

Research paper

Multi-year profiles of T3 are positively correlated with corticosterone in male bowhead whale baleen

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ARTICLE INFO

Keywords:

Bowhead whale
Triiodothyronine
Corticosterone
Testosterone
Stable isotopes

ABSTRACT

Thyroid hormones play an important role in the regulation of growth, development, metabolism, thermoregulation, and migration. Very little information exists on patterns of thyroid hormone concentrations in healthy mysticete whales, as many studies have focused on ill, entangled, or stranded whales, making it difficult to interpret thyroid hormone trends. In this study, we used a unique sample-set of bowhead whale baleen plates to explore the long-term interrelationships between triiodothyronine (T3), the most biologically active thyroid hormone, corticosterone, testosterone, and nitrogen isotope ratios ($\delta^{15}\text{N}$) (proxies for stress, reproduction, and diet, respectively) to investigate the role T3 may play in the physiology of healthy cetaceans. Baleen plates were collected between 1998 and 2011 from eight subsistence-harvested male bowhead whales across the Eastern Canadian Arctic. Each baleen plate generated 88–158 serial samples, representing ~11–22 years of life for each individual whale. T3 concentrations ranged from 0.61 to 21.62 ng/g and varied seasonally in just two whales. Most whales showed no correlation between T3 and seasonal fluctuations in testosterone or $\delta^{15}\text{N}$, suggesting that variation in T3 is not driven by seasonal shifts in reproductive cycles, consumer trophic level, or migration. However, a strong positive correlation between T3 and corticosterone was observed in every whale, which we hypothesized was due to non-seasonal factors that simultaneously increase metabolic rate and physiological stress. The positive correlation between T3 with corticosterone suggests that in mysticete whales, some stressors may require increased energetic output.

1. Introduction

Historically, most wildlife endocrine studies have focused on hormones produced by the hypothalamic-pituitary-gonadal (HPG) axis and the hypothalamic-pituitary-adrenal (HPA) because they provide information on reproductive rates and stress physiology (Kersey and Dehnhard, 2014), which are important determinants for the conservation of wildlife populations. However, many conservation threats, such as anthropogenic disturbances, climate change, and shifts in the food web, may cause other physiological changes, including alterations in metabolism or diet, which can also have population-level consequences (reviewed in Birnie-Gauvin et al., 2017). Thyroid hormones (THs) play an important role in the regulation of metabolic activity, which varies due to changing environmental or physiological demands, and despite

their potential as informative biomarkers, THs are often overlooked in wildlife endocrine studies (Behringer et al., 2018).

THs (thyroxine, T4 and triiodothyronine, T3) are synthesized and secreted by the thyroid gland, and are controlled by the hypothalamic-pituitary-thyroid (HPT) axis (Behringer et al., 2018). THs modulate several metabolic and ontogenetic processes, including the pattern and timing of skeletal development and maintenance (Bassett and Williams, 2016), growth and maturation (Eworo et al., 2015; Forhead and Fowden, 2014), development of the brain (Bernal, 2005; Horn and Heuer, 2010), thermogenesis and the maintenance of body temperature (Behringer et al., 2018; Forhead and Fowden, 2014; Schermer et al., 1996; Silva, 2011), and reproduction in both males and females (Gao et al., 2014; Silva et al., 2018; Singh et al., 2011; Wagner et al., 2009). One of the primary functions of the HPT axis is to regulate the

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<https://doi.org/10.1016/j.ygcen.2025.114800>

Received 25 March 2025; Received in revised form 8 August 2025; Accepted 15 August 2025

Available online 18 August 2025

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production of THs across seasons (reviewed in Dardente et al., 2014; Zwahlen et al., 2024) and in response to changing energetic demands (Behringer et al., 2018), with several studies observing decreased TH levels during fasting (Brecchia et al., 2006; Schaebs et al., 2016) or starvation (Harris et al., 1978), and increased levels during a surplus (Bishop et al., 2009) or with higher quality food (Behringer et al., 2018). Based on these observations, many studies have assumed that TH levels consistently reflect nutritional state; however, many intrinsic and extrinsic processes may influence THs simultaneously, which can make TH data difficult to interpret. Additionally, the correlation between THs and energetic demands appears stronger in terrestrial mammals than marine mammals, whose large fat reserves may mediate the need to reduce metabolic activity during periods of nutritional deficits (Behringer et al., 2018; Lockyer, 2007).

Analyzing multiple hormones simultaneously can provide insights into the role THs play in the physiological state of marine mammals. Glucocorticoids (GCs) are mediated by the HPA axis in response to a stressor (Dickens and Romero, 2013) and increased levels of circulating GCs result in altered metabolism and behaviour, facilitating coping with and recovery from the current stressor (MacDougall-Shackleton et al., 2019). Common stressors experienced by marine mammals include predation, stranding, entanglement, injury, illness, capture, and negative energy balance (Atkinson et al., 2015; Ayres et al., 2012; Rolland et al., 2017). GCs are generally assumed to increase in response to all types of stressors, including nutritional stress (Busch and Hayward, 2009; Dallman et al., 1993), while THs are often assumed to decline during nutritional stress and remain relatively steady otherwise (reviewed in Behringer et al., 2018). Thus, it has been assumed that THs and GCs will be inversely correlated during nutritional stress, and not correlated during non-nutritional stressors (Brecchia et al., 2006; Harris et al., 1978). However, this model does not account for many other potential influences on THs, such as thermal environment and life stage, and it has not been adequately explored in cetaceans. THs also play a role in vertebrate reproduction, which can be altered if THs shift from normal levels, leading to infertility in females and abnormal sperm function and morphology in males (Gao et al., 2014; Krassas et al., 2010; Singh et al., 2011; Wagner et al., 2009); therefore, assessing correlations between THs and reproductive hormones, could provide further information into the relationships between endocrine axes.

Hormone concentration data can be further contextualized by employing a multidisciplinary approach that includes stable isotope proxies. Stable isotope analysis is used to assess food web structure, ecological niche, migration, and diet of wildlife (Bodey et al., 2011; Walter et al., 2014). Ratios of both carbon ($\delta^{13}\text{C}$) and nitrogen isotopes ($\delta^{15}\text{N}$) vary with dietary sources and trophic level, although relatively large variation in $\delta^{13}\text{C}$ with different sources of primary production is useful for inferring habitat use, while typically larger trophic enrichment of ^{15}N makes $\delta^{15}\text{N}$ useful for assessing consumer trophic level (Bodey et al., 2011). Therefore, measuring stable isotopes in addition to THs may provide a more complete assessment of hormonal regulation with respect to nutritional state.

Very little information exists on long-term TH patterns in marine mammals, especially mysticete whales. Most studies on endocrine function of mysticetes have used matrices that provide endocrine data from a relatively brief moment in time, such as blubber or feces (Graham et al., 2021; Lemos et al., 2020). However, long-term patterns in THs in mysticete whales can be reconstructed from measurements along baleen plates (Ajó et al., 2020, 2024; Lysiak et al., 2023, 2018). Baleen grows slowly and continuously over years, and in adult balaenids (right whales and bowhead whales), a single piece of baleen can represent a decade or more of the whale's life, essentially representing a chronological time series arrayed across a single linear structure. It has been confirmed that patterns of hormone concentrations accumulated along the baleen plate reflect known life histories (Hunt et al., 2014, 2016b, 2017; Lysiak et al., 2018). For example, progesterone in baleen from female North Atlantic right whales (*Eubalaena glacialis*; NARW) peaked in regions of the baleen

that were grown during pregnancies (Hunt et al., 2016b), while GCs were elevated during periods of stress and during pregnancies (Ajó et al., 2020; Lysiak et al., 2018).

Several studies have also documented seasonal oscillations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ along baleen plates, reflecting seasonal changes in diet and/or distribution as whales feed within isotopically distinct regions (Aguilar et al., 2014; Hobson and Schell, 1998; Matthews and Ferguson, 2015). $\delta^{15}\text{N}$ cycles in baleen may also reflect seasonal foraging cycles, oscillating between periods of greater and potentially reduced food intake (Aguilar et al., 2014; Hobson and Schell, 1998; Matthews and Ferguson, 2015). Matthews and Ferguson (2015) matched higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in summer-grown baleen with higher baseline values across the summer range of Eastern Canada-West Greenland (EC-WG) bowheads, and suggested they forage year-round, but could not rule out reduced foraging during winter as an additional source of isotopic cycling. Stable isotope data have proven especially useful for interpretation of baleen hormone patterns, as the annual cycles of stable isotope ratios can be used to estimate baleen growth rates and thus timelines of endocrine fluctuations (Lysiak et al., 2018).

Previous TH studies using mysticete baleen have focused on stranded, entangled, or chronically ill individuals (Ajó et al., 2020, 2024; Lysiak et al., 2018), and thus it has been unclear how and why THs vary over time in healthy individuals. Baleen plates from subsistence-harvested male bowhead whales provide an opportunity to examine THs in presumed-healthy mysticetes, which could therefore be useful for assessing TH patterns in relation to season, GCs, reproductive hormones, and $\delta^{15}\text{N}$. The objectives of this study were to: 1) explore seasonal patterns in T3 (the active form of thyroid hormone); and 2) assess the relationships between T3 and corticosterone (the dominant GC present in baleen), testosterone (the main reproductive hormone in males), and $\delta^{15}\text{N}$ (proxy for foraging), which would allow us to address hypotheses about the role T3 may play in stress responses, reproduction, and nutrition, respectively. If THs are involved in energetic demands, we predicted T3 concentrations would vary seasonally, and more specifically would be positively correlated with $\delta^{15}\text{N}$ and negatively correlated with corticosterone, as bowhead whales are thought to reduce their food consumption during the winter (Matthews and Ferguson, 2015). If THs are involved in male reproduction, we predicted a seasonal trend in T3, and a correlation between T3 and annual cycles of testosterone, which is elevated during the purported breeding season (Hunt et al., 2022).

2. Methods

2.1. Sample collection

Baleen plates were collected from male bowhead whales ($n = 8$) hunted by Inuit from locations across the eastern Canadian Arctic between 1998–2011 (Fig. 1). Each whale was harvested in the summer or early fall, and morphological data were collected and recorded within 24–48 h of death (Table 1). Whale body length was measured from snout to fluke using measuring tape and these measurements were used to estimate ages (Hunt et al., 2022), which ranged from 10 to 153 yrs. Most baleen plates included the embedded root (the portion within the gum tissue), preserving the entire plate including the most recent growth. One plate was cut at the gumline, thereby excluding the most recent 20–25 cm or ~1–1.5 yr of growth (Table 1). Baleen plates were frozen at $-25\text{ }^{\circ}\text{C}$ shortly after collection.

2.2. Sample preparation

Algae and other surface materials were removed from baleen plates using scrubbing pads and scalpels, and then plates were air dried (for details see Matthews and Ferguson, 2015). Starting at the base (proximal end with most recent growth), baleen plates were drilled at 2 cm increments along the entire length using a hand-held rotary tool with a 1/

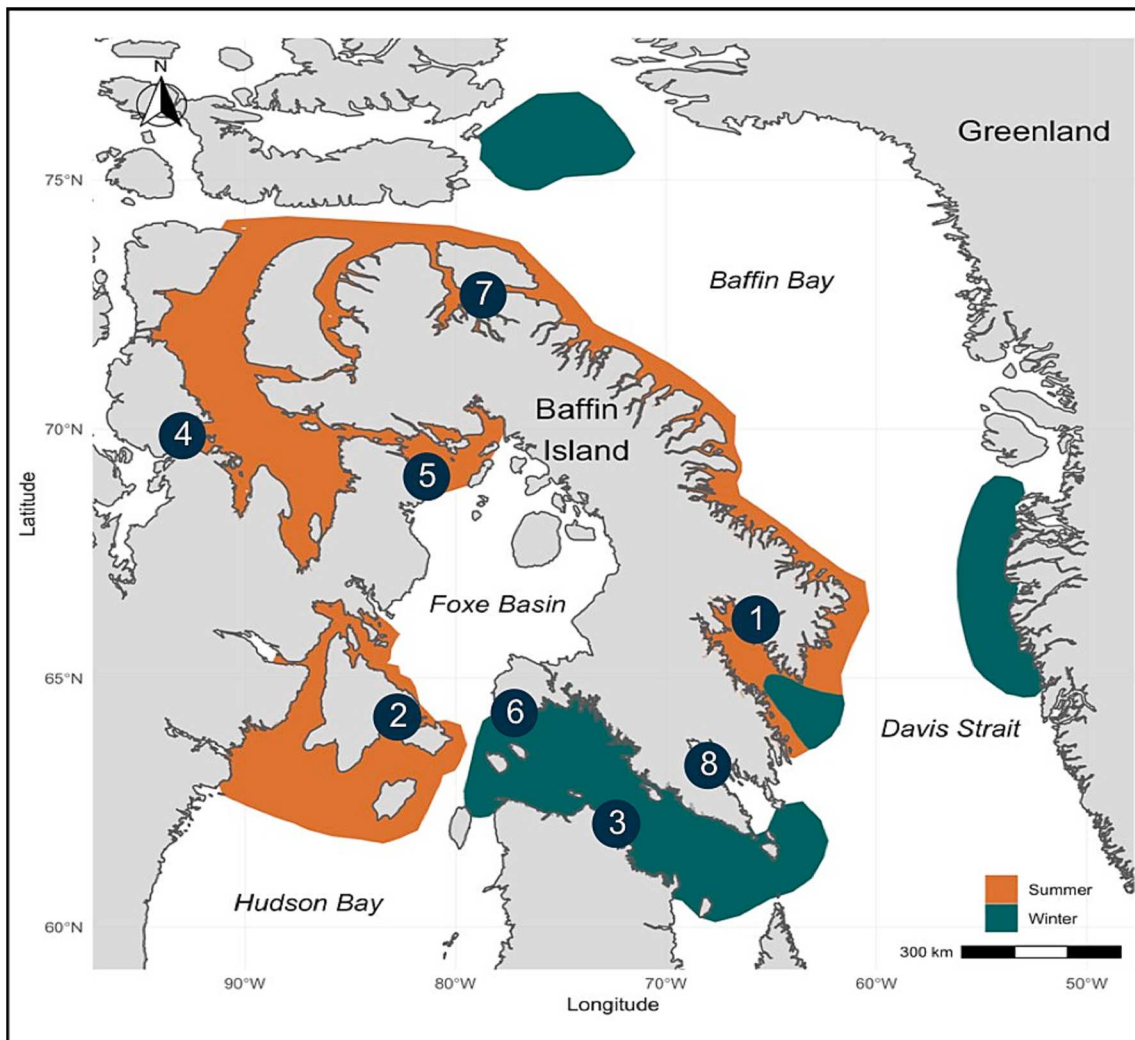


Fig. 1. Locations where baleen was collected from 8 bowhead whales from the Eastern Canada-West Greenland (EC-WG) population. Numbers on map correspond to whales listed in [Table 1](#). Winter (green) and summer (orange) distributions were (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.) reproduced from [Matthews and Ferguson \(2015\)](#).

16-inch drill bit, producing a powdered sample from each sampling location. Given that adult bowhead baleen growth rates range from 16 to 25 cm per year ([Schell et al., 1989](#)), 2-cm sampling increments represent approximately 1 to 1.5 months of growth, and the longest plates (330 cm) represent over a decade of growth. Baleen powder samples were stored frozen at -80°C until the hormone extraction process.

2.3. Hormone extraction

Hormones were extracted from baleen following [Hunt et al. \(2017\)](#). We placed 100 mg of baleen powder into a borosilicate glass tube and added 6 ml of 100 % methanol. The sample was put on a plate shaker for 2 h and centrifuged for 15 min at 3000 rpm, after which 4.5 ml of the supernatant was removed, transferred to a new glass tube, and dried under nitrogen at 45°C for 4–6 h. Samples were reconstituted in 0.50 ml of assay buffer (X065 assay buffer, Arbor Assays, Ann Arbor, MI, USA), vortexed for 1 min, and transferred to a cryovial and frozen at -20°C until hormone analysis. Final data were corrected to account for the portion of supernatant that could not be recovered from the baleen powder (1.5 ml).

2.4. Hormone assays and validation

T3 and corticosterone were measured using commercially available T3 and corticosterone enzyme immunoassay kits (EIA; Arbor Assay, catalogue #K056 and #K014, Ann Arbor, MI). Testosterone data from the same individuals were measured and previously published in [Hunt et al. \(2022\)](#). To preserve the limited sample volumes and improve assay precision for low-dose samples, we modified the manufacturer's protocols as follows: for the T3 assay, we reduced the volume of standards and samples (50 μl of standards/samples, as in [Hunt et al., 2017](#)); and for both assays, the standard curve was extended by serial dilution to produce one additional low-dose standard, with the final T3 standard curve spanning 39.06–5,000 pg/ml and the final corticosterone standard curve spanning 78.125–10,000 pg/ml. Both assays had previously passed parallelism validations for bowhead baleen extract, and the corticosterone assay had also passed an accuracy (matrix effect) validation ([Hunt et al., 2017](#)). However, accuracy had not been assessed for the T3 assay; therefore, we performed an accuracy validation for this assay. To test for accuracy, we spiked four standards with a pool of bowhead baleen extract derived from samples with relatively low apparent T3 concentration. The spiked standards were assayed alongside standards spiked only with buffer and the pooled baleen extract was also assayed individually to determine the amount of endogenous hormone in the pool.

Table 1
Morphological data for 8 male Eastern Canada-West Greenland bowhead whales from which baleen plates were collected (Matthews and Ferguson, 2015).

Whale Number	Whale ID	Date Collected (month/year)	Total body length (m)	Baleen length (cm)	Age estimated from body length ^d
1	NSA-BM-98-01	07/1998	12.75	266 ^{a,c}	22
2	BM-CH-2000-001	08/2000	11.65	270 ^{b,c}	15
3	BM-01-2008	08/2008	14.88	319 ^{a,c}	78
4	BM-NSA-2008-001	09/2008	10.51	181 ^{a,c}	10
5	BM-NSA-2008-002	08/2008	13.43	235 ^{a,c}	29
6	BM-NSA-2009-03	09/2009	15.77	330 ^{a,c}	~153
7	BM-NSA-2010-01	08/2010	12.80	230 ^{a,c}	23
8	BM-NSA-2011-01	08/2011	14.33	298 ^{a,c}	48

^a Total length (entire plate, including growth within gum tissue).

^b Erupted length (cut at the gumline).

^c Full length of baleen was not sampled for hormone analyses, due to sample quantity limitations

^d (Hunt et al., 2022).

The results were graphed as observed vs. expected, with results assessed for linearity and slope (acceptable slope is within 0.7–1.3; ideal slope = 1; Grotjan and Keel, 1996.). The T3 assay exhibited acceptable accuracy for bowhead baleen extract (slope = 0.94; R² = 0.98; Fig. 2). Following successful validation, baleen extracts were assayed individually at full-strength (1:1; undiluted) in both assays. To minimize effects of intra- and inter-assay variation, each whale’s samples were randomized within and across assay plates, and all assays for a given hormone, for a given whale, occurred on the same day, with identical lot numbers for all reagents.

We followed standard QA/QC protocols for hormone analysis, including assaying each sample, control, and standard in duplicate, and

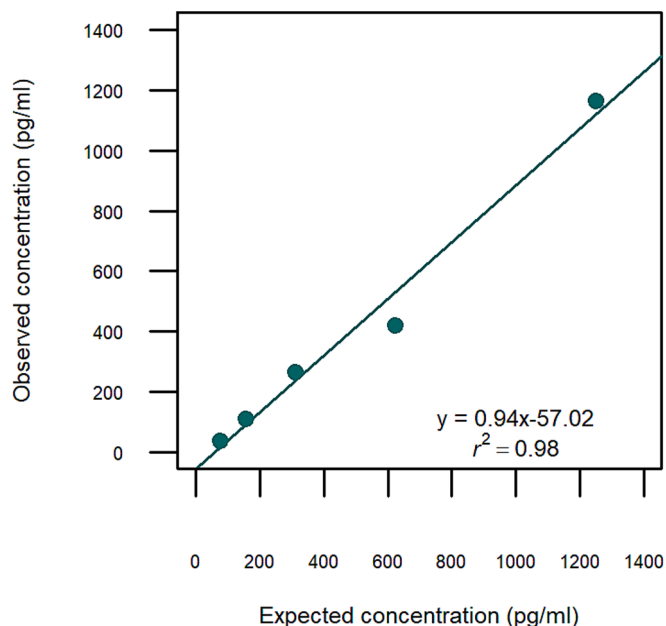


Fig. 2. Accuracy plot for T3 assay tested with bowhead whale baleen extract.

inclusion of a full standard curve, non-specific binding wells, controls, and zero-dose wells in every assay. Any samples with a coefficient of variation (CV) between duplicates of greater than 10 % was re-assayed; CV’s for this analysis were calculated from the optical density of each well. All standard curves were additionally inspected for normal NSB/zero ratio, normal controls, and expected sigmoidal shape of standard curve. Final results were converted to ng of immunoreactive hormone per g of baleen powder.

2.5. Stable isotope data

δ¹⁵N was previously measured in baleen plates from the same individuals; details can be found in Matthews and Ferguson (2015). Briefly, ~1 mg of each baleen sample was analysed using isotope ratio mass spectrometry, and stable nitrogen isotope ratios were reported in delta notation (δ) as parts per thousand (‰) deviation from the isotope ratio of atmospheric N₂. Data were normalized using reference materials calibrated to international standards, and analytical precision based on repeated measures of a reference material (not used in calibrations) and duplicate sample measurements were ≤ 0.11 ‰.

2.6. Data analysis

T3 and corticosterone concentrations were interpolated from assay standard curves using four-parameter logistic curve fits, using GraphPad Prism (Version 8.1.2; San Diego, CA). We investigated seasonality in T3 by calculating the autocorrelation function (ACF) using the Forecast package (Hyndman et al., 2025) in R Studio (Posit Team, 2024). The ACF calculates the correlation coefficient between the original time series and itself at various lags, and is useful for identifying patterns such as cycles from repeating positive (and negative) correlations (e.g., seasonality). We also examined variation in T3 relative to variation in corticosterone, and previously measured testosterone and δ¹⁵N data in the same plates (Hunt et al., 2022; Matthews and Ferguson, 2015), using cross correlation functions (CCF) also calculated using the Forecast package. The CCF calculates the correlation coefficient between two different time series at various time lags, and is useful for determining the relationship between two variables (e.g., whether they vary synchronously, or if one precedes/follows the other). The maximum lag at which the ACF was calculated was 10log₁₀(T) where TT is the length of the time series and the maximum lag for the CCF was 10log₁₀(T/2). For both ACF and CCF, the approximate 95 % confidence limits were calculated as ±1.96T^{-1/2} based on the null hypothesis of white noise (Hyndman, 2015). For the CCF, TT is the shorter length of both time series. Samples at 0 cm (newest baleen growth) were removed from ACF and CCF analyses due to high hormone concentrations observed in each plate.

3. Results

3.1. Seasonality in T3

T3 was detected in all baleen samples, with concentrations ranging from 0.61-21.62 ng/g. ACFs revealed seasonality in T3 concentrations in two baleen plates (from whales BM-NSA-2008–001 and BM-01–2008); however, the remaining six plates exhibited no seasonality in T3 concentrations (Fig. 3). BM-NSA-2008–001 and BM-01–2008 showed significant positive correlations at lags 3 and 4, respectively, indicating seasonal fluctuations every 6–8 cm of growth (i.e., given sampling interval of 2 cm).

3.2. T3 and δ¹⁵N

A negative correlation was observed between T3 and δ¹⁵N at lag 0 for BM-NSA-2009–03 and lag 1 for BM-NSA-2010–01 (Fig. 4). The

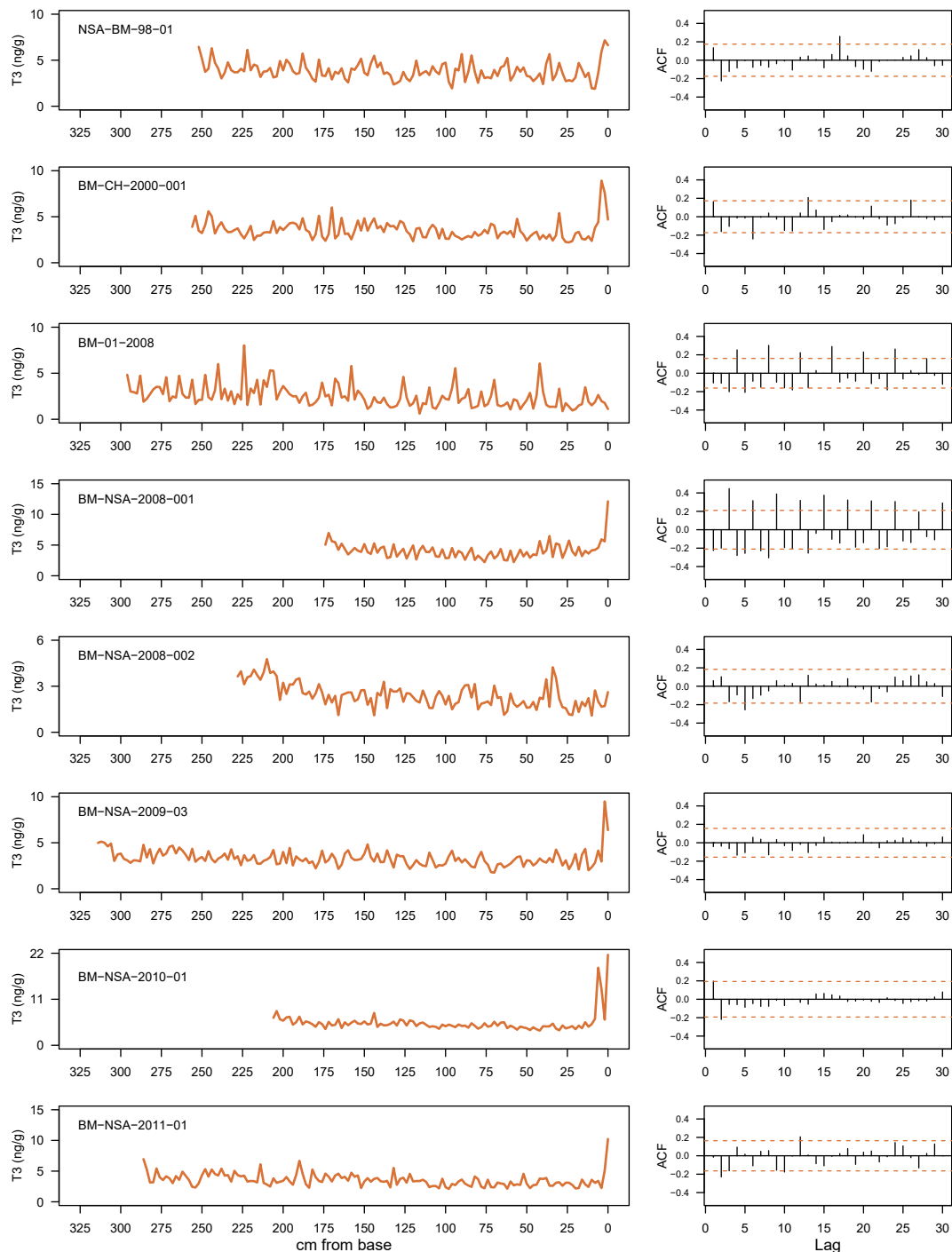


Fig. 3. T3 profiles measured along baleen plates from 8 male bowhead whales and corresponding auto-correlation plots. Seasonality in T3 concentrations was observed in BM-NSA-2008-001 and BM-01-2008, while the other six whales, showed no seasonality. Autocorrelations falling outside the dashed lines provide evidence of statistical significance at the 5 % level at that lag (Hyndman and Athanasopoulos, 2018.). Lag unit is 2 cm (the sample increment).

remaining six plates showed no correlation between T3 and $\delta^{15}\text{N}$.

3.3. T3 and corticosterone

T3 and corticosterone concentrations were positively correlated in each plate. CCF analysis indicated that T3 and corticosterone were positively correlated at lag 0 in all plates, with the exception of BM-01-2008, which showed the strongest positive correlation at lag 1 (Fig. 5).

3.4. T3 and testosterone

T3 and testosterone were positively correlated in BM-NSA-2008-002; however, no correlation was observed in the seven remaining whales (Fig. 6).

4. Discussion

Patterns of THs in mysticete whales are not well understood, as most previous TH studies have either used matrices that provide endocrine

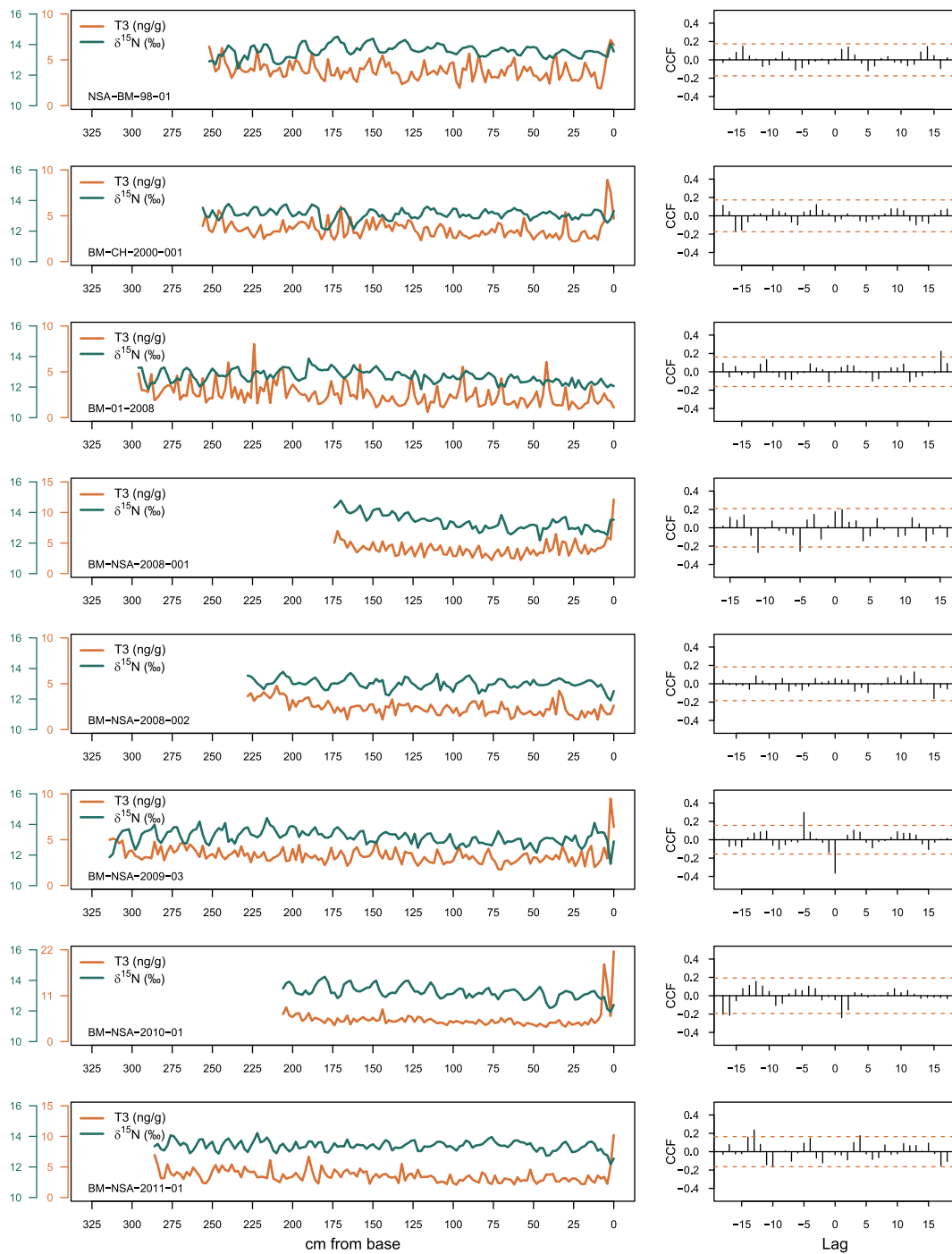


Fig. 4. T3 and $\delta^{15}\text{N}$ profiles measured along baleen plates from 8 male bowhead whales and corresponding cross-correlation plots. A negative correlation was observed at lag 0 for whale BM-NSA-2009-03, while a negative correlation was observed at lag 1 for BM-NSA-2010-01. No correlation was observed between T3 and $\delta^{15}\text{N}$ for the remaining six whales. Cross-correlations falling outside the dashed lines provide evidence of statistical significance at the 5% level at that lag (Hyndman and Athanasopoulos, 2018). Lag unit is 2 cm (the sample increment).

data for a relatively short period of time or have been collected from stranded, entangled, or chronically ill individuals (Ajó et al., 2020, 2024; Lysiak et al., 2018). We used a unique multivariate dataset from presumed-healthy harvested bowhead whales, which allowed us to investigate T3 patterns in relation to season, GCs, testosterone, and $\delta^{15}\text{N}$ to better understand the role that T3 may play in healthy mysticete whales. If THs are primarily involved in the modulation of metabolism, we predicted to see a seasonal trend in T3, a positive correlation between T3 and $\delta^{15}\text{N}$, and a negative correlation between T3 and corticosterone, since bowhead whales are thought to reduce foraging

throughout the winter (Matthews and Ferguson, 2015). We also predicted to see a correlation between T3 and testosterone, if T3 was involved in seasonal mating (Brown et al., 2007). The lack of seasonality in T3 concentrations, which were uncorrelated with $\delta^{15}\text{N}$ and testosterone, suggest that T3 may not be solely involved in modulation of energy metabolism or reproduction, or that other factors may be more influential on T3 production and thus mask our predicted outcomes. Additionally, the positive correlation between T3 and corticosterone observed here challenges the assumption that THs and GCs are often negatively correlated, and suggests that certain stressors may require

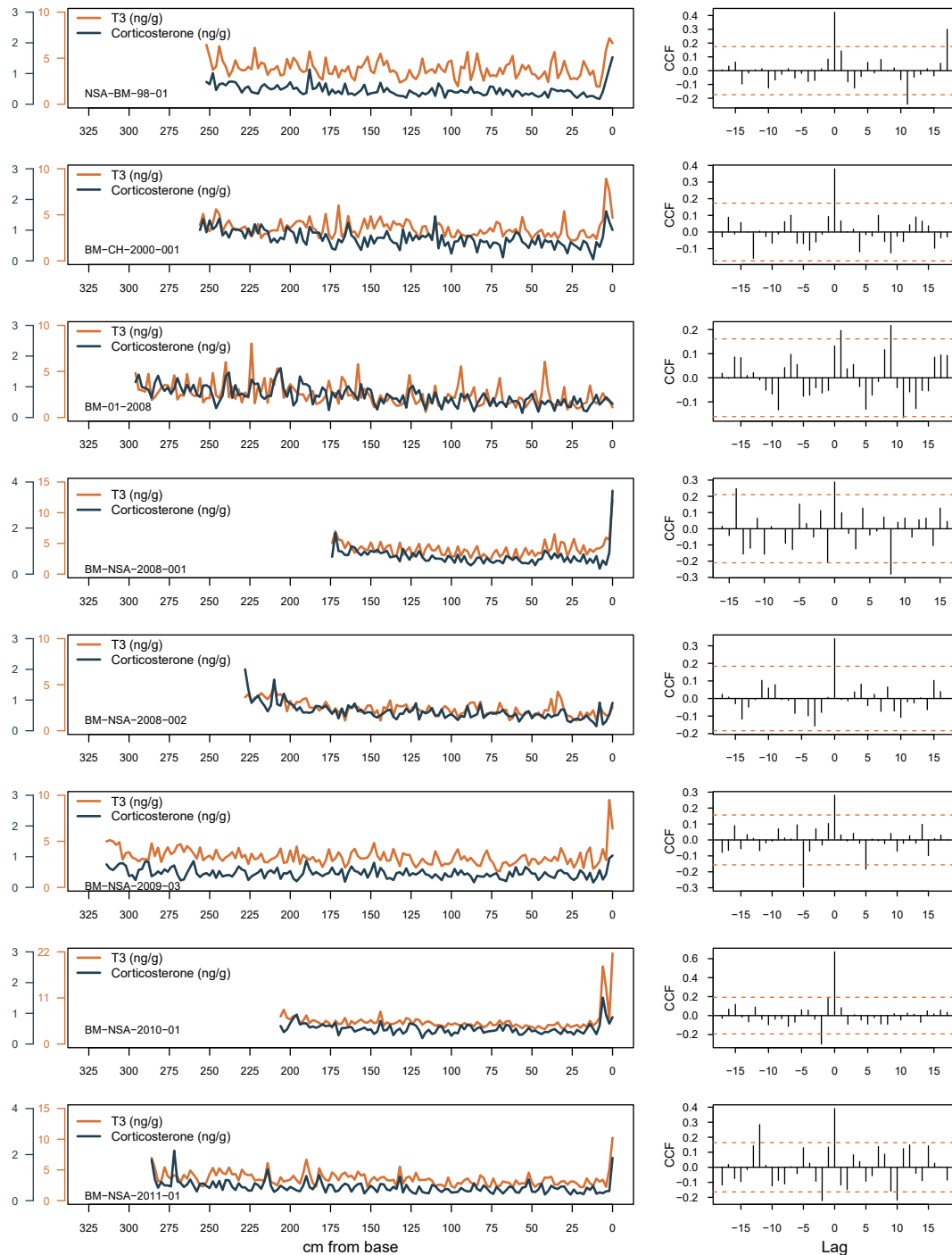


Fig. 5. T3 and corticosterone profiles measured along baleen plates from 8 male bowhead whales and corresponding cross-correlation plots. A positive correlation was observed between T3 and corticosterone in each whale. A positive correlation at lag 0 was observed in 7 whales, while whale BM-01-2008 exhibited a positive correlation at lag 1. Cross-correlations falling outside the dashed lines provide evidence of statistical significance at the 5 % level at that lag (Hyndman and Athanasopoulos, 2018). Lag unit is 2 cm (the sample increment).

increased metabolic rate.

Experiments in captive mammals suggest that during periods of nutritional deficits, the HPT axis becomes down-regulated, resulting in a reduction of THs (Behringer et al., 2018; Boelen et al., 2008). Many studies investigating THs in relation to nutritional state have also measured GCs, as GCs are thought to increase during times of nutritional stress (Busch and Hayward, 2009; Dallman et al., 1993); thus, it has been hypothesized that GCs and T3 would have an inverse relationship, with GCs increasing and T3 decreasing when an animal experiences nutritional stress (Ayres et al., 2012; Gobush et al., 2014). The unexpected

positive correlation between T3 and corticosterone observed in each whale in this study may be explained by events that increase physiological stress (high GCs) and require increased metabolic rate (high T3). For example, Gobush et al. (2014) observed a positive correlation between T3 and GCs in Hawaiian monk seals and hypothesized that the trend could be due to adequate yet stressful foraging behaviour. If monk seals were successfully foraging, while having to compete with other predators, it is possible that they would exhibit both high T3 and GC levels (Gobush et al., 2014). Since the EC-WG bowhead whale population is approaching carrying capacity (Biddlecombe et al., 2025), an

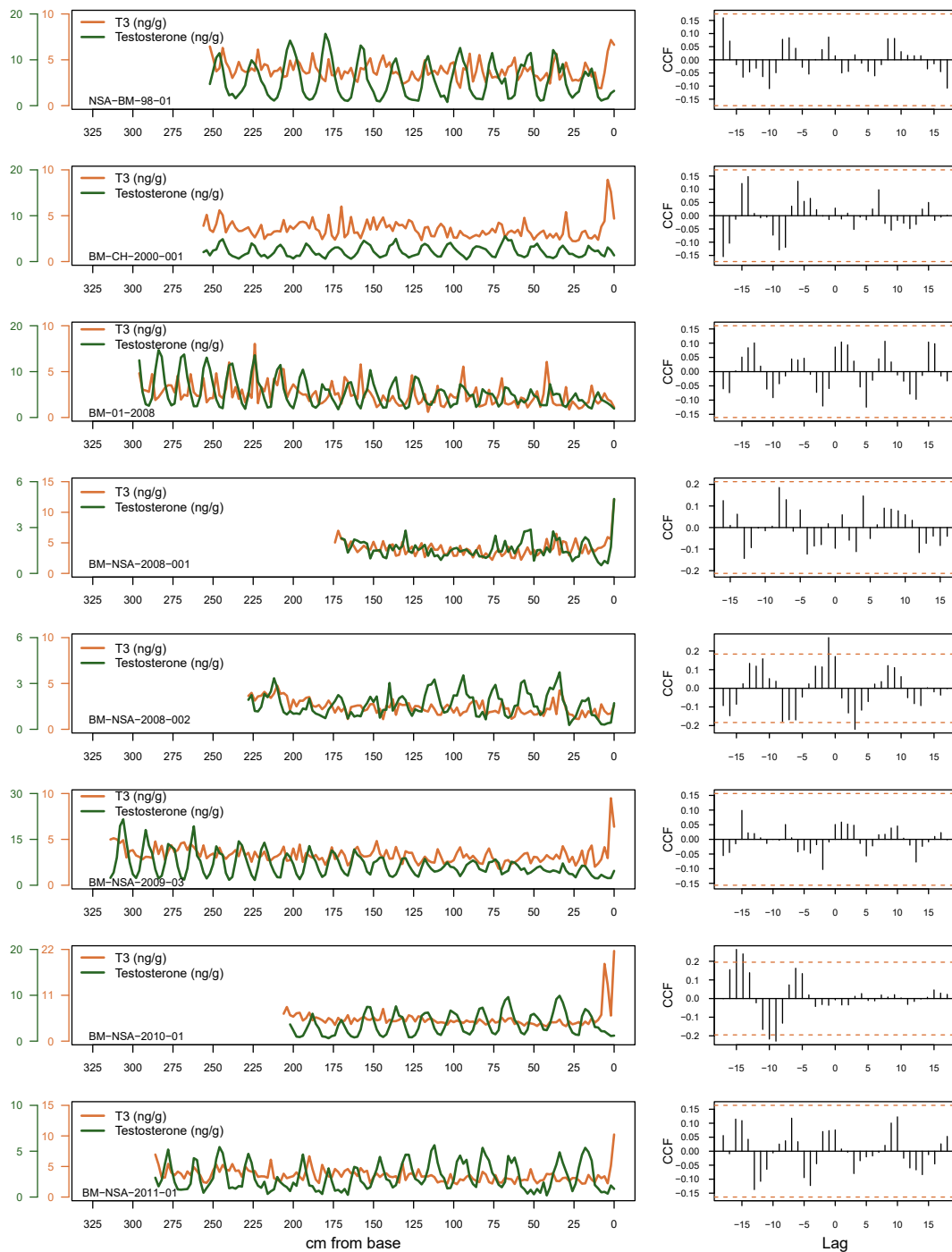


Fig. 6. T3 and testosterone profiles measured along baleen plates from 8 male bowhead whales and corresponding cross-correlation plots. A positive correlation was observed between T3 and testosterone in whale BM-NSA-2008-002 but no correlation was observed between the remaining seven whales. Cross-correlations falling outside the dashed lines provide evidence of statistical significance at the 5 % level at that lag (Hyndman and Athanasopoulos, 2018). Lag unit is 2 cm (the sample increment).

increase in foraging competition may result in a simultaneous increase in GC levels and metabolic rate. A similar pattern has been noted in entangled leatherback turtles, which showed a positive correlation between corticosterone and thyroxine (the precursor to T3), with entanglement thought to represent a stressor that requires increased energetic output (i.e., increased swimming effort while towing heavy gear Hunt et al., 2016a). Similarly, T3 and GCs increased simultaneously in a fatally entangled right whale, again possibly related to the energetic demands of swimming while entangled (Lysiak et al. 2018).

Thermoregulatory output may also contribute to the positive

correlation between T3 and corticosterone. For example, Lemos et al. (2020) found that gray whales with poor body condition had higher fecal T3 concentrations than whales with good body condition, and also observed a positive correlation between fecal T3 and GCs. Since cetacean blubber acts as an insulator, whales with reduced blubber thickness may need to increase their metabolic rate to maintain normal body temperature (Parry, 1949); therefore, this could mean that in cetaceans, nutritional stress may result in increased secretion of THs, rather than the decreased THs noted in studies of captive terrestrial mammals (Brecchia et al., 2006; Harris et al., 1978; Schaebs et al., 2016). Those

stressors that result in a reduction of blubber thickness and body condition, such as entanglement and starvation, could therefore result in a positive correlation between THs and GCs due to thermoregulatory effects. However, bowhead whales in this study were not entangled and unlikely in poor body condition; therefore, other factors likely contributed to this positive correlation.

We predicted to see seasonal fluctuations in T3, a positive correlation between T3 and $\delta^{15}\text{N}$, and a negative correlation between T3 and corticosterone, under the possibility that bowheads continue foraging but possibly at a reduced rate during the winter (Matthews and Ferguson, 2015). Seasonal fluctuations in T3 concentrations were, however, observed in baleen plates from two whales. Based on annual bowhead baleen growth rates of 16–25 cm yr⁻¹ (Schell et al., 1989) and our assumption that 2 cm represents ~ 30 days of growth (Lysiak, 2008), BM-01–2008 and BM-NSA-2008–001 experienced seasonal changes in T3 that occurred two to three times per year. Several biological events may impact metabolic rate seasonally, including thermoregulation, mating, fasting, and migration (Cristóbal-Azkarate et al., 2016; Gobush et al., 2014). However, these events are presumably experienced by most bowhead whales, yet the seasonal pattern in T3 was only observed in two whales in this study. In free-ranging ground squirrels, inconsistent TH patterns were observed, which was attributed to environmental factors impacting TH dynamics, potentially masking any seasonal trends in TH production (Williams et al., 2019). The lack of seasonality in T3 and lack of correlation between T3 and $\delta^{15}\text{N}$ observed in most whales could indicate that EC-WG bowhead whales forage year-round, without a reduction in winter foraging. However, it is also possible that environmental heterogeneity experienced by bowhead whales may also mask seasonal fluctuations in THs and warrants further investigation.

Although BM-01–2008 and BM-NSA-2008–001 were the only whales to exhibit seasonal fluctuations in T3, they did not share any obvious similarities, based on the morphological data collected, and interestingly, BM-01–2008 was one of the largest and oldest whales in the dataset, while BM-NSA-2008–001 was the youngest and smallest. Testosterone in baleen from BM-01–2008 showed a decrease in amplitude over time, while BM-NSA-2008–001 lacked seasonal fluctuations in testosterone altogether (Hunt et al., 2022). It is possible that a lack of seasonality in testosterone reveals an underlying trend in T3 or that non-mating male bowhead whales are behaving differently than mating whales; however, due to our small sample size and lack of age ranges, it is difficult to ascertain what these trends mean in an ecological context.

Correlations between THs and testosterone have been observed in males of several species, including Iranian fat-tailed rams (*Ovis aries*; Zamiri and Khodaei, 2005), white-breasted hedgehogs (*Erinaceus roumanicus*; Rutovskaya and Diatrotov, 2022), Tegul lizard (*Salvator merianae*; Zena et al., 2020, 2019), the edible dormouse (*Glis glis*; Jalilae and Assenmacher, 1983), red foxes (*Vulpes vulpes* L.; Maurel and Boissin, 1981), and Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants (Brown et al., 2007), and it is thought that THs play a role specifically in seasonal reproductive function (Cyr and Eales, 1996; Dawson et al., 2001; Rutovskaya and Diatrotov, 2022). We predicted a positive correlation between T3 and testosterone if T3 was involved in reproduction; however, a correlation was only observed in one out of eight whales. In elephants, a negative trend between T3 and testosterone was observed but only in males with clear, annual musths (Brown et al., 2007), and since seasonal fluctuations in testosterone were observed in almost each bowhead whale in this study (Hunt et al., 2022), we expected to see a similar trend. While we know that normal function of the thyroid gland is important for reproduction in both sexes (Choksi et al., 2003), the mechanisms involved are not well understood, and since mating in bowheads may also coincide with other physiological events, such as migration, changes in thermoregulation, and feeding, these factors may mask or contribute to the lack of correlation observed between T3 and testosterone.

By comparing T3 with corticosterone, $\delta^{15}\text{N}$, and testosterone, we hoped to better understand the role T3 plays in healthy mysticete

whales. Correlations between T3 and $\delta^{15}\text{N}$ and T3 and testosterone observed in just two and one whale, respectively, may have been spurious since $\delta^{15}\text{N}$ and testosterone were highly seasonal and spurious correlations are more likely to occur when one or both variables is highly autocorrelated (Dean and Dunsmuir, 2016).

Unexpected, yet consistent, correlation between T3 and corticosterone concentrations was in opposition to the commonly observed negative correlation exhibited in many terrestrial mammals. This study focused solely on male bowhead whales, which may have limited our findings. Future studies should continue to investigate the relationships between the HPT, HPG, and HPA axes, in both sexes, in a wider range of age classes, to determine if there are other trends that were not observed in this study. It would also be useful to simultaneously collect drone images and biological samples, including blubber, blow, or fecal samples to investigate relationships between THs and body condition. Continued effort in understanding trends in THs could potentially provide additional tools for assessing the health of wild whale populations, which is imperative to their successful management and conservation.

CRediT authorship contribution statement

Justine M. Hudson: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kathleen Hunt:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marianne Marcoux:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **C.Loren Buck:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **Cory J.D. Matthews:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank Hunters and Trappers Organizations (HTOs) and wildlife officers in communities across Nunavut and Nunavik, and Nunavut Tunngavik Incorporated (P-Y Daoust) for collecting baleen samples. We would also like to thank Fisheries and Oceans Canada staff (T. Naaykens, C. Willing, L. Dueck, B. Dunn, P. Hall, T. Kelley) for assisting with baleen collection and subsampling, along with Brenden Dufault (University of Manitoba) for assisting with statistical analyses. JMH would also like to thank the University of Manitoba, NSERC Create Program, and the NSF grant #1656063 “Research Coordination Network (RCN): Predicting vertebrate responses to a changing climate: modeling genomes to phenomes to populations (G2P2PoP).

Data availability

Data will be made available on request.

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