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Prevalence and Abundance of Cyamid “Whale Lice” (*Cyamus ceti*) on Subsistence Harvested Bowhead Whales (*Balaena mysticetus*)

Andrew L. Von Duyke,[1,2] Raphaela Stimmelmayr,[1] Gay Sheffield,[3] Todd Sformo,[1] Robert Suydam,[1]
Geof H. Givens[4] and John C. George[1]

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ABSTRACT. We present findings on the prevalence and abundance of cyamid ectoparasites (*Cyamus ceti*) or “whale lice” on bowhead whales (*Balaena mysticetus*) harvested for subsistence in the Bering, Chukchi, and Beaufort Seas from 1973 to 2015. Cyamids were present on 20% of the 673 whales that were examined for cyamid ectoparasites. Logistic regression was used to determine factors associated with cyamid prevalence. The probability of cyamid presence increased with age, length, and improving body condition, but decreased over the past 35 years. Cyamid presence was also more probable on whales harvested in the spring than on those harvested in the fall. When present, cyamid abundance was typically low (< 10 per whale). Case histories provide ancillary information about the relationships between abundance of cyamids and their bowhead hosts. Environmental change and increasing anthropogenic disturbances are expected to occur in the Arctic regions inhabited by bowheads. We recommend continued monitoring of subsistence harvested whales for cyamids, as well as further investigations into the roles of environmental and anthropogenic variables in cyamid prevalence and abundance, as part of a comprehensive program of Arctic ecosystem assessment.

Key words: cyamid; whale lice; *Cyamus ceti*; ectoparasite; bowhead whale; *Balaena mysticetus*; Arctic; Bering Sea; Chukchi Sea; Beaufort Sea

RÉSUMÉ. Nous présentons nos constatations en matière de prévalence et d’abondance de l’ectoparasite cyamidae (*Cyamus ceti*) ou « pou des baleines » se trouvant sur la baleine boréale (*Balaena mysticetus*) capturée à des fins de subsistance dans la mer de Béring, la mer des Tchouktches et la mer de Beaufort entre 1973 et 2015. Les cyamidae étaient présents sur 20 % des 673 baleines qui ont été examinées dans le but d’y trouver des ectoparasites cyamidae. La régression logistique a servi à déterminer les facteurs liés à la prévalence de cyamidae. La probabilité de la présence de cyamidae augmentait en fonction de l’âge, de la longueur et de l’amélioration de l’état corporel, mais elle a diminué au cours des 35 dernières années. De plus, la présence de cyamidae était également plus probable chez les baleines capturées au printemps que chez les baleines capturées à l’automne. Lorsque présents, les cyamidae étaient généralement de faible abondance (< 10 par baleine). Les cas types fournissent des renseignements supplémentaires sur les relations entre l’abondance de cyamidae et les baleines hôtes. Des changements environnementaux et de plus grandes perturbations anthropiques sont attendus dans les régions arctiques où évolue la baleine boréale. Nous recommandons la surveillance continue des baleines attrapées à des fins de subsistance pour en détecter les cyamidae. Nous recommandons également des études plus approfondies afin de déterminer le rôle des variables environnementales et anthropiques en matière de prévalence et d’abondance des cyamidae, dans le cadre d’un programme exhaustif d’évaluation de l’écosystème arctique.

Mots clés : cyamidae; pou de la baleine; *Cyamus ceti*; ectoparasite; baleine boréale; *Balaena mysticetus*; Arctique; mer de Béring; mer des Tchouktches; mer de Beaufort

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INTRODUCTION

Cyamids (Crustacea, Amphipoda), also known as “whale lice,” are ectoparasites that feed on the epidermis of whales (Rowntree, 1983, 1996; Schell et al., 2000). They are able to stay attached to the surface of their cetacean hosts through several adaptions, including sharp grasping claws and a flattened shape (Fig. 1). Although they are common to many cetacean species, some cyamid species are host-specific. For instance, *Cyamus ovalis*, *C. gracilis*, and *C. erraticus* can be found only on right whales (*Eubalaena* spp.) (Kaliszewska et al., 2005). Similarly, the bowhead

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[1] North Slope Borough Department of Wildlife Management, PO Box 69, Barrow, Alaska 99723, USA
[2] Corresponding author: Michigan Technological University – SFRES, 1400 Townsend Drive, Houghton, Michigan 49931, USA; Andrew.VonDuyke@north-slope.org
[3] Alaska Sea Grant, University of Alaska Fairbanks - Northwest Campus, Pouch 400, Nome, Alaska 99762, USA
[4] Givens Statistical Solutions, LLC, 4913 Hinsdale Drive, Fort Collins, Colorado 80526, USA

FIG. 1. Numerous cyamid "whale lice" (*Cyamus ceti*) on the surface of a 9 m long female bowhead whale (*Baleana mysticetus*) harvested in Barrow in 2004 (ID 04B03). Note the depth to which cyamids embed their claw-like appendages (inset) into the whale's epidermis. Also note the presence of distinct age classes. (Large photo: North Slope Borough, Department of Wildlife Management. Inset photo: Taken by Todd Sformo at the Advanced Instrumentation Laboratory, University of Alaska Fairbanks.)

whale (*Balaena mysticetus*), another member of the family Balaenidae closely related to the right whale, has a closely associated cyamid ectoparasite (*Cyamus ceti*, Fig. 1).

Long-term visual health assessments of North Atlantic right whales (*Eubalaena glacialis*) suggest a relationship between the spatial distribution and relative abundance of cyamids and the health status of their host (Pettis et al., 2004). For example, orange cyamids (*C. erraticus*) occur in relatively low numbers on all healthy adult right whales (R. Rolland, pers. comm. 2015; J. Seger, pers. comm. 2016), where their spatial distribution is largely confined to genital and mammary folds. But the occurrence of these cyamids in large numbers on the host's dorsal surface, particularly around the blowholes, has been associated with poor health (Schick et al., 2013; J. Seger, pers. comm. 2016). Such infestations have been observed in "last-sighting" photos, after which the whales were presumed dead (Pettis et al., 2004). In another example, a North Atlantic right whale, entangled by a line around its rostrum that prevented feeding, became almost entirely covered with cyamids before the animal's eventual death from starvation (Moore et al., 2006; M. Moore, pers. comm. 2015; R. Rolland, pers. comm. 2015). Presumably, the reduced swimming speed of physically compromised whales allows cyamids to proliferate by occupying more "environments" that are hydrodynamically favorable (Rowntree, 1996).

Although the Bering-Chukchi-Beaufort Seas (BCB) population of bowheads is currently large and increasing (Givens et al., 2016), its remote Arctic home range means that these whales are a difficult species to monitor, and little is known about their cyamid ectoparasites. Bowheads are legally hunted by Native Alaskans, and postmortem examinations of subsistence harvested bowhead whales have been conducted for more than 40 years in cooperation with the Alaska Eskimo Whaling Commission and village whaling captains' associations. This investigation reviews the harvest records collected by the National Marine Fisheries Service in the 1970s and the North Slope Borough Department of Wildlife Management from the early 1980s to the present. Our fundamental goal was to better understand the factors associated with cyamid prevalence and abundance on BCB bowhead whales, and this work presents, to our knowledge, the first such long-term investigation.

Our specific objectives were to characterize cyamid prevalence and abundance with respect to demographic, morphological, seasonal, and body condition variables of bowhead whales. A further objective was to improve the basic understanding of cyamid ecology. To do so, we compiled and analyzed data from all harvest records of bowheads that were visually inspected for cyamids.

METHODS

In cooperation with the Alaska Eskimo Whaling Commission and village Whaling Captains' Associations, postmortem examinations of subsistence harvested bowhead whales were conducted by the National Marine Fisheries Service in the 1970s and by the North Slope Borough Department of Wildlife Management from the early 1980s to the present. Upon landing, the exposed skin of the whale (including the gape of the mouth, eyelids, blowholes, genital slit, and peduncle, as well as any skin depressions, scars, cracks, or wounds) was examined for cyamid ectoparasites. The presence, location, and relative abundance of cyamids were noted, as were other biometric and demographic data. Detailed descriptions of the methods used to collect whale biometric and demographic data can be found in George (2009).

Because harvested bowheads typically had fewer than 10 cyamids present, and the count distribution was highly skewed (e.g., the median count was 2, but the highest three cyamid totals were recorded as 201, 200, and 100; see Fig. 2), absolute cyamid abundance was not formally analyzed. Instead, our analyses focused on cyamid presence.

We fit logistic regression models to predict the probability of cyamid presence. The response variable for all models was an indicator variable for cyamid presence (present = 1, absent = 0). Sex of the whale (SEX, female = 1 and male = 0) was determined by external visual examination. The presence of scars (SCAR, present = 1, absent = 0) was ascertained from the observer comments recorded in the harvest records for each whale. Whales were scored as having scars if any wounds, gouges, cracks, killer whale (*Orcinus orca*) bites, line entanglements, or ship strikes

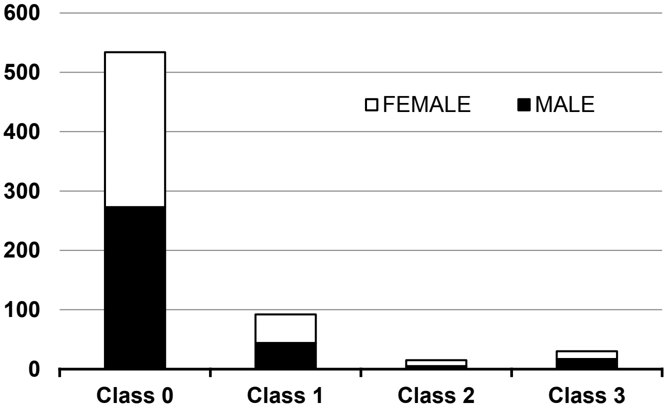


FIG. 2. Bar chart classifying 671 of the 673 bowhead whales examined for cyamids (excluding two whales of undetermined sex). Classes indicate the number of cyamids detected on harvested whales during gross examination immediately upon landing. Class 0: none detected. Class 1: 1–5 cyamids detected. Class 2: 6–10 cyamids detected. Class 3: more than 10 cyamids detected. Classification data were scored from observer comments on the bowhead whale harvest data forms.

were present. Total body length (LEN) was measured as the straight-line distance from the distal end of the rostrum to the inside of the fluke notch. Whale age (AGE) was estimated via several methods, including aspartic acid racemization of eye lens tissue (George et al., 1999), stable isotope analysis of the baleen (Lubetkin et al., 2008), and corpora counts in the ovaries (George et al., 2011). We also considered the whale's body condition (COND) as an explanatory variable. We defined COND as the residuals from a "body condition model" that predicts the whale's girth as a function of its length. Because we ran two families of logistic regression models based on two different data sets (see Tables 1 and 2), we generated residuals from two separate body condition models:

1. body condition model 1 (used in Table 1 models)

$$\mathrm{GIRTH}_{ax} = 124.5 + 0.56\cdot\mathrm{LEN}_{cm}$$
$$(R^2 = 0.88, F_{1,\,124} = 935.8, p = 2.2 \times 10^{-16})$$

2. body condition model 2 (used in Table 2 models)

$$\mathrm{GIRTH}_{ax} = 166.0 + 0.52\cdot\mathrm{LEN}_{cm}$$
$$(R^2 = 0.79, F_{1,\,495} = 1890, p = 2.2 \times 10^{-16})$$

where GIRTH_{ax} = axillary girth of the whale, which is measured as one-half of the whale's circumference (cm) taken from the dorsal centerline to the ventral centerline and adjacent to the posterior insertion of the pectoral flippers; LEN_{cm} = total length of the whale, measured as the straight-line distance (cm) from the distal end of the whale's rostrum to the inside of the fluke notch.

The sign and magnitude of the residuals from these models indicate whether a whale is fatter or thinner than predicted for its length and thereby act as an index that characterizes body condition (COND). To assess temporal relationships, we included a variable for the season (SEAS, where spring = 0 and fall = 1) and the year (YEAR) in which each whale was harvested.

Our first set of models (Table 1, models 1 – 5) considered the following six explanatory variables: AGE, SEX, SCAR, COND, SEAS, and YEAR. We did not include AGE and LEN in the same models because of collinearity (Pearson's product-moment correlation, $r = 0.77$, $p < 2.2 \times 10^{-16}$). Rather, using the same data set, we replaced AGE with LEN and re-ran our models using the same procedures (Table 1, models 6 – 10). The sample size for all models in the first analysis ($n = 126$) was substantially less than the number of examined whales because relatively few whales in our harvest records had an age estimate to associate with their length and girth measurements. However, by considering whales with length and girth measurements, regardless of the presence of an age estimate, it was possible to model cyamid presence with a sample size that was almost four times as large ($n = 497$). This set of models (Table 2) considered the variables LEN, COND, SEX, SCAR, SEAS, and YEAR. We generated these models with the same procedures used for those in Table 1.

All analyses were conducted using R Statistical Software (R Core Team, 2014). Our modeling procedure began by constructing all possible univariate models. We next constructed a "full" model. For the first analysis (Table 1), because LEN and AGE are highly correlated, it was necessary to construct two variants of the "full" model, each including five explanatory variables in common (SEX, SCAR, COND, SEAS, YEAR) and differing only in the inclusion of LEN or AGE. For the second analysis (Table 2) the "full" model included LEN, COND, SEX, SCAR, SEAS, and YEAR. Starting with each variant of the "full" model, we used backward elimination to sequentially drop variables based on the highest non-significant *p*-value until all remaining variables were significant at $\alpha = 0.05$. Finally, for the highest-performing additive effect models, we considered the influence of interaction terms. Model performance was then compared and ranked by corrected Akaike's Information Criterion ($\mathrm{AIC_C}$). We considered the best models to be those with $\Delta\mathrm{AIC_C}$ scores below 2 when compared to the highest-ranking model (Burnham and Anderson, 2002). Among these, it is reasonable to prefer the most parsimonious model that retains all statistically significant effects.

We also ran chi-squared tests to assess whether cyamid presence was associated with sex, the village where each whale was harvested, and the harvest season (i.e., spring or fall). To consider the relationship between body condition and age, we compared the mean age of whales with body condition scores above the 80th percentile to that of whales with body condition scores below the 20th percentile. The mean length and age of whales harvested in the spring vs. fall were compared using *t*-tests. Annual patterns in the percentage of harvested whales with cyamids, as well as the mean annual length of harvested whales, were assessed for temporal autocorrelation using the "acf" function in R.

TABLE 1. Ranked logistic regression models estimating the probability of cyamid presence (n = 126). No models include variables for both AGE and LEN because of collinearity. Models 1–5 are the five highest ranked models to include the variable AGE. Models 6–10 are the five highest ranked models to include the variable LEN. Explanatory variables are shown in the column headers. Colons indicate interactions. Model 1 (bold) is the highest performing model.

			Estimated coefficient								
ID	AIC_C	ΔAIC_C	AGE[1]	LEN[2]	COND	SEX	SCAR	SEAS	YEAR	AGE:YEAR	LEN:YEAR
1	**111.93**	**0.00**	**4.157***	–	–	–	–	–	–	**−0.002***	–
2	112.73	0.81	0.024**	–	–	–	–	–	−0.082*	–	–
3	112.75	0.83	–	–	–	–	–	–	−0.083**	1.2×10^{-5}**	–
4	113.42	1.49	0.030**	–	–	–	−1.013	–	−0.065	–	–
5	113.69	1.77	2.912	–	–	–	–	–	−0.036	−0.001	–
6	119.13	7.20	–	13.057*	–	–	–	–	–	–	0.037*
7	119.46	7.53	–	0.181*	–	–	–	–	−0.080*	–	–
8	119.47	7.54	–	–	–	–	–	–	−0.081*	–	9.1×10^{-5}**
9	121.19	9.26	–	0.177*	0.002	–	–	–	−0.078*	–	–
10	121.26	9.33	–	14.668	–	–	–	–	0.011	–	−0.007

[1] Age estimates from stable isotope analyses, corpora counts, or aspartic acid racemization.

[2] Body length is used as a proxy for age.

** Values significant at ≤ 0.01; * significant at ≤ 0.05.

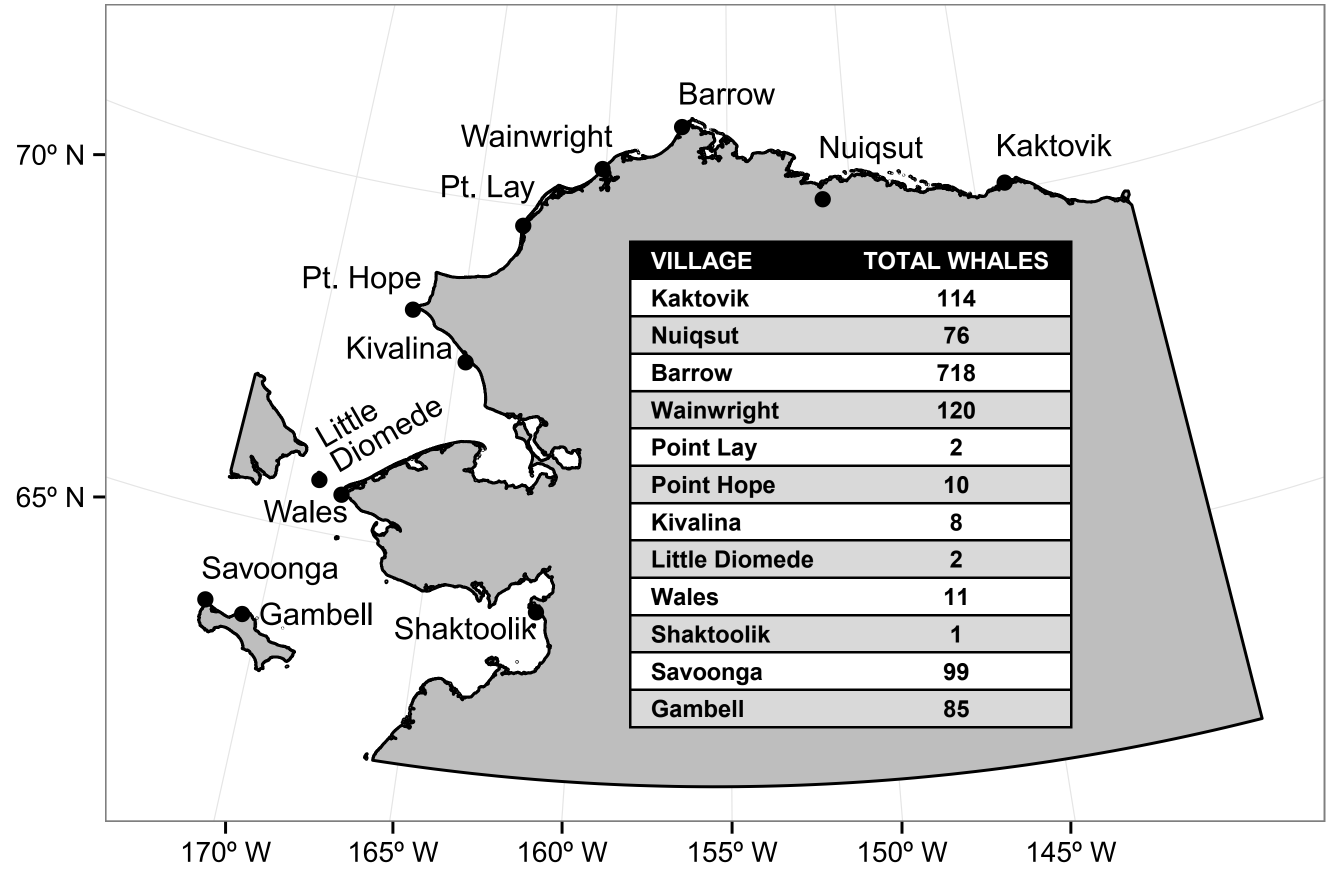
To evaluate the conditions that may be related to cyamid abundance on harvested bowheads, we also qualitatively assessed the written observations from the harvest records in our database. A selection of case studies is provided in Table 3.

RESULTS

We compiled records from 673 harvested bowheads that had been visually examined for ectoparasites from 1973 to 2015. This sample included 341 males (51%) and 332 females (49%). Cyamids were present on a total of 137 (20%) of the whales examined. Of the whales with cyamids, 67% had 1–5 cyamids present (Fig. 2, Class 1), whereas the remaining 33% had 6 or more cyamids (Fig. 2, Classes 2 and 3). There was no significant difference between male and female bowheads in the proportion with cyamids present (Fig. 2; χ^2 = 0.43, df = 1, p = 0.51; n = 666). Although some villages (e.g., Barrow) harvest far more bowheads than others (Fig. 3), there was no significant difference by village in the proportion of examined whales with cyamids present (χ^2 = 6.5, df = 5, p = 0.26, n = 673). Season was significantly related to the proportion of harvested bowheads with cyamids (χ^2 = 4.75, df = 2, p = 0.03, n = 730), with more spring whales having cyamids present. The mean age of whales with a body condition index (i.e., residuals from the "body condition model" described above in the methods) above the 80th percentile was 32 years, and the mean age of whales whose body condition index was below the 20th percentile was 22.8 years. However, a t-test showed no significant difference (t = 0.93, df = 44, p-value = 0.18). A comparison of the mean length and age of harvested bowheads by season shows that spring whales are significantly longer (t = −2.28, df = 660, p = 0.02) and older (t = −2.78, df = 149.9, p = 0.006) than fall whales. We also observed a pattern that might suggest periodicity in the percentage of whales with cyamids over time and in the mean annual length of harvested bowheads (Fig. 4). These patterns were significantly related (R^2 = 0.27, $F_{1,34}$ = 12.7, p = 0.001). Analysis of the annual mean lengths of harvested bowheads showed a significant positive temporal autocorrelation at a three-year time lag. There was no significant autocorrelation in the proportion of whales with cyamids (See Fig. 4).

The models in Table 1 were based on a subset of data in which an age estimate was associated with each examined whale (n = 126). Two sets of models are shown in Table 1: models 1–5 included AGE and excluded LEN, whereas models 6–10 did the opposite. Model 1 was the highest ranked model in the entire set of models in Table 1, and suggests that older whales have a higher probability of cyamid presence than younger whales. Model 1 also included a significant interaction between AGE and YEAR. Models 2–5 all had ΔAIC_C scores below 2, and are therefore comparable in performance to model 1. These top five models all included the variables AGE, YEAR, and/or their interaction. Model 4 was an exception in that it also included the variable SCAR. Models 6–10 in Table 1 utilized LEN as a surrogate for age. While LEN is statistically significant in models where it replaced AGE, altogether, these models have a poorer fit. The effect of SCAR and COND were not found to be important in the highest ranked models, and when present, were not significant. Although the performance of models 6–10 was substantially lower (e.g., model 6 had the lowest ΔAIC_C = 7.20), their structure was similar to the higher-ranking models in their inclusion of an age proxy (LEN), YEAR, and/or their interaction.

The models in Table 2 were based on data from examined whales regardless of whether they had an associated age estimate (n = 497). The top ranked model (model 1) was also the only model with a ΔAIC_C score below 2. This model suggests that a whale's length (LEN) is significantly related to the probability of cyamid presence, but the effect of this variable is complicated by an interaction with the



VILLAGE	TOTAL WHALES
Kaktovik	114
Nuiqsut	76
Barrow	718
Wainwright	120
Point Lay	2
Point Hope	10
Kivalina	8
Little Diomede	2
Wales	11
Shaktoolik	1
Savoonga	99
Gambell	85

FIG. 3. Map of coastal villages in northern and western Alaska where bowhead whales were examined for the presence of cyamids. Inset table indicates the approximate number of whales landed in each village (1973 to 2015).

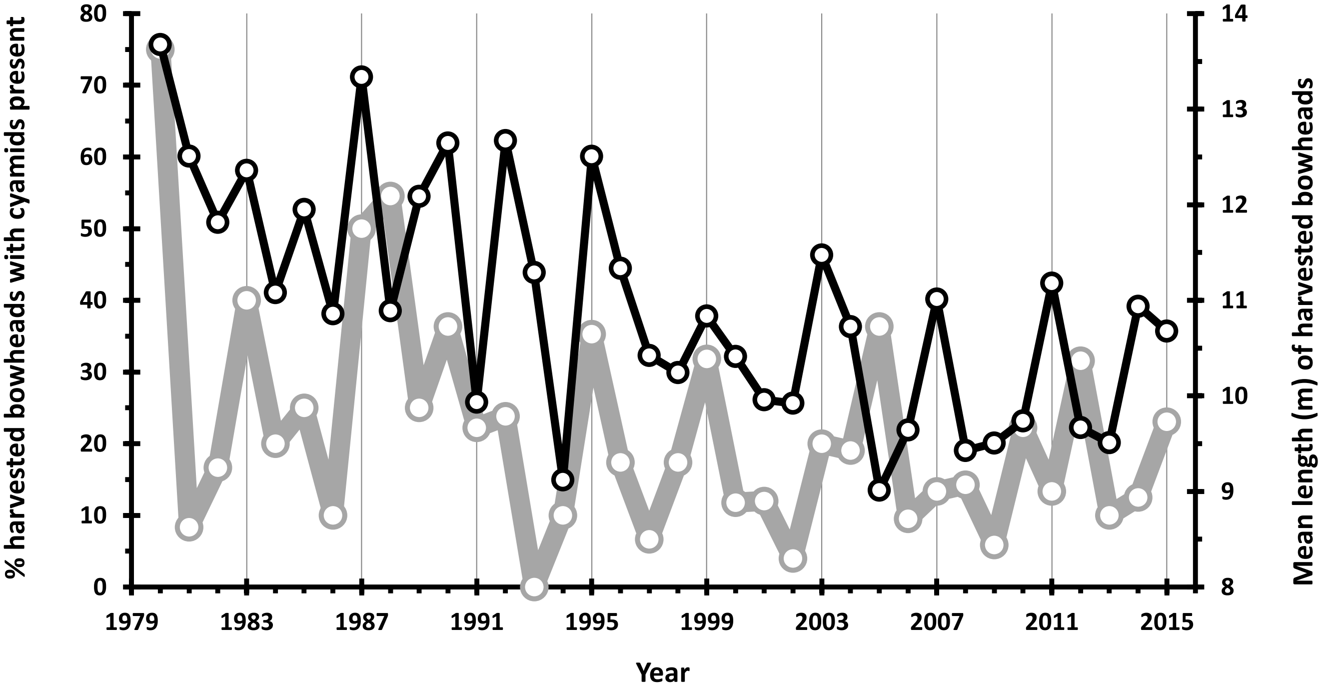


FIG. 4. The dots on the gray line indicate the percentage of harvested whales with cyamids present each year. Those on the black line indicate the mean length (m) of bowheads harvested annually. There was a statistically significant positive temporal autocorrelation of the mean lengths at the three-year time lag, but no significant autocorrelation in the percentage of whales with cyamids. Mean length and the percentage of whales with cyamids were significantly related ($R^2 = 0.27$, $F_{1,34} = 12.7$, $p = 0.001$).

TABLE 2. Ranked logistic regression models estimating the probability of cyamid presence ($n = 497$). These models consider LEN only as an analog for age. Explanatory variables are shown in the column headers. Colons indicate interactions. Model 1 (bold) is the highest performing model.

			Estimated coefficient							
ID	AIC_C	ΔAIC_C	LEN[1]	COND	SEX	SCAR	SEAS	YEAR	LEN:SEAS	COND:SEAS
1	**456.58**	**0.00**	**0.002**	**0.003***	–	–	**−3.143****	–	**0.212***	–
2	459.93	3.35	0.104*	0.004*	–	–	−0.840***	–	–	–
3	460.98	4.40	0.095*	0.004*	–	–	−0.808***	−0.014	–	–
4	461.97	5.39	0.010*	0.004	–	–	−0.084***	–	–	8.5×10^{-5}
5	462.78	6.20	0.104*	0.004*	–	−0.192	−0.831***	−0.013	–	–
6	464.84	8.26	0.104*	0.004*	−0.011	−0.193	−0.831***	−0.013	–	–
7	466.36	9.78	–	–	–	–	−0.774***	–	–	–
8	472.25	15.67	0.102*	–	–	–	–	–	–	–
9	473.13	16.55	–	0.004*	–	–	–	–	–	–
10	473.72	17.14	–	–	–	–	–	−0.026	–	–
11	476.83	20.25	–	–	–	0.223	–	–	–	–
12	477.06	20.48	–	–	0.096	–	–	–	–	–

[1] Length (LEN) used as an index of age.

*** values significant at ≤ 0.001; ** significant at ≤ 0.01; * significant at ≤ 0.05.

season of harvest (SEAS). An analysis of deviance confirms that the model terms for LEN and LEN:SEAS together significantly affect the probability of cyamid presence ($p = 0.005$). Body condition (COND) was also significant and was positively associated with the probability that cyamids were present. Despite their lower performance, models 2–6 (Table 2) were very consistent with model 1 in the use of LEN, COND, and SEAS.

A review of selected case histories provides ancillary information concerning the abundance of cyamids and their complex relationships with bowhead whales. A very old and large bowhead had high cyamid abundance (Table 3, whale 95B09, aged 172). So too did smaller or younger whales (Table 3, whales 14B04, 04B03) and four other sexually immature whales (i.e., < 13.9 m long; see Nerini et al., 1984). Severely physically compromised whales also had high cyamid abundance. Examples include whale 15KK01 (Table 3) which had "about 100" cyamids present; and whale 08G01, which had an apparent chronic injury to its lower spine. This whale was described as having "numerous" cyamids present, "large patches of cyamids on skin of lower body and genital slit," and with a drawing indicating "lots of bugs" posterior to the genital slit. Its skin was reported as "thin," and the skin-blubber boundary was described as "tough." In contrast, whale 99B14, despite a severe line entanglement and poor physical condition, did not have cyamids present. Finally, scarring and skin damage (e.g., 15B20, 15KK01, 92B11, 82WW01, and 76B20) were associated with cyamid presence in 21% ($n = 29$) of examined whales with cyamids.

DISCUSSION

Although cyamids were detected on 20% of harvested bowhead whales, cyamid abundance tended to be very low. For example, 95% of the bowheads examined for cyamids had fewer than 10 individuals present (Fig. 2). Because cyamids have no free-swimming aquatic life-stage (Rowntree, 1983, 1996), parasite transmission among bowheads likely occurs via direct contact. In addition to direct contact between whales, cyamid proliferation also requires successful attachment to the host. Unlike right whales, bowheads have no callosities upon which cyamids can grip. Thus, the presence of damaged skin, which is more likely to occur in older whales, increases the chances that whale-to-whale parasite transmission will be successful. Given the low cyamid prevalence, very low absolute numbers of cyamids, and the absence of callosities, the transmission of cyamids from host to host may be dependent upon the frequency of whale-to-whale interactions and the accumulation of skin damage. Whereas the rate of parasite transmission may be low, the very long lifespan of bowheads (George et al., 1999) makes it plausible that older whales have had more opportunities for the direct transfer of cyamids from another host through increased intraspecific interactions. Moreover, the accumulation of skin damage over time may increase the likelihood of successful parasite transmission by providing the structure to which cyamids can grip. This hypothesis is supported by the preferred models of cyamid presence (Table 1, model 1 and Table 2, model 1), each of which included AGE or LEN (a surrogate for age) as a variable that was positively related to the probability of cyamid presence. The same patterns can be seen in lower performing models, in which AGE and LEN are often significant predictors. These findings are consistent with written comments from our database (Table 3) that relate the spatial use of cyamids to whale epidermal cracks, dents, scars, and injuries, all of which tend to accrue with age.

The positive association of body condition to cyamid presence (Table 2; model 1) was a surprising trend. Presumably, whales in poor body condition swim more slowly, thereby increasing the chances that cyamids can stay

TABLE 3. Selected case studies of bowhead whales that were harvested for subsistence in Alaskan waters. Whales are listed in chronological order beginning with the most recent.

ID	Year	Sex	Length (m)	Age (years)	Cyamid abundance[1]	Comments
15B20	2015	♀	11.9	no age estimate	~ 30	*Barrow*: In a scar and immediately behind the blowhole. Few on mandible.
15KK01	2015	♂	12.8	no age estimate	~ 100	*Kaktovik*: Old bomb recovered from lower back contained in a large abscess capsule. Dozens of cyamids present in “indented” surface area located over abscess capsule. Harpooner said that the whale “dove differently”—likely compromised by chronic injury. Several chronic internal lesions not directly associated with old wound indicated general poor health.
14B04	2014	♂	9.0	no age estimate	> normal	*Barrow*: Recovered dead in the spring lead at Barrow, this whale was struck and lost near Wainwright (~ 190 km southwest of Barrow) and drifted north over a period of about four days. Many cyamids (0.5 cm to 2.0 cm) were seen scattered over the head, body, peduncle, and flukes. Four days is likely insufficient time for the cyamids to have proliferated. However, they may have dispersed across a larger area of the whale’s body because of the reduced flow rate of water.
08G01	2008	♂	14.3	no age estimate	heavily infested	*Gambell*: The attending commissioner from the Alaska Eskimo Whaling Commission related the following observations to G. Sheffield: Numerous large patches of cyamids on skin of lower body and genital slit. Black skin [epidermis] was reported as thin and the *mangtak*[2] tough. Large patches of cyamids on the middle lower portion of the body and genital slit. The hunters noted that the whale had two 5 cm diameter circular “swollen” scars on dorsal region ~ 25–30 cm and 3–4 m anterior to peduncle. When first spotted, the whale was “oblivious to the approach” of the whaling crew, did not swim, and repeatedly dove and surfaced in one place. The whale dove normally when it was struck, taking down two floats. But it “swam at a slow pace.” The description suggests that this bowhead was physically compromised and behaved abnormally.
04B03	2004	♀	9.1	~ 1.0	~ 100	*Barrow*: Whale lice, near the eye and along the mouth ~100 in two groups (at least).
99B14	1999	♂	14.2	64.0	none reported	*Barrow*: Severely entangled in crab lines through the mouth and around the peduncle. Considered to be in poor condition, with severe lacerations and gray skin. The examiners did not report cyamids on this animal. We reexamined all photographs of 99B14 and did not see cyamids.
95B09	1995	♂	17.5	172.0	lots of lice	*Barrow*: Whale 95B09 was the largest male measured at Barrow in our database and also among the oldest whales recorded. It was described as having “lots of lice,” as well as areas of the vertebral column with spondylosis, a condition that has not been described in other BCB bowheads (Paul Nader, pers. comm. 1995).
92B11	1992	♂	15.0	no age estimate	20–30	*Barrow*: Many (20–30) cyamids in old, healed, depressed lesion.
82WW01	1982	♀	17.7	64.9	45–50	*Wainwright*: 15–20 cyamids on eroded area on chin. About 30 larger cyamids in scar.
76B20 around	1976	♀	14.3	39.5	hundreds	*Barrow*: Hundreds of cyamids covering soft-scarred area on back and genital area.

[1] Qualitative assessments of cyamid abundance are based on observations recorded by examiners.

[2] *Mangtak* = Alaskan Yupik term for the epidermis and outer blubber layers of the whale, which are consumed for food.

attached and proliferate, whereas whales in good condition swim faster, making it more difficult for cyamids to stay attached. The relationship between body condition and age may explain this relationship. The positive association between bowhead age and body condition may be the result of lower foraging efficiency in young post-wean individuals with underdeveloped baleen racks. Later in life, when mature whales have a fully formed baleen rack, their body condition scores tend to increase (George, 2009; George et al., 2015). Additionally, if bowhead longevity is a function of body condition, then older whales (i.e., those demonstrated to be more likely to have cyamids) should have higher body condition scores. Our data suggest a weak relationship between age and body condition ($p = 0.18$), with whales in the best condition (body condition index ≥ 80th percentile) about a decade older on average than those in poor condition (body condition index ≤ 20th percentile). Given the growth dynamics of bowheads throughout their maturation process, it seems likely that the association between body condition and cyamid presence may be at least partially associated with the metric that we used to score body condition.

In addition to AGE, the most parsimonious model in Table 1 also included an interaction between AGE and YEAR, which was negatively associated with cyamid presence (Table 1, model 1). The negative slope of YEAR indicates that, with the passage of time, the probability of cyamid presence on harvested bowheads decreases. Given evidence that older bowheads tend to have cyamids present, we speculated that interannual variation in the demographic composition of harvested bowheads may be influential. Indeed, since 1981, there has been a pronounced downward trend in the size of bowheads harvested in the fall ($R^2 = 0.56$, $p = 5.6 \times 10^{-7}$, $n = 33$), but not in the spring ($R^2 = 0.02$, $p = 0.39$, $n = 35$). A mechanistic explanation for these trends likely involves many factors. One consideration is that the current growth rate of the BCB bowhead population (Givens et al., 2016) makes it plausible that their age distribution is shifting over time toward greater numbers of younger whales. Another possibility concerns the implications of a Barrow Whaling Captains' Association decision to open the fall whaling season later in the year, when air temperatures are cooler and smaller migrating bowheads are more abundant, thereby decreasing the chance of harvesting large bowheads. Inter-seasonal variation (SEAS) was significant and included as part of the most parsimonious model in Table 2. The negative relationship between SEAS and cyamid presence indicates that, as the indicator variable increases from 0 (spring) to 1 (fall), the probability of cyamid presence decreases. Because whales caught during the spring hunts are, on average, longer and older, we surmised that the demography of harvested bowheads was also important at the inter-seasonal time scale. This inter-seasonal variability is also likely to be related to many factors, but Iñupiat hunting practices, which differ between the spring and fall, may play a major role. Although some villages tend to harvest larger whales, Barrow, which accounts for a major proportion of our data, tends to harvest smaller bowheads. Given the complexities within this system, including ice dynamics, hunter selectivity, population dynamics, and many other factors, the temporal trends in cyamid presence and whale size should be interpreted with caution until a more detailed analysis can be undertaken.

Ancillary data from our harvest records suggested no apparent trends relating to the abundance of cyamids. Our records did document high cyamid abundance in a bowhead with a spinal abnormality; similarly, it has been reported that humpback whales (*Megaptera novaeangliae*) with severe spinal abnormalities and very poor body condition became heavily infested (Osmond and Kaufman, 1998; Félix et al., 2007). However, few other harvest records indicated elevated abundance of cyamids on bowheads in poor body condition. Moreover, contradicting reports of young, healthy, or small whales with higher cyamid abundance also existed in our records. Other than associations with skin depressions and deep wounds, meaningful patterns associated with cyamid abundance were not apparent from our harvest reports. Typically, most harvested bowheads had few or no cyamids present and were generally in very good condition (Philo et al., 1993; Willetto et al., 2002; Stimmelmayr, 2015). Another consideration is that, given the overall good health of this population, low cyamid abundance per whale, and low cyamid prevalence, successful parasite transmission from host to host may simply be a rare event. Finally, other cyamid species have been shown to have varying levels of cold tolerance (Best, 1979). Perhaps because bowheads are the only mysticete that consistently winters in Arctic waters, this species (*C. ceti*) may be close to its physiological limit and at the edge of its ecological niche.

Because cyamids are difficult to observe and document on free-ranging whales (Rowntree, 1983), few systematic studies of these parasites exist. This investigation suggests that most BCB bowheads do not carry cyamid parasites, and those that do tend to have low cyamid abundance. Our models also indicate that demographic variables (e.g., age and size), body condition, and temporal variables (e.g., year and season of harvest) are significant predictors of cyamid presence. Further investigations are needed in order to disentangle the complexities of ice dynamics, population ecology, and hunting selectivity from the basic ecology of bowheads and their cyamid parasites. For example, subadult (post-weaning) bowhead body condition has been shown to improve as sea ice cover declines (George et al., 2015). Bowhead productivity may increase in response, thereby increasing the chances of cyamid transmission from host to host through density-dependent effects. Further complicating matters are the effects of environmental change within Arctic marine ecosystems, which are anticipated to continue into the future (Moore and Laidre, 2006; Moore et al., 2014). Maritime traffic and industrial development are anticipated to increase in response to declining sea ice cover (Reeves et al., 2012) and will likely lead to higher anthropogenic disturbance levels.

Whether, how, and to what extent bowheads will respond to these and other changing environmental stressors remains to be seen. There is reason to believe that, given the bowhead's longevity and evolutionary strategy of "weathering" environmental variability (Burns, 1993; George et al., 1999), its response(s) to environmental perturbations may not be readily detectable. Cyamid prevalence and abundance appear to be associated with demographic, physiological, or anthropogenic factors, which are also subject to change with the environment. Visual examinations for cyamids are relatively easy to perform on harvested bowheads. We therefore recommend that similar assessments of cyamid prevalence and abundance be conducted on harvested bowheads and other large whale species in Arctic regions to further develop a basic ecological understanding of these species as part of comprehensive Arctic ecosystem assessment programs (Moore et al., 2014).

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