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SYMPOSIUM

Conservation Physiology of an Uncatchable Animal: The North Atlantic Right Whale (*Eubalaena glacialis*)

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Synopsis The North Atlantic right whale, *Eubalaena glacialis* (NARW), a critically endangered species that has been under intensive study for nearly four decades, provides an excellent case study for applying modern methods of conservation physiology to large whales. By combining long-term sighting histories of known individuals with physiological data from newer techniques (e.g., body condition estimated from photographs; endocrine status derived from fecal samples), physiological state and levels of stress can be estimated despite the lack of any method for nonlethal capture of large whales. Since traditional techniques for validating blood assays cannot be used in large whales, assays of fecal hormones have been validated using information on age, sex, and reproductive state derived from an extensive NARW photo-identification catalog. Using this approach, fecal glucocorticoids have been found to vary dramatically with reproductive state. It is therefore essential that glucocorticoid data be interpreted in conjunction with reproductive data. A case study correlating glucocorticoids with chronic noise is presented as an example. Keys to a successful research program for this uncatchable species have included: consistent population monitoring over decades, data-sharing across institutions, an extensive photo-identification catalog that documents individual histories, and consistent efforts at noninvasive collection of samples over years. Future research will require flexibility to adjust to changing distributions of populations.

Introduction

Large whales are increasingly affected by a variety of anthropogenic impacts, including entanglement in fishing gear, exposure to noise (e.g., from seismic exploration, shipping, and military sonar), toxins, pollutants, pathogens, and global change in climate (Cassoff et al. 2011; Doney et al. 2011; Pompa et al. 2011; Davidson et al. 2012; Frisk 2012). A conservation-physiology approach could be particularly useful for delineating chronic cumulative impacts, assessing sublethal impacts, and establishing mechanistic cause-and-effect linkages (Cooke et al. 2013, 2014; Hunt et al. 2013). Unfortunately, large whales present serious challenges for employing many tools of classic physiology because there is no feasible method of nonlethal capture that would enable sampling the blood of these species. From the perspective of the field physiologist, large whales are essentially "uncatchable animals." In the case of the mysticetes (baleen whales), there are not even any comparable small species in captivity that could be used to develop alternative techniques.

Fortunately, recent advances in nonlethal and noninvasive sampling methods have made even the largest species of whales amenable to study. The techniques of conservation physiology available today for the study of large whales include analysis of alternative types of samples that can substitute for blood, e.g., feces (Rolland et al. 2005, 2007a; Hunt et al. 2006), respiratory vapor (Hogg et al. 2009; Hunt et al. 2013), biopsies of skin and blubber (Mansour et al. 2002; Kellar et al. 2006, 2009), and visual assessment of health using photographs as proxies for physiological samples (Pettis et al. 2004; Rolland et al. 2007b). When these methods are combined with long-term study of identified individuals

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with known life-histories, it is possible to piece together a picture of physiological response to anthropogenic disturbance even for an "uncatchable" species (e.g., Rolland et al. 2012). We present here a case study of research on the North Atlantic Right Whale, *Eubalaena glacialis* (NARW) as an example of the problems, possibilities, and approaches of studying conservation physiology in an endangered large whale.

The North Atlantic right whale

The NARW is one of the rarest species of mysticete whale, with approximately 500 individuals remaining (North Atlantic Right Whale Consortium 2014). The species is currently classified as Endangered under the US Endangered Species Act of 1974, the Canada Species at Risk Act of 2002, and the International Union for the Conservation of Nature (Reeves et al. 2007; Reilly et al. 2012). The range of the NARW extends from Florida to Iceland, although most known distributions occur along the eastern seaboard of the United States and Canada (Fig. 1). In summer, NARWs feed on aggregations of copepods in the northern parts of this range, including the Bay of Fundy and the Nova Scotian Shelf. In late fall, most males and nonpregnant females disappear to poorly documented wintering grounds (though see Cole et al. 2013), while pregnant females and some juveniles migrate southward to the southeastern coast of the United States, where the females calve in mid-winter. In spring, females and calves migrate north and are re-joined by additional whales for feeding in Cape Cod Bay and the Great South Channel east of Cape Cod. The NARW has been called the "Urban Whale" (Kraus and Rolland 2007) because the calving grounds, migration routes, and feeding grounds all are located in areas heavily affected by fishing activity, shipping traffic, coastal runoff, and many other anthropogenic impacts.

NARWs are individually identifiable via unique patterns of white "callosities" (areas of thickened skin colonized by white cyamid crustaceans) on their heads, along with unique pigmentation, scars, and marks (Kraus et al. 1986). Images for sightings of right whales have been collected in a unified photo-identification catalog for this species, known as the NARW Identification and Sightings Database ("NARW ID/Sightings Database" hereafter; North Atlantic Right Whale Consortium, www.narwc.org). This database currently contains over 700,000 images of 685 individual whales, with records spanning 80 years (North Atlantic Right Whale Consortium 2014). Thus, most individual NARW have long histories of sightings, are of known age-class and sex and, in the case of females, usually have a known calving history. The existence of this database has been key to development of a research program in conservation physiology for this species.

Major modern sources of mortality in NARW include collisions with vessels (shipstrikes) and entanglements in fishing gear (Kraus et al. 2005; Moore et al. 2005, 2007; Knowlton and Brown 2007; Knowlton et al. 2012). Either of these events may kill whales outright or may cause a period of chronic injury and stress. For example, 83% of adult NARW bear scars indicative of an entanglement at some time, with many whales having experienced multiple episodes (Knowlton et al. 2012). Sublethal effects of these entanglements are unknown. Many regulatory changes have been implemented to reduce shipstrikes and entanglements. While shipstrikes appear to have decreased recently, incidence of serious entanglements (defined as entanglements causing wounds deeper than 8 cm, and/or whales still bearing fishing gear) has significantly increased over the past three decades (Knowlton et al. 2012; Laist et al. 2014).

The NARW population also experiences unexplained acute declines in reproductive rate. During the 1990s, inter-calving intervals of females lengthened from a mean of 3 years to 5.8 years (Kraus et al. 2007). In recent years, numbers of calves have increased, but fecundity remains low relative to the reproductive rates of the closely related southern right whale (*Eubalaena australis*; Best 1994). The causes of reduced reproduction in NARW are unclear but are hypothesized to include poor body condition, stress, inbreeding, toxins or contaminants, and disease (Reeves et al. 2001; Kraus et al. 2007; Rolland et al. 2007b). In the late 1990s, concerns about impaired reproduction led to development of tools to assess and monitor the potential causes (Reeves et al. 2001), resulting in one of the first long-term research programs on conservation physiology of a large whale (Rolland et al. 2007a, 2007b).

Techniques of conservation physiology used for NARW

Physiological research on NARW has largely followed two parallel and complementary tracks: development of methods for the collection and analysis of data for alternative types of samples (other than blood and plasma), and development of photographically based assessments of health that can be linked to physiological status.

Alternative types of samples

Samples that are feasible to collect from large whales include fecal samples, samples of respiratory vapor

Fig. 1 Range and habitats of the North Atlantic right whale (*Eubalaena glacialis*). Image used with permission of the New England Aquarium. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

(blow), and biopsies (small samples of skin and blubber) collected by darts. Each of these methods has advantages and disadvantages (reviewed by Hunt et al. 2013). Fecal samples, for example, are entirely noninvasive and the analytic techniques are well-developed (Rolland et al. 2005, 2006; Hunt et al. 2006), but rates of opportunistic collection tend to be low. However, the use of specially trained scat-detection dogs can dramatically increase that rate (Rolland et al. 2006), although this method results in a higher percentage of samples from unknown individuals (i.e., dogs often locate samples that are floating far from any identified whale). Nevertheless, long-term studies provide the opportunity for the accumulation of a large archive of samples, and genetic profiling can assist in associating a fecal sample with an individual whale (Gillett et al. 2008, 2010). In contrast, blow sampling is a technique that shows great promise for improving sampling rate, but field techniques and analytic methods are still in their infancy (Hogg et al. 2009; Hunt et al. 2013, 2014). Finally, biopsies are collected regularly from NARW for genetic analyses (reviewed by Noren and Mocklin 2012). We focus on fecal sampling below, as fecal samples are the best-validated alternative samples used for endocrine studies.

The NARW archive of fecal samples

Collection of fecal samples from NARW began in 1999 and continues today. Although the rate of collection on any given day is low, extending the effort across multiple research vessels for more than a decade has resulted in gradual accumulation of an unparalleled archive of cetacean fecal samples. Over 375 fecal samples have been collected over the past 15 years. Approximately one-third of these samples are from known individuals with detailed sightings.

Validation of endocrine assays without blood samples

The NARW fecal archive has been used extensively for endocrine studies. Currently each fecal sample is analyzed for a suite of fecal hormone metabolites (FHMs) covering six classes of gonadal, adrenal, and thyroid hormones (Rolland et al. 2005; Hunt et al. 2006). A recurring issue with development of these FHM assays has been the infeasibility of standard methods of validation (e.g., ACTH challenges, comparisons to plasma) in large whales. Fortunately, the NARW ID/Sightings Database is detailed enough that most individual NARW can be categorized accurately with regard to sex, age-class, and, importantly, reproductive state. Therefore, rather than attempting to correlate FHMs with plasma hormones, FHMs can be compared directly with the whale's known physiological state (e.g., pregnancy, lactation, maturity, health). For example, if elevated concentrations of progestins in feces can correctly identify pregnant females, then the assay of fecal progestins can be said to be a reliable measure of pregnancy, eliminating the need for correlations with plasma progesterone.

Using this approach we have been able to demonstrate that FHMs do reflect NARW's physiological state with a high degree of accuracy (Rolland et al. 2005, 2007a; Hunt et al. 2006). For example, the majority of whales can be sexed accurately by fecal androgen/estrogen ratio, levels of fecal progestins are always elevated by several orders of magnitude in pregnant females, mature males are characterized by a combination of lower levels of fecal progestins and high levels of fecal androgens, and lactating females are distinguishable from other categories by a combination of relatively low levels of progestins and androgens, and high levels of estrogens (Rolland et al. 2005, 2007a).

Photographs as a potential source of physiological information

Due to cetaceans' lack of fur and their reliance on a subcutaneous layer of blubber as a major energetic reserve, photographs can reveal considerable information about health that is relevant for physiological studies. Lateral photographs of right whales at the surface have been assessed for several variables related to health-status, such as dorsal contour behind the blowholes (reflecting stores of blubber and hence relative energetic reserves), skin lesions, presence of orange cyamids (ectoparasites) along the margins of the blowholes, and "rake marks" anterior to the blowholes (Pettis et al. 2004; Rolland et al. 2007b). These parameters are scored on an ordinal scale and constitute a quantifiable "visual health assessment" that can serve as a proxy for individual health (Pettis et al. 2004; reviewed by Rolland et al. 2007b). Additionally, aerial photographs have been used to capture an overhead view of the morphology of the body. These aerial photographs can be analyzed to determine the whale's contour and girth relative to its length (e.g., photogrammetry), which can reveal nuanced details of nutritional condition, and sometimes can be useful for diagnoses of pregnancy (Perryman and Lynn 2002; Rolland et al. 2007b; reviewed by Hunt et al. 2013). Overall, photographs have become an increasingly rich source of information about the relative health of individual whales, enabling better interpretation of physiological data. Note also that techniques exist for assessing the thickness of blubber directly via ultrasound (Moore et al. 2001; Miller et al. 2011, 2012), although this requires close approach and direct contact with the whale.

Example: Assessing stress in NARW

A common goal of conservation physiology is the assessment of stress, often via analysis of adrenal glucocorticoids (Lennox and Cooke 2014). Recent reviews have indicated that levels of fecal glucocorticoids consistently elevate in response to anthropogenic stressors, across a wide range of taxa (e.g., Dantzer et al. 2014). For chronic stress in particular, integrative assessments of glucocorticoids (e.g., feces) appear to be more reliable than plasma-based measures (Dickens and Romero 2013). Our experience indicates that data on fecal glucocorticoids are best interpreted in conjunction with other hormones and/or with known individual life histories.

Fecal glucocorticoids vary with reproductive state

A key discovery was that concentrations of glucocorticoids in NARW feces are consistently and significantly elevated in whales of certain reproductive states, particularly adult males and pregnant females (Fig. 2; Hunt et al. 2006; Rolland et al. 2007a). This pattern has also been reported in other mammalian species (e.g., Dantzer et al. 2010). It is tempting to consider reproduction itself as a type of stressor. However, reproduction is not an emergency response, and the term "stressor" typically has a connotation of an unexpected event that evokes an emergency response (McEwen and Wingfield 2003). Rather, reproduction can be considered an energetic burden that increases allostatic load (McEwen and Wingfield 2003). Such increases in allostatic load may not be true stressors but nevertheless can cause changes in concentrations of glucocorticoids, and this must be borne in mind when interpreting data on levels of glucocorticoid.

Importantly, this means that elevated levels of fecal glucocorticoids in NARW can only be interpreted correctly if the reproductive state of the whale is known. For example, consider a fecal sample with a glucocorticoid concentration of 178 ng/g. This is well above the median fecal glucocorticoid concentration of 28 ng/g for the overall NARW population. In the absence of any other information, can a sample with unusually high fecal glucocorticoids confidently be said to be from a "stressed" whale (using "stressed" here in the classic sense of distressed or unhealthy)? No—as should be clear from Fig. 2, such a sample could also be from a normal, healthy pregnant female. The same issue can (theoretically) occur at a population-wide level; if the NARW population were to experience an increase in the percentage of females that are pregnant or the percentage of males that are mature breeding animals, both of which are presumably good things, this will likely result in an increase in overall median levels of fecal glucocorticoids for the entire population. In sum, "high cort is not always bad," for an individual or for a population. However, given further information on reproductive state the picture becomes clearer. In the example given above, this sample was in fact from a mature male, and 178 ng/g is unusually high for mature males (compare to Fig. 2). In fact, that particular whale was severely entangled—the sample was collected opportunistically during a disentanglement effort—and the whale disappeared (presumed to have died) shortly after the sample was collected. This example illustrates that an individual's glucocorticoid data are best analyzed in conjunction with information about the whale's reproductive state and individual history. Even in the absence of detailed individual history, adding reproductive hormones to the fecal analytic panel can considerably improve the interpretation of glucocorticoid data (Dantzer et al. 2010, 2014; Goymann 2012). Routine assessment of reproductive hormones has recently been recommended for studies of conservation physiology of other marine vertebrates as well (Labrada-Martagon et al. 2014).

Are right whales stressed by chronic noise from shipping?

Underwater noise has been an issue of particular interest for conservation physiology of marine mammals (National Research Council 2005; Nowacek et al. 2007; Frisk 2012), with research focusing on underwater noise from military sonar, seismic exploration, and commercial ships. Of these three acoustic impacts, noise from ships has been the most difficult to study because of the near-complete lack of a control group—a population, season, or location during which chronic noise from shipping can be reduced or eliminated. Research on NARW has provided one of the first cases in which this question could be addressed for a large species of whale. Every year since 1999, fecal samples have been collected from NARW during July–September in the Bay of Fundy, Canada. In the year 2001, this sampling effort coincided with the tragic terrorist attacks of September 11, 2001. Shipping traffic and underwater noise were sharply reduced in the Bay of Fundy for several days after this event (Rolland et al. 2012). Compared with the four subsequent years, levels of fecal

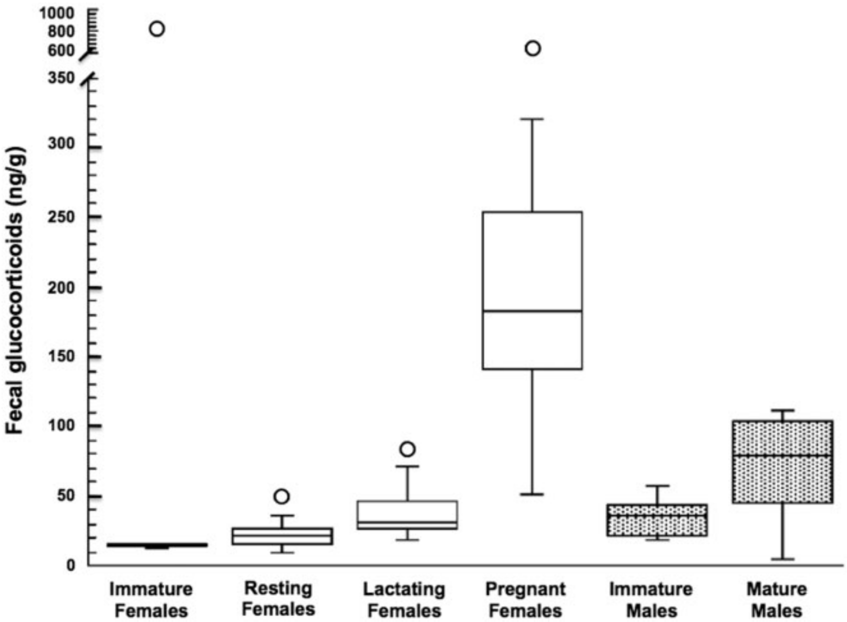

Fig. 2 Fecal glucocorticoids in NARW of different age-classes, sexes, and reproductive states. A "resting" female is an adult female of reproductive age who is neither pregnant nor lactating. Data are shown as boxplots; the center line is the median, the box includes 25–75% of the data, and whiskers include 5–95% of the data.

glucocorticoids were significantly lower in 2001 after September 11 (compared with before September 11; Fig. 3). There were no obvious changes in availability of food or in other potential stressors in 2001; the most likely explanation appears to be that NARW may be chronically stressed by noise from shipping.

Two aspects of this study deserve mention. First, reproductive data were critical for the analysis, e.g., only after analysis of such data was it clear that pregnant females and mature males should be excluded from analysis so as to eliminate the effect of normal elevations in glucocorticoids due to reproductive state. Second, we were able to study an unanticipated change in an anthropogenic stressor only because of long-term, ongoing commitment to collecting fecal samples, surveying populations, and conducting photographic identification. This remains the only study that has correlated underwater noise from shipping with measures of adrenal stress in a large whale.

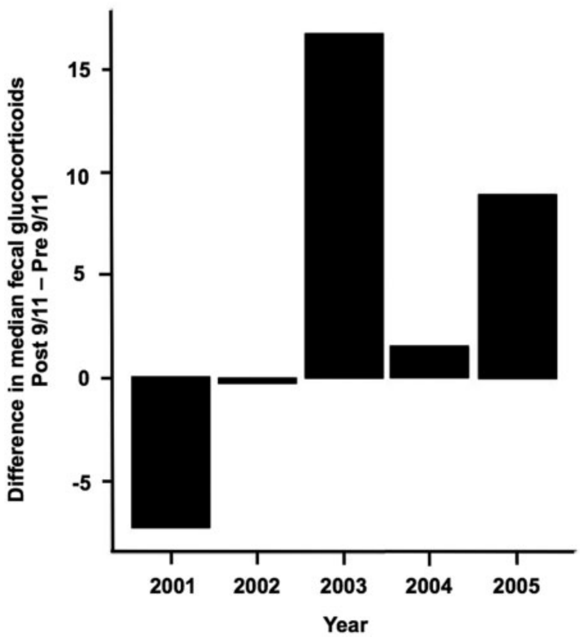

Fig. 3 Difference median fecal glucocorticoids of NARW after September 11 when compared with prior to September 11, over 5 different years. The terrorist attacks in 2001 resulted in reduced ship traffic and reduced underwater noise after September 11. Reproduced with permission from Rolland et al. (2012).

Key components for a successful research program

As the above examples indicate, research on the conservation physiology of NARW has been extremely fruitful despite the considerable difficulties of working with a highly endangered and "uncatchable" species. Important factors in developing a feasible and effective research program in conservation physiology have included:

- Consistent survey effort with cross-institutional collaboration. Physiological research on NARW has been possible due to ongoing multi-decade, long-term research that includes consistent annual surveys of the population at the calving grounds, during migration, and at feeding grounds in the spring and summer (Brown et al. 2007). This effort required the cooperation, through the North Atlantic Right Whale Consortium (www.narwc.org), of multiple institutions across numerous states and a vast stretch of coastline. The benefits of this collaborative approach are most apparent in the case of the NARWC Identification and Sightings Database, which combines photographs and sighting records from research groups along the east coast (Hamilton et al. 2007). This model could be applied to other cases in which a migratory species is studied by different research groups in different areas.

- Consistent collection of samples. Noninvasive collection of samples has, in many species, been performed on a temporary basis limited to rather short funding cycles. The NARW fecal database now spans 15 years of continuous collection of fecal samples, and those samples have been contributed by several different research teams. In many years, sample collection has been piggy-backed onto the survey efforts described above, enabling sample collection to continue even through gaps in funding, with funding secured later for laboratory analyses. We note further that it has been useful to have a single point-person contacting all teams, coordinating collection protocols, and reiterating focus on the collection of samples every year. Although such an archive of fecal samples may only accumulate slowly, once it reaches a certain size (and particularly if it contains samples from known individuals), later the archive can be mined repeatedly for multiple studies and for the development of additional analytic tools (e.g., fecal aldosterone and fecal thyroid hormone, both added in recent years). Important patterns in fecal hormones were, in many cases, only detected after 5 or more years of collecting samples.
- The value of a photo-identification catalog for providing known individual histories. It is impossible to overstate the value of having long-term, detailed, individual histories from known individuals, particularly given that standard physiological validations cannot be used. Only with the individual sighting records of the NARW ID/Sightings Database could we match data from alternative types of samples, such as data on fecal hormones, to an independently known physiological state. Creation and maintenance of such a photo-identification database is not trivial and requires on-going collection of new photographs, photo-analysis to "match" new photographs to known whales, and resolution of problem cases. The NARW ID/Sightings Database has been the foundation for a multitude of studies on the conservation physiology, general biology, and management of this species (Kraus and Rolland 2007).
- Physiology explicitly included in conceptual models. Initial attempts to model the responses of large whales to anthropogenic stressors (i.e., noise) did not include physiology, but rather focused on behavior (e.g., National Research Council 2005). More recently, however, a few teams conducting research on marine mammals have broadened this conceptual model to include any type of anthropogenic disturbance and have explicitly included physiology in the model (e.g., New et al. 2013), thereby renewing focus on physiology as applied to conservation of large whales.
- Flexibility in the face of changing climate and distribution. NARW distribution may now be changing. For the majority of this long-term study, the Bay of Fundy has been a consistent feeding ground for NARW in the summer. Since 2010, fewer NARW than usual have been sighted in the Bay of Fundy, with a portion of the population apparently moving to some as-yet-unknown alternative feeding site(s) (North Atlantic Right Whale Consortium 2013, 2014; S. Kraus, personal observations). These changes in distribution may be, in part, short-term fluctuations, but global change in climate is probably also a contributing factor. This change in distribution presents some logistical challenges, and it is likely that long-term physiological research on other taxa may face similar issues in the future. Conservation physiologists may soon be faced with not just the familiar task of documenting changes that occur in a well-studied population, but also with re-locating and following populations as they shift their distribution and phenology in response to changing climate (e.g., Carvalho et al. 2011; Guisan et al. 2013).

Conclusions

Future directions for NARW physiological research are diverse. A continued focus is the nature of the cetacean stress response, and particularly identification of which (of many) anthropogenic stressors are having the most serious effects. One fruitful avenue of research could be combining data on aldosterone and thyroid hormone with glucocorticoid data; these three hormones can react differently to different types of stressors, and a combination approach may enable discrimination of the physiological effects of stressors of different types (e.g., Ortiz and Worthy 2000; Ayres et al. 2012; Gobush et al. 2014). Statistical methods will be needed that can help unify information from multiple-measure datasets. Several new analytical tools are available that need further validation, both for methods of collecting data in the field and for laboratory analytic techniques (e.g., respiratory vapor analysis, blubber hormone analysis, aerial photographic methods using drones). Finally, efforts are underway to combine behavioral and physiological data with traditional ecological data into large-scale, long-term population models, as has been done recently with southern elephant seals (New et al. 2013).

Research on the conservation physiology of large whales, particularly the mysticetes, will always be logistically challenging, but this study of NARW shows that it is possible. We believe that the NARW program can serve as a model for research on the conservation physiology of large species for which traditional methods of capture and sampling may not be feasible. Long-term study of known individuals remains, in our estimation, the best approach for elucidating the physiological effects of anthropogenic impacts on these rare and difficult-to-study animals.

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