ICES Journal of
Marine Science

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2019), doi:10.1093/icesjms/fsz177

Utilization of pop-up satellite archival transmitting tags to evaluate thorny skate (*Amblyraja radiata*) discard mortality in the Gulf of Maine groundfish bottom trawl fishery

Ryan Knotek [1,2]*, Jeff Kneebone[2], James Sulikowski[3], Tobey Curtis[4], Joseph Jurek[5], and
John Mandelman[2]

[1]*School for the Environment—Marine Science and Technology Program, University of Massachusetts Boston, 100 William T. Morrissey Blvd., Boston, MA 02125, USA*
[2]*Anderson Cabot Center for Ocean Life, New England Aquarium, 1 Central Wharf, Boston, MA 02110, USA*
[3]*Marine Science Department, University of New England, 11 Hills Beach Rd., Biddeford, ME 04005, USA*
[4]*Highly Migratory Species Management Division, NOAA National Marine Fisheries Service, 55 Great Republic Dr., Gloucester, MA 01930, USA*
[5]*Northeast Fishery Sector II, Gloucester, MA 01930, USA*

**Corresponding author: tel: + 1 518 879 4084; e-mail: ryan.knotek001@umb.edu.*

Knotek, R., Kneebone, J., Sulikowski, J., Curtis, T., Jurek, J., and Mandelman, J. Utilization of pop-up satellite archival transmitting tags to evaluate thorny skate (*Amblyraja radiata*) discard mortality in the Gulf of Maine groundfish bottom trawl fishery. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsz177.

Received 24 January 2019; revised 2 August 2019; accepted 7 August 2019.

Thorny skate (*Amblyraja radiata*) remain one of the most overfished species in the Gulf of Maine (GOM) despite being designated as a prohibited (zero-possession, mandatory release) species by the New England Fishery Management Council in 2003. To better understand the extent to which discard mortality (DM) occurring after incidental capture in the GOM groundfish bottom trawl fishery may be impeding recovery, 75 individuals (55–94 cm total length, TL) were tagged with pop-up satellite archival transmitting (PSAT) tags and monitored for up to 28 days following capture under representative commercial trawl fishing practices. Data recovered from 61 PSAT-tagged skate were analysed with a longitudinal survival analysis to estimate DM and identify influential capture-related variables. DM rate was a function of TL, with larger skates (>70 cm; DM = 16.5%) experiencing lower mortality than smaller conspecifics (55–70 cm; DM = 24.5%). From our results, we estimate annual thorny skate DM in the GOM groundfish bottom trawl fishery to be 79.2 ± 0.2 mt, which accounts for <1% of the existing stock biomass in the GOM (8400 mt). This study confirms that thorny skate are relatively resilient to bottom trawl fishing practices in the GOM, and suggests that other sources of mortality may be impeding population recovery.

Keywords: best-practices, depth time-series, electronic tagging, longitudinal survival analysis, northeast multispecies fishery, Rajiformes

Introduction

In the US Gulf of Maine (GOM), skate species managed under the Northeast Skate Complex Fishery Management Plan (FMP) are both harvested and taken as bycatch by fisheries operating in the region. Under the FMP, fishing mortality for seven species is managed through a single complex-wide quota on total allowable landings (NEFMC, 2003). However, highly restrictive species-specific regulations such as retention limits and complete prohibitions (i.e. zero-possession) on commercial landings have been enacted to reduce mortality on overfished populations (NEFMC, 2003; Curtis and Sosebee, 2015). Although these measures may mitigate the impact of direct harvest (Waring, 1984; Hoenig and Gruber, 1990; Sulikowski *et al.*, 2003), some species still experience high rates of incidental capture (as bycatch), and discard mortality (DM) can continue to have significant impacts on skate populations because of their life history characteristics (e.g. slow growth, late maturation, and low fecundity). In fact, high DM rates may even perpetuate population declines by impeding species recovery (Davis, 2002).

Thorny skate (*Amblyraja radiata*) are one of the most overfished species in the GOM, with National Oceanic and Atmospheric Administration (NOAA) Northeast Fisheries Science Centre (NEFSC) bottom trawl survey biomass indices currently near 55 year lows (i.e. 0.17 kg tow^{-1}, <5% of the biomass target; NMFS, 2017). In response to this chronically poor stock status, the Northeast Skate Complex FMP prohibited this species in 2003 to reduce fishing mortality associated with commercial landings. However, thorny skate biomass in the GOM has declined further because the prohibition (Sosebee *et al.*, 2016), thereby suggesting that other sources of mortality, and/or environmentally driven distributional shifts (e.g. Nye *et al.*, 2009), are impeding stock recovery. For example, DM associated with the groundfish bottom trawl fishery, which was recently estimated to account for 72.6% (or 322.8 metric tonnes, mt) of total annual thorny skate live-discards in the GOM (Sosebee *et al.*, 2016), may represent a significant source of mortality.

DM in the GOM groundfish bottom trawl fishery was previously addressed by Mandelman *et al.*, (2013), wherein short-term mortality was 23% for 351 skates that were caught under representative trawl conditions and monitored in submerged enclosures for 72 h. However, the authors urged caution when considering the adoption of this estimate for stock assessments because of uncertainties associated with the 72-h cross-sectional results, particularly the compromised state (i.e. listless or moribund) of surviving skates at the completion of the 72-h trials, and the greater mortality (54%) evident in a subsample ($n = 35$) of thorny skate that were transported to shore-based tanks and monitored for 7 days. Long-term DM beyond 72 h has been reported for several other fish species (Kaimmer and Trumble, 1998; Knotek *et al.*, 2018; Schram and Molenaar, 2018), and shown to extend upwards of 27 days post-capture in a simulated trawl-capture with Pacific halibut, *Hippoglossus stenolepis* (Davis and Olla, 2001). However, the extent to which confinement stress throughout monitoring and/or transport or shielding from post-release predation, two potential limitations of confinement studies (Portz *et al.*, 2006), affected the 23% DM estimate of Mandelman *et al.*, (2013) is unknown. Nonetheless, the NEFMC incorporated the 23% DM rate into stock assessments under Framework Adjustment 2 to the Northeast Skate Complex FMP (NEFMC, 2014). Given the impact of assumed DM rates on annual catch limits and quotas set for the Northeast Skate Complex, a further investigation of trawl-caught thorny skate DM with monitoring periods exceeding 72 h is warranted to address the aforementioned uncertainties and confirm the accuracy of current DM estimates.

Pop-up satellite archival transmitting (PSAT) tags are powerful fisheries-independent tools for monitoring post-release fate over extended durations (Campana *et al.*, 2009). These tags can be rapidly applied (externally) to an animal prior to release, and allow the animal to swim freely and interact with its environment for a user-defined period prior to reporting their archived data via the Argos satellite system. These data can then be used to infer the post-release fate of an animal, determine the timing of mortality (if evident), and evaluate the effects of the capture-and-handling process on survival. Although PSAT tags have not previously been used to investigate skate DM, they have been used to examine movement patterns of several skate species including the common skate (*Dipturus batis*; Wearmouth and Sims, 2009), Arctic skate (*Amblyraja hyperborea*; Peklova *et al.*, 2014), and big skate (*Beringraja binoculata*; Farrugia *et al.*, 2016) over long-term periods (weeks to months), thereby demonstrating their utility for DM estimation. For these reasons, the objective of this study was to derive DM estimates for trawl-caught thorny skate over extended monitoring periods via PSAT tags. In addition to estimating DM rates, this study aimed to identify the most influential factors (e.g. fishing conditions and practices, individual biological traits, and degree of capture-related physical trauma) that affect thorny skate mortality, which could then be incorporated into a best-practice framework to reduce mortality in the GOM groundfish bottom trawl fishery.

Methods

Study site and fishing protocol

At-sea trials ($n = 9$ single-day trips) to collect information on thorny skate condition and DM rate following capture with typical commercial fishing practices in the GOM groundfish bottom trawl fishery were conducted during August and September 2016 ($n = 7$ days) and September 2017 ($n = 2$ days) in the coastal waters off northern Massachusetts (Figure 1). All trials occurred aboard a mid-sized (∼13 m) commercial fishing trawl vessel, the F/V *Mystique Lady* (Gloucester, MA), and tows ($n = 27$) were conducted using a standard trawlnet (16.51 cm codend mesh; 20.12 m headrope length; 21.95 m footrope length; 8.90 cm cookie sweep) with 127 cm trawl doors. Fishing was conducted in depths that ranged from 55 to 161 m and occurred on predominately soft-bottom substrate in calm seas (<1 m wave height) for durations of 30–240 min and at speeds of 2–4 kts. Bottom seawater and air temperatures were measured during all tows and on-deck sampling with HOBO temperature loggers (Onset Computer Corp., Bourne, MA) affixed to the headrope of the trawlnet and to the topside of the vessel, respectively. The temperature logger on the topside of the vessel was housed in an RS1 Solar Radiation Shield (Onset Computer Corp.) to more accurately measure on-deck air temperatures. From these measurements, the temperature gradient evident during each sampling event was calculated as the difference between bottom seawater and air temperatures. Temperature gradients during this study reflect "worst-case scenario" summer temperature regimes in the GOM (elevated bottom to surface seawater gradients and highest air temperatures), which are known to exacerbate capture-related stress in congeneric species of skate from this region (e.g. >9°C temperature gradients; Cicia *et al.*, 2012).

Sampling procedure

Following each tow, the catch was deposited on-deck and the total catch weight (in kg) was estimated by the vessel captain. Fishers then followed standard commercial practices in the GOM trawl fishery when culling/sorting catch. This included sorting of the catch by species into fish totes (71 cm × 41 cm × 28 cm) either by hand or by inserting a fish pick (a hand-held tool with a metal hook or nail for lifting and manoeuvering catch) into the wing musculature. To examine the effect of air exposure on DM, individuals were sampled continuously over a period of ∼75 min from the initial air exposure of the net codend, which represents

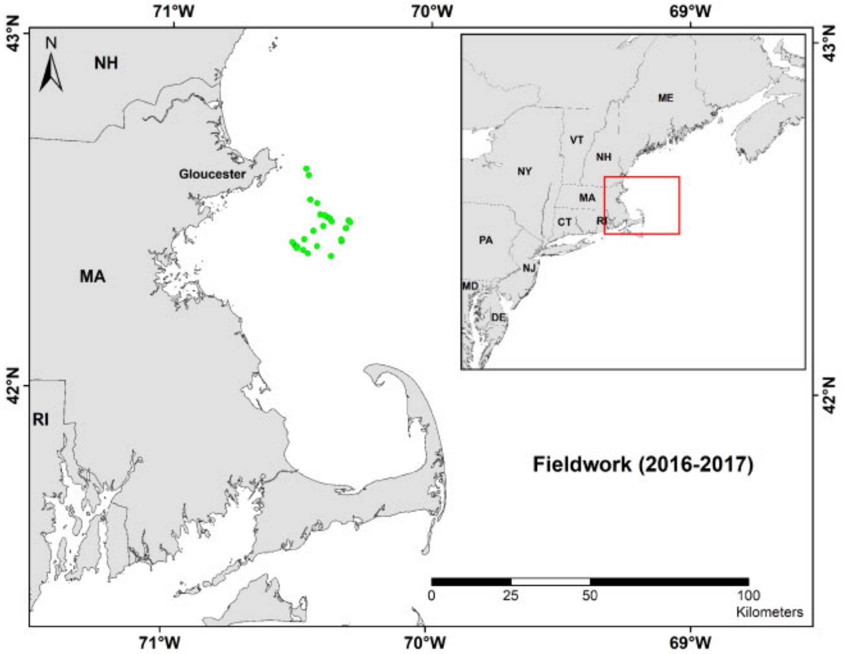

Figure 1. Individual two locations ($n = 27$; depicted as points) from the fieldwork conducted in August and September (2016–2017) aboard the F/V Mystique Lady in the Gulf of Maine.

Table 1. Injury code classifications based on overt physical trauma adapted from Mandelman *et al.* (2013) that were used to evaluate the condition of trawl-caught thorny skate.

Code	Description
1	None to minor physical trauma (<10 mm lacerations, no haemorrhaging or internal bleeding) and normal coloration
2	Moderate physical trauma (11–20 mm lacerations, slight to moderate haemorrhaging or internal bleeding) and may or may not show signs of discoloration
3	Severe physical trauma (>20 mm lacerations, extensive haemorrhaging or internal bleeding) and body discoloration

All skates were evaluated by a single researcher to avoid any subjectivity in scoring.

the maximum elapsed on-deck time prior to discard in the fishery.

For each skate sampled, the sex and total length (TL; cm) were recorded. Maturity status was also recorded, with male skates considered mature when claspers were long and fully calcified (Ruocco *et al.*, 2006), and female skates recorded as mature based on palpitation for developing egg cases or having a distended/vascularized cloaca (i.e. suggesting recent parturition; Sosebee, 2005). Each skate was also assigned a nominal injury code based upon the level of overt physical trauma as originally described in Mandelman *et al.*, (2013; Table 1; Supplementary Figure S1). Injury assessments for all skate were conducted by a single researcher and therefore were not subject to interpretational bias. Skate were then released, with the exception of a subsample described in the following section.

Monitoring the fate of discarded skate

To examine the fate of discarded thorny skate, a subset of 75 individuals (55–94 cm TL) were tagged with PSAT tags (Model: PSATLIFE, Lotek Wireless Inc., St John's, Newfoundland, Canada). These tags measured pressure (i.e. depth) and ambient water temperature at 10-s intervals over 14- or 28-day deployment periods. Following this period, the tags were programmed to detach, float to the surface, and transmit the archived data compiled into 5-min bins. Higher resolution data (i.e. 10-s intervals) were only accessible in cases where the tag was physically recovered and directly downloaded using the "Tag Talk" program (Lotek Wireless Inc.). Tags were affixed near the centre of one of the skate's pectoral wings using a method modified from Wearmouth and Sims (2009), wherein a monofilament line and two pairs of 1″ Petersen discs and baffles were crimped on either side of the skate's wing musculature (dorsal and ventral; Figure 2). To minimize the potential impact of sampling and tagging on post-release fate, individual skates were processed as quickly as possible (1–6 min). Prior to at-sea sampling, tag attachment/retention trials were performed at the University of New England Marine Science Centre (Biddeford, ME) with captive thorny skate (55–65 cm TL) to confirm that our attachment technique resulted in no tag shedding and/or tag-induced mortality up to 28 days post-tagging. Tags were not applied to skate <55 cm TL because of concerns that the PSAT tags would compromise the mobility of smaller individuals and therefore potentially result in tag-induced mortality.

PSAT tags were strategically deployed on individuals across a range of tow and air exposure durations, and for each injury code

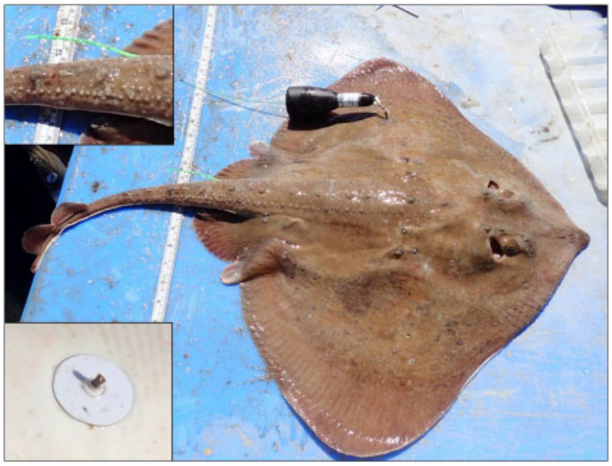

Figure 2. Pop-up satellite archival transmitting tag (Lotek LIFE LAT3500) attachment method using monofilament line and two pairs of 1″ Petersen discs and baffles secured on either side of the skate (dorsal and ventral). Image in the lower-left corner displays the Petersen disc/baffle/crimp pair on the ventral side of the skate. Image on the top-left corner displays the Floy® dart tag that was inserted at the base of the tail for all skates ≥30 cm total length.

and handling method (i.e. hand sorting vs. fish pick), in order to assess the impact of several variables experienced during typical commercial fishing conditions. Furthermore, PSAT tags (14-day deployment) were also deployed on dead skates ($n = 2$) to establish "negative control" movement signatures, which would be used in subsequent analyses to infer mortality events.

Survival analysis

We utilized a longitudinal survival analysis to model the probability of survival as a function of time (e.g. Cox and Oakes, 1984; Benoît *et al.*, 2012, 2015). In this analysis there were four primary objectives. First, PSAT tag depth time-series data were examined to determine the fate of our subsampled skates. Second, the fishing conditions and biological covariates associated with each subsampled skate were evaluated to identify, which covariates were best able to predict survival following discard. Third, using this subset of covariates, a suite of survival mixture models (SMMs; developed by Benoît *et al.*, 2012, 2015) were fitted to explain survival and ultimately provide DM estimates. Finally, best-practice frameworks were formulated based upon the subset of covariates to mitigate thorny skate mortality. All analyses were performed using R 3.4.5 (R Core Team, 2017), and when applicable, statistical significance was accepted at $p < 0.05$.

Depth-variance survival test

To determine the fate of individual discarded animals, we first converted pressure data collected by the PSAT tags to depth using the package "rtide" (Thorley *et al.*, 2017) and removed any tidal-noise associated with the tidal cycle of the area with the "oce" package (Kelley and Richards, 2017). Depth time-series for each skate were then subjected to a modified depth-variance survival test adapted from Capizzano *et al.*, (2016), with an additional clause to ensure the test was not falsely classifying extended periods of on-bottom (live) behaviour as mortality events (details in Supplementary Material). If skate survived throughout the monitoring period they were treated as right-censored data because their fate is unknown following tag detachment (i.e. time of death occurs after the monitoring period). If mortality was confirmed (i.e. a censored event), time of death was estimated as the time bin with the first non-significant result in the sequence leading up to the end of the trial. One individual was recaptured alive ~8 days after release, but died shortly after being released again. Because this mortality event could not be attributed to the original capture event, its time-series was truncated to the recapture event and was treated as a right-censored (i.e. alive) observation at the point of recapture.

Assessment of fishing conditions and practices, individual biological traits, and injury

For this step of the analysis we considered all covariates (i.e. fishing conditions and practices, individual biological traits, and injury scores) that could influence survivorship of trawl-caught thorny skate. Initial examination of correlation between covariates and relevant interactions (i.e. TL and catch weight, TL and air exposure, and air temperature and air exposure) using a Pearson correlation revealed that interactions terms were all highly collinear with respect to catch weight ($r = 0.97$) or air exposure ($r = 0.97$). Therefore, interaction terms were not considered in the survival analysis.

The empirical Kaplan–Meier estimator (Cox and Oakes, 1984), a non-parametric analysis that provides an estimate of the survival function by following the proportion of live skate throughout the time-at-large and in the absence of censored values, was utilized to generate preliminary graphical depictions of the influence of each covariate on survivorship, and to provide an empirical estimate of survival that can be used to assess the fit of SMMs developed in later steps.

The multivariate (semi-parametric) survival analysis known as the Cox proportional-hazards model (CPHM; Cox, 1972; Therneau and Grambsch, 2000) was then used to identify, which covariates (i.e. tow duration, fishing depth, temperature gradient, catch weight, handling method, air duration, TL, sex, maturity, and injury score) predicted the survival of discarded thorny skate following the methodologies outlined in Knotek *et al.* (2018). This model is defined as:

$$\hat{h}(t) = h_0(t)^{(X'\beta + Z'b)}, \qquad (1)$$

where $\hat{h}(t)$ is the hazard function at time t (i.e. the risk of incidental morality occurring at time t) determined by a non-parametric baseline hazard function $h_0(t)$, a suite of relevant covariates X', and a Gaussian random effect Z' (with tow as the subject) to account for any within-tow correlations (Benoît *et al.*, 2010; Knotek *et al.*, 2018). To estimate parameters in this model we used partial maximum likelihood (Cox, 1972; Ripatti and Palmgren, 2000). Model building was twofold: (i) identify whether or not the random effect was appropriate, and (ii) find the most parsimonious set of covariates to predict survival (details in Supplementary Material; Benoît *et al.*, 2010; Knotek *et al.*, 2018).

Model building revealed a fixed-effects modelling approach was appropriate (i.e. random effect of tow was not significant; $p = 0.97$) and TL was the only covariate that predicted survival (see Supplementary Table S2 for model building output). TL was then converted into a categorical predictor (binned every 10 cm) to reflect size classes used in NEFSC bottom trawl surveys, and to allow us to identify, which of the TL-specific DM rates (generated in subsequent steps) best reflected the size-distribution of thorny skate discards in the GOM. Log-rank tests were then performed to test for differences in the underlying survival function between size classes and if the resulting *p*-value was not significant ($p > 0.05$), these classes were combined. This led to the consolidation of bins >70 cm TL (χ^2: 0.48 to 0.82) and bins ≤70 cm TL ($\chi^2 = 0.70$). TL was therefore used as a two-level categorical covariate in subsequent analyses.

Predicting post-release survival based upon relevant covariates

To estimate post-release survivorship rates, we chose to use a parametric survival analysis modelling approach (i.e. SMMs) developed by Benoît *et al.* (2012, 2015). This approach is favourable because of its ability to explain the survivorship of thorny skate over time with longitudinal data, and estimate the time at which survivorship asymptotes (i.e. survival rate). The underlying model of the SMMs is defined as:

$$\hat{S}(t) = \pi \cdot \exp\left[-(\alpha \cdot t)^{\gamma}\right] + (1 - \pi), \qquad (2)$$

where $\hat{S}(t)$ is the probability of survival at time t. The probability of a skate being adversely affected by capture-and-handling is denoted by π and the survival function for these skate is explained by $\exp[-(\alpha \cdot t)^{\gamma}]$, which is assumed to follow a Weibull distribution that includes scale and shape parameters, α and γ, respectively. The skates not adversely affected by capture-and-handling are assumed to have a survival probability of 1, as natural mortality was assumed to be negligible during the relatively short-duration of the tag monitoring period (14–28 days). In Equation (2) the survival rate is defined as $\hat{S}(t) = 1 - \pi$ because as $t \to \infty$, $\exp[-(\alpha \cdot t)^{\gamma}]$ eventually leads to nil survival for affected individuals, leaving only the non-affected skate alive. To incorporate the influence of TL on survivorship, α and π parameters can be manipulated to address the effect of the covariates on the survival rate over time and/or the probability of a skate being adversely affected, respectively. This approach produces several competing models according to the different assumptions of how TL impacts survivorship (Table 2). All model variants were fit using maximum likelihood methodology (additional details provided in Benoît *et al.*, 2012, 2015) and convergence and fit were evaluated by overlaying the 95% confidence bands from Kaplan–Meier estimates with the predicted survival functions. Model fits were also compared using Akaike's Information Criterion corrected for small samples sizes (AICc; Burnham and Anderson, 2002), wherein ΔAICc values (relative to lowest AICc value between models) were used to identify the model variant(s) most suited for predicting the survival function (details in Supplementary Material; Burnham and Anderson, 2002). Based upon a comparison of ΔAICc (Table 2) there was similar support for several of the competing models and therefore no single-model could be considered a best-fit. Therefore, model averaging (of SMMs) based on Akaike weights (e.g. Lukacs *et al.*, 2010; Benoît *et al.*, 2010; details in Supplementary Material) was used to generate a single survival rate for each size class that reflected the suite of model variants according to their ΔAICc values (e.g. Knotek *et al.*, 2018).

Estimation of DM on a fishery-scale

To estimate fishery-wide DM for thorny skate in the GOM groundfish bottom trawl fishery, we used a modified modelling approach described by Knotek *et al.* (2018). Here, model averaged survival rates (see above) were converted into DM rates (i.e. 1—survival rate), then applied to the most recently available estimate of total annual live-discards (by weight) in the fishery to derive an estimate of DM (in mt). However, since recent NEFSC bottom trawl data suggest that ∼95% of all thorny skate occupying the GOM are <74 cm (Sosebee *et al.*, 2016), only the DM rate associated with the smaller-size category (55–70 cm TL) was used to estimate DM. Finally, to account for model variant-specific parameter uncertainty and variability in fishery-scale estimates of DM, Monte Carlo simulations based on bootstrapping (Efron and Tibshirani, 1993; details in Supplementary Material) were used with this approach to derive the final fishery-scale estimate (mean and standard deviation) of DM.

Results

Fieldwork and capture characteristics

In all 612 thorny skate (24–94 cm TL; 305 male and 307 female) were captured and sampled after being handled by hand ($n = 323$) or with a fish pick ($n = 289$; Table 3). The majority of skates was categorized as having minor (i.e. injury code 1; 38.4%) to moderate (i.e. injury code 2; 44.0%) overt physical trauma with the fewest observations made for severely injured skate (i.e. injury code 3; 17.6%; Table 3). Tows that captured thorny skate were primarily composed of common commercial groundfish species (e.g. grey sole, *Glyptocephalus cynoglossus*; yellowtail flounder, *Pleuronectes ferruginea*; winter flounder, *Pseudopleuronectes americanus*; haddock, *Melanogrammus aeglefinus*; and Atlantic cod, *Gadus morhua*), monkfish (*Lophius americanus*), spiny dogfish (*Squalus acanthias*), skate (e.g. little skate, *Leucoraja erinacea*; winter skate, *Leucoraja ocellata*; and barndoor skate, *Dipturus laevis*), and to a lesser extent, invertebrates (e.g. American lobster, *Homarus americanus*; and rock crab, *Cancer borealis*). Total estimated catch weight per tow ranged from 29 to 907 kg. Bottom seawater and air temperature ranged from 6.3 to 8.3°C and 16.5 to 26.8°C, respectively, whereas the temperature gradient between the two locations varied from 9.3 to 19.6°C (Table 4).

Monitoring the fate of discards and negative controls

Of the 75 PSAT tags deployed, 59 transmitted Argos data and 35 were physically recovered and/or returned and directly downloaded, including two tags that did not transmit. In total, we retrieved data from 61 of the 75 PSAT tags (81.3%) via transmission ($n = 30$) and/or physical recovery and direct download ($n = 31$). Tags that only provided Argos transmissions, including one of the two negative controls (i.e. known dead skate), yielded an average of 88.7% (out of 4032 expected observations) and 72.3% (out of 7888 expected observations) of the time-series data in 5-min resolution for 14- and 28-day deployment periods, respectively. In contrast, physically downloaded tags provided access to the entire time-series in 10-s resolution for the 14- and 28-day deployment periods (i.e. 120 960 and 236 640 observations, respectively).

Depth-variance survival test

The depth-variance survival test identified seven mortality events (see Supplementary Table S1 for individual mortality event information), with the majority ($n = 5$ individuals) of capture-related DM having occurred within 18 h of release. However, two mortalities did occur at 241 and 263 h post-release (Figure 3). After

Table 2. Model variant results for survival mixture models (SMMs) that modelled thorny skate survival as a function of total length (TL) treated as a two-level categorical covariate.

Model variants	Parameters		Model fitting	Discard mortality rates	
	α	π	ΔAICc	55–70 cm TL	>70 cm TL
Weibull 2[a]	f(size)	1	5.195	100	100
Mixture 2[b]	f(size)	Constant	–	21.63 [0.11]	21.63 [0.11]
Mixture 3[c]	Constant	f(size)	2.540	21.98 [0.11]	5.13 [0.08]
Mixture 4[d]	f(size)	f(size)	0.370	22.16 [0.11]	6.67 [0.13]
			Model average	24.53 [0.06]	16.50 [0.07]

TL's effect on survivorship was modelled under different assumptions of model parameters α and π, which were treated either as fixed (equal to 1), constant (estimated), or as a function of TL categories, f(size). Model variant fit is represented by the change in Akaike's Information Criterion corrected for small sample sizes (ΔAICc) relative to the lowest AICc value (indicated with a dash "–"). Model averaged discard mortality rates (in %; derived from survival rates generated by SMMs) are presented as the mean [standard error] from Monte Carlo simulations ($n = 5000$) with parametric bootstrapping to simulate model uncertainty.

[a] Common survival function for each total length category.

[b] Common survival function within each total length category for a fixed proportion of affected individuals.

[c] Common survival function for affected individuals, with the proportion affected dependent on total length category.

[d] Common survival function within each total length category, where the proportion of affected individuals also depends on total length category.

Table 3. Number of trawl-caught thorny skate sampled as either observational samples or tagged with pop-up satellite archival transmitting (PSAT) tags for each category of handling method, sex, and injury code.

	Handling method		Sex		Injury code		
Sample	Hand	Fish pick	Male	Female	Code 1	Code 2	Code 3
Observation	323	289	305	307	235	269	108
PSAT	39	34	40	33	19	28	26

Negative control PSAT-tagged skate ($n = 2$) are not included in this table.

Table 4. Mean [minimum, maximum] values of the fishing conditions, practices, and individual traits observed for thorny skate released as either observational samples or with pop-up satellite archival tags (PSAT).

Variable	Observational		PSAT	
Tow duration (min)	141	[37, 236]	137	[40, 236]
Depth (m)	101	[55, 161]	99	[75, 161]
Temperature (°C)				
Bottom seawater	7.2	[6.3, 8.3]	7.1	[6.4, 8.3]
Air (on-deck)	20.8	[16.5, 26.8]	19.6	[16.5, 26.9]
Gradient	13.6	[9.3, 19.6]	12.5	[9.9, 19.6]
Catch weight (kg)	354	[29, 907]	468	[29, 907]
Air exposure (min)	30.7	[3.7, 76.7]	30.2	[5.8, 69.5]
Total length (cm)	46.9	[24.0, 94.0]	70.6	[55.5, 94.0]

mortality occurred, PSAT tags generally remained attached to dead skates for 121–489 h before dislodging and floating to the surface. Surviving skates ($n = 53$) occupied depths ranging from 22.9 to 184.0 m (mean ± standard deviation: 89.8 ± 19.0 m) and displayed vertical movement behaviour that can be broadly categorized as periods remaining at-depth (maximum span of 102 h) with brief off-bottom forays (associated with diel-cycles), and on/off shelf movement (Supplementary Figure S2). Ultimately, these behaviours made it possible to characterize the status of skate (live or dead) throughout a time-series and identify mortality events.

Discard survival rates and estimates of fishery-scale DM

Model variants (i.e. SMMs) fit the 95% confidence bands relatively well (i.e. within the centre of the bands) with the exception of the time frame preceding the first mortality in the smaller category (55–70 cm TL). However, model fit largely improved over time for this category (Figure 4). Individual model variants generated a range of size-specific DM rates according to the various model assumptions (Table 2). For example, Weibull 2 assumed that all skate were adversely affected (nil survival), whereas Mixture 4 allowed the survival function and proportion of adversely affected skate to vary by size category (6.7 and 22.2% mortality for larger and smaller skate, respectively; Table 2). However, because each variant carried different Akaike weights (Table 2) with no clear best-fitting model (according to Benoît *et al.*, 2012), model averaging was used to generate a single overall DM rate for each size category that incorporated model variant DM rates based on their relative contribution to the survival function (i.e. Akaike weight). This approach estimated that larger skate have a lower DM rate (16.5 ± 0.1%) than smaller thorny skate (24.5 ± 0.1%; Table 2). Based upon the mortality rate for the smaller category and average annual estimates of bottom trawl thorny skate live-discards (i.e. 322.8 mt in 2014; Sosebee *et al.*, 2016), annual DM for the GOM groundfish bottom trawl fishery is ∼79.2 ± 0.2 mt.

Discussion

Thorny skate DM in the GOM groundfish bottom trawl fishery

This study demonstrated the utility of PSAT tags for assessing the long-term survivorship of a benthic skate species following discard from one of the GOM's largest commercial fisheries. By modelling PSAT tagging data in concert with detailed observations collected during the capture event, a size-dependent DM rate was identified that suggested larger thorny skate (DM rate = 16.5%) experience lower mortality than smaller conspecifics (DM rate = 24.5%) when caught in bottom otter trawls under "worst-case scenario" summer temperature regimes (Cicia *et al.*, 2012). Furthermore, given the average size of thorny skate in the GOM, the DM rate estimate for the smaller category (55–70 cm TL) was determined to best reflect the size-distribution of

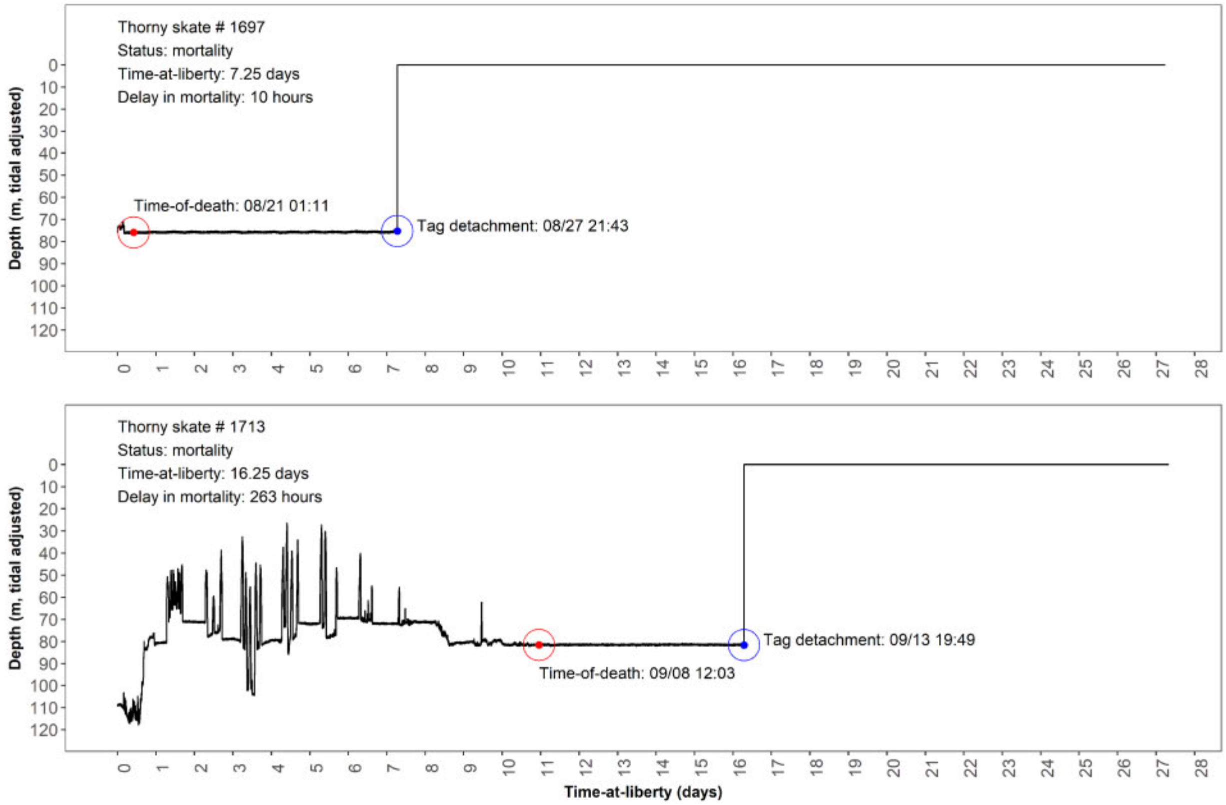

Figure 3. Tide-adjusted depth time-series (solid line) obtained from pop-up satellite archival transmitting tags (10-s resolution) deployed on two thorny skate that exhibited immediate (top panel) and delayed (∼10 days; bottom panel) mortality. Transmission characteristics are provided in the upper left corners of the figures. Time of death derived from the depth-variance survival test and time of tag detachment (i.e. pop-up) are both indicated with a dot/circle and annotated with text, respectively.

discards and the overall DM rate in the bottom trawl fishery. This overall DM rate is consistent with the previous estimate (23%) reported by Mandelman *et al*., (2013) and is markedly lower than estimates for other trawl-caught species of skate (Laptikhovsky, 2004; Enever *et al*., 2009; Mandelman *et al*., 2013; Saygu and Deval, 2014; Tsagarakis *et al*., 2015), which suggests thorny skate are fairly resilient to capture-and-handling in this fishery.

Our results indicate that the majority of thorny skate DM following capture in bottom trawls occurred within 18 h of discarding; however, longer term manifestations of DM were also evident up to 10 days post-release. Previous studies with trawl-caught skate in the Bristol Channel and Gulf of St Lawrence (Enever *et al*., 2009; Benoît *et al*., 2012) found that DM occurred entirely within 24 h post-release when using monitoring periods of up to 64 and 110 h, respectively. In contrast, extended monitoring periods (up to 28 days) in this study revealed delayed DM events, which corroborates recent observations of little and winter skate captured in the New England scallop dredge fishery (Knotek *et al*., 2018). Of note, most previous studies of skate DM have not been able to quantify delayed DM because of abbreviated monitoring periods (≤5 days) associated with traditional confinement methods (i.e. on-board holding tanks and submerged cages; Kaiser and Spencer, 1995; Endicott and Agnew, 2004; Laptikhovsky, 2004; Enever *et al*., 2009; Benoît *et al*., 2012; Mandelman et al., 2013; Depestele *et al*., 2014; Saygu and Deval, 2014; Tsagarakis *et al*., 2015; Sulikowski *et al*., 2018), thereby making our PSAT tag-derived results more reliable and robust to both short and delayed DM events. Nonetheless, the occurrence of delayed DM for thorny skate in this study was relatively low, which confirms that the 54% (7 days) DM rates reported by Mandelman *et al*., (2013) were more likely an artefact of confinement stress than a result of capture-and-handling (Portz *et al*., 2006).

The impact of capture-related and biological factors on DM rates

All of the mortalities documented in this study can be attributed to the effects of capture-and-handling in the GOM groundfish bottom trawl fishery, and are not considered a reflection of natural mortality. Natural mortality in these types of studies (e.g. Benoît *et al*., 2012; Mandelman et al., 2013; Depestele *et al*., 2014; Knotek *et al*., 2018) is considered negligible because the monitoring period is relatively short compared to the lifespan of elasmobranchs (e.g. ∼16 years for thorny skate in the GOM; Sulikowski *et al*., 2005), and any predation within this time frame would have likely been because of decreased predator avoidance abilities from the effects of the capture event (Raby *et al*., 2014). Therefore, DM rates for trawl-caught thorny skate were driven by capture-related factors that included the size of the animal, the degree of incurred physical trauma, thermal stress, and stressors associated with air exposure during the capture-and-handling process.

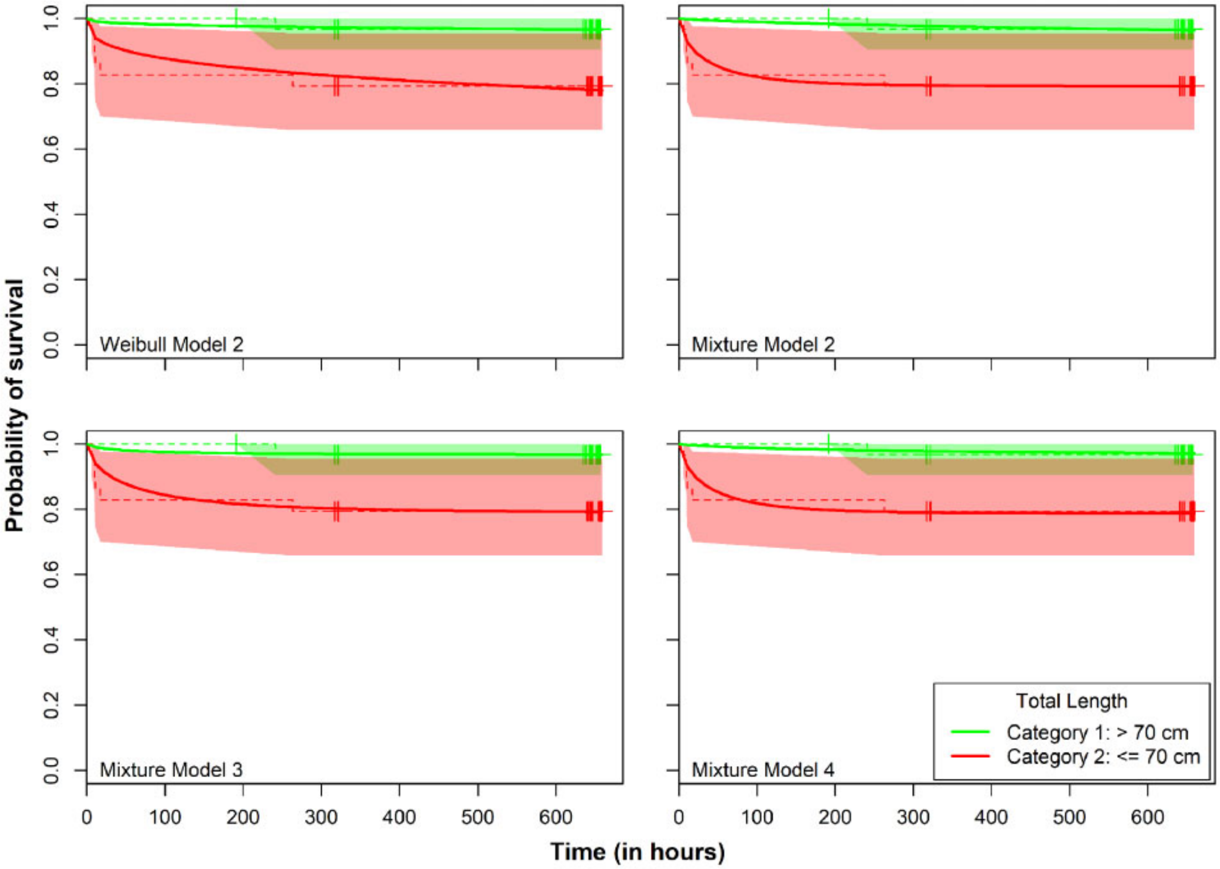

Figure 4. Probability of survival over time for thorny skate with respect to size-category for each model variant (indicated in the bottom-left corner of each panel). Dashed lines and shaded areas represent Kaplan–Meier estimates and 95% confidence bands up until the last observation for each size category. Censored observations are indicated with "+" along the Kaplan-Meier estimate (i.e. dashed line). Solid lines show the model variant prediction.

TL was identified with our modelling approach as the most influential factor affecting trawl-caught thorny skate DM. In this size-dependent relationship, smaller thorny skate displayed a higher degree of DM than larger conspecifics, which has similarly been reported for skate discarded from beam trawls in the North Sea (Depestele *et al.*, 2014), and speculated for thornback skate, *Raja clavata*, and brown skate, *Raja miraletus*, captured in bottom trawls in the eastern Mediterranean (Saygu and Deval, 2014). In addition, size has also been shown to influence at-vessel mortality (i.e. mortality occurring at or prior to landing) for ray species (family Dasyatidae and Myliobatidae) captured in the prawn trawl fishery off of northern Australia (Stobutzki *et al.*, 2002). In all of these scenarios, increased survivorship of larger individuals may be the result of a thicker integument providing added protection (Mandelman *et al.*, 2013; Depestele *et al.*, 2014), having a larger body mass and core body temperature that is less sensitive to ambient temperature changes (Spigarelli *et al.*, 1977), and/or having more energetic reserves to cope and recover from the capture-and-handling process. This size-dependent relationship may have also been an artefact of tag-induced mortality wherein individuals in the smaller category (55–70 cm TL) were more susceptible to the adverse effects associated with carrying PSAT tags. However, there was no relationship between smaller size and increased mortality within this size category (Supplementary Table S1), and no mortality was observed during the initial 28-day retention trials that were conducted on skates measuring 55–65 cm TL (i.e. the smallest tagged in the field study). As such, there is no evidence to suggest that our results were greatly confounded by tag-induced mortality.

Thorny skate DM rates were also influenced by the degree of physical trauma incurred during the capture event in this study. For example, the DM rate (based on live-dead proportion) increased by 25% across injury scores (code 1 = 6%; code 2 = 9%; code 3 = 31%). Injury is a well-documented factor impacting DM in skates (e.g. Depestele *et al.*, 2014; Knotek *et al.*, 2018; Sulikowski *et al.*, 2018) and has been previously shown to influence DM for trawl-caught thorny skate in the Gulf of St Lawrence (Benoît *et al.*, 2012). Furthermore, higher degrees of physical trauma (injury codes 2 and 3) were likely the underlying driver for longer term (delayed) manifestations of thorny skate mortality; wherein sublethal injuries (e.g. puncture wounds and lacerations) could have compromised the skate's integument and epidermal mucus layer, and led to osmoregulatory dysfunction, secondary infections, and/or susceptibility to disease (Luer, 2014; Cook *et al.*, 2019).

Though there was evidence that injury influenced DM, higher incidental PSAT tag non-reporting rates for skate that incurred more severe physical trauma (injury codes 2 and 3) limited our ability to comprehensively evaluate the effect of injury on mortality. For example, while all tags reported from animals with no to minor injuries (code 1), non-reporting rates rose to 14.3% ($n = 4$) and 34.6% ($n = 9$) for skate that suffered moderate (code 2) to more severe injuries (code 3), respectively. This trend becomes particularly relevant to the study if we consider the scenario of non-reporting rates as an artefact of DM events; wherein tags were either damaged during a scavenging event or inhibited from transmitting following premature detachment from the dead skate (via decomposition/scavenging) and the tag washing ashore and/or being covered by debris before the pre-programmed transmission at 14 or 28 days after deployment. Had more tags reported for the higher injury codes, it is likely that additional mortality events would have been documented and the degree of physical trauma would have had a more pronounced role in establishing DM rates. Therefore, the estimated mortality rates for skates with injury codes 2 and 3 should be considered minimums.

Despite the effect of TL and injury on thorny skate DM, this species seems capable of surviving extended tow durations of up to 3.9 h, prolonged bouts of air exposure up to 70 min, and large-scale temperature gradients up to 19.6°C, to which many skate species have previously shown susceptibility. For example, mortality increased with tow duration for trawl-caught cuckoo skate, *Leucoraja naevus*, small-eyed skate, *Raja microocellata*, blonde skate, *Raja brachyura*, and thornback skate in the Bristol Channel (Enever *et al.*, 2009) and smooth skate, *Malacoraja senta*, in the GOM (Mandelman *et al.*, 2013). Though there are inherent limitations in evaluating tow duration (i.e. inability to pinpoint the exact time skate entered the codend; Neilson *et al.*, 1989), thorny skate are likely more resilient to longer periods of compaction in the codend because of their larger size and more rigid morphology that provides added physical protection (Sulikowski *et al.*, 2005; Natanson *et al.*, 2007). To this end, Mandelman *et al.*, (2013) reported that trawl-caught smooth skate were 10.9% more likely to incur severe injuries than thorny skate in the GOM, which is further substantiated by the nearly 82% of trawl-caught thorny skate sustaining only minor to moderate injuries in the present study.

Individual and cumulative effects of prolonged bouts of air exposure and abrupt changes in bottom seawater to air temperature did not appear to result in high levels of thorny skate DM. Previous studies have demonstrated that both the individual (e.g. 30-min air exposure or 18.1°C temperature gradient; Knotek *et al.*, 2018) and cumulative (e.g. interaction of 50-min air exposure and 9.1°C temperature gradient; Cicia *et al.*, 2012) impacts of these factors have resulted in increased DM for little and winter skate. However, in this study trawl-caught thorny skate were capable of surviving both the individual and cumulative effects of more pronounced exposure events (up to 20 min longer) and abrupt temperature gradients (up to a 10.5°C larger gradient) than was reported as being lethal in little and winter skates (Cicia *et al.*, 2012; Knotek *et al.*, 2018). The reasons for this resiliency are unknown, but nonetheless, it suggests that thorny skate may be tolerant of acute hypoxia and thermal stress.

Management implications and conclusions

This study confirms that thorny skate are relatively resilient to bottom trawl fishing practices in the GOM, with annual DM accounting for <1% of the existing stock biomass in the region (Sosebee *et al.*, 2016; NMFS, 2017). This suggests that factors other than DM (e.g. environmentally driven change; Di Santo, 2015) may be contributing to the impaired recovery of this species that has been evident in the 15 years since its prohibition. However, given that thorny skate biomass is currently at only 2.3% of its highest historical level (i.e. 364 million mt in 1966; Sosebee *et al.*, 2016) the population is likely highly sensitive to even small-scale sources of mortality, such as DM. Furthermore, the impact of DM on thorny skate population recovery is further elevated if extensive fishing effort occurs within areas of high thorny skate biomass (Knotek *et al.*, in prep.). Therefore, best-practices aimed at reducing mortality in this fishery should still be taken into consideration in fisheries management, especially when providing collateral benefits to other non-target species/size classes. This could include best-practice handling methods such as prioritizing the immediate release of skates to reduce time on-deck and air exposure and encouraging fishers to avoid picking skate in areas of vital organs (i.e. cranial, pericardial, and abdominal cavities). Other factors to consider include mitigation measures that address animal size; however, traditional best-practices such as size limitations are not applicable for this species given its prohibited status. Bycatch avoidance strategies are therefore a likely more appropriate option, particularly the avoidance of areas where smaller skate are found in abundance. Lastly, given the gear-specific nature of DM, future research efforts should be directed towards evaluating mortality in the other major gear-types responsible for thorny skate discarding, including scallop dredge, sink gillnet, and bottom longline gears.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

Data collection in this study was made possible by research scientists from the Anderson Cabot Centre for Ocean Life at the New England Aquarium, who assisted us throughout this study during fieldwork. This study was approved by the New England Aquarium Institutional Animal Care and Use Committee (Protocol 2016-02).

Funding

Funding for this research was provided by the 2015 NOAA NMFS Bycatch Reduction Engineering Program (Award # NA15NMF4720373).

References

Benoît, H. P., Capizzano, C. W., Knotek, R. J., Rudders, D. B., Sulikowski, J. A., Dean, M. J., Hoffman, W. *et al.* 2015. A generalized model for longitudinal short-and long-term mortality data for commercial fishery discards and recreational fishery catch-and-releases. ICES Journal of Marine Science, 72: 1834–1847.

Benoît, H. P., Hurlbut, T., and Chassé, J. 2010. Assessing the covariates influencing discard mortality of demersal fishes in four fisheries using a semi-quantitative indicator of survival potential. Fisheries Research, 106: 436–447.

Benoît, H. P., Hurlbut, T., Chasse, J., and Jonsen, I. D. 2012. Estimating fishery-scale rates of discard mortality using conditional reasoning. Fisheries Research, 125–126: 318–330.

Burnham, K. P., and Anderson, D. R. 2002. Model Selection and Multimodel Inference: A Practical Information Theoretic Approach, 2nd edn. Springer-Verlag, New York.

Campana, S. E., Joyce, W., and Manning, M. J. 2009. Bycatch and discard mortality in commercially caught blue sharks *Prionace glauca* assessed using archival satellite pop-up tags. Marine Ecology Progress Series, 387: 241–253.

Capizzano, C. W., Mandelman, J. W., Hoffman, W. S., Dean, M. J., Zemeckis, D. R., Benoît, H. P., and Langan, J. A. 2016. Estimating and mitigating the discard mortality of Atlantic cod (*Gadus morhua*) in the Gulf of Maine recreational rod-and-reel fishery. ICES Journal of Marine Science, 73: 2342–2355.

Cicia, A. M., Schlenker, L. S., Sulikowski, J. A., and Mandelman, J. W. 2012. Seasonal variations in the physiological stress response to discrete bouts of aerial exposure in the little skate, *Leucoraja erinacea*. Comparative Biochemistry and Physiology—Part A: Molecular & Integrative Physiology, 162: 130–138.

Cook, K. V., Hinch, S. G., Drenner, S. M., Raby, G. G., Patterson, D. A., and Cooke, S. J. 2019. Dermal injuries caused by purse seine capture result in lasting physiological disturbances in coho salmon. Comparative Biochemistry and Physiology—Part A: Molecular & Integrative Physiology, 227: 75–83.

Cox, D. R. 1972. Regression models and life tables. Journal of the Royal Statistical Society, 34: 187–200.

Cox, D. R., and Oakes, D. 1984. Analysis of Survival Data. Chapman and Hall Ltd, London.

Curtis, T. H., and Sosebee, K. A. 2015. Landings composition of the northeast US skate, Rajidae, wing fishery and the effectiveness of prohibited species regulations. Marine Fisheries Review, 77: 1–8.

Davis, M. W. 2002. Key principles for understanding fish bycatch discard mortality. Canadian Journal of Fisheries and Aquatic Sciences, 59: 1834–1843.

Davis, M. W., and Olla, B. L. 2001. Stress and delayed mortality induced in Pacific halibut *Hippoglossus stenolepis* by exposure to hooking, net towing, elevated sea water temperature and air: implications for management of bycatch. North American Journal of Fisheries Management, 21: 725–732.

Depestele, J., Desender, M., Benoît, H. P., Polet, H., and Vincx, M. 2014. Short-term survival of discarded target fish and non-target invertebrate species in the "eurocutter" beam trawl fishery of the southern North Sea. Fisheries Research, 154: 82–92.

Di Santo, V. 2015. Ocean acidification exacerbates the impacts of global warming on embryonic little skate, *Leucoraja erinacea* (Mitchill). Journal of Experimental Marine Biology and Ecology, 463: 72–78.

Efron, B., and Tibshirani, R. 1993. An Introduction to the Bootstrap. Chapman and Hall, New York.

Endicott, M., and Agnew, D. J. 2004. The survivorship of rays discarded from the South Georgia longline fishery. CCAMLR Science, 11: 155–164.

Enever, R., Revill, A. S., and Grant, A. 2009. Discarding in the North Sea and on the historical efficacy of gear-based technical measures in reducing discards. Fisheries Research, 95: 40–46.

Farrugia, T. J., Goldman, K. J., Tribuzio, C., and Seitz, A. C. 2016. First use of satellite tags to examine movement and habitat use of big skates *Beringraja binoculata* in the Gulf of Alaska. Marine Ecology Progress Series, 556: 209–221.

Hoenig, J. M., and Gruber, S. H. 1990. Life-history patterns in the elasmobranchs: implications for fisheries management. NOAA Technical Report NMFS, 90: 1–16.

Kaimmer, S. M., and Trumble, R. J. 1998. Injury, condition, and mortality of Pacific halibut bycatch following careful release by Pacific cod and sablefish longline fisheries. Fisheries Research, 38: 131–144.

Kaiser, M. J., and Spencer, B. E. 1995. Survival of by-catch from a beam trawl. Marine Ecology Progress Series, 126: 31–38.

Kelley, D., and Richards, C. 2017. oce: Analysis of Oceanographic Data. R Package Version 0.9-23. https://CRAN.R-project.org/package=oce (last accessed 1 September 2018).

Knotek, R. J., Rudders, D. B., Mandelman, J. W., Benoît, H. P., and Sulikowski, J. A. 2018. The survival of rajids discarded in the New England scallop dredge fisheries. Fisheries Research, 198: 50–62.

Laptikhovsky, V. V. 2004. Survival rates of rays discarded by the bottom trawl squid fishery off the Falkland Islands. Fishery Bulletin, 102: 757–759.

Luer, C. A. 2014. Novel Compounds from Shark and Stingray Epidermal Mucus with Antimicrobial Activity against Wound Infection Pathogens. Mote Marine Laboratory, Sarasota, FL.

Lukacs, P. M., Burnham, K. P., and Anderson, D. R. 2010. Model selection bias and Freedman's paradox. Annals of the Institute of Statistical Mathematics, 62: 117–125.

Mandelman, J. W., Cicia, A. M., Ingram, Jr, G. W. , Driggers W. B. III , Coutre, K. M., and Sulikowski, J. A. 2013. Short-term post-release mortality of skates (family Rajidae) discarded in a western North Atlantic commercial otter trawl fishery. Fisheries Research, 139: 76–84.

Natanson, L. J., Sulikowski, J. A., Kneebone, J. R., and Tsang, P. C. 2007. Age and growth estimates for the smooth skate, *Malacoraja senta*, in the Gulf of Maine. Environmental Biology of Fishes, 80: 293–308.

National Marine Fisheries Service (NMFS). 2017. Status review report: thorny skate (*Amblyraja radiata*). Final Report to National Marine Fisheries Service, Office of Protected Resources. February 2017. 60 pp.

Neilson, J. D., Waiwood, K. G., and Smith, S. J. 1989. Survival of Atlantic halibut (*Hippoglossus hippoglossus*) caught by longline and otter trawl gear. Canadian Journal of Fisheries and Aquatic Sciences, 46: 887–897.

New England Fishery Management Council (NEFMC). 2003. Northeast Skate Complex Fishery Management Plan. NEFMC, Newburyport, MA.

New England Fishery Management Council (NEFMC). 2014. Framework Adjustment 2 to the Northeast Skate Complex Fishery Management Plan. NEFMC, Newburyport, MA.

Nye, J. A., Link, J. S., Hare, J. A., and Overholtz, W. J. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the northeast United States continental shelf. Marine Ecology Progress Series, 393: 111–129.

Peklova, I., Hussey, N. E., Hedges, K. J., Treble, M. A., and Fisk, A. T. 2014. Movement, depth and temperature preferences of an important bycatch species, Arctic skate *Amblyraja hyperborea*, in Cumberland Sound, Canadian Arctic. Endangered Species Research, 23: 229.

Portz, D. E., Woodley, C. M. and Cech, 2006. Stress-associated impacts of short-term holding on fishes. Reviews in Fish Biology and Fisheries, 16: 125–170.

Raby, G. D., Packer, J. R., Danylchuk, A. J., and Cooke, S. J. 2014. The understudied and underappreciated role of predation in the mortality of fish released from fishing gears. Fish and Fisheries, 15: 489–505.

R Core Team. 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Ripatti, S., and Palmgren, J. 2000. Estimation of multivariate frailty models using penalized partial likelihood. Biometrics, 56: 1016–1022.

Ruocco, N. L., Lucifora, L. O., Díaz de Astarloa, J. M., and Wöhler, O. 2006. Reproductive biology and abundance of the white-dotted skate, *Bathyraja albomaculata*, in the Southwest Atlantic. ICES Journal of Marine Science, 63: 105–116.

Saygu, I., and Deval, M. C. 2014. The post-release survival of two skate species discarded by bottom trawl fisheries in Antalya Bay, eastern Mediterranean. Turkish Journal of Fisheries and Aquatic Sciences, 14: 1–2.

Schram, E., and Molenaar, P. 2018. Discards Survival Probabilities of Flatfish and Rays in North Sea Pulse-Trawl Fisheries (No. C037/18). Wageningen Marine Research, 41 p.

Sosebee, K., Miller, A., O'Brien, L., McElroy, D., and Sherman S. 2016. Update of thorny skate (*Amblyraja radiata*) commercial and survey data. US Department of Commerce, Northeast Fisheries Science Center Reference Document, 16–08. 145 pp.

Sosebee, K. A. 2005. Maturity of skates in northeast United States waters. Journal of Northwest Atlantic Fishery Science, 35: 141–153.

Spigarelli, S. A., Thommes, M. M., and Beitinger, T. L. 1977. The influence of body weight on heating and cooling of selected Lake Michigan fishes. Comparative Biochemistry and Physiology Part A: Physiology, 56: 51–57.

Stobutzki, I. C., Miller, M. J., Heales, D. S., and Brewer, D. T. 2002. Sustainability of elasmobranchs caught as bycatch in a tropical prawn (shrimp) trawl fishery. Fishery Bulletin, 100: 800–821.

Sulikowski, J. A., Benoît, H. P., Capizzano, C. W., Knotek, R. J., Mandelman, J. W., Platz, T., and Rudders, D. B. 2018. Evaluating the condition and discard mortality of winter skate, *Leucoraja ocellata*, following capture and handling in the Atlantic monkfish (*Lophius americanus*) sink gillnet fishery. Fisheries Research, 198: 159–164.

Sulikowski, J. A., Kneebone, J., Elzey, S., Jurek, J., Danley, P. D., Howell, W. H., and Tsang, P. C. 2005. Age and growth estimates of the thorny skate (*Amblyraja radiata*) in the western Gulf of Maine. Fishery Bulletin, 103: 161–168.

Sulikowski, J. A., Morin, M. D., Suk, S. H., and Howell, W. H. 2003. Age and growth estimates of the winter skate (*Leucoraja ocellata*) in the western Gulf of Maine. Fishery Bulletin, 101: 405–413.

Therneau, T. M., and Grambsch, T. M. 2000. Modeling Survival Data: Extending the Cox Model. Springer, New York.

Thorley, J., Fleishman, A., and Miller, L. 2017. rtide: Tide Heights. R Package Version 0.0.4. https://CRAN.R-project.org/package=rtide.

Tsagarakis, K., Nikolioudakis, N., Papandroulakis, N., Vassilopoulou, V., and Machias, A. 2015. Survival of discards in a Mediterranean bottom trawl fishery. Mytilene, Lesvos Island, Greece: Panhellenic Symposium on Oceanography and Fisheries.

Waring, G. T. 1984. Age, growth and mortality of the little skate off the northwest coast of the United States. Transactions of the American Fisheries Society, 113: 314–321.

Wearmouth, V. J., and Sims, D. W. 2009. Movement and behaviour patterns of the critically endangered common skate *Dipturus batis* revealed by electronic tagging. Journal of Experimental Marine Biology and Ecology, 380: 77.

Handling editor: Michael Pol