



ORIGINAL ARTICLE

## A whale of an opportunity: Examining the vertical structure of chlorophyll-*a* in high Arctic waters using instrumented marine predators

KRISTIN L. LAIDRE<sup>1,2\*</sup>, MADS PETER HEIDE-JØRGENSEN<sup>2</sup>, MILES L. LOGSDON<sup>3</sup>, LEON DELWICHE<sup>3</sup> & TORKEL GISSEL NIELSEN<sup>4</sup>

<sup>1</sup>Polar Science Center, Applied Physics Laboratory, University of Washington, Seattle, Washington, USA; <sup>2</sup>Greenland Institute of Natural Resources, Nuuk, Greenland; <sup>3</sup>School of Oceanography, University of Washington, Seattle, Washington, USA; <sup>4</sup>National Institute of Aquatic Resources, Section for Oceanecology and Climate, Technical University of Denmark, Charlottenlund, Denmark

### Abstract

Sixty hours of direct measurements of fluorescence were collected from six bowhead whales (*Balaena mysticetus*) instrumented with fluorometers in Greenland in April 2005 and 2006. The data were used to (1) characterize the three-dimensional spatial pattern of chlorophyll-*a* (*Chl-a*) in the water column, (2) to examine the relationships between whale foraging areas and productive zones, and (3) to examine the correlation between whale-derived *in situ* values of *Chl-a* and those from concurrent satellite images using the NASA MODIS (Moderate Resolution Imaging Spectroradiometer) EOS-AQUA satellite (MOD21, SeaWiifs analogue OC3M and SST MOD37). Bowhead whales traversed 1600 km<sup>2</sup>, providing information on diving, *Chl-a* structure and temperature profiles to depths below 200 m. Feeding dives frequently passed through surface waters (>50 m) and targeted depths close to the bottom, and whales did not always target patches of high concentrations of *Chl-a* in the upper 50 m. Five satellite images were available within the periods whales carried fluorometers. Whales traversed 91 pixels collecting on average 761 s (SD 826) of *Chl-a* samples per pixel (0–136 m). The depth of the *Chl-a* maximum ranged widely, from 1 to 66 m. Estimates of *Chl-a* made from the water-leaving radiance measurements using the OC3M algorithm were highly skewed with most samples estimated as <1 mg m<sup>-3</sup> *Chl-a*, while data collected from whales had a broad distribution with *Chl-a* reaching >9 mg m<sup>-3</sup>. The correlation between the satellite-derived and whale-derived *Chl-a* maxima was poor, a linear fit explained only 10% of the variance.

**Key words:** Bowhead whale, chlorophyll-*a*, fluorometer, MODIS, remote sensing

### Introduction

The spring phytoplankton bloom constitutes the single most important biological event in the marine Arctic ecosystem, with cascading impacts that reach the top of the food chain (Arrigo & Van Dijken 2003; Heide-Jørgensen & Laidre 2004). With the advent of advanced ocean colour satellite instruments, there has been an explosion of the use of these data to estimate biological, biogeochemical, and physical parameters such as the surface concentration of chlorophyll-*a* (*Chl-a*) (Carder et al. 1999; Sathyendranath 2000; Miroslaw & Stramski

2004; Heide-Jørgensen et al. 2007a). This is especially true in remote localities such as polar environments, where year-round observations are difficult, effort is low, and ice-associated primary production often cannot be monitored with traditional methods (Dierssen & Smith 2000; Burenkov et al. 2001). While space-based remote sensing techniques allow for the characterization of regional dynamics of phytoplankton abundance over broad scales of space and time by relying on measurements of water-leaving radiance (estimating *Chl-a* as the total return of reflectance through the optical depth of the water

\*Correspondence: K. L. Laidre, Polar Science Center, Applied Physics Laboratory, University of Washington, 1013 NE 40<sup>th</sup> Street, Seattle, WA 98105, USA. E-mail: klaidre@apl.washington.edu

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column) (Morel & Maritorena 2001; Clarke et al. 2006), little insight is gained concerning the three-dimensional dynamics of the environment and vertical structure of *Chl-a* in the water column.

Disko Bay, located between sub-Arctic waters of southwest Greenland and the high Arctic waters of Baffin Bay, is among the most productive springtime coastal sites in West Greenland (Levinsen et al. 2000; Madsen et al. 2001, 2008a, 2008b; Heide-Jørgensen & Laidre 2004; Heide-Jørgensen et al. 2007a) (Figure 1). During winter, the water column is well mixed and

the lack of light and the seasonal ice coverage inhibits net growth of phytoplankton. After sea ice break-up solar radiation and melt water warm and dilute the surface layer, trapping nutrients in a stable surface layer that stimulates the phytoplankton bloom. When initiated, the exponential growth of phytoplankton quickly depletes the surface layer of nutrients (Nielsen & Hansen 1995, 1999; Pedersen et al. 2006) and after the bloom sediments to the bottom.

An aggregation of approximately 1200 bowhead whales (*Balaena mysticetus* Linnaeus, 1758) that are

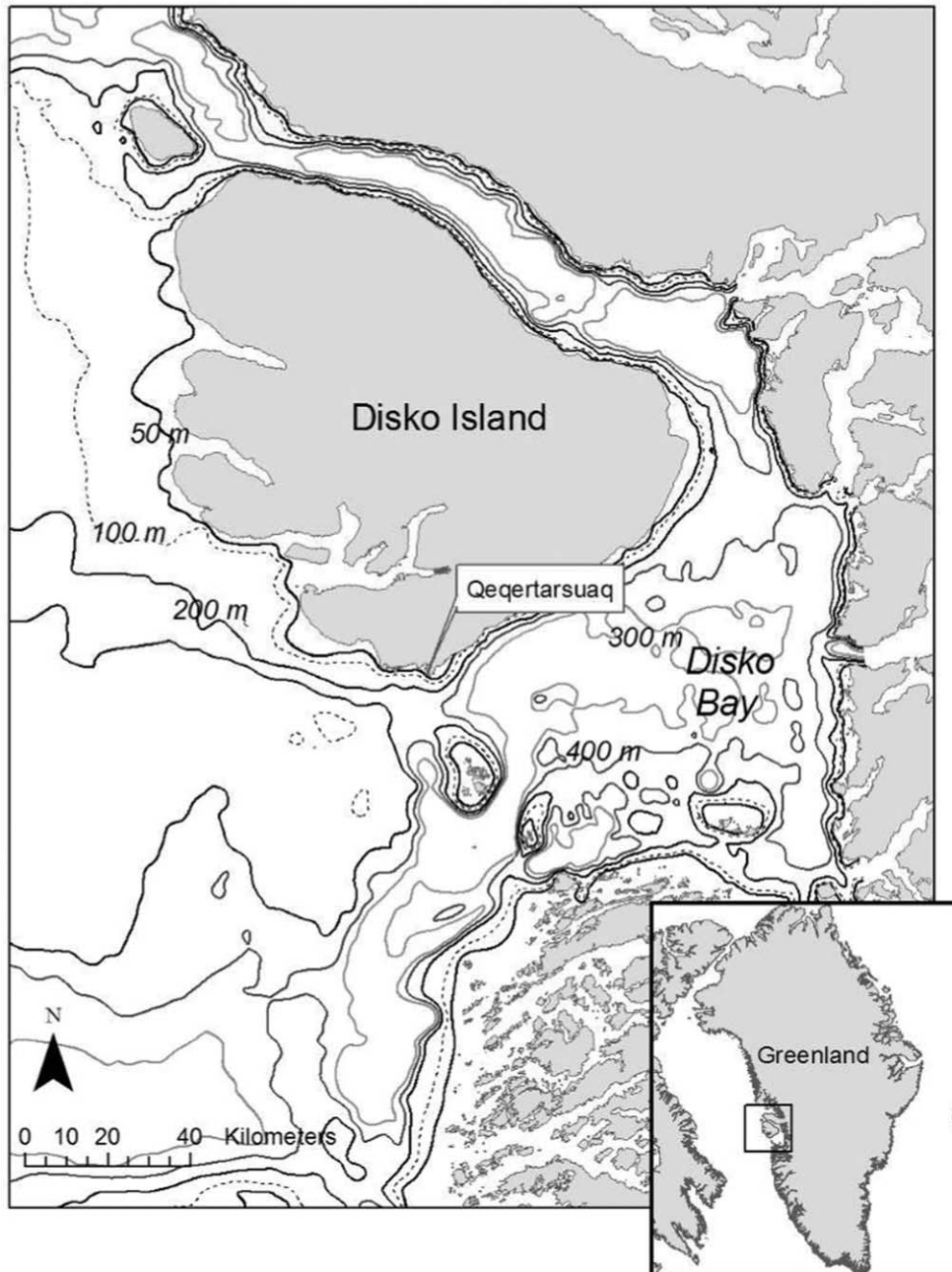


Figure 1. Study area in West Greenland together with bathymetric structure of the sea floor in Disko Bay. All data were collected near the town of Qeqertarsuaq <70 km from the coastline.

part of a population extending between eastern Canada and West Greenland (Heide-Jørgensen et al. 2007b) arrive in Disko Bay in February and remain in the area until May, where they feed intensively on secondary producers (i.e. amphipods and copepods *Calanus glacialis*, *C. hyperboreus*, and *C. finmarchicus*). These whales traverse optically complex coastal waters at the peak primary production bloom in the Arctic and tagging methods are well developed (i.e. Heide-Jørgensen et al. 2003, 2006; Laidre et al. 2007). Therefore they offer an ideal opportunity to serve as oceanographic sampling platforms in high-latitude waters.

In this study, we instrumented bowhead whales with fluorometers (archival dive-temperature-fluorescence) to sample the water column in Disko Bay. These data were used to (1) examine bowhead whale diving patterns relative to the patterns of *Chl-a* and temperature in the Disko Bay water column in spring, and (2) derive and interpolate *in situ* water column fluorescence estimates of *Chl-a* corresponding to a satellite-derived surface transect of the whales' movement. We present a description of the spatial variation in the vertical structure of *Chl-a* in Disko Bay along with corresponding estimates of *Chl-a* derived from the MODIS (Moderate Resolution Imaging Spectroradiometer) satellite-derived global algorithm and variation in wavelength specific band ratios. This study demonstrates the utility of marine top predators as autonomous physical and biological samplers for extending the interpretation of remotely sensed data into the vertical structure of the water column. This is particularly useful in the high-latitude polar ecosystem, where seasonally ice-covered waters limit ship access to open water periods and make logistics difficult and costly.

## Materials and methods

### *Bowhead whale instrumentation and data collection*

Bowhead whales were instrumented with WetLabs (Corvallis, Oregon) fluorometers (Fluorescence Nephelometric Turbidity Unit, FLNTUB) in Disko Bay, West Greenland in April 2005 and 2006 (Figure 1). Fluorometers were mounted on a cylindrical float (28 × 8 cm) which included a VHF transmitter (Telonics, Mesa, Arizona) and an ARGOS satellite-linked tag (Wildlife Computers SPOT4, Redmond, Washington) for instrument recovery (Figure 2). Floats were attached to the whales using stainless steel harpoon tips (25 × 100 mm). All tags were deployed using an 8-m long fibreglass pole from a small open boat approximately 4–5 m away from the whale (cf. Heide-Jørgensen et al. 2003, 2006). During pursuit, the float tags



Figure 2. Instrument attached to bowhead whales with 1.5-m long wire and small harpoon head imbedded in the blubber layer. A WetLabs FLNTUB fluorometer was fixed to a float using hose clamps. Flotation (orange float) kept the tag at the surface for instrument recovery after the package was released from the whale, and the tag was relocated using a satellite (top left of orange float) and VHF transmitter (top right of orange float). The package corroded off the whale after 24–48 h using a magnesium bolt. Photo by M. P. Heide-Jørgensen.

were held in a PVC housing mounted to the pole. Once the harpoon tip was imbedded in the blubber of the whale, the float was released from the housing. The float was tethered to a 1.5-m long stainless steel wire with a corrosive magnesium bolt which released the float from the whale after a set period of time (generally 3–4 days; however, some floats stayed on longer). Floats were recovered using real-time ARGOS satellite locations (Harris et al. 1990) and a fine-scale VHF search conducted using directional antennas mounted on a 50-foot boat (*r/v* Porsild, Arctic station, Copenhagen University) or from a small boat. The FLNTUBs sampled fluorescence, pressure (resolution 1 m), and temperature (resolution 0.001 °C) every second at a resolution of 1 m.

After tags were retrieved, data were downloaded to a PC for processing and analysis. Voltage readings from the FLNTUBs were downloaded and converted to *Chl-a* using standard equations developed by WetLabs (ECOView software). These *Chl-a* values were calibrated against *in situ* *Chl-a* measurements from the waters of Disko Bay (see Heide-Jørgensen et al. 2007). All samples where depth was 0 m were removed from the data sets together with values of *Chl-a* that were less than or equal to 0 mg m<sup>-3</sup>. Satellite positions were received when the whales surfaced to breathe; and a linear interpolation between each known whale location was used to create a simulated whale location every second through horizontal *x-y* space for the entire tracking period. ARGOS location qualities of LC-0 or better were flagged and used as good quality. We assumed a constant swim speed during the period of time the tag was on the whale, a reasonable assumption based

on behavioural data collected from bowheads in the past (Heide-Jørgensen et al. 2003).

*Chl-a* profiles were created using the 'griddata' function in MathWorks MATLAB software. The interpolated length scale (cell size) was determined based on visual inspection of the dive track and total distance traversed by the whale. The distance between each surface interval (i.e. ARGOS position received when the whale surfaced to breathe) was used as the basis for the horizontal cell size and vertical cell size was 1 m (same as that of the pressure transducer). A linear interpolation method was used to estimate the *Chl-a* of each cell based on a Delaunay triangulation.

#### Satellite data product

Data were obtained from the NASA Moderate Resolution Imaging Spectroradiometer (MODIS: EOS AQUA satellite). Daily data products used included *Chl-a* (MOD21, SeaWifs analogue OC3M) and 4 µm sea-surface temperature (MOD37, SST). These atmospherically corrected and georegistered products have a spatial resolution of 1 km (Gordon & Wang 1994; O'Reilly et al. 2000; Martin 2004).

The data work flow included the use of Windows Image Manager WimSoft® for importing and spatial sub-setting of MODIS data prior to construction of a geodatabase in the ESRI ArcGIS® grid format. Cell values were extracted from each image corresponding to the same day and location as the *in situ Chl-a* sampled from the bowhead whales. Thus, *in situ* measurements of *Chl-a* concentration were spatially comparable with daily remotely-sensed estimates of water-leaving radiance and *Chl-a* for all cloud-free days.

#### Spatial and statistical analysis

All pixels within each daily MODIS image were assigned a unique cell ID value. Geographic positions along the whale track together with associated *Chl-a*, temperature, and band ratios were associated to MODIS *Chl-a* and temperature values in each individual cell using ArcGIS 9 (Hawth's Tools extension, www.spatial ecology.com). Summary statistics of whale fluorometric data were obtained in

each pixel. The pixel was considered to be the smallest sampling unit and standardized the analysis. We calculated whale-derived (WD) *Chl-a* maximum in each pixel (from the fluorometer), associated depth and temperature, and mean WD *Chl-a* through all depths. Pixel-based summaries of data collected from instrumented whales were correlated with summaries of satellite-derived (SD) *Chl-a* data in each pixel. The distribution of *Chl-a* values along the whales' trackline was characterized by both mean and maximum WD *Chl-a*. WD sea temperatures at 1 and 2 m depths were correlated to satellite-derived SST. Statistics used included linear models, KS-tests, and ANOVAs using  $p < 0.05$  as the level of significance.

## Results

#### Bowhead whale data

Six bowhead whales were instrumented with fluorometers in April 2005 ( $n = 5$ ) and 2006 ( $n = 1$ ) along the south coast of Disko Island (Figure 1, Table I). Dates of deployment spanned 22 April to 1 May (Laidre et al. 2007). Approximately 60 h of measurements (every second) were collected from the whales. Spatial coverage of Disko Bay was focused between the coastline and 50 km offshore. Whales did not range farther than 100 km off the coast while instrumented. Whales travelled in a number of different vectors from their tagging sites and covered approximately 200 km (straight line distance) along the south coast of Disko Island (Figure 3).

Diving behaviour was variable, with mean dive depths ranging between 53 m (SD 35) and 94 m (SD 124). The maximum depth reached by an instrumented whale was 380 m (whale 02-05), which was deeper than maximum depths for other whales (ranging between 110 and 234 m). Most whales' dives were focused in the upper 200 m of the water column, with surfacing intervals 7–9 min apart. Mean dive durations ranged from 3 min (SD 2) to 13 min (SD 11) and the maximum dive duration in this study was 41 min. In general, whales spent the largest proportion of their time in the

Table I. Bowhead whales instrumented with fluorometers in Disko Bay, West Greenland between April and May 2005–2006. Maximum *Chl-a* encountered by each whale over the tracking period is based on mean *Chl-a* values for each integer depth (in metres).

Whale ID	Date deployed	Time deployed	Deployment duration	Sex and size of whale	<i>Chl-a</i> max (SD) (mg m <sup>-3</sup> )	Depth at <i>Chl-a</i> max (m)
01-05	22/4/05	13:56	6 h, 44 min	M, 15–18 m	4.63 (0.69)	12
02-05	26/4/05	17:12	8 h, 15 min	F, 15–18 m	21.22 (2.49)	5
03-05	28/4/05	15:30	5 h, 28 min	U, 15–18 m	7.84 (2.22)	8
04-05	3/5/05	11:30	13 h, 50 min	F, 12–15 m	6.12 (1.60)	8
05-05	1/5/05	18:11	7 h, 57 min	F, 12–15 m	6.06 (1.22)	6
01-06	1/5/06	18:55	17 h, 5 min	U, 15 m	2.87 (0.22)	13

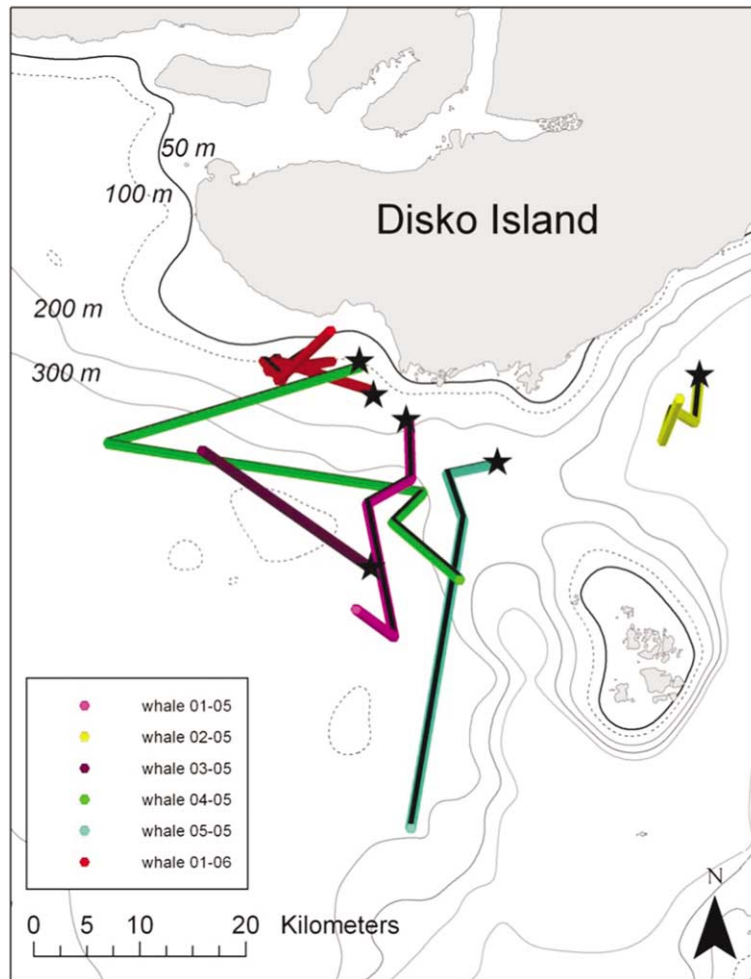


Figure 3. Spatial coverage of Disko Bay by whales instrumented with fluorimeters in 2005 and 2006. Black stars show the start location or tagging site. Depth contours are shown for reference. All good-quality ARGOS locations were used to reconstruct the whales' tracks, representing a minimum distance travelled.

upper 10 m of the water column (Table II) due to surfacing behaviour. Dives did not always target the most productive strata of the water column (as

indicated by the patches of high *Chl-a*) and instead whales frequently dove to the bottom, where *Chl-a* levels were low. The dive profiles did, however, allow

Table II. Fraction of time spent in 10-m bins of the water column (between 0 and 100 m) for each instrumented whale. Time spent at 0 m (when the whale was at the surface and the fluorimeter was exposed to air) was not included in the analysis, thus fractions are representative of the sub-surface use of the water column.

	Whale ID					
	01-05	02-05	03-05	04-05	05-05	01-06
1–10 m	0.44	0.32	0.12	0.20	0.24	0.30
11–20 m	0.30	0.28	0.06	0.11	0.17	0.05
21–30 m	0.09	0.13	0.08	0.09	0.13	0.05
31–40 m	0.04	0.13	0.15	0.10	0.13	0.07
41–50 m	0.01	0.05	0.20	0.10	0.10	0.07
51–60 m	0.01	0.03	0.15	0.14	0.06	0.07
61–70 m	0.01	0.01	0.15	0.10	0.05	0.08
71–80 m	0.01	0.01	0.05	0.05	0.04	0.15
81–90 m	0.01	0.01	0.02	0.05	0.03	0.09
91–100 m	0.01	0.01	0.01	0.03	0.02	0.04
>100 m	0.07	0.04	0	0.03	0.03	0.04

for a robust characterization of the *Chl-a* and temperature composition in the waters traversed by the whales from the surface down to at least 200 m.

In 2005, 42.5 h of *Chl-a* and temperature data were collected from whale tags at depths between

0 and 380 m. In 2006, 0.6 h were sampled between depths of 0 and 111 m. WD *Chl-a* values ranged between 0.01 and 33 mg m<sup>-3</sup> (Figure 4a–f) and all whales dove well beneath the optical depth used for satellite-based observations. The establishment,

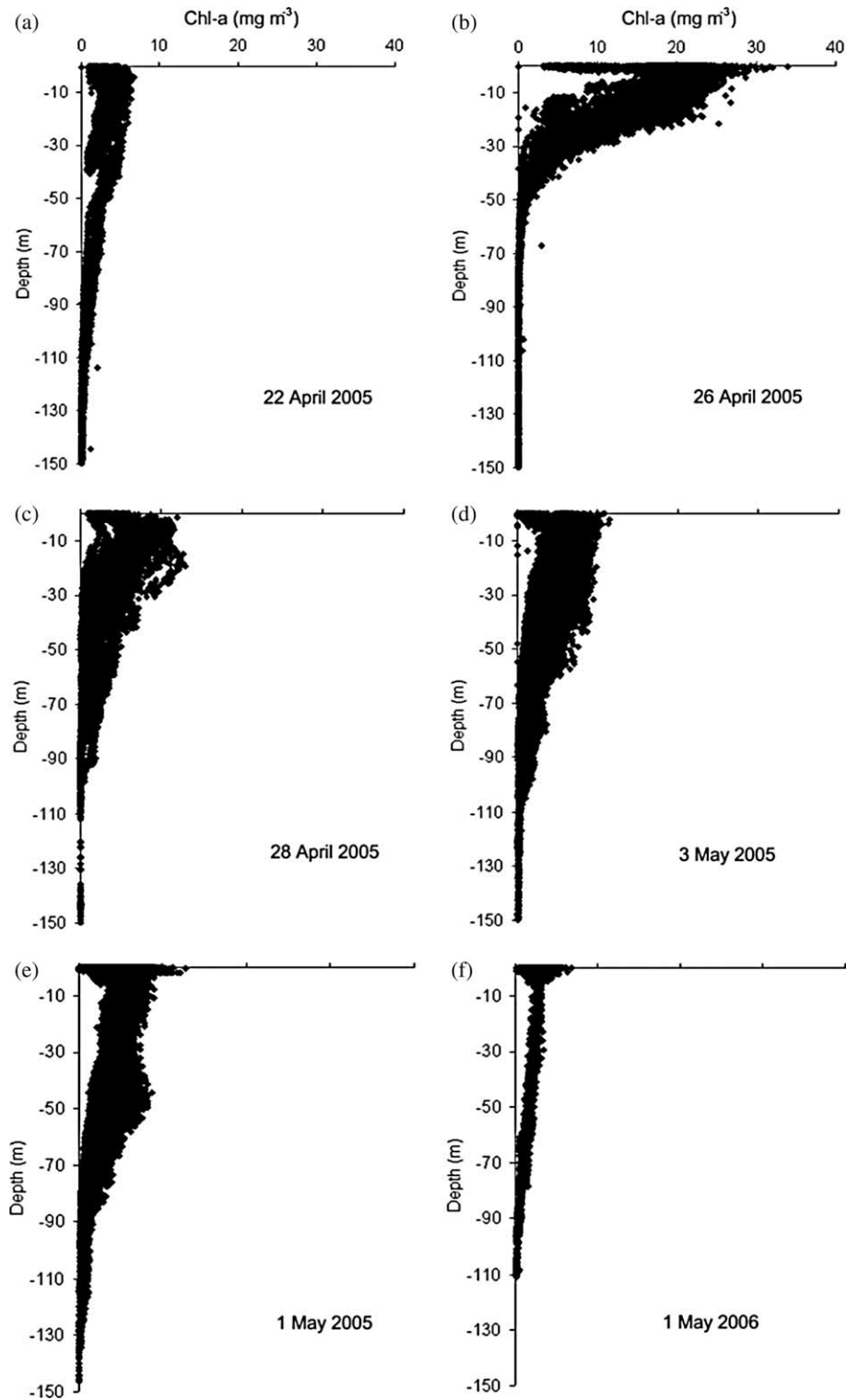


Figure 4a–f. *Chl-a* and depth profiles from six whales instrumented in Disko Bay, West Greenland in April and May 2005 and 2006. Note the succession of the phytoplankton bloom is apparent.



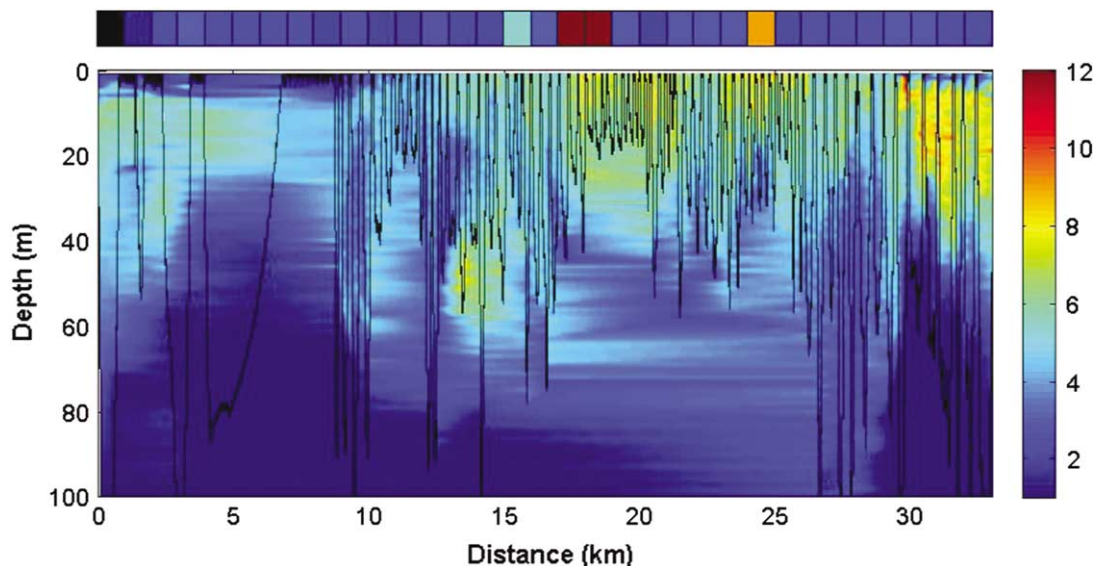


Figure 5. Whale 05-05 *Chl-a* interpolation in  $\text{mg m}^{-3}$  (colour panel), dive profile (black lines), and corresponding MODIS OC3M pixel values along the trackline (top squares correspond to 1 km cells). Whale was tagged and tracked on 1 May 2005, for trackline see Figure 3. Both water column and satellite *Chl-a* are referenced to the same colour scale. The  $x$ -axis is the total number of kilometres (straight line distance) covered by the instrumented whale.

build-up and sedimentation of the phytoplankton bloom over a 1.5-week period can be seen from the series of WD *Chl-a* values between 22 April and early May. Values increased from  $<5$  to  $35 \text{ mg m}^{-3}$ , one order or magnitude in one week (Figure 4a–f). The overall succession and depth distribution of the phytoplankton recorded by the whale tags is comparable to the *Chl-a* depth profiles recorded simultaneously at a permanent sampling station 1 nm south of Qeqertarsuaq (Madsen et al. 2008b).

Mean values of WD *Chl-a*, when binned by 1 m increments, ranged between  $2.9$  (SD  $0.2$ )  $\text{mg m}^{-3}$  and  $21.2$  (SD  $2.5$ )  $\text{mg m}^{-3}$ . Temperatures were negative throughout the first 80–100 m below the surface and increased to positive values below 100 m. Interpolation of WD *Chl-a* demonstrated horizontally patchy and variable *Chl-a* concentrations along each whale's trackline. WD *Chl-a* maximum values occurred at a wide range of depths, between 1 and 66 m (Table I).

#### Satellite data

Five MODIS images were available within the time periods the whales carried fluorometers in Disko Bay. Tagged whales traversed a total of 91 individual pixels where estimates of *Chl-a* and water-leaving radiance by wavelength were available. The number of pixels in each MODIS image that spatially coincided with whale movements ranged from 5 to 44 (mean 18, SD 16). In each pixel, on average, 761 (SD 826) measurements were sampled by whales at a range of depths (1–136 m). The WD *Chl-a* maximum in each pixel ranged widely ( $0.9$ – $12.7$

$\text{mg m}^{-3}$ ) and occurred over a range of depths (1 and 66 m). Of the *Chl-a* maxima obtained in each pixel, 71% occurred at depths above 10 m, 20% occurred at depths between 11 and 30 m, and 1% occurred below 30 m. The temperature value at the WD *Chl-a* maximum ranged from  $-0.5$  to  $-1.6^\circ\text{C}$ .

#### Comparison between data sets for *Chl-a*

Interpolation of *Chl-a* along whale tracklines demonstrated considerable variability in the depth and extent of *Chl-a* patches (Figure 5). This was apparent in all profiles created from instrumented whales. Large patches of high concentration of *Chl-a* were detected at a range of depths down to about 50 m. The correlation of these data with corresponding pixel values (Figure 5, top row of boxes) estimated by the MODIS OC3M was poor and not significant. Low values of SD *Chl-a* were found along all whale tracklines, and when SD values were high, they infrequently corresponded with high levels of WD *Chl-a*, even at depths  $>10$  m. The correlation between the MODIS OC3M algorithm *Chl-a* values and WD *Chl-a* max was also poor. A linear fit to the data explained 10% of the variance and MODIS estimated on the order of 30% of the *Chl-a* in the water column ( $y = 0.3x + 6.2$ ,  $R^2 = 0.11$ ).

The frequency distribution of WD and SD *Chl-a* values in each of the 91 pixels was significantly different ( $p < 0.05$ ) (Figure 6). The distribution of values obtained from the MODIS OC3M algorithm (mean  $1.9 \text{ mg m}^{-3}$ , SD  $3.4$ ) was highly skewed to the left with most values estimated as  $<1 \text{ mg m}^{-3}$ .

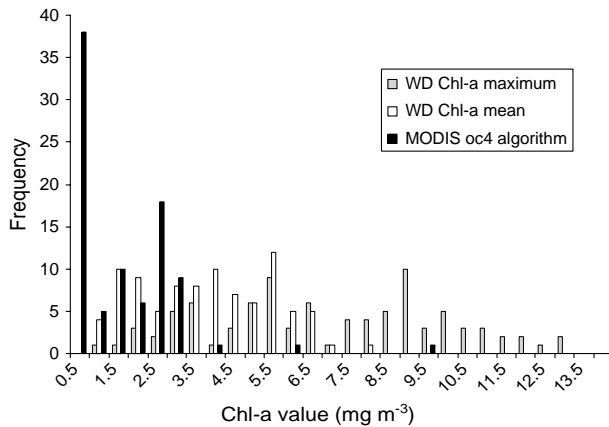


Figure 6. Distribution of *Chl-a* values obtained from three different sources in a given pixel in the study: WD *Chl-a* maximum, WD *Chl-a* mean and MODIS OC3M global algorithm value.

Low *Chl-a* concentrations were often predicted by the satellite (range 0.2–22.3 mg m<sup>-3</sup>). Conversely, both the mean WD *Chl-a* (mean 3.6 mg m<sup>-3</sup>, SD 1.7, range 0.6–7.9) and maximum WD *Chl-a* (mean 6.7 mg m<sup>-3</sup>, SD 3.0, range 0.9–12.7) had broad distributions with ranges outside of those suggested by SD measurements (Figure 6). There was no obvious *Chl-a* peak within either WD mean or WD maximum *Chl-a* distribution. With the exception of extremely low values, the WD mean distribution was in slightly better agreement with the satellite estimates (Figure 6). The interpolated profile of whale WD temperature suggests that the warmer temperatures at deeper depths (+ deg C, part of the West Greenland current) could be detected beyond depths of 100 m (Figure 7). The linear correlation between WD SST (1 m depth) and MODIS SST

was good (Figure 8); however, WD values were almost 60% below those estimated by MODIS ( $y = 0.58x - 0.61$ ,  $R^2 = 0.30$ ).

## Discussion

Previous studies on the foraging behaviour of bowhead whales in Disko Bay have documented high variability in depths of foraging dives (Laidre et al. 2007), with whales apparently foraging between 80 and 200 m. In early spring feeding studies, these dives frequently corresponded to depths close to the complex bottom topography along the slope of Disko Bay. This may be due to bowhead whales in Disko Bay targeting pre-ascension stage copepods, which occur in high density patches near the bottom in early spring (Madsen et al. 2001).

In this study, bowhead whale dives did not always target the most productive areas of the water column, as measured by the relationship between terminal depth and high concentrations of *Chl-a*. Instead, and contrary to our expectation, whales often traversed these productive areas and dives terminated in areas with relatively low *Chl-a* concentrations when compared to the upper 50 m of the water column. The upper 50 m is known to be an important area for copepods, which ascend from depth in spring and feed on the phytoplankton (*Chl-a*) at the surface. However, in the case of bowhead whales in Disko Bay, it may be energetically more efficient to search for high density copepod patches near the bottom before they ascend (Laidre et al. 2007). Thus the primary production levels in the upper 50 m may not have much influence on where whales spend their time, at least in early spring before the copepod ascension. It is possible that after

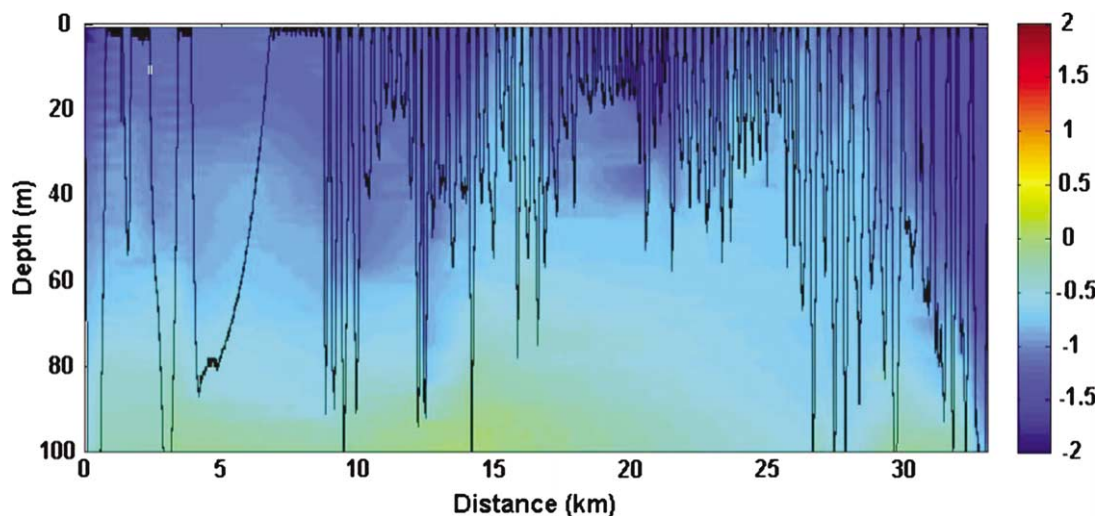


Figure 7. Whale 05-05 temperature interpolation (°C) (colour panel) and dive profile (black lines). Whale was tagged and tracked on 1 May 2005, for trackline see Figure 3. The x-axis is the total number of kilometres (straight line distance) covered by the instrumented whale.



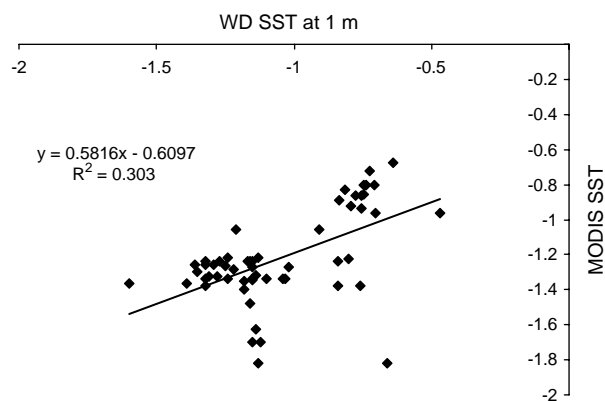


Figure 8. Relationship between the estimates of WD sea-surface temperature and MODIS sea-surface temperature product (MOD37). Temperatures are in degrees Celsius.

copepods ascend, the whales' strategy changes and they target surface waters and have a closer association with high levels of *Chl-a*. We infer that whales forage at the terminal points of their dives, although obtaining specific data to demonstrate that this is the case is difficult.

The synoptic spatially continuous portal of ocean primary production supplied by satellite-based ocean colour instruments offers coverage that is impossible to achieve with traditional ship-based or moored instrumentation. These techniques allow for the characterization of regional dynamics of phytoplankton abundance over broad scales of space and time, especially in remote areas where there is considerable interest in mapping and monitoring changes. However, given that water-leaving radiance measurements only estimate *Chl-a* as the total return of reflectance through the optical depth of the water column (Morel & Maritorena 2001; Clarke et al. 2006), little insight is gained concerning the three-dimensional structure of *Chl-a*, especially below the optical depth.

Several studies have demonstrated the utility of marine mammals as adaptive samplers for areas of high oceanographic interest (Boehlert et al. 2001; Boyd et al. 2001; Lydersen et al. 2002; Biuw et al. 2007; Boehme et al. 2008a, 2008b; Charrassin et al. 2008; Costa et al. 2008; Teo et al. 2009), and this study expands on previous work by integrating and comparing autonomous *in situ* sampling with satellite-based observations. Few *in situ* studies are available to corroborate satellite-derived coastal measurements of production in the Arctic, where storms, variable wind-induced mixing, and coastal upwelling increase the complexity of in-water optical properties. The instrumentation of bowhead whales to concurrently sample the Arctic environment provided a useful comparison to the global satellite data algorithms frequently used in high-latitude waters. At the same time, this approach offered previously unob-

tainable three-dimensional data along unique transects on coastal *Chl-a* structure in Disko Bay.

The MODIS OC3M satellite-derived *Chl-a* estimates correlated poorly to *in situ* WD *Chl-a* values and estimated <30% of the actual *Chl-a* in the water. This algorithm measured low concentrations of *Chl-a* despite much higher *Chl-a* levels in the water column even at shallow depths (Figures 5 and 6). This finding was not surprising given similar poor results in other polar seas (Dierssen & Smith 2000; Burenkov et al. 2001). Global calibrations of geophysical algorithms tend to be poorly correlated with actual values at high latitudes (Bailey & Werdel 2006; Heide-Jørgensen et al. 2007) despite proving robust in more temperate waters (Gohin et al. 2008). Global algorithms are designed for less optically complex open ocean environments (Carder et al. 1999; Sathyendranath 2000; Miroslaw & Stramski 2004; Heide-Jørgensen et al. 2007). The coastal waters of the high Arctic experience rapid changes in phytoplankton abundance and concentration of dissolved organic matter, and it is highly unlikely that the spatial and temporal progression of these variables is correctly captured by satellite observations.

It is important to note that not all potential maximum depths in a given pixel were sampled by diving whales. Thus the whale-derived *Chl-a* maximum is indicative of the potential maximum value of *Chl-a* at a given location, not the absolute maximum. Regardless, the WD *Chl-a* measurements revealed far more structure below the water surface and higher *Chl-a* concentrations than reported based on satellite data. Furthermore, the spatial precision of the analysis was limited by the degree of error around the good-quality Argos locations. In the future, similar studies using cetaceans would benefit from the GPS technologies presently being developed and tested for marine mammals.

The use of both *in situ* fluorometers and satellite water-leaving radiance algorithms for estimating *Chl-a* involve the fluorescence and absorption of photons of light by phytoplankton. These measurable processes vary predictably with the concentration of *Chl-a*. However, the mechanisms behind the derivation of *Chl-a* estimates differ methodologically. Satellite-based water-leaving radiance algorithms use the signal at two or more bands in the electromagnetic spectrum of light. The higher the *Chl-a* concentration the more light is absorbed, and therefore the less light is received at the satellite sensor. Conversely, fluorometers deployed in the water column rely upon the fluorescence properties of *Chl-a* absorbing a photon at shortwave high-energy light and then re-emitting it at a longer wavelength of light with lower energy to provide an *in situ* estimate of concentration of phytoplankton cells.

The data collected from instrumented whales are based solely on an artificial source of light and are thus useful in characterizing properties of the water which are independent of the environmental setting in which it is found. Conversely, the data collected by the satellite are based on solar or natural light as well as backscattering through the atmosphere and water column, and document the cumulative effects of numerous interactions with the environment. This distinction recognizes that optical properties through the depth of the water column are structurally complex. When limited to two-dimensional surface observations, the interpretation of structure often fails.

Satellite-based observations from the NASA Moderate Resolution Imaging Spectroradiometer (MODIS: EOS AQUA) satellite capture the spatial variability of the normalized water-leaving radiance at a single time stamp over a broad spatial extent (resolution of 1 km). Bowhead whales equipped with fluorometers in coastal waters travel continuously in space and time and dive every 5–7 min. Each approach offers a unique perspective of characterizing the spatial and temporal variation of the three-dimensional dynamics of the marine environment.

Top predators offer a platform for sampling the marine environment in areas that cannot be adequately or reliably obtained with standard sampling techniques (Reid & Croxall 2000; Boyd & Murray 2001; Charrassin et al. 2002, 2004; Fraser & Hofmann 2003; Nicholls et al. 2008). Consequently, biological autonomous sampling systems have immense potential to contribute to oceanographic and satellite-based data in a cost-effective manner (Boehlert et al. 2001; Boyd et al. 2001; Lydersen et al. 2002, 2004; Biuw et al. 2007; Boehme et al. 2008a, 2008b; Charrassin et al. 2008; Costa et al. 2008). In this paper we also examined whether marine predators could be used to collect and provide robust data to examine the spatial distribution of chlorophyll-*a* in the high Arctic. This was combined with optical properties of water-leaving radiance from space-based observations and used to extend the three-dimensional picture of primary production in a coastal zone. This study demonstrates that both the estimates of *Chl-a* derived by global ocean colour algorithms as well as the spatial variation of those estimates relative to *in situ* fluorescence measurements are not well correlated. Thus, innovative methods for collecting detailed *in situ* data are necessary for both calibrating and validating data collected from satellites.

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