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FEATURE ARTICLE

Combining telemetry and fisheries data to quantify species overlap and evaluate bycatch mitigation strategies in an emergent Canadian Arctic fishery

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ABSTRACT: Greenland halibut *Reinhardtius hippoglossoides* are bottom-dwelling flatfish that support commercial and community fisheries in Baffin Bay, Canada. Recently, exploratory inshore summer fisheries have raised concerns surrounding the bycatch of Greenland sharks *Somniosus microcephalus* and Arctic skate *Amblyraja hyperborea*, which are susceptible to overfishing due to their conservative life history traits. To explore fisheries selectivity and opportunities for bycatch mitigation, we combined pop-up satellite archival tags (PSATs) and fisheries data to assess habitat overlap and catch trends across these 3 species. PSAT data showed variable inter-specific overlap, with Greenland sharks primarily inhabiting depths <1000 m (725 ± 193 m), Greenland halibut inhabiting a narrower depth range (1030 ± 113 m), and Arctic skates overlapping depths (950 ± 225 m) of both species. However, fisheries data suggested high inter-specific overlap at deepest depths, with peak catch-per-unit-effort (CPUE) of all species at depths 800–1000 m. A marked decline in Greenland shark CPUE was observed throughout the fishing season which was best explained by cumulative fishing pressure. Combined tagging and fisheries data suggest that targeting specific seasonal habitat will not decrease bycatch, and inshore summer longline fisheries should be evaluated in the context of potentially high elasmobranch mortality, with enforced bycatch handling practices and alternative mitigation measures (e.g. gear modification or reduced soak times) required.

KEY WORDS: Greenland shark · *Somniosus microcephalus* · Greenland halibut · Arctic skate · PSAT · Electronic tagging

Bycatch of Greenland shark *Somniosus microcephalus* following depredation of Greenland halibut *Reinhardtius hippoglossoides* on a deep-set longline, Arctic Canada.

Photo: Angela L. Young

1. INTRODUCTION

Bycatch of non-targeted species in commercial fisheries is a global conservation concern that influences the sustainability of fish populations and ecosystem function (Davies et al. 2009). Bycatch reduction is challenged by limited engagement in mitigation strategies, lack of coordinated management across governances, and biological data gaps for key species (Lewison et al. 2011). Robust life history information for non-target species can improve bycatch mitigation strategies but is often lacking for species of low commercial value, including many elasmobranch species (sharks, skates, and rays) that can comprise a high

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proportion of fisheries bycatch. Elasmobranch bycatch reduction is a current priority due to reported population declines (Davidson et al. 2016, Pacoureau et al. 2021) and their high proportion of threatened species across marine vertebrate groups due in part to slow growth, long lifespans, and late maturity (Hoffmann et al. 2010, Dulvy et al. 2014, 2017).

Longline fisheries have the highest rates of elasmobranch bycatch (Oliver et al. 2015) due to non-selectivity and the susceptibility of olfactory predators to bait fisheries, further challenged by highly variable post-release survival (Musyl & Gilman 2019, Whitney et al. 2021). However, the elevated sensory capabilities of many elasmobranchs also present alternative mitigation strategies such as magnetic or odour deterrents (Jordan et al. 2013), though effectiveness of these strategies appears to be region- and species-specific (Grant et al. 2018). Other terminal gear modifications have also been shown to reduce mortality following longline capture, such as increased use of circle hooks (Godin et al. 2012). However, limited effectiveness of gear modifications and the persistence of elasmobranch bycatch continue to generate calls for innovative approaches to reduce catch and decrease mortality of vulnerable species.

An alternative strategy to gear modification is to define habitat use of targeted and bycatch species, identifying regions of minimal spatiotemporal overlap for more selective fishing practices. Advancements in telemetry technology are providing novel insights into marine animal habitat use (for review see Hussey et al. 2015), and electronic tags such as pop-up satellite archival tags (PSATs) can provide horizontal and vertical data to estimate fisheries interactions (Queiroz et al. 2016, 2019, Crossin et al. 2017) beyond traditional metrics such as catch-per-unit-effort (CPUE) data alone. Such telemetry data have successfully informed diverse conservation strategies (Bograd et al. 2010, Hays et al. 2019) for fish species including spiny dogfish *Squalus acanthias* (Carlson et al. 2014), Atlantic bluefin tuna *Thunnus thynnus* (Galuardi & Lutcavage 2012), swordfish *Xiphias gladius* (Braun et al. 2019), and Atlantic halibut *Hippoglossus hippoglossoides* (Murphy et al. 2017) by delineating stock boundaries, quantifying population mixing, and distinguishing migratory ecotypes. Using satellite telemetry proactively to define the habitat of key species may allow informed management strategies for bycatch avoidance at the inception of a developing fishery.

The development of fisheries in the Canadian Arctic is viewed as an important means to support socioeconomic growth but raises concerns over ecological impacts (Tai et al. 2019), particularly those in semi-enclosed regions that respond more rapidly than oceanic systems to anthropogenic stressors (Caddy 1993). Cumberland Sound, a large semi-enclosed embayment (~94 000 km^2) off Baffin Island (Qikiqtaaluk) in Nunavut, Canada, contains a deep basin (>1000 m) that supports a small-scale commercial fishery for Greenland halibut *Reinhardtius hippoglossoides* based in the community of Pangnirtung (see Fig. 1). This fishery provides economic support in a region with limited socioeconomic opportunities (Treble 2008, Hussey et al. 2017) but also results in bycatch of Greenland shark *Somniosus microcephalus* and Arctic skate *Amblyraja hyperborea* (DFO 2008). The fishery traditionally operates during winter months using benthic longlines set through sea ice, but increasingly mild winters and unpredictable sea ice conditions have shortened ice-fishing seasons (Walsh et al. 2003, Hussey et al. 2017), driving interest in developing a summer fishery to harvest remaining quota and expand fisheries opportunities. The Government of Nunavut conducted a dedicated summer exploratory fishery using a commercial longline vessel with full observer coverage in 2009 and 2010 (Young 2009, 2010). Summer longlines harvested an additional ~32 t of Greenland halibut each year (compared to 164 ± 142 t in the winter fishery 1989–2006; DFO 2008), and resulted in elasmobranch bycatch (1500 Arctic skates and >700 Greenland sharks over 2 seasons) that far exceeded yearly averages in the winter fishery (272 ± 414 Arctic skates, 83 ± 67 Greenland sharks yr^{-1}, 1989–2006; DFO 2008). Given forecasts of worsening winter ice conditions (Wang & Overland 2009, Collins et al. 2013) and the potential expansion of regional summer fishing efforts (Wheeland & Devine 2015, 2016), development of effective bycatch mitigation measures for these vulnerable species is a priority.

Robust population estimates and management plans are currently limited in Atlantic Canada for Greenland sharks and Arctic skates, with no assessments, status reports, or action plans available from the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Broader regional assessments have categorized Greenland sharks as Vulnerable (IUCN Red List of Threatened Species; Kulka et al. 2020), data deficient (Henriksen & Hilmo 2015), and unassessed (Davis et al. 2013), and Arctic skates are listed as Least Concern based on the premise of a distribution largely 'outside the reach of current fishing activity' (Kulka et al. 2016), which may change with fisheries expansion. However, Greenland sharks possess the most extreme life history traits described for elasmobranchs (growth rates of <1 cm yr^{-1}, potential female age-at-maturity >100 yr, and estimated lifespans of multiple centuries; Hansen 1963, Yano et al. 2007, Nielsen et al. 2016). These vulnerable life history traits coupled with further fisheries development will likely increase the risk of overfishing for both species. This necessitates data-informed mitigation strategies that allow selective Greenland halibut fisheries while also reducing Greenland shark and Arctic skate bycatch and maintaining socioeconomic benefits to local communities.

This study evaluated the degree of habitat overlap across target and bycatch species and analyzed exploratory fishery data to assess the potential implementation of bycatch mitigation strategies. Longline catch data and PSAT deployments on Greenland halibut, Greenland sharks, and Arctic skates were combined to assess summer depth and temperature habitat in Cumberland Sound. PSAT and observer data from a 2 yr exploratory summer fishery were compared to (1) use fisheries CPUE data to explore the primary factors influencing catch rates, (2) explore the utility of PSAT data to reflect and potentially inform fisheries CPUE, and (3) determine whether a depth–temperature niche in Greenland halibut could be targeted to reduce bycatch. Results provide an initial viability assessment of fisheries-targeted depths/temperatures and/or spatiotemporal closures to decrease shark and skate bycatch in an emergent fishery in the Canadian Arctic, with applicability to other developing community fisheries.

2. MATERIALS AND METHODS

2.1. Exploratory fisheries data

To assess the potential of a summer fishery for Greenland halibut in Cumberland Sound, the Government of Nunavut in conjunction with the community of Pangnirtung administered a 2 yr exploratory fishing effort in Cumberland Sound (Fig. 1) (Young 2009, 2010). During summer fishing, fisheries observers participated in all trips (100% coverage) and collected metadata associated with longline sets and catch. In 2009 (from 4 Sept–25 Oct), the F/V 'Stelie II' deployed longlines throughout the interior of Cumberland Sound (Fig. 1), with fishing depths ranging from 256–1189 m. In 2010 (between 1 Aug and 21 Sept), the F/V 'L'anse Amour Venture' focused fishing effort in deep-water regions with the highest Greenland halibut catch in the previous year, fishing depths from 582–1097 m (Fig. 1). Longlines consisted of 600–2400 hooks line^{-1} in both years, using either a combination of hook sizes (14, 15, 16; 2009) or one hook size (15; 2010). Soak times ranged from 6–68 h, with most sets (78%) between 12 and 24 h. For each bottom longline set, catch metrics for Greenland halibut, Greenland shark, and Arctic skate were recorded (number of individuals; total mass (kg) as directly measured [Greenland halibut and Arctic skate] or estimated [Greenland shark]), as well as set date, location (latitude and longitude), modal fishing depth (m), number of hooks, and soak time. CPUE was subsequently calculated for each species as:

$$\text{CPUE} = \text{individuals}\ (\text{hooks})^{-1} \times 10^{3} \qquad (1)$$

where individuals represents the number of individuals captured during the set and hooks is the number of hooks deployed. CPUE was multiplied by a factor of 10 (here, 10^3) to make final values more tractable, as is common in CPUE calculations and reporting (Dunn et al. 2000); CPUE is consequently interpreted here as individuals per 1000 hooks.

Significant predictors of CPUE for each of the species studied were analysed using generalized additive models (GAMs) implemented in the R package 'mgcv' (Wood 2018). CPUE is a strictly non-negative, right-skewed, continuous response (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m702p001_supp.pdf) and was assumed to follow a conditional Tweedie distribution with a power parameter (p) that was automatically optimised within the fitting function. The global model took the form:

$$\begin{gathered}\log(\mu_i) = \alpha + s_{1,\text{Year}_i}\,(\text{Season}_i) + s_{2,\text{Year}_i}\,(\text{Depth}_i)\\ + s_{3,\text{Year}_i}\,(\text{Soak time}_i) + f_1\,(\text{Long}_i,\text{Lat}_i) + f_4\,(\text{Soak time}_i)\\ + f_5\,(\text{Long}_i,\text{Lat}_i) + \text{Year}_i\\ \text{CPUE}_i \sim \text{Tweedie}(\mu_i,\text{p}) \qquad (2)\end{gathered}$$

where α is the intercept and $s_{1,\ldots,n}$ are penalised thin plate spline regression functions of the n^{th} covariate, and f_1 is an isotropic smooth (i.e. smooth–smooth interaction) of latitude and longitude to model any spatial variation linked to fishing location. Models were fit using restricted maximum likelihood smoothing parameter estimation, with the maximum basis dimensions of each smooth function left at their default settings (see Section 2 in the Supplement).

Preliminary inspection of the data revealed pronounced seasonal variation in nominal CPUE that could have several biological or fishery-dependent explanations (Fig. S2). To help differentiate between these potential mechanisms, 3 different variables were considered for modelling seasonal trends (i.e. the season term in Eq. 1): day of the year, which implies biological changes in abundance and/or catchability; the cumulative catch within each annual fish-

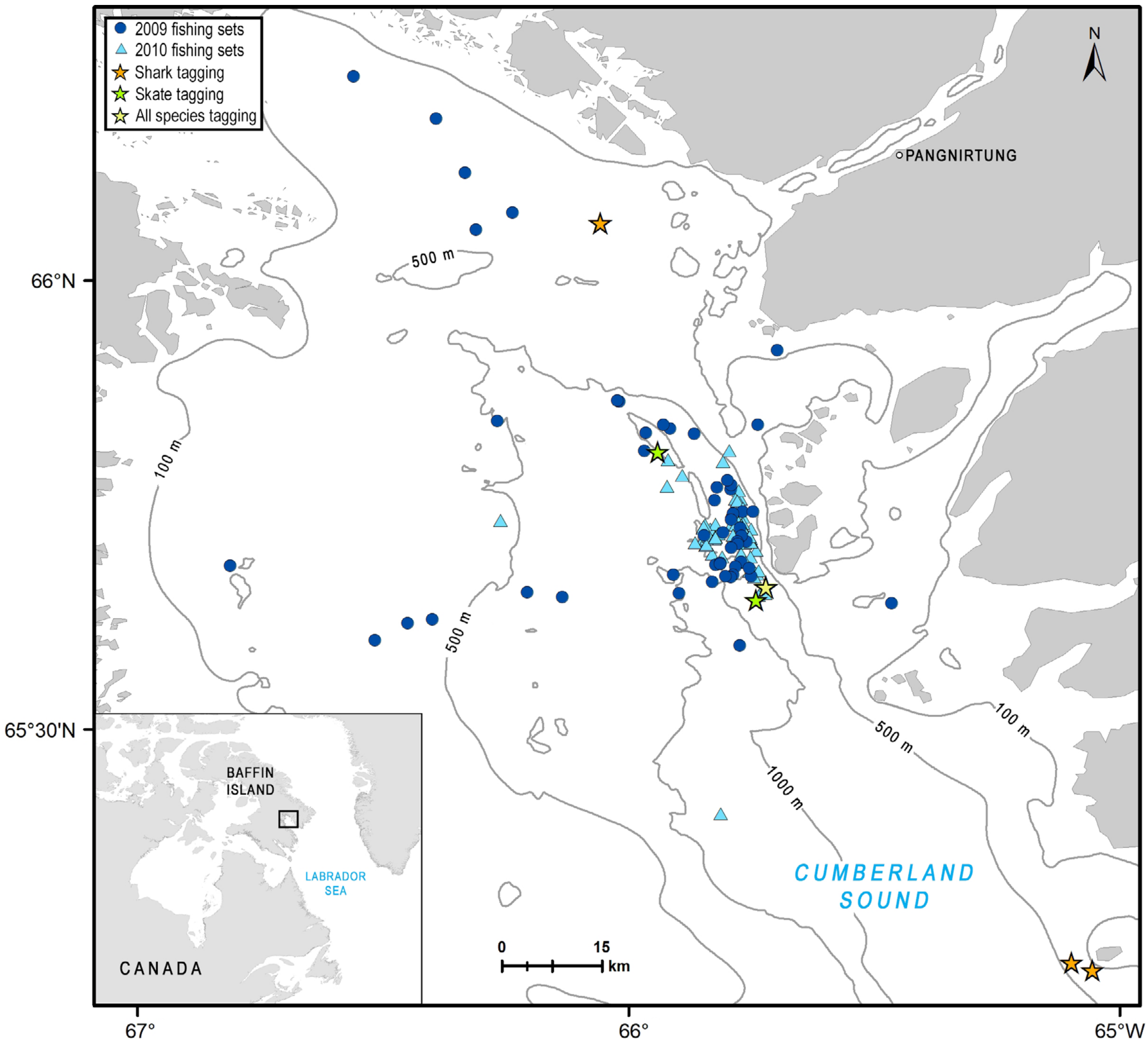

Fig. 1. Tagging and longline set locations in Cumberland Sound, Baffin Island, Nunavut, Canada. Fishing locations in 2009 (circles) and 2010 (triangles) represent deep longline sets for Greenland halibut as part of the exploratory summer fishery over 2 yr. Electronic tag deployments (star symbols; coloured by species) on Greenland halibut (n = 7), Greenland shark (n = 3), and Arctic skates (n = 6) were from the MV 'Nuliajuk' in August 2010 and 2011. Solid grey lines within Cumberland Sound: bathymetry (depth in m)

ing season (defined as the total number of individuals caught across all previous sets), which aims to model seasonal stock depletion by the fishery; and set number within each fishing season, which attempts to model variation linked to the behaviour of the survey vessel e.g. moving between patches. All seasonal terms were modelled as factor-smooth interactions with year (s_{1,Year_i}), which allowed the shape of the seasonal smooth to vary between years (Pedersen et al. 2019). However, we also included simplified models that assumed a constant seasonal effect across both years of the study in our candidate set (see Section 3 in the Supplement for further details on model specifications).

Model selection was performed by minimisation of Akaike's information criterion ($\mathrm{AIC_c}$) from a candidate set that included all permitted combinations of the explanatory variables (Burnham & Anderson 2004). To avoid fitting problems due to correlated predictors, different measures of seasonality were prevented from appearing in the same model (all pairwise concurvity >0.68; Fig. S4). Correlation among the remaining terms was low (pairwise concurvity <0.33), so no additional constraints were placed on model membership.

For each term retained in the top model, we report Bayesian approximate p-values from Wald-like tests implemented in package 'mgcv' (Wood 2018) along with an estimate of the effect size, calculated as the change in deviance explained when the model is refitted minus the term of interest. Additionally, because GAMs model the response as a function of non-linear smoothers, even significant predictors may only influence CPUE over a limited range of values. To characterise such threshold effects, the 'derivative' function in the R package 'gratia' (Simpson 2021) was used to identify regions of each fitted spline where CPUE was significantly changing (i.e. where the 95% simultaneous CIs around the first derivative do not overlap 0). Goodness-of-fit of the final models was checked using a simulation-based approach implemented via the R package 'DHARMa' (Hartig 2022) and revealed no significant deviations from the expected distribution of residuals (Fig. S5). All R code and data used for CPUE modelling are available in the Supplement (Sections 1–7).

2.2. Satellite tag deployment on target species

Tagging of fish with PSATS (MiniPATs; Wildlife Computers) took place in Cumberland Sound, Baffin Island, Canada, during August 2010 and 2011 (Fig. 1). Greenland halibut, Greenland sharks, and Arctic skates were captured on bottom-set longlines by a hired commercial vessel (2010) and a research vessel (2011) in Cumberland Sound. Longlines consisted of ~1900 m of bottom line with 1500–2000 circle hooks (Mustad Duratin, sizes 15 and 16) affixed on 1 m braided gangions baited with squid (Argentine shortfin squid *Illex argentinus*), with most fishing set soak times ranging from 12–24 h (mean ± SD: 21 ± 10 h). Upon retrieval, Greenland halibut and Arctic skates were carefully removed from hooks to minimize damage and placed in holding tanks onboard the fishing vessel prior to tagging.

For Greenland halibut, miniPATs were attached externally through insertion of a titanium dart head into the muscle tissue on the dorsal surface mid-way along the dorsal fin, by locking the dart head under the pterygiophores following the methods of Loher & Seitz (2006). MiniPATs were attached to the dart head via a 15 cm, 300 lb test monofilament leader coated with polyolefin shrink tubing to minimize irritation and tissue abrasion.

For Arctic skates, tags were attached by feeding 15 cm of stainless-steel leader wire through the midsection of the wing and securing it with 2 small circular plastic plates affixed on the dorsal and ventral surface. The dorsal plate was crimped, while on the ventral surface the wire was either twisted or crimped to lock the leader/tag in place following the methods of Wearmouth & Sims (2009).

For Greenland sharks, individuals were removed from the main longline in water using a small zodiac vessel and secured alongside using straps around the main body (caudal fin and posterior to the pectoral fins). Tags were then externally attached using a large umbrella-style Domeier dart tag (Domeier et al. 2005) inserted at the base of the dorsal fin via a stainless-steel hand-held tagging pole and secured to the plastic dart via a 12 cm stainless steel tether coated with polyolefin shrink tubing.

Following tagging procedures (~3 min), tagged Greenland halibut and Arctic skates were held for ~15 min onboard the vessel and monitored on release to ensure normal swimming behaviour. Similarly, for Greenland sharks, straps and hooks were removed and the sharks were released and monitored for upright swimming and strong tailbeats; duration of handling and tagging was ~20 min.

MiniPATs were programmed to record depth and ambient temperature at different time intervals (see Table 1). Shorter deployments (30, 40, or 70 d) were used to retrieve higher data resolution, and longer deployments (100 or 300 d) were used to obtain multi-season data and to potentially capture more spatial coverage (i.e. long-distance movements previously reported in Peklova et al. 2012, 2014). Tag deployments were programmed to optimize data resolution based on battery capacity (see Table 1 for tagging duration and sampling frequency for all individuals). The setting for automatic premature release of the tag at a constant depth was disabled because of the expectation that benthic-associated halibut and skates may have periods of minimal movement.

For all species, tag pop-off locations combined with bathymetry and water column structure data were used to filter tracks to include only movements within Cumberland Sound. This was necessary given the incapacity for horizontal track reconstruction using light level data due to depth of animal occurrence. Following data filtering, depth and temperature data for conspecifics were pooled for calculations of species-specific depth and temperature distributions, kernel density estimates of thermal-depth niche, and inter-specific comparisons. For all analyses of intra- and inter-specific vertical habitat use, data from the day of tagging and the day of tag release were removed to eliminate potential bias from tagging stress (day of tagging) and from post-release tag movement through the water column (day of tag release). Unweighted pooling of individuals allowed for maximum use of available depth/

temperature data, while recognizing that a higher proportion of data will be contributed by some individuals (see Table 1 individual for days of data by individual). For Greenland sharks, restricting data to within Cumberland Sound limited days of data per individual (see Table 1) but was accepted to optimize regional specificity for fisheries comparisons.

To assess the ability of tagging data to accurately reflect fisheries catch patterns, distributions of tag-recorded depths were compared to CPUE across the range of fishing depths. To directly assess the correlation between tagging data and fisheries catch, tag-recorded depth frequency was plotted against CPUE across set depths (n = 88).

Mean (±SD) depth and temperature were calculated for each individual and each species (pooled individuals). Contour plots of time-at-depth and time-at-temperature across time-of-day were generated to visualize diel focal depths and temperature and associated variability. All days with depth and temperature data from each individual were used. Time of day, depth, and temperature were binned: 30 min, 5 m, and 0.05°C. Kernel density estimates of thermal-depth niche were also generated, with the proportion of time in each bin calculated and plotted with 10% isolines, with forms for each species showing 95% of all data.

3. RESULTS

3.1. Exploratory Greenland halibut summer fishery data

The exploratory summer fishery in 2009 and 2010 deployed a total of 114 bottom longline sets, of which 89 sets (51 in 2009; 38 in 2010) had adequate recorded data for CPUE analyses. These 89 sets resulted in landings of ~66.9 mt (estimated round weight) of Greenland halibut (35.3 mt in 2009; 31.6 mt in 2010). Set depths ranged from 256–1189 m, with the majority (85%) at depths >800 m where most Greenland halibut were caught (Fig. 2). Mean (±SD) CPUE (reported throughout as ind. per 1000 hooks) for both years combined were 74 ± 53 for Greenland halibut, 3 ± 3 for Greenland shark, and 8 ± 11 for Arctic skate, with Greenland shark and Arctic skate CPUE exceeding that of Greenland halibut for the shallowest sets (<600 m; Fig. 2). Greenland shark bycatch ranged from 0–38 ind. set^{-1}, with 474 and 185 individuals caught in 2009 and 2010, respectively, resulting in a total of 659 individual sharks caught (7 ± 8 ind. set^{-1}) in sets with adequate metadata across the 2 yr. Arctic skate bycatch was the highest recorded bycatch by number of individuals in both years, with 863 and 677 individuals caught in 2009 and 2010, respectively, for a total of 1540 individual skates caught

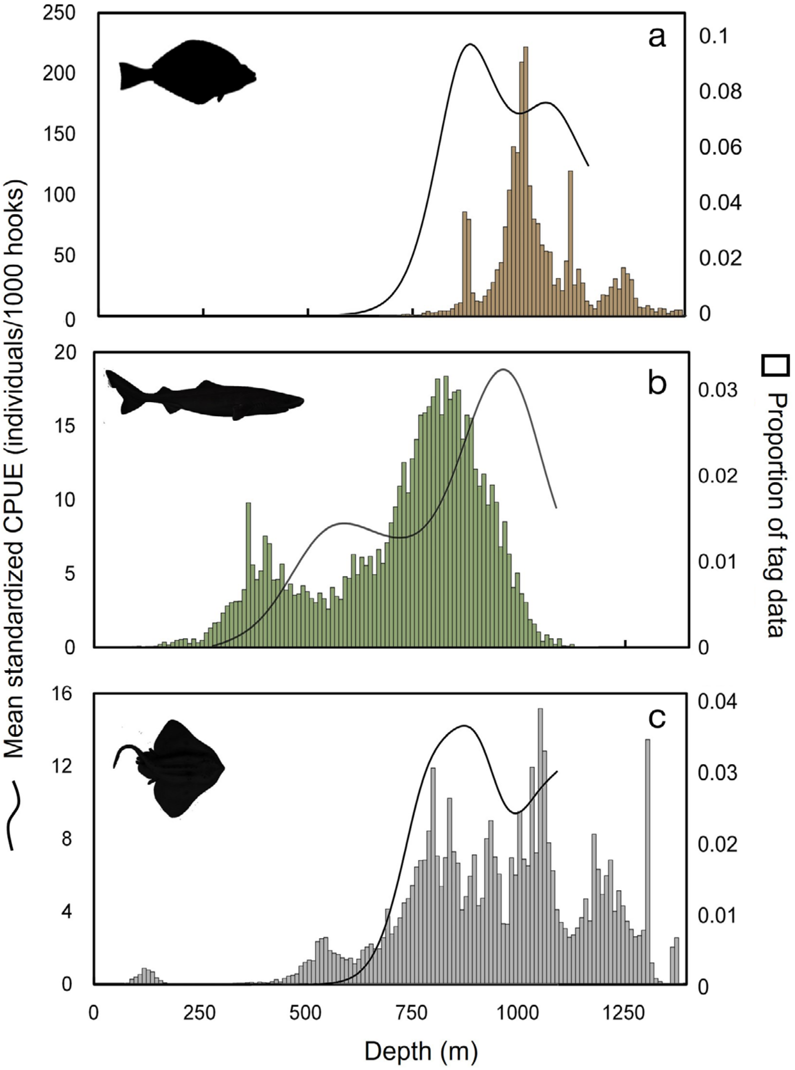

Fig. 2. Using depth data from electronic tags to track fisheries catch-at-depth for 3 species in Cumberland Sound, Nunavut, Canada. Histograms (coloured bars) show frequency of electronic tag–recorded depths (10 m bins; right *y*–axis) for (a) Greenland halibut *Reinhardtius hippoglossoides*, (b) Greenland shark *Somniosus microcephalus*, and (c) Arctic skate *Amblyraja hyperborea* in Cumberland Sound, Baffin Bay, Nunavut, Canada, during the summer/fall seasons. Trendlines are thin plate regression splines representing mean catch-per-unit-effort (CPUE) from fitted generalized additive models

(21 ± 25 ind. set^{-1}) across the 2 yr. Greenland sharks and Arctic skates constituted the majority of bycatch, with other captured species including roughhead grenadier *Macrourus berglax*, invertebrates, soft coral, and a single harp seal *Pagophilus groenlandicus*. Greenland shark bycatch occurred across set depths, while the majority of Greenland halibut and Arctic skate catch was at depths >700 m (Fig. 2).

3.2. Comparison of fisheries and electronic tag data

Data were successfully retrieved from tags deployed on 7 Greenland halibut, 3 Greenland sharks, and 6 Arctic skates (Table 1 shows total days of retrieved data across individuals). Tags remained on Greenland halibut and Greenland sharks for the full pre-programmed deployment, while 3 of 6 tags on Arctic skates released prematurely (Table 1), potentially due to tearing of the wing musculature (Peklova et al. 2014). Overall, data recovery and filtering resulted in 629 d of data (range: 70–199 d ind.$^{-1}$) for Greenland halibut, 275 d (30–70 d ind.$^{-1}$) for Arctic skates, and 86 d (6–40 d ind.$^{-1}$) for Greenland sharks (Table 1). For Greenland sharks, data filtering resulted in one filtered track for an animal with a pop-off location outside the Sound, for which water column thermal structure clearly changed upon exit from the Sound (Table 1). For halibut and skates, all pop-off locations were within the Sound, and there was no evidence from bathymetry (i.e. shallower depths at exit of the Sound where a sill is located) that animals left and returned to the Sound during the tracking period. For one halibut with the longest tracking time (300 d), track length was filtered to remove winter months to make inter-specific comparisons appropriate to season (Table 1). While Greenland shark data were most limited by sample size and filtering data according to animal presence in the Sound, data were deemed representative of behaviour based on >34 000 post-filtering measure-

Table 1. Electronic tag data for individual Greenland halibut, Greenland shark, and Arctic skate tagged and released in Cumberland Sound, Baffin Island, Nunavut, Canada, in 2011 and 2012. TL: total length. Duration: between tag deployment and tag release/reporting—parentheses indicate cases where tags detached before the pre-programmed date (all other tags remained on fish for the full pre-programmed tracking period). Mean values are reported as mean ± SD

Species	No.	TL (cm)	Duration (d)	Sampling rate (min)	Mean depth (m)	Mean temp (°C)	Max. depth (m)
Greenland halibut							
Reinhardtius hippoglossoides	1	95	100	5	946 ± 85	2.3 ± <0.1	1132
	2	84	70	2.5	1006 ± 55	2.4 ± <0.1	1133
	3	85	70	2.5	1032 ± 112	2.4 ± <0.1	1389
	4	88	100	5	1124 ± 125	2.4 ± <0.1	1386
	5	85	70	2.5	980 ± 92	2.3 ± <0.1	1118
	6	90	100	5	1105 ± 93	2.4 ± <0.1	1380
	7	nd	300 (119)[a]	10	961 ± 106	2.6 ± 0.1	1386
All	–	**88 ± 4**	**629**	–	**1030 ± 113**	**2.4 ± <0.1**	**1389**
Greenland shark							
Somniosus microcephalus	1	300	40	2.5	800 ± 147	2.4 ± 0.3	1123
	2	315	40 (6)[b]	2.5	387 ± 87	2.1 ± 0.4	1260
	3	320	40	2.5	668 ± 191	2.2 ± 0.4	1116
All	–	**312 ± 10**	**86**	–	**725 ± 193**	**2.3 ± 0.3**	**1260**
Arctic skate							
Amblyraja hyperborea	1	73	40	1.25	1134 ± 142	2.7 ± 0.1	1329
	2	66	30 (40)	1.25	761 ± 135	2.5 ± 0.1	1349
	3	72	57 (100)	5	260 ± 334	0.4 ± 0.9	1005
	4	62	70	2.5	876 ± 247	2.1 ± 0.4	1338
	5	64	38 (70)	2.5	1206 ± 173	2.5 ± 0.1	1383
	6	69	40	1.25	892 ± 140	2.5 ± 0.1	1115
All	–	**68 ± 4**	**275**	–	**950 ± 225**	**2.5 ± 0.4**	**1383**

[a] Greenland halibut 7 recorded data for the full deployment (300 d), but data were only used from days in summer and fall (n = 119 d)

[b] Greenland shark 2 reported 40 d of data, but only data from within Cumberland Sound were used (n = 6 d)

ments of both depth and temperature and previous tag deployments in the Sound (Campana et al. 2015). Consequently, data were considered adequate for statistical analyses of both temperature and depth measurements.

Depth distributions from tags were consistent with CPUE data in Greenland halibut and Arctic skates, with tag-recorded depth peaks correlating with catch (Fig. 2). Tag data for Greenland sharks appeared to track a bimodal depth distribution, with a dominant peak at ~800 m and a secondary peak at ~400 m, which mirrored the shape of CPUE-at-depth distribution but with offset peak depths (deeper peak depths in CPUE; Fig. 2).

3.3. Electronic tag data: depth and temperature

Greenland halibut depth and temperature distributions were consistent within and across individuals, with individual mean depths ranging from 946–1124 m and mean temperatures of 2.3–2.6°C (Table 1). Greenland halibut depth was highly centered around 1000 m (Fig. 3a) with a pooled mean of 1030 ± 113 m, with 95% of data >860 m and 55% of data >1000 m (Table 1). Pooled mean temperature for Greenland halibut was 2.4 ± <0.1°C; temperature SD was < ±0.1°C for most individuals, demonstrating an extremely narrow thermal distribution (Table 1, Fig. 3b).

Greenland sharks were distributed throughout the water column, with a broader range of mean depths across individuals (Table 1). Overall, Greenland sharks showed highest use of depths between 700 and 1000 m (Fig. 3a), with 2.3% of depth data >1000 m. Water temperatures were more variable within and across Greenland sharks (Table 1), ranging from 1.6–2.7°C due to movement through the water column (Fig. 3b). Reported data summaries are in the context of relatively small sample size of Greenland sharks tagged compared to Greenland halibut and Arctic skates, and should be interpreted as such.

Arctic skates showed inter-individual variability in both depth and temperature distributions (Table 1),

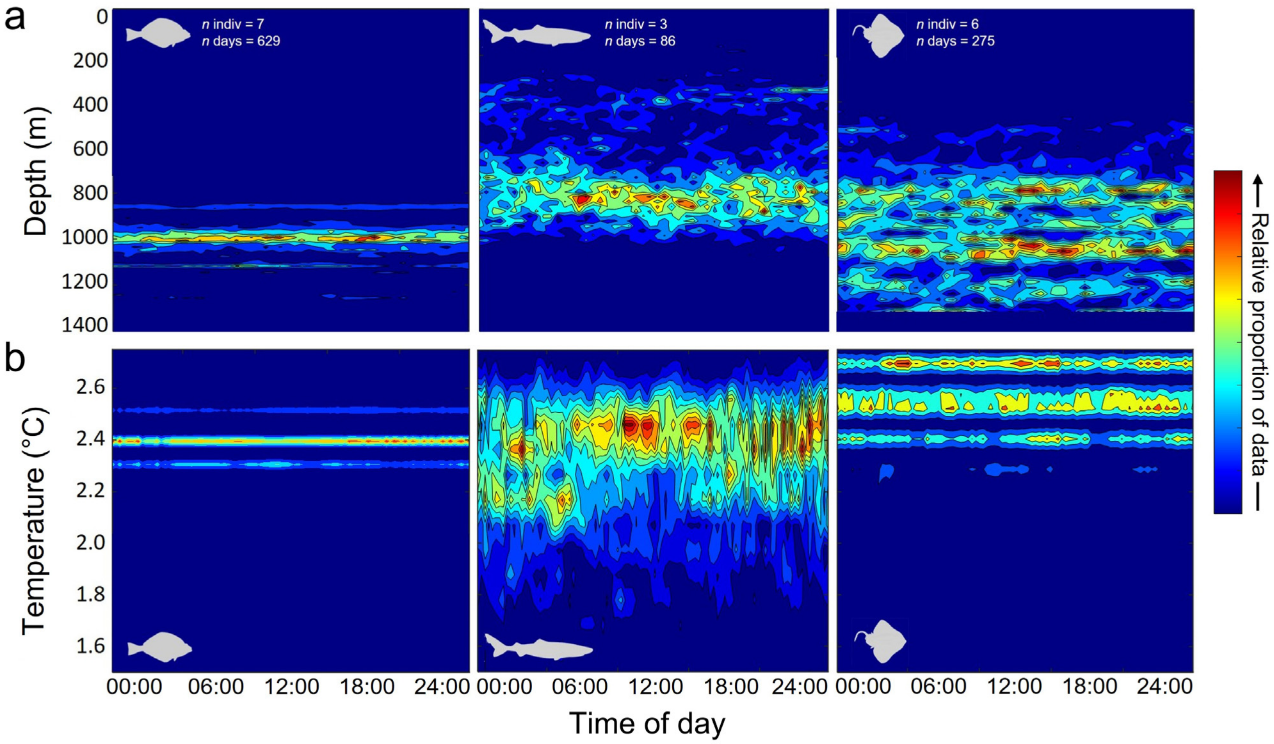

Fig. 3. Proportion of time spent at depth and temperature for electronically tagged fish species that are targeted (Greenland halibut *Reinhardtius hippoglossoides*) or common bycatch (Greenland shark *Somniosus microcephalus* and Arctic skate *Amblyraja hyperborea*) in a summer longline fishery operating in Cumberland Sound, Nunavut, Canada. (a) Greenland halibut were highly restricted to depths between 950 and 1050 m, while Greenland sharks and Arctic skates showed variable depth distributions. (b) Combined temperature data showed narrow depth ranges for all species (<1°C), with extremely narrow thermal niche for Greenland halibut (2.4 ± 0.1°C). Data shown are for all full days for all individuals of each species in which telemetry geolocation data indicated that tagged individuals remained in the Cumberland Sound region (no. of individuals and no. of days shown for each species) during the summer/fall seasons

resulting in varying bands of focal depths (between 600 and 1400 m) and temperatures (between 2.2 and 2.7°C) in overall data distributions (Fig. 3). Variability in temperature was lower within individual skates than across individuals due to different temperature-at-depth across the narrow depth bands that varied by individual (Table 1, Fig. 3).

Kernel density estimates of thermal-depth envelopes showed higher overlap between Greenland sharks and skates than between Greenland halibut and Greenland sharks and no overlap between Greenland halibut and skates (Fig. 4). Overlap between Greenland halibut and Greenland sharks was at depths of 932–991 m and temperatures of 2.4–2.5°C, representing 1.6 % of Greenland shark depth-temperature data and 11.2 % of Greenland halibut data. Arctic skate thermal-depth envelopes were distributed from 700 to >1300 m and 2.4 to >2.8°C. However, at core depths that were similar to those of Greenland halibut (1000–1100 m), Arctic skate temperatures were higher (2.7–2.8°C) than those of Greenland halibut (2.3–2.5°C) due to some skates occupying depths >1100 m where temperatures were higher (Fig. 4). While Greenland shark thermal-depth envelopes overlapped with Greenland halibut only at depths <1000 m, and with Arctic skate at depths <1050 m (Fig. 4), deep dives for >1 h to depths of >1100 m were observed in all tagged sharks (Table 1, Fig. 5), resulting in the minimal observed depth-thermal overlap at deeper depths with both Greenland halibut and Arctic skate.

3.4. Environmental and methodological predictors of fishery CPUE

Final GAMs fitted to fisheries observer data explained 62–79 % of deviance in CPUE of Greenland sharks, Greenland halibut, and Arctic skates (Table 1). Set depth and cumulative effort within a fishing season were consistently retained in the best-fitting models for all species (Table 1) and had a high degree of support, with Akaike weights that were 2.5–8 times higher than their closest competitors (Tables S1–S3).

3.4.1. Depth effects

Depth was consistently retained in the top models for all species, with CPUE tending to increase at greater depths (Table 2, Fig. 6). However, the relationship was non-linear and varied among species in a manner that was broadly consistent with depth use patterns from tag data (Fig. 2). Greenland halibut and Arctic skate CPUE was effectively zero up to a depth of ~500 m, whereupon it increased sharply up to a depth of 750 m before plateauing (a single deep set at the extreme of the fished range was excluded from the analysis as it exerted a strong influence on the tail of the spline; see Figs. S9–S12). In contrast, Greenland shark CPUE was characterised by a pronounced shoulder at shallower depths, initially increasing up to a depth of 500 m, where it stabilised before increasing again at depths > 830 m to a peak at 900–1000 m. This pattern broadly mirrors that observed in tag data although transposed approximately 100 m deeper (Fig. 2).

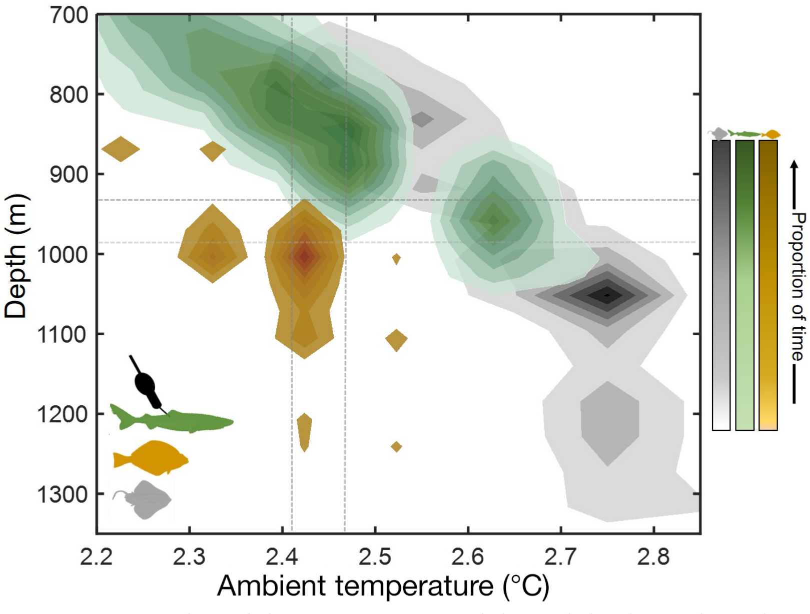

Fig. 4. Bivariate kernel density estimations of thermal-depth envelopes for 3 fish species during the ice-free period in Cumberland Sound, Nunavut, Canada. Depth and temperature data were recorded by electronic tags deployed on fisheries-targeted Greenland halibut *Reinhardtius hippoglossoides* (orange) and common bycatch species Greenland shark *Somniosus microcephalus* (green) and Arctic skate *Amblyraja hyperborea* (grey). Isolines represent 10 % increments of data. Dashed grey lines show thermal-depth ranges where tag data for Greenland halibut and Greenland shark overlap

3.4.2. Seasonal/fisheries effects

CPUE of all species varied over the course of the fishing season. However, the predictor that best explained these

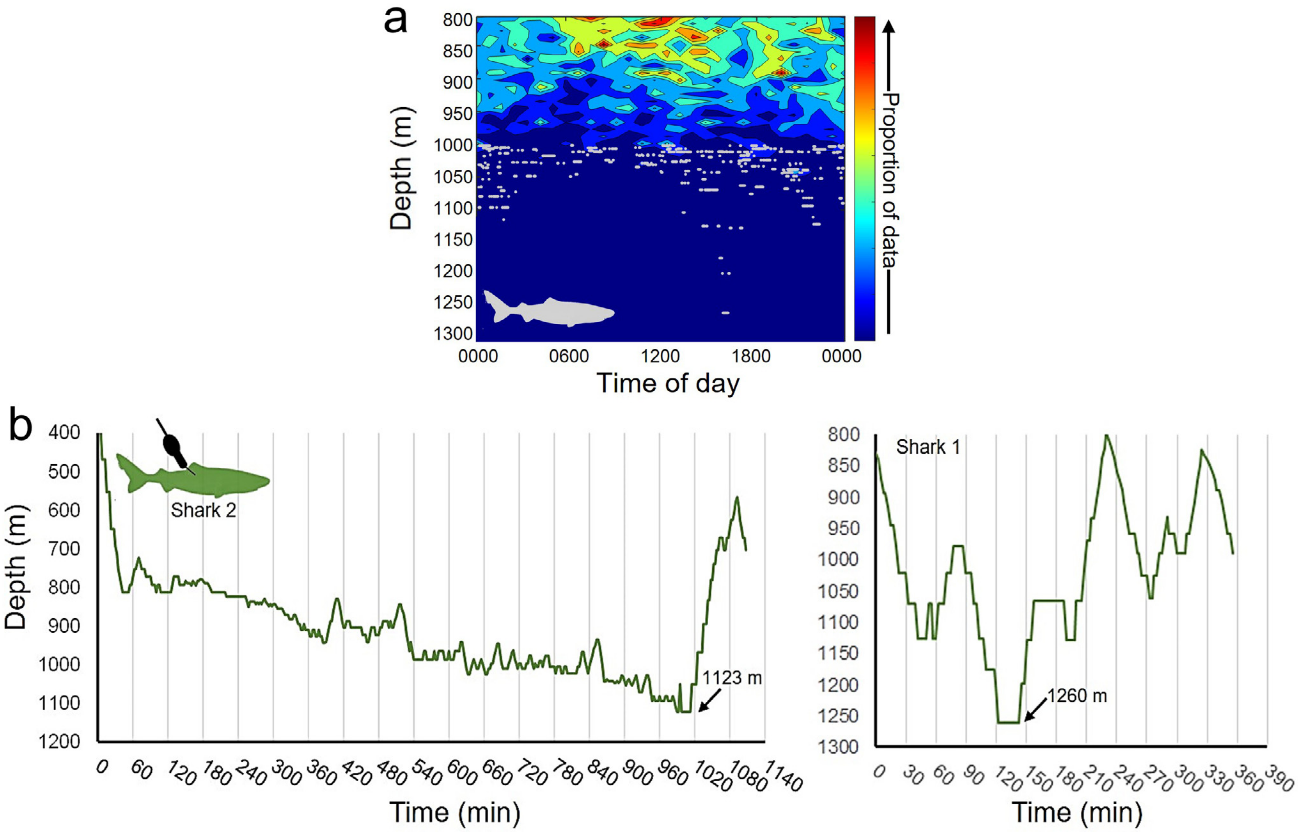

Fig. 5. Prolonged deep dives by Greenland shark *Somniosus microcephalus* in Cumberland Sound, Nunavut, Canada. (a) Compilation of deeper (>800 m) depth data from electronic tags indicates that Greenland sharks spent minimal time at depths >1050 m and are potentially depth-limited by the bathymetry of Cumberland Sound, with only a narrow region with depths >1000 m (see Fig. 1). Deeper dives (grey points) are minimally represented in overall data due to infrequency (~2% of data). However, (b) prolonged deep dives were observed in individual sharks. Sharks were capable of extended dives (16 h) from 800 to >1100 m (first panel in b) as well as shorter (20 min) 'bounce-dives' to depths of 1260 m (rightmost panel)

Table 2. Final generalized additive model fit to catch-per-unit-effort of Greenland shark, Arctic skate, and Greenland halibut. For each variable, results are presented as p-values from Wald-like tests along with the estimated degrees of freedom (edf) and change in the proportion of null deviance explained (%DE) when the term is excluded from the model. For variables modelled as factor-smooth interactions, summary statistics are presented for smooths fit separately to each year, while the %DE represents the overall contribution of the 2-way interaction. The overall adjusted R^2 and DE for the model are also shown. Cumulative catch: total individuals caught since start of annual fishing season. Dashes (–) indicate variables that did not appear in the top model for each species following Akaike's information criterion model selection; see Tables S1–S3

Variable	Year	Greenland shark			Arctic skate			Greenland halibut		
		F (edf)	p	%DE	*F* (edf)	p	%DE	*F* (edf)	p	%DE
Cumulative catch	2009	25.1 (3.9)	<0.001	48.3	2.6 (1.2)	0.11	2.4	–	–	–
	2010	30.5 (2.7)	<0.001		11.6 (1.0)	0.001				
Set		–	–	–	–	–	–	5.2 (6.8)	< 0.001	8.2
Depth		8.9 (4.7)	< 0.001	16.1	2.6 (4.2)	0.035	54.4	3.2 (4.5)	0.017	18.3
Soak time		9.0 (5.2)	< 0.001	17.1	–	–	–	–	–	–
Location		–	–	–	–	–	–	3.5 (7.9)	0.001	12.9
		R^2 adj. = 0.76 %DE = 83.2			R^2 adj. = 0.30 %DE = 56.4			R^2 adj. = 0.79 %DE = 87.7		

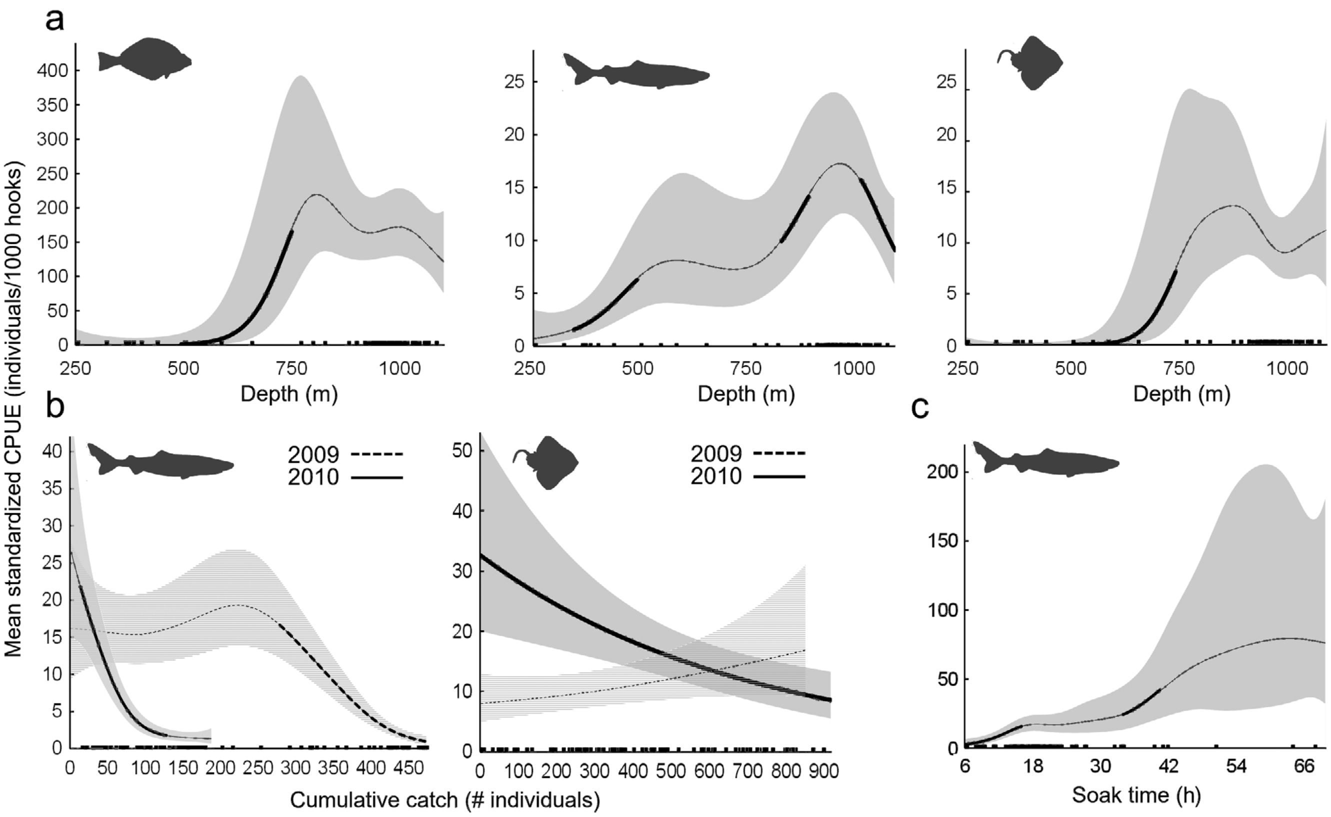

Fig. 6. Partial effect plots showing marginal relationships between catch-per-unit-effort (CPUE) of Greenland halibut, Greenland shark, and Arctic skate over 2 consecutive years and (a) fishing depth, (b) cumulative fishing effort, and (c) soak time. Trendlines are thin plate regression splines from fitted generalized additive models (GAMs) along with 95% CIs (shaded ribbon). Trendlines shaded in grey: global smoothers fitted to pooled data from both years, whereas multiple lines represent year-by-smooth interactions (lower left panels). Emboldened sections of splines represent regions of significant change based on the simultaneous confidence intervals around the first derivatives. Ticks along *x*-axis show distribution of raw CPUE data used in GAM analyses. Plots are only shown for explanatory variables that were retained in the final model for a given species

seasonal trends differed (see Sections 3 & 4 in the Supplement for detailed results and diagnostics of GAM analyses). For the Greenland shark and Arctic skate, cumulative catch over the fishing season was found to be the best predictor of CPUE, with the shape of the seasonal relationship differing across the 2 yr of the study (Akaike weights of models containing a cumulative catch × year interaction were >4- and >8-fold higher than with other seasonal predictors for skate and shark, respectively; Tables S2 & S3). The effect of cumulative catch was particularly strong for Greenland sharks, explaining almost 50% of the total deviance (Table 2). CPUE of Greenland sharks declined seasonally with greater cumulative catch in both years; however, this decline occurred more abruptly in 2010 than 2009 (Fig. 6). Derivative analysis indicated that in the first year of the fishery, shark CPUE initially remained relatively constant at a mean of 17 individuals per 1000 hooks (95% CI: 15.7–19.3) until 276 individuals had been captured, whereafter it declined significantly for the remainder of the season, reaching a minimum of 1.0 individual per 1000 hooks (95% CI: 0–3.0) once 486 had been caught. In the second year of the study, CPUE at the start of the fishing season was slightly higher (mean: 24.5; 95% CI: 18.1–31.8) but began to decline almost immediately and stabilised at a low mean of 1.5 (95% CI: 0.86–2.0) after just 125 individuals had been captured (Fig. 6).

For Arctic skates, the relationship between CPUE and cumulative catch was weaker and less consistent between years (2.8% of total deviance explained; Table 2). No significant seasonal trend in CPUE was observed in 2009, although there was a tendency for CPUE to increase with higher cumulative catch (Table 2, Fig. 6). In 2010, skate CPUE was initially higher than in 2009 (2009: mean: 8.1; 95% CI: 5.1–13.1; 2010: mean: 32.6; 95% CI: 20.0–53.0) but declined significantly throughout the fishing season, reaching a minimum of 8.6 (95% CI: 5.6–13.3) after 919 individuals had been captured (Fig. 6).

The seasonal trend in CPUE of Greenland halibut was more complex than that observed for bycatch species and was best explained by set number within fishing season, with a similar multimodal pattern observed in both years of the study (models with other seasonal predictors had essentially no support, with Akaike weights <0.01; Table S1). CPUE was characterised by an initial increase, followed by a decrease and then a second peak in sets deployed towards the latter part of the season (Fig. S9).

3.4.3. Soak time effects

In addition to depth and cumulative fishing effort, soak time was also selected in the top model for the Greenland shark (Fig. 6). Shark CPUE tended to be higher in sets with longer soak times, with significant increases detected between 6–16 h and >34 h. Mean CPUE was estimated to be 46% lower (95% CI: −84 to 21%) at a soak time of 12 h compared to the median of 18.5 h and 200% higher (95% CI: 78–410%) at soak times of 36–48 h. Soak time was not a significant predictor of Greenland halibut or Arctic skate CPUE over the range of times used in this study (6–68 h). Fishing location was also a significant predictor of halibut CPUE but was not retained in the best-fitting models for Arctic skate or Greenland shark once the effects of depth were taken into account.

4. DISCUSSION

Multi-species electronic tagging data and fisheries catch data were combined to assess depth-thermal habitat use, CPUE trends, and opportunities for bycatch reduction in an emergent Arctic fishery. Tagging data suggested minimal overlap of Greenland halibut and Greenland sharks at deepest depths, but the observed high Greenland shark CPUE at these depths likely precludes bycatch reduction using spatiotemporally targeted fisheries effort. Tag-recorded depth distributions corresponded to modelled CPUE data for the benthic Greenland halibut and Arctic skate, but the high CPUE of Greenland sharks at the extremes of tag-recorded depths indicates that tag data alone may be a limited predictor of bycatch risk in vertically mobile species. The observed bycatch of Greenland sharks and Arctic skates and the marked seasonal declines in Greenland shark CPUE suggest the need for alternative bycatch mitigation measures for sustainable fishing practices.

Electronic tag data revealed some degree of species-specific depth and temperature distributions during the ice-free season in Cumberland Sound. The movement of all Greenland halibut to depths >1100 m from shallower tagging depths indicates consistent use of the greatest available depths with narrow associated thermal ranges (2.4 ± <0.1°C), similar to prior observations (Peklova et al. 2012). Arctic skates were more broadly distributed across regional bathymetry, with a wider depth-thermal niche than Greenland halibut despite similar benthic association (Fig. 4). Vertically mobile Greenland sharks were most broadly distributed, likely driven by a combination of physical parameters (bathymetry limitation during movements) and/or behavioural traits (prey-seeking in the water column) consistent with previously observed association with shallow to deep environments (Beck & Mansfield 1969, Campana et al. 2015, Gallant et al. 2016). Greenland halibut were stenothermic at 2.3–2.4°C (72% of data), with an even narrower temperature range than that observed during the ice-covered season (1.6–2.6°C; Peklova et al. 2012). However, shared use of these temperatures by both Arctic skates and Greenland sharks will likely limit the effectiveness of temperature-targeted fishing to avoid elasmobranch bycatch.

Overall, the low overlap at deepest depths (>1000 m) of Greenland halibut and Arctic skate PSAT data with that of Greenland sharks suggested that fisheries targeting deepest depths could facilitate Greenland shark bycatch reduction. However, while Greenland shark mean CPUE did decrease at depths >1000 m, overall bycatch was still high at these deepest set depths compared to those <800 m (Fig. 6). Capture at depth corresponds to tag-recorded dives to >1000 m observed here and elsewhere (Fisk et al. 2012, Campana et al. 2015), and use of deeper waters in Cumberland Sound could represent benthic association with extended deep dives (~8 h to depths >1000 m) to optimal Greenland halibut fishing depths. Observed depredation (e.g. multiple tangles along a recovered longline, excessive loss of gangions; N. Hussey pers. obs.) in this system and elsewhere (Grant et al. 2020) suggest Greenland sharks may alter typical behaviour to move along the seafloor depredating catch. Scavenging behaviour (Leclerc et al. 2011) and high olfactory capabilities (Ferrando et al. 2016, 2017, Yopak et al. 2019) make a response to ~2000 baited hooks and struggling hooked fish (i.e. Greenland halibut and Arctic skates) likely, as these species are observed in Greenland shark diets (Nielsen et al. 2014, 2019). Deep diving in Greenland sharks may be partially influenced by variations in feeding cues, inter-individual and ontogenetic variability, bathymetry of the system occupied, and data sample size limitations (i.e. here based on 3 tagged individuals). A larger-scale study across a gradient of fishing effort combined with additional research tools (e.g. animal-borne data loggers; Barkley et al. 2020) would allow more definitive identification of Greenland shark interactions with fishing gear.

Seasonal declines in Greenland shark CPUE were observed in 2 years with different fishing timeframes (Fig. 6). Post-capture mortality occurred due to handling practices including dismemberment of entangled sharks, with estimates of 50 % mortality (~285 sharks) in 2009 and presumably similar rates in the following year (Young 2009, 2010). It is unknown how these mortality rates extend to broader Arctic fisheries, but similar practices during the ice-fishing season (Davis et al. 2013) suggest that fisheries-associated mortality may contribute to the observed seasonal CPUE declines. Seasonal migration patterns may also contribute to CPUE trends, as late summer emigration from inshore fjords to offshore waters has been observed in Arctic regions (Campana et al. 2015, Hussey et al. 2018), and multi-year acoustic telemetry monitoring of Greenland sharks in Scott Inlet (northern Baffin Island) showed emigration from coastal to offshore regions with sea ice formation (Edwards et al. 2021). However, the weak effect of date-by-year in GAM analyses (see Section 3 in the Supplement) makes seasonal emigrations a less likely explanation than localized reduction in shark numbers due to mortality. There is also some evidence for Greenland shark site fidelity to coastal sites over multiple years (e.g. 15 % of tagged sharks in Edwards et al. 2021), indicating that continued fishing pressure on a seasonal population in Cumberland Sound could decrease abundance if a philopatric group exists. In addition, the more rapid decline of Greenland shark CPUE in 2010 than the previous year may indicate a local population that failed to fully recover to pre-2009 levels. Given the limitations of CPUE data here (i.e. 2 yr of data; a single-vessel exploratory fishery per season) and the well-described challenges of using shark CPUE to determine population trajectories (Baum et al. 2005, Burgess et al. 2005), confident interpretation of these trends requires additional data.

Seasonal CPUE trends for Arctic skates were inconsistent, marginally increasing over time in 2009 and significantly decreasing in 2010. These contrasting trends may relate to variable fishing depths (i.e. shallower sets at the start of 2009 compared to 2010) or other patterns of skate spatiotemporal abundance, but overall trends were less striking than those of Greenland sharks with no apparent impact of fishing mortality. While Arctic skates have been shown to undertake larger-scale movements (~30 to >100 km; Peklova et al. 2014, P. Puskar et al. unpubl. data), multi-year acoustic telemetry data suggest that this species can be site-attached for long periods of time in Cumberland Sound (P. Puskar et al. unpubl. data). This site fidelity could lead to population declines in regions of focused fishing effort (Sguotti et al. 2016, Jaiteh et al. 2017, Karnad et al. 2020), necessitating longer-term monitoring of population trends given the high numbers caught and higher vulnerability in semi-enclosed seas (Ulman et al. 2020) such as Cumberland Sound.

The conclusion that targeting specific depth-thermal habitat or specific timeframes will be ineffective for bycatch reduction of Greenland sharks and Arctic skates necessitates consideration of other mitigation measures. Reducing soak time effectively reduced Greenland shark bycatch over specific timeframes, as has been observed for other elasmobranch species (Erickson & Berkeley 2008, Morgan & Carlson 2010). While Greenland halibut CPUE could reasonably be expected to be lower with short soak times, no effect was observed on halibut CPUE; this may be a result of the interacting effects of hooked fish escapes and depredation by Greenland sharks (High 1980, Ward et al. 2004, Haimovici & Ávila-da-Silva 2007), though soak time (in hours) relationships with CPUE can be confounded by non-static effectiveness of baited longlines over time (Peterson et al. 2017). Regardless, short soak times resulted in lowest Greenland shark CPUE and did not reduce catch rates of the targeted species. As such, short (<10 h) soak times could be explored in this fishery to assess Greenland shark bycatch reduction and maintenance of adequate Greenland halibut catch.

Modification of fishing gear has been effective in reducing elasmobranch bycatch, though preliminary gear modification trials with Greenland sharks have indicated that odor- and magnetic-deterrent hooks are ineffective (Grant et al. 2018), while monofilament gangions may reduce catch compared to braided nylon gangions (Grant et al. 2020). However, monofilament is unlikely to reduce skate bycatch due to a lack of cutting teeth, and magnetic hooks have mixed effects across species (O'Connell et al. 2011). The high levels of elasmobranch bycatch observed and the lack of clear solutions to mitigate bycatch underscore the need for additional research into effective mitigation measures to reduce bycatch encounter rates and mortality in Cumberland Sound summer fishery operations.

Until effective strategies to reduce bycatch are demonstrated, the implementation of safe and efficient handling practices to improve post-release survival rates (Davis et al. 2013, Edwards et al. 2019b) and elimination of intentional mortality upon capture (e.g. severing tails of sharks to disentangle from gear; Davis et al. 2013) is likely a viable management approach. The propensity for Greenland sharks to roll and wrap longline gear around their body will require methods to untangle sharks, formal practices to cut and repair gear, and acceptance of gear loss and damage. In contrast, the primary concern for Arctic skates is a gaffing practice for removal from gear that can result in fatal damage to the mouth region (Endicott & Agnew 2004), which may be relatively simple to resolve. Better handling practices may be particularly effective in reducing mortality rates of Greenland sharks, as the majority of sharks caught on bottom longlines are alive when brought to the surface, are observed to swim off after proper release, and have recorded stress responses similar to temperate/tropical species (Barkley et al. 2017), though robust post-release survival data are still lacking (Edwards et al. 2019b). By extension, this highlights the value of ongoing observer coverage, enforcement presence and handling education in a developing fishery.

The depth-thermal 'floors' (i.e. maximum depths, minimal temperatures, or water column features that bound the majority of movements) observed in Greenland sharks have been reported for other migratory, vertically mobile fish in the open ocean (e.g. carcharhinid and lamnid sharks, billfishes, tunas) (Bernal et al. 2017, Madigan et al. 2021) and have potential relevance to fisheries practices. While the vast majority of pelagic species' movements are within these depth/temperature thresholds (i.e. 'typical' behaviour), tag-recorded occasional dives to maximum depths and minimum temperatures often far exceed these thresholds (Ward & Myers 2005). As such, longline catch-at-depth of pelagic fishes can be much higher than tag-recorded depth data would predict. For example, bigeye tuna *Thunnus obesus* in the Central Pacific Ocean have shown peak catches at depths exceeding the majority of recorded depth distributions (Ward & Myers 2005), and capture at atypically deeper depths has been demonstrated broadly across pelagic species (Zhu et al. 2012). It is therefore possible that for vagile pelagic predators, depth data extremes (e.g. deepest 1–2%) may better represent depths of susceptibility to bottom- or midwater-set longline gear. Future studies using telemetry data to assess bycatch risk for vertically active predators may be more effective if these extremes are considered primary at-risk depths along with core vertical distributions. The data here also demonstrate the utility of PSATs on deep-sea benthic fauna, incentivizing further development of methods to accommodate the challenges of tracking these species (Edwards et al. 2019a). For example, satellite tracking of Patagonian toothfish *Dissostichus eleginoides* in the South Atlantic and big skate *Beringraja binoculata* in the Gulf of Alaska revealed movement dynamics and seasonal depth distributions that were previously undescribed (Brown et al. 2013, Farrugia et al. 2016). Tracking studies for deep-sea species have been relatively rare thus far (Edwards et al. 2019a), despite the global distribution of deep-sea fisheries (Clark et al. 2016) and marked species declines in associated deep-sea fauna (Devine et al. 2006). These data limitations underscore the value of improved biological information for data-deficient benthopelagic species.

Bycatch reduction for a more effectively targeted and selective fishery depends on improved mitigation techniques and stakeholder engagement. Continuation of the summer longline fishery in Cumberland Sound should be evaluated in the context of bycatch levels of Arctic skates and Greenland sharks, while also further exploring reduced soak times and gear modifications. Enforced best handling practices for bycatch and observer monitoring of fisheries practices will be an effective mitigation tool in the immediate future and will need to be enacted through transparent discussions among all involved stakeholders. Depth-thermal niches here provide baseline data to track change over time, and expanded satellite telemetry studies will refine our understanding of the species' habitat use. Given the pronounced temperature regime change in the Arctic (Overpeck et al. 1997, Stone 2015) and apparent stenothermic behaviour in Greenland halibut and other polar species, further data from target species will be needed to assess species-specific susceptibility to fisheries and a changing environment. Telemetry and catch data are mutually informative and in complement can identify species-specific behavioural changes and vulnerability to fisheries and changing oceans. These combined approaches will allow more informed predictions of ecosystem change and improve the efficacy of ongoing wild fisheries toward more sustainable practices.

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