

## ECOPHYSIOLOGY

# Paradoxical escape responses by narwhals (*Monodon monoceros*)

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Until recent declines in Arctic sea ice levels, narwhals (*Monodon monoceros*) have lived in relative isolation from human perturbation and sustained predation pressures. The resulting naivety has made this cryptic, deep-diving cetacean highly susceptible to disturbance, although quantifiable effects have been lacking. We deployed a submersible, animal-borne electrocardiograph-accelerometer-depth recorder to monitor physiological and behavioral responses of East Greenland narwhals after release from net entanglement and stranding. Escaping narwhals displayed a paradoxical cardiovascular down-regulation (extreme bradycardia with heart rate  $\leq 4$  beats per minute) superimposed on exercise up-regulation (stroke frequency  $>25$  strokes per minute and energetic costs three to six times the resting rate of energy expenditure) that rapidly depleted onboard oxygen stores. We attribute this unusual reaction to opposing cardiovascular signals—from diving, exercise, and neurocognitive fear responses—that challenge physiological homeostasis.

**A**voidance behaviors by animals exposed to threatening stimuli are generally grouped into two integrated but mutually exclusive categories: flight or fight reactions and freeze reactions (1–3). Also termed active and passive defenses (2), both afford the opportunity for escape but with vastly different physiological consequences. Fleeing mammals show physiological responses typical of exercise (i.e., tachycardia, elevated respiration rates, and metabolic up-regulation) (2, 4), mediated by sympathetic pathways of the autonomic nervous system. Conversely, immobility during sedentary “freezing” is associated with bradycardia [reduced heart rate (HR)] and metabolic down-regulation (5, 6) via parasympathetic pathways coupled with dynamic sympathetic changes in muscle tonus and blood pressure (7). This dual escape system is so distinct that central neural control involves separate anatomical regions of the mammalian brain and motor pathways (1, 7) and underlies the inability of animals to simultaneously freeze and flee when frightened (1, 3).

Although fear pathways are well documented for terrestrial species (2–7), far less is known about these pathways for marine mammals, whose escape responses are complicated by limited access to oxygen when submerged (8–10). The tempering of physiological functions through bradycardia, peripheral vasoconstriction, apnea, and metabolic down-regulation characteristic of freeze reactions is similar to the mammalian dive response

(8–10). Because of this, we might expect that mammals specialized for diving are preadapted to react to perceived threats through an innate, oxygen-conserving freeze response to prevent hypoxic damage to tissues (11). Extreme bradycardia has been reported for marine mammals during forcible submergence (10) and escape from underwater entrapment (12), albeit under unnatural conditions. How such a freeze-type reaction integrates with the routine diving physiology of wild marine mammals, particularly in deep-diving species, has not been determined.

We monitored the behavior, biomechanics, and cardiovascular and energetic responses that occur during escape reactions by free-ranging narwhals. As one of the deepest-diving cetaceans, narwhals may exceed 1500 m in depth when foraging (13). Furthermore, as year-round occupants of the Arctic pack ice, narwhals have long remained mostly isolated from anthropogenic activities, making this highly adapted species unusually vulnerable to disturbance (14–17).

We recorded the behavior and sedentary HRs of nine narwhals immediately after release from net entanglement and stranding during annual indigenous hunts in August 2014 and August 2015 in Scoresby Sound, East Greenland (table S1) (18). Of these animals, five were instrumented for long-term monitoring via a submersible electrocardiograph-accelerometer-depth monitor (ECG-ACC; tube length: 16 cm; diameter: 3 cm) secured by suction cups on the dorsal side of the animal (Fig. 1) (19). The ECG-ACC and data were subsequently retrieved by using incorporated VHF and satellite tags to locate the floating instrument once it fell off 0.4 to 3 days later.

Upon release, narwhals displayed a paradoxical escape response that included momentary disorientation followed by profound bradycardia while fleeing. Compared with a normal dive (Fig. 1C), the first dives after release (Fig. 1D) showed a rapid onset of intense bradycardia typically attri-

buted to freeze reactions (7). HRs as low as 3 to 4 beats  $\text{min}^{-1}$  (bpm) occurred upon submergence during a prolonged descent to depth and were maintained until the final minutes of rapid ascent (Figs. 1 and 2). This extreme bradycardia, which we term “cardiac freeze,” was most apparent during the first five escape dives occurring within  $62.6 \pm 11.9$  ( $\pm$ SEM) min ( $n = 5$  narwhals) of release (Fig. 2, A and B). Bradycardia during cardiac freeze represented a  $>94\%$  reduction in HR relative to when narwhals rested on the water surface (fig. S1). This compares with a 34 to 50% reduction in HR from resting levels for semi-aquatic mammals as motor activity declines during sedentary freeze responses to threatening stimuli when freely diving (20) or on land (21). In each case, the cardiac response to perceived threats was characterized by the rapid onset and development of marked bradycardia.

Average minimum heart rate ( $HR_{\text{MIN}}$ ),  $6.2 \pm 0.54$  ( $\pm$ SEM) bpm ( $n = 31$  dives), was relatively invariable for escaping narwhals (Fig. 2C). Conversely,  $HR_{\text{MIN}}$  during post-escape periods declined asymptotically with dive depth (Fig. 2C), following trends reported for free-ranging sea lions (22), bottlenose dolphins, and Weddell seals (19). Depending on dive depth and duration, the cardiac freeze displayed by escaping narwhals could last more than 10 min during individual dives. Routine bradycardia was gradually reestablished during sequential dives at the end of the escape period (Fig. 2A) and defined the subsequent post-escape period (Fig. 2B) beginning 45 to 90 min after release.

Unexpectedly, the escape response of narwhals included high levels of flight superimposed on the powerful bradycardia. Rather than remain immobile as usual for bradycardia periods associated with true freeze reactions (1, 5, 6), escaping narwhals displayed stroke frequencies (SFs) that were equivalent to or faster than those performed during routine, post-escape dives (Figs. 1 and 3). The highest SFs occurred during the ascent phase of escape [ $40.6 \pm 3.0$  ( $\pm$ SEM) strokes  $\text{min}^{-1}$ ,  $n = 5$  narwhals] and post-escape [ $36.6 \pm 2.6$  ( $\pm$ SEM) strokes  $\text{min}^{-1}$ ,  $n = 5$  narwhals] dives; these levels were approximately twice the average SF during routine 15-m dives when transit swimming [ $18.9 \pm 3.1$  ( $\pm$ SEM) strokes  $\text{min}^{-1}$ ,  $n = 49$  1-min samples for five narwhals].

The interplay between opposing physiological signals during escape altered the response of the heart to submerged exercise (Fig. 3). Unlike other marine mammals (19, 23), the HR of narwhals showed little change with increasing SF during escape dives (Fig. 3A), as described by

$$HR = 7.95 + 0.10SF \quad (1)$$

( $n = 423$  HR-SF samples for five narwhals,  $R^2 = 0.08$ ,  $P < 0.0001$ ). HR is measured in beats per minute and SF is in strokes per minute for 25 dives of moderate depth (45 to 473 m) (18).  $R^2$  is the coefficient of determination. Mean HR during escape dives was  $10.0 \pm 0.23$  ( $\pm$ SEM) bpm ( $n = 423$  HR-SF samples), regardless of depth or

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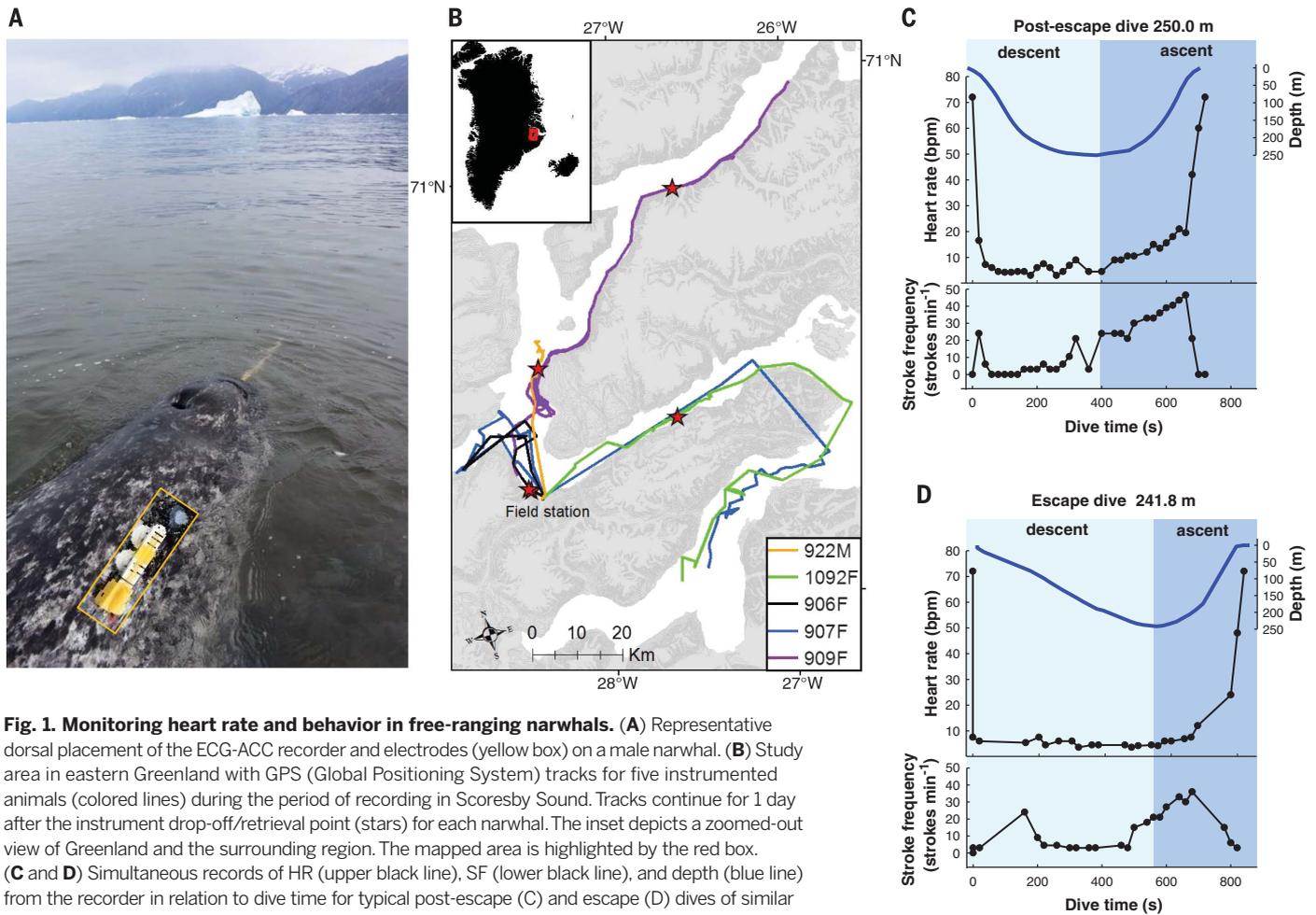
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level of exercise from gliding to 50 strokes  $\text{min}^{-1}$ , implying parasympathetic neural dominance.

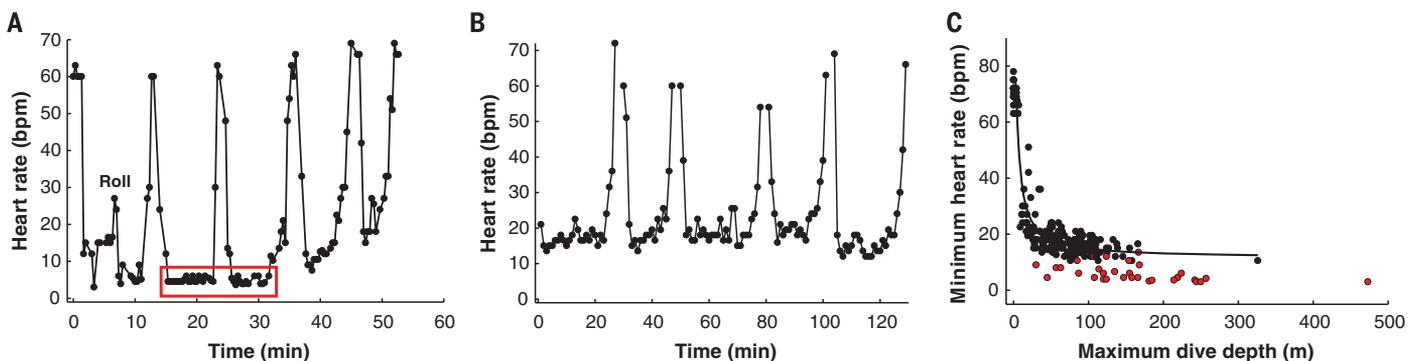
During subsequent post-escape dives, narwhals displayed a continuum of cardiac responses that depended on the duration of prior entanglement

and stranding (Fig. 3, B to D) (18). Like exercising seals and dolphins (19, 23), HR increased with SF in narwhals during post-escape dives. However, the level of exercise-induced change, evident from the slope of the HR-SF relationship, differed

significantly with handling duration [analysis of covariance (ANCOVA) on interactions,  $P < 0.001$ ,  $F = 178.42$ ,  $df = 2, 1009$ ]. Short handling times resulted in an increase in HR with SF consistent with flight, suggesting either parasympathetic

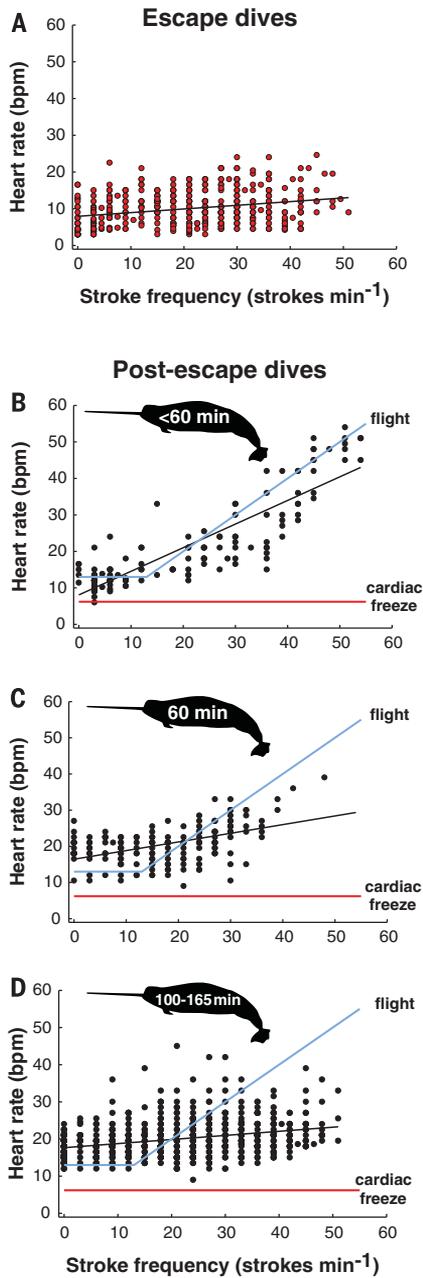


**Fig. 1. Monitoring heart rate and behavior in free-ranging narwhals.** (A) Representative dorsal placement of the ECG-ACC recorder and electrodes (yellow box) on a male narwhal. (B) Study area in eastern Greenland with GPS (Global Positioning System) tracks for five instrumented animals (colored lines) during the period of recording in Scoresby Sound. Tracks continue for 1 day after the instrument drop-off/retrieval point (stars) for each narwhal. The inset depicts a zoomed-out view of Greenland and the surrounding region. The mapped area is highlighted by the red box. (C and D) Simultaneous records of HR (upper black line), SF (lower black line), and depth (blue line) from the recorder in relation to dive time for typical post-escape (C) and escape (D) dives of similar depths for narwhal 1092F. The blue backgrounds denote descent (light) and ascent (dark) periods. Data points represent 20-s averages. Note the rapid onset and intensity of bradycardia and the lack of correlation between HR and stroking during the escape dive (D).

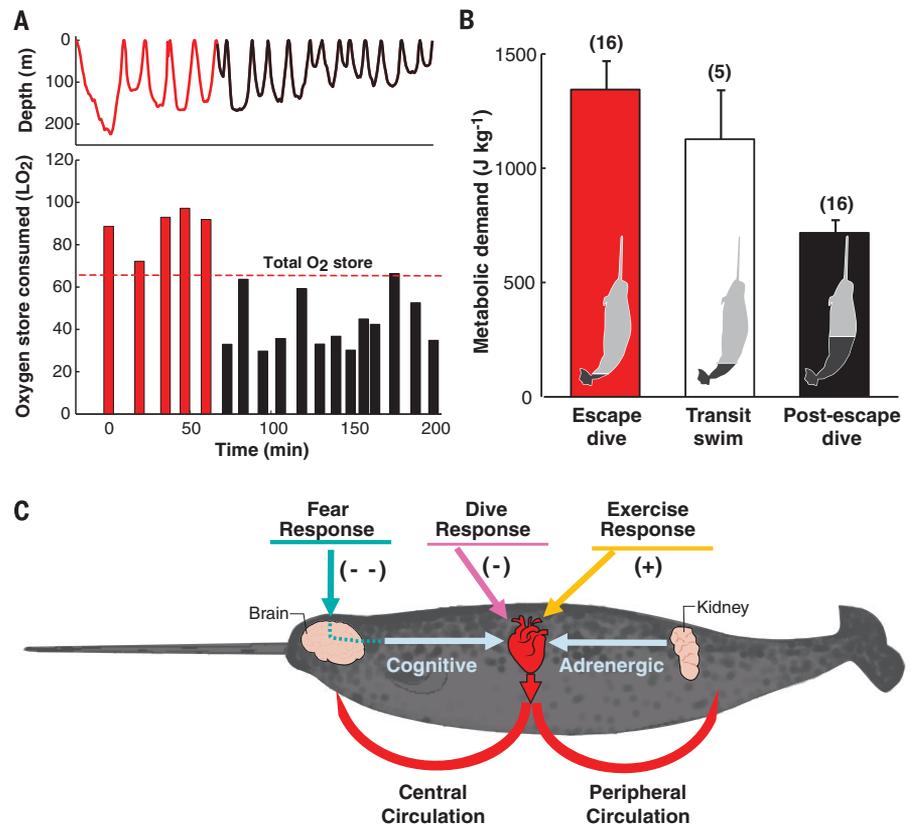


**Fig. 2. The effect of escape responses on bradycardia in diving narwhals.** HR in relation to time for a female narwhal (909F) during (A) sequential escape dives after release and (B) depth-matched dives to 103 to 136 m occurring 44 to 52 hours later. The red box in (A) highlights periods of extreme bradycardia (“cardiac freeze”). (C) Minimum

HRs for escape (red circles) and post-escape (black circles) dives as a function of maximum dive depth for five narwhals. The least squares regression model (black line) for post-escape dives is described by  $HR_{\text{MIN}} = 11.50 + 334.73/\text{depth} - 459.54/\text{depth}^2 + 42.67/\text{depth}^3$  ( $R^2 = 0.93$ ,  $P < 0.0001$ ,  $n = 211$  dives). Points represent 20-s averages.



**Fig. 3. Relationship between heart rate and stroke frequency in diving narwhals after entanglement and stranding.** (A) Extreme bradycardia during the first five escape dives immediately after release ( $n = 423$  samples of 20 s each for five narwhals). (B to D) Effect of prior handling duration on the HR-SF relationship during post-escape dives. Inset icons denote short [(B)  $n = 132$  samples, one narwhal], moderate [(C)  $n = 177$  samples, two narwhals], and long [(D)  $n = 706$  samples, two narwhals] handling times. Two-factor general linear models (black lines) are compared with predicted relationships for a cardiac freeze response (red lines based on average minimum HR during escape dives) and flight-dominated responses (blue lines predicted from HR-SF relationships for freely swimming marine mammals) (18).



**Fig. 4. Energetic costs and physiological model for escape reactions by narwhals.** (A) Estimated oxygen consumption during individual dives (lower panel bars) for sequential escape (red) and post-escape (black) dives (upper panel line) by narwhal 907F. The total available oxygen store (red dashed line) for the narwhal is shown. (B) Metabolic demands for five narwhals during escape dives (red bar), surface swimming (white bar), and post-escape dives (black bar). Values in parentheses are the number of depth-matched dives or swimming segments. Bar height and whiskers represent means + 1 SEM. Gray shading in icons denotes the proportion of oxygen stores used to support the dive or swim. (C) Relative effect of diving, exercise, and neurocognitive fear responses on heart function during escape reactions. Cognitive and adrenergic pathways (highlighted in blue) provide additional short- and long-term signals, respectively, to the cardiovascular system.

withdrawal from bradycardia or increased sympathetic neural influence (Fig. 3B). Longer handling caused a progressive shift toward cardiac freeze (Fig. 3, C and D) (18). Although overall HR was elevated, the slope of the HR-SF relationship for narwhals handled the longest (Fig. 3D) was statistically indistinguishable from that measured for narwhals during escape dives (Fig. 3A) (ANCOVA on interactions,  $P = 0.6201$ ,  $F = 0.245$ ,  $df = 1, 1125$ ), which demonstrates a sustained effect when aversive stimuli are protracted.

A key benefit of bradycardia and metabolic down-regulation during freeze responses by aquatic vertebrates is oxygen conservation when submerged (10, 11). However, such savings are negated in narwhals because of the addition of flight on profound bradycardia during escape (Fig. 4, A and B). Combining predicted maintenance costs (24) with locomotor costs of 1.7 to 1.9  $J\ kg^{-1}\ stroke^{-1}$  and 5.3 to 5.4  $J\ kg^{-1}\ stroke^{-1}$  for routine swimming and maximum aerobic performance, respectively (fig. S2) (18, 25), we found that the mean metabolic cost of escape dives by narwhals was significantly greater

(Student's  $t$  test,  $t_{15} = 4.29$ ,  $P = 0.0006$ ) than for post-escape dives of similar duration (7 to 9 min) and depth (116 to 137 m). The cost of escape dives also exceeded the energetic cost of surface transit swimming (Fig. 4B).

The effect of these costs on diving narwhals is apparent from the percentage of body oxygen stores consumed (LO<sub>2</sub>) (Fig. 4, A and B). Serving as a critical metric for diving mammals, the depletion of blood, lung, and muscle oxygen leads to anaerobiosis and, ultimately, cessation of a dive as aerobic limits are breached (8, 9). Using tissue oxygen contents from wild narwhals (18, 26), total oxygen stores averaged  $56.9 \pm 5.3$  ( $\pm$ SEM) LO<sub>2</sub> for our instrumented narwhals. Combined with metabolic demands calculated from stroking costs (Fig. 4B), typical escape dives required 97% of the narwhal's onboard oxygen store, often exceeding predicted aerobic dive limits (Fig. 4A). This compares with 52% of the store used to support post-escape dives of similar duration and depth. Alternatively, escaping narwhals, like beaked whales (25), frequently avoided anaerobiosis by decreasing dive duration.

Overall, this study reveals a complex escape response by narwhals that requires the integration of often opposing physiological signals from diving, exercise, and neurocognitive fear responses (Fig. 4C). This complexity is not without consequences. Coordination of diverse neural signals with adrenergic pathways (3, 4) is needed to maintain the protection of key hypoxia-sensitive organs (i.e., the brain) (8–10) when evading threats while submerged. With the dive response sensitive to exercise (23), depth (19), cognitive control (27, 28), and now escape reactions (Figs. 1 to 4), this protection may be challenged. For rats, simultaneous vagal neural inputs for diving bradycardia and fear bradycardia can promote sudden death (11). For narwhals, extreme bradycardia superimposed on flight responses (Figs. 1 to 3) coupled with comparatively high energetic costs (Fig. 4) and predicted low concentrations of neuroprotecting globins characteristic of deep-diving mammals (29) creates exigent conditions for maintaining tissue oxygenation and physiological homeostasis.

In light of these findings, the susceptibility of deep-diving cetaceans (30), including narwhals (14, 17), to anthropogenic disturbances such as oceanic noise may not be surprising. Although species-specific responses to threats may differ, the Arctic seascape has changed for marine mammals, with the rapid degradation in polar ice cover (14) and concomitant increased opportunities for predation (15), human hunting (16), and shipping and seismic exploration (17). Historically, wild narwhals avoided threats such as killer whales and icebreakers by relying on slow, covert movements and sinking to depths beneath the cover of ice or moving to shallows unreachable by pursuing predators (26, 31–33). With the advent

of novel, unpredictable threats, the escape response of narwhals has broadened by necessity and warrants consideration when evaluating the effects of human activities on this and other deep-diving cetaceans.

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#### SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/358/6368/1328/suppl/DC1  
Materials and Methods  
Supplementary Text  
Figs. S1 and S2  
Table S1  
References (34, 35)

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### The flight of the narwhal

Animals tend to respond to threats with the well-known behaviors of fight, flee, or freeze, each of which requires a different suite of physiological responses. Marine mammals face particular challenges because they may flee into an environment where oxygen is not available and pressure must be accommodated. Williams *et al.* placed a submersible electrocardiograph, depth, and acceleration recorder on narwhals after they were freed from entanglement. The animals displayed contrary cardiovascular responses simultaneously, which placed extreme stress on the cardiovascular system and the tissues that it protects.

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