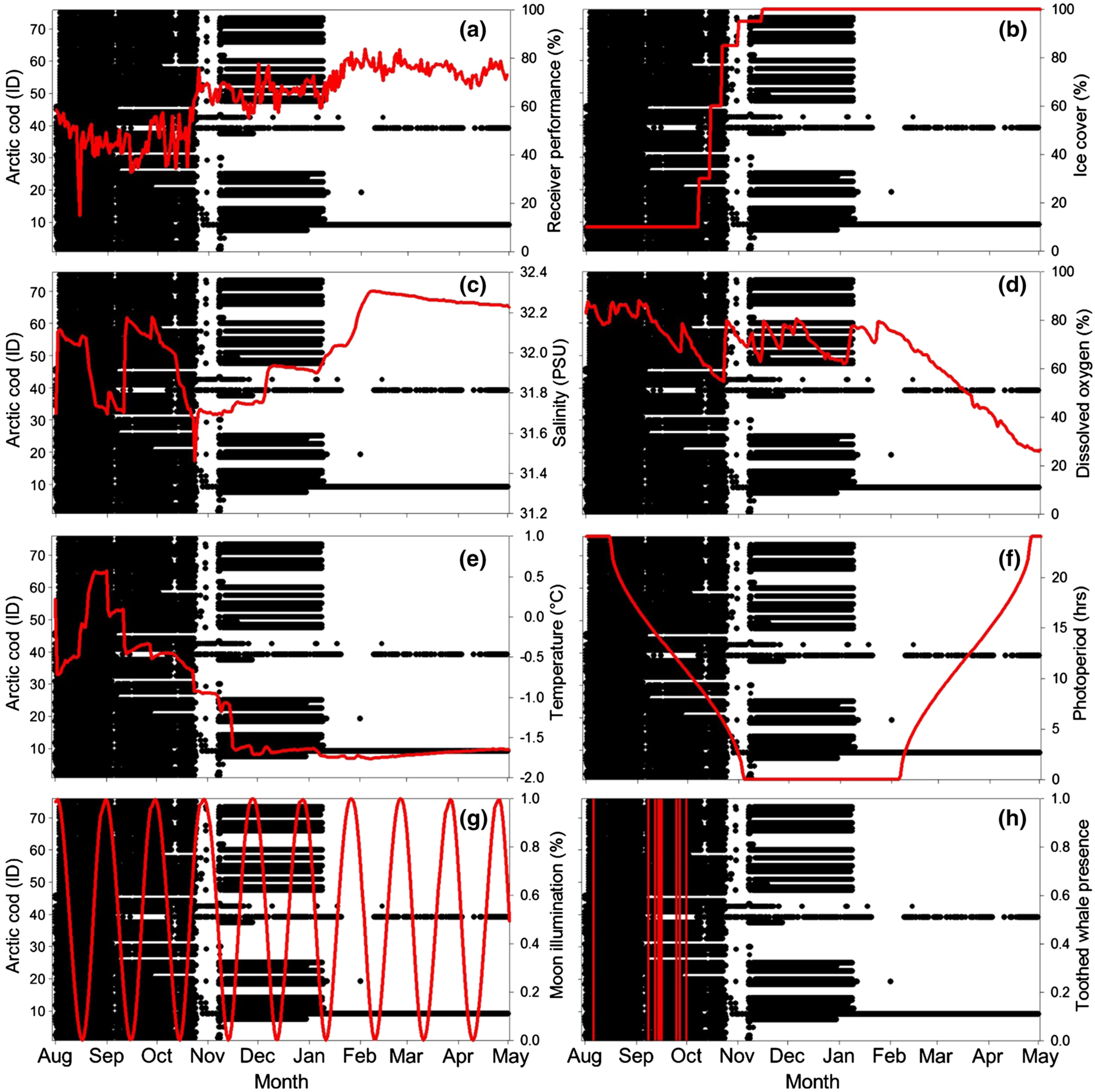

Fig. 3 Arctic cod presence and absence in relation to various factors. *Black dots* represent cod detections and *red lines* represent: **a** receiver array performance (%); **b** ice cover within the bay (%); **c** salinity (PSU); **d** dissolved oxygen (%); **e** water temperature (°C); **f** photoperiod (h); **g** moon illumination (%); and **h** toothed whale presence. (Color figure online)

was favoured, whereas in the ice-covered period, the entire northern half of the bay was used more consistently.

Discussion

Arctic cod captured and released in Resolute Bay, in July/August 2012, showed an extended residence in both open-water and ice-covered periods. During their overall residence, the majority of the Arctic cod showed two separate periods of residence: an initial residence (82 days) during the open-water period and a second residence (63 days) during the ice-covered period. This was separated by a 15-day general absence during the latter stages of ice formation, beginning at around 80 % cover. When resident in the bay, a preference for the deep area to the north was shown during the open-water period, with wider use of shallower areas under ice cover. Spatial use between tagging groups and individuals showed

Table 2 Parameter estimates from generalised linear mixed model predicting Arctic cod presence in Resolute Bay relative to predatory and abiotic factors

Predictor variables	Value	SE	*t* value	*P*
Intercept	186.110	19.308	9.64	<0.001
Sea ice coverage	−0.058	0.005	−10.99	<0.001
Salinity	−5.957	0.596	−9.99	<0.001
Dissolved oxygen	0.014	0.006	2.17	0.03
Sea temperature	−0.359	0.027	−1.34	0.18
Photoperiod	0.198	0.022	8.85	<0.001
Moon illumination	−0.010	0.001	−6.68	<0.001
Month	0.520	0.068	7.69	<0.001
Whale presence/absence	−0.302	0.139	−2.18	0.03
Random effect				
Cod ID estimated variance ± SE = 2.73 ± 1.65				
Residual estimated variance ± SE = 1.32 ± 1.15				

The autocorrelation parameter estimate (Φ) was 0.42

SE standard error

close consistency, indicating that the majority of individuals sampled were representative of one large mobile school, rather than several smaller schools. This represents the first account of a mass behavioural pattern exhibited by this species, over an extended time period. Two explanations for the observed pattern are proposed: (1) response to changing environmental conditions necessary for physiological acclimation and (2) changes in the distribution of prey resources relative to changes in predation risk.

Arctic cod are relatively eurythermal and euryhaline for a high-latitude fish species, and the observed variability fell within their known physiological tolerances (Bradstreet et al. 1986); however, the rate of change in environmental variables can influence habitat selection as the result of the time required for physiological acclimation (Goddard et al. 1992). It appears that a combination of environmental factors were influencing Arctic cod presence/absence within the bay area during the study period. Despite low variation in water temperature (∼1.5 °C) and salinity (∼0.8 PSU), and high correlation with sea ice cover, Arctic cod were more probable to be absent at higher sea ice cover and salinities, and lower water temperatures and dissolved oxygen (DO) proportions. These four variables in concert probably influenced the initial mass departure from the bay during ice formation. Fish plasma typically freezes between −0.5 and −0.8 °C (Goddard et al. 1992), and the initial mass departure coincided directly with a rapid (≤24 h) drop in water temperature across this boundary. Arctic cod are cold-adapted species, producing antifreeze in order to inhabit sub-zero water temperatures (Osuga and Feeney 1978). Arctic cod in Disko Bay, Greenland, were found to contain high levels of antifreeze in the summer months, relative to other local fish species (Enevoldsen et al. 2003); however, the exact timing consistency between the temperature drop and the initial mass exodus merits future investigation. The deeper waters outside the shallow bay would have remained more stable during ice formation, in terms of the measured environmental variables, allowing the Arctic cod to gradually acclimate over the 15-day absence, and then return under full ice cover.

Moon phase was negatively associated with cod presence. It is possible that the approach of the full moon may have triggered departure from the bay to perform a biological function, such as spawning. Lunar/tidal cycles have been strongly linked to spawning activity in tropical and subtropical fish species, but to date, little evidence has been presented for this phenomenon in temperate and polar regions (McMullin et al. 2009). However, it has been hypothesised that sex steroid concentrations in Atlantic cod are linked to lunar cycles (Fraser Cameron, University of Iceland, Unpublished data), and second mass departure does fall within the expected spawning period, November to March (Hop and Gjøsæter 2013).

Throughout the open-water period, increased predation risk from mammalian and avian predators in the shallow bay, would have been balanced by increased resource availability (Craig et al. 1982). Freshwater inputs and sewage outflow would have stimulated productivity (Turek and Center 1987; Hop and Gjøsæter 2013), while Arctic cod, visual predators (Benoit et al. 2010), would have further benefited from enhanced feeding opportunities in shallow sunlit waters, explaining the significant positive relationship with photoperiod. Despite a significant negative relationship with cod presence, toothed whale presence did not trigger a mass exodus on any occasion, during the open-water period. A trade-off between resource availability and predation risk is further supported by spatial use within the bay over the initial residence period. The highest RI values were recorded at most northerly deeper (>20 m) receiver sites, in closest proximity to the sewage outlet. In addition to increased nutrient inputs, the deeper depression would have offered partial refuge, relative to the shallower areas. This observation was consistent with Welch et al. (1993), who found cod to favour depressions within shallow embayments.

During ice formation/cover and the polar winter, increased salinity and sunlight limitation would have restricted primary productivity (Turek and Center 1987); thus, DO and food resources would be continually reduced. Also, plankton abundance in the adjacent Allen Bay was documented to be markedly reduced in the prolonged presence of large cod schools (Crawford and Jorgenson 1996), which would have also occurred in Resolute Bay over the course of both residences. The mature Arctic cod would have maintained or even increased energy requirements for

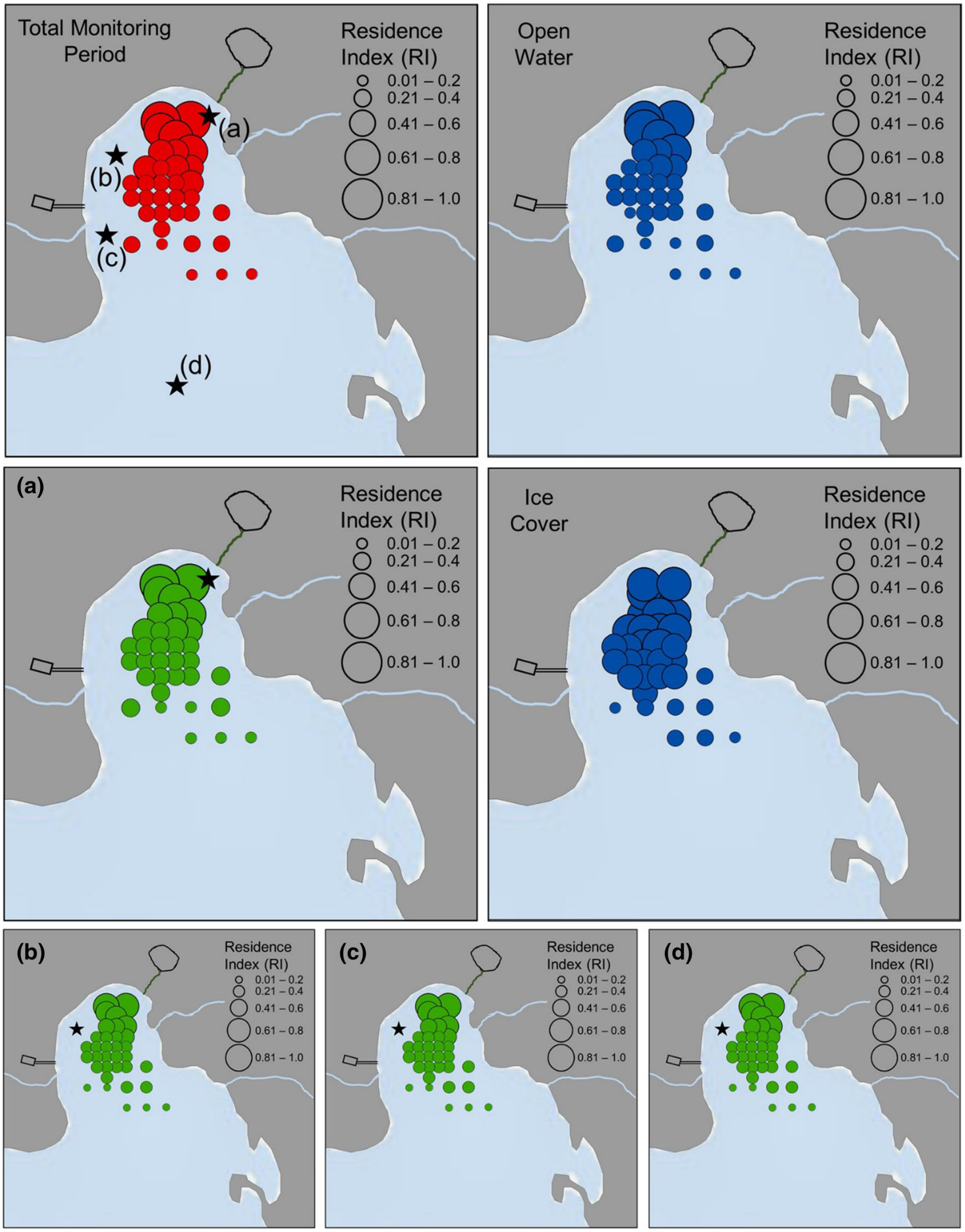

Fig. 4 Arctic cod Residence Index (RI) by acoustic receiver station. *Top left* (*red circles*) represents mean RI for all tagged Arctic cod across the entire monitoring period 1 August 2012–30 April 2013. *Stars* represent tagging locations of Arctic cod. *Blue circles* represent mean RI for all cod recorded for >8 days in both open-water and ice-covered periods ($n = 27$); *top right* for the open-water period 1 August to 30 September 2012; and *middle right* for the ice-covered period 10 November 2012 to 10 January 2013. *Left central* and *bottom row* (*green circles*) represent mean RI for Arctic cod by capture location (**a**–**d**, indicated by *stars*) across the entire monitoring period 1 August 2012–30 April 2013. (Color figure online)

gonadal growth as spawning season approached (Lambert and Dutil 2000; Hop and Gjøsæter 2013). At the time of the initial mass exodus, increasing ice cover in the adjacent channel would have displaced toothed whales from the region and greatly reduced the threat of avian predation. This would have afforded the Arctic cod the first opportunity to exploit alternative resources outside of the bay, with an additional benefit of reduced predation risk.

On return to the shallow embayment, during the second residence under full ice cover, a larger area, including deep area in the north and the adjacent shallower areas, was used more commonly. This was consistent with the findings of Crawford and Jorgenson (1993), who describe Arctic cod schools to spread out under high ice cover relative to open water. Predation pressure by birds and toothed whales would have been eliminated in the ice-covered period; thus, shallow areas could have been used with decreased risk. Additionally, reduced primary productivity under ice cover may have increased stagnation in the deep-water pocket, and/or necessitated increased spatial use in search of more sparsely distributed food resources. During the winter months following the second mass exodus, cod could be more reliant on bioluminescence in deeper water, either predating directly on bioluminescent zooplankton, or using the light they produce to locate other food sources (Benoit et al. 2010).

The sample size and multiple sampling locations in this study were presumed to have provided a sufficient representation of the overall Arctic cod presence in Resolute Bay, during the monitoring period. It must be noted that rod and reel as a capture technique tend to favour bolder individuals and transmitter size limited the minimum size of cod tagged, thus, potentially presenting a bias in the representation of the general population. All but eight of the 85 tagged individuals were detected on multiple days. There are several possible reasons the other eight were never detected. Of these eight, four were released at the mouth of the bay [release location (d)] and may not have ever entered the bay. It is also possible that any of these eight cod were subject to immediate predation or tag failure. For the rest of the cod that were detected, the monitoring period was limited by the battery lives of the tags and receivers. As such, it was not possible to know whether these individuals returned to the bay area in the following months, i.e. do the same individuals inhabit the bay in consecutive years? Double tagging for extended battery life would be required to answer this question.

Conclusions

The results of this study indicate that in both open-water and ice-covered periods, a shallow Arctic embayment constituted an important habitat for Arctic cod. The employment of acoustic telemetry allowed, for the first time, consistent monitoring of the movements of a large number of individual Arctic cod across open-water, ice-formation and ice-covered periods. The presence and absence of these fish within Resolute Bay was apparently driven by a combination of environmental factors, and a trade-off between resource availability and predation risk. From the parameters measured in this study, it has only been possible to speculate on the exact variables contributing to the distinct pattern observed; thus, future focused investigation is required to identify the specific contributing factors. While present in the bay, it appears that the majority of the tagged cod were part of a single school, and therefore a single biological unit. Extended open-water residence of Arctic cod supports the role of shallow embayments as feeding grounds for both avian and marine mammal predators in the high Arctic (Crawford and Jorgenson 1993; Geoffroy et al. 2011). Ultimately, it is hypothesised that a combination of physiological process, a spatial shift in resource availability, predation risk and possibly a biological trigger for spawning, defined Arctic cod distribution.

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