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Diel changes in acoustic and catch estimates of krill biomass

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Abstract:

Krill-biomass estimates can be compromised by diel variabilities in acoustic backscatter and the catch efficiencies of various nets. This paper describes an effort to quantify these variabilities at fine temporal and spatial scales during a three-day experiment at a fixed location, using high-resolution, stratified Bioness samples and echo-integration, and assuming a fixed distribution of krill orientations. Night-time catches in the krill scattering layer (SL) were 15 times the acoustic estimates. The situation was reversed during daytime, when the acoustic estimates in the SL were 5 times larger than the catches. This collectively resulted in a ±10-dB gradual diel cycle in the difference of vertically integrated biomass from both sampling methods. Use of a strobe light on the Bioness reduced avoidance of the net by krill and significantly increased (x10) daytime catches in the SL, but had no significant effect on night-time catches. The difference in volume-backscattering strength at 120 and 38 kHz ($\Delta S_{v120-38}$) in the densest parts of the SL agreed with predictions using a target-strength (*TS*) model and an assumed normal distribution of tilt (mean θ= 11°; s.d. = 4°). The $\Delta S_{v120-38}$ was smaller for lower densities and during night-time. It appears that the $\theta$and, therefore, *TS* distributions of krill significantly change during their diel vertical migrations. At twilight and at night, when they are feeding and swimming vertically, they exhibit lower mean *TS* and $\Delta S_{v120-38}$ and react less to strong strobe-light pulses, in contrast to daytime. Diel patterns in *TS* and net avoidance should be taken into account in krill-biomass assessments that use round the clock acoustic-survey data and multi-frequency *TS* models for target classification.

Keywords: avoidance, diel vertical migration, feeding, *in situ* orientation, krill, *Meganyctiphanes norvegica*, St Lawrence Estuary, strobe light, target strength, *Thysanoessa raschi*

1. Introduction

Krill biomass estimates can be obtained from net sampling or acoustic surveys, which are often conducted 24-hrs day^{-1} to minimize the use of ship time (e.g. Harvey and Devine, 2007; Reiss *et al.*, 2008). Large differences (~8 dB) between daytime and night-time acoustic estimates were first attributed to diel changes in the krill orientation distributions, based on modelled effects of animal tilt (θ; the angle relative to the horizontal) on target strength (*TS*) (Sameoto, 1980; Everson, 1982; 1983; Simard *et al.*, 1986; Greenlaw, 1977). *In situ* measurements of θ have exhibited a wide range of distributions varying from $\theta \approx 0$ with a small s.d. to much larger and variable θ (Sameoto, 1980; Lawson *et al.*, 2006). Sameoto (1980) observed a diel change in *in situ* krill orientations, but Lawson *et al.* (2006) did not. All of these different results reveal a large variability of *in situ* θ. Nevertheless, *in situ* orientation is considered a major source of uncertainty in the *TS* used for acoustical estimation of krill biomass (McGehee *et al.*, 1998; Stanton and Chu, 2000; Demer and Conti, 2004 and 2005; Chu and Wiebe, 2005; Lawson *et al.,* 2006).

When there are no diel differences, a constant distribution of θ can be used in krill *TS* models for assessment surveys. For example, to assess Antarctic krill (*Euphausia superba*) biomass from acoustic survey data collected only during daylight hours, a normal distribution (N) with mean θ=11° and s.d.=4° is used (CCAMLR, 2005). However diel differences can exist. Krill tracked during night-time have shown extensive and rapid vertical excursions between a phytoplankton-rich surface layer and their daytime depth (Sourisseau *et al.*, 2008). Such vertical displacements cause night-time distributions of θ to have much larger means and s.ds. than their daytime counterparts. Therefore, if krill *TS* is modelled with a fixed daytime-distribution of θ, krill biomass estimated from 24-hrs day^{-1} assessment surveys will be negatively biased. Moreover, measurements of volume backscattering strength ($S_V = TS + 10\log(N)$; where *N* is the number of animals m^{-3}) and the frequency response of krill (Stanton and Chu, 2000) will also be modulated by θ. Multifrequency S_v are often used to acoustically identify krill (e.g. Reis *et al.*, 2008, and reference therein) and estimate their length distributions (Lawson *et al.*, 2008).

For estimates of krill biomass from instrumented multiple-net samplers, avoidance of the net by krill is the predominant source of uncertainty. For example, large differences (>10 dB) have been observed for daytime vs. night-time estimates of adult krill (e.g. Sameoto, 1980; Everson and Bone, 1986; Cochrane and Sameoto, 1991; Cochrane *et al.*, 1991). To reduce avoidance, researchers have mounted lights in front of the nets to ‘freeze’ the animals before their capture (Sameoto *et al.*, 1993). However, large diel variability in the effectiveness of lights has been noted. Comparing the results of four tows with and without a continuous light on, the night-time catch of *Meganyctiphanes norvegica* increased by two to three times while daytime catch was 10-20 times higher with the light on (Sameoto *et al.*, 1993). Krill size did not appear to be a factor in these results. During the long night of Antarctic fall, use of a strobe light on three tows only improved the catches of large individuals and increased the krill biovolume catch by 1.5 times (Wiebe *et al.* 2004). Given the large variability of responses, many more studies are needed to accurately assess the effects of a strobe light on the catch of krill, particularly its diel variability.

This paper describes an experiment where acoustic and net sampling measurements are made with high spatial and temporal resolutions at a same site over a 3-day period to assess the effects of krill diel vertical migration (DVM) behaviour on acoustic and net estimates of krill biomass. The objectives are to: 1) document the changes in catchability, strobe light effect, krill *TS* and S_v differences at 120 and 38 kHz ($\Delta S_{v\ 120\text{-}38}$) due to DVM; 2) quantify the potential effects of DVM on biomass estimations from 24-hrs day^{-1} acoustic or net surveys; and 3) examine the effects of DVM on the efficacies of multi-frequency acoustic techniques for remotely identifying taxa and krill lengths. In all cases, account is made for the inherent natural variability in the evaluated parameters.

2. Material and methods

The regional krill aggregation at the head of the Laurentian Channel in the St. Lawrence Estuary (Figure 1, Simard and Lavoie, 1999) was sampled intensively and simultaneously with acoustics and nets aboard the R/V “Coriolis II” from 4-7 Sept. 2003 (for details see Sourisseau *et al.*, 2008). Krill, which largely dominate the pelagic biomass in this area, were sampled with a one-m^2 instrumented multiple-net Bioness sampler equipped with one-mm mesh black nets. The Bioness was equipped with a strobe light (model ST-400c 35-candelas xenon lamp; Novatech Design Ltd.) flashing, when activated, for 20 µs every 0.5 s. The strobe light was only activated on some tows during the third day. Short oblique tows (~15 min, ~2.5 kts), were repeated virtually every hour and sampled four layers (0-20, 20-40, 40-100 and 100-150 m) spanning the whole water column, resulting in a total of 289 samples. The tow rate was increased to 1.25 tow h^{-1} on the third day to allow for tows with the activated strobe. Sampling was intensified during night-time to better monitor this more variable phase of DVM. For comparison with acoustic estimates, catches from the 0-20 m layer were halved to account for the non-ensonified zero to 10 m layer.

Acoustics measurements

Two echosounders (Simrad EK60) operating at 120 and 38 kHz and configured with split-beam hull-mounted transducers (beamwidths = 3° and 7° respectively) were used to observe DVM of krill and estimate their biomass. The range from the sea-surface to a depth of 10 m was not sampled because of the transducer depths (five metres), near-fields, and ringing. Both echosounders were calibrated with the standard sphere method (Foote *et al.*, 1987). Volume backscattering coefficients (s_v; $m^2\ m^{-3}$) at 120 kHz that exceeded the estimated noise levels were integrated in bins (2-m vertically by 10-s or 10 pings horizontally) for a comparison with Bioness catches (Simmonds and MacLennan, 2005; Simard *et al.,* 2000). The sound speed and absorption coefficients, computed from Bioness CTD profiles, were used in the calculation of s_v.

There is much uncertainty comparing acoustic estimates of krill with catch estimates because: the echosounders sample much larger volumes than the nets (e.g. 50 fold more at 150-m range); the krill are patchily organized (observed with optical and acoustic sensors by Sameoto *et al.*, 1993); and the water sampled beneath the ship differs somewhat from that sampled by the net towed behind the ship, particularly in areas where current directions change with depth (Sourisseau *et al.*, 2008). Despite these difficulties, the acoustic data were averaged over depth-distance rectangles which were later crossed with the Bioness nets.

The s_v were converted to biomass using a conversion factor based on the simplified stochastic distorted-wave Born approximation (SDWBA) krill *TS* model (Demer and Conti, 2005; Conti and Demer, 2006), as corrected by Demer *et al.* (2008), and length-to-mass relationships (Simard and Lavoie, 1999). This model was adopted by the Committee for the Conservation of Antarctic Marine Living Resources (CCAMLR, 2005). This model is tuned for *Euphausia subperba,* assuming constant density contrast, g=1.0357, and sound speed contrast h=1.0279 (derived from *ex situ* measurements; Foote, 1990), and N(11°, 4°). These values of g and h fall within the measured range for the two euphausiid species in this study (Kogeler *et al*., 1987).

The conversion factor was computed (Reiss *et al.*, 2008) as the ratio of the krill weight and backscattering cross-section (σ_{bs}), each weighted by the krill total length-distribution. This model resulted in $\overline{TS}$ =-78.6 dB re one m^2 for *T. raschi* (total length *L*=19-33 mm, mean=27.0 mm, unimodal distribution; wet weight=0.041-0.223 g, mean=0.128 g), and $\overline{TS}$ =-76.6 dB re one m^2 (*L*=22-42 mm, mean=34.4 mm, unimodal distribution; wet weight=0.071-0.669 g, mean=0.355 g). The conversion factor for total krill was $\overline{TS}_w$=-70.15 dB·g^{-1}, which is one dB lower than the constant value of $\overline{TS}_w$=-69 dB g^{-1} previously used for this area (Simard and Lavoie, 1999). The biomass m^{-3} (*B*) was calculated from:

$$B = \frac{s_V}{10^{\left(\overline{TS}_w/10\right)}} . \qquad (1)$$

Differences in volume backscattering strengths (S_v; dB re one m^{-1}) at 120 and 38 kHz ($\Delta S_{v\ 120\text{-}38}$) were computed over four-metre high by five-minute bins. Histograms of $\Delta S_{v\ 120\ \text{-}38}$ were computed for the night-time 10-30 m and the daytime 90-150 m dense krill SLs. This was done for increasing S_v thresholds at 120 and 38 kHz corresponding to three signal-to-noise ratios and packing densities of the small krill patches in the large insonified volumes: -90 and -85 dB; -90 and -80 dB (~ 1 krill m^{-3}); and -80 and -70 dB (~ 10 krill m^{-3}), respectively. The predicted $\Delta S_{v\ 120\text{-}38}$ distribution from the SDWBA model with N(11°, 4°) tilt distribution was computed for the total krill length distribution.

3. Results

The contribution of copepods to the S_v was negligible (<-86 dB) because of their low densities (maximum=50 individuals m^{-3} during the first 52 hrs), and low mean *TS* ($\overline{TS}$ ~-103 dB for a 2-3 mm long copepod at 120 kHz; Stanton and Chu, 2000). Similarly, the hyperiid amphipod *Themisto libellula* did not contribute appreciably to the S_v because of their very low mean densities relative to euphausiids. However, the S_v was slightly contaminated from small pelagic fish in the upper water column (daily maximum ~-83 dB re 1 m^{-1}; Figure 2), and by excursions of a few small demersal organisms (*in situ TS* from -70 to -50 dB) into the water column during night-time (Sourisseau *et al.*, 2008).

The catch of zooplankton principally comprised, in decreasing order of biomass: *T. raschi* (3.7±9.9 individuals m^{-3}), *M. norvegica* (0.5±2.7 individuals m^{-3}), *T. libellula* (0.1±0.3 individuals m^{-3}) and *Calanus finmarchicus* (32.6±126.8 individuals m^{-3}). Only euphausiids (*L*=19-42 mm), which dominated biomass, are considered further.

The krill at the study site exhibited typical night-time asynchronous DVM behavior (Pearre, 2003). They formed a dense SL during daytime between 100 m and the bottom (~150 m) (Figure 2). At dusk, all this layer synchronously moved nearer to the surface (0-40 m), with high concentrations in the 10-20 m depth where the echo integration started (Figure 2). While most of the krill remained there over night, some descended to form SLs at intermediate depths, down to their daytime depths. At dawn, all of the krill descended, reforming the dense daytime SL. Analyses of phytoplankton pigment from krill stomachs and measurements of ADCP vertical velocity data (c.f. Sourisseau *et al.,* 2008) suggest that krill moved between the surface and intermediate SLs during the night-time.

The $\Delta S_{v\ 120\text{-}38}$ pattern during DVM is illustrated in Figure 2c. During night-time $\Delta S_{v\ 120\text{-}38}$ in the 10-30 m depth layer ranged from 1-20 dB, with a mean of 6.84

(s.d.=2.73) and a distribution slightly skewed towards high values (Figure 3). During the daytime in the 90-150 m SL, the $\Delta S_{v\ 120\ -38}$ ranged from 0-16 dB with a distribution skewed towards low values and a mean of 8.59 dB (s.d.=2.98). Increasing the S_v thresholds in computing the $\Delta S_{v\ 120\ -38}$ gradually shifted the distribution towards high values and filtered out the few high values. The $\Delta S_{v\ 120-38}$ distribution in the densest parts of the daytime krill SL (Figure 3b, white bars) corresponded to the predictions from the SDWBA *TS* model used for the total krill length distribution observed.

During the daytime, the acoustic estimates of krill biomass were systematically higher than corresponding Bioness catches (Figure 4a), by a factor of three to six, on average (five to eight dB relative change) (Wilcoxon test, p < 0.001). In the dense SL > 100 m, the average catch represented only 20% of the acoustic estimate (0.43/2.11, Table 1). At night-time, the situation was reversed; the Bioness generally caught more krill than were acoustically-estimated (Figure 4b, Table 1, Wilcoxon test, p < 0.001). In the dense night-time SL in the surface layer, the average catch was 15 times higher than the acoustic estimate (6.18/0.40, Table 1). During night-time, at depths > 40 m, the differences between the two estimates tended to be smaller and sometimes even in favor of acoustics (Figure 4b, grey area). Net samples during the ascent and descent phases of the DVM mimicked the night-time samples (Figure 4c). Night-time acoustic estimates were significantly lower (K-S test, p < 0.001) than daytime ones, by a factor of ~ 4, on average (Table 1).

Use of the strobe light increased the Bioness catches by a factor of ~10 during daytime (Table 1). This increase was particularly significant (K-S test, p < 0.001) in the dense krill SL in the lower two strata, but not significant (K-S test, p > 0.08) in the less dense upper strata (Table 1; Figure 4a, crossed circles). At night-time, the strobe light did not have any significant effect (K-S test, p > 0.22) in any strata (Figure 4b, Table 1). As expected, the strobe light had no significant effect (K-S test, p > 0.27) on acoustic densities, either during daytime or night-time (Table 1).

The two series of biomass estimates from the acoustics and net catches (each integrated from 10 m to the seafloor) differed significantly (Wilcoxon test, p=0.05), and the zero-lag correlation between them was nil (Kendall τ=0.003, p=0.98). The time-series of the differences in the two krill biomass estimates exhibited diel fluctuations (Figure 5). The amplitude of the diel fluctuations was ±~10 dB (Figure 5). The strongest shift occurred soon after dusk, where the acoustic estimates were minimal relative to the catches. They then gradually increased over night and reached a plateau near noon. This pattern was particularly evident during the first two night-times (Figure 5). The strobe light reduced the amplitude of the diel fluctuations by significantly increasing the daytime catches (K-S test, p < 0.001), without a significant night-time effect (K-S test, p > 0.11), thereby significantly reducing the daytime difference (K-S test, p < 0.001).

The estimated biomass from the series of net samples with a strobe was slightly higher than the mean biomass acoustically estimated with data collected from 10 m to the bottom (Table 2), but this difference was not significant (K-S test, p > 0.29). Acoustic estimates were five times higher than catch estimates during daytime, while they were 3.9 times lower for night-time. Therefore, daytime acoustic surveys might produce 1.4 fold (121/86.8, Table 2) more biomass than night-time catch surveys. When a strobe light was used, the catch estimate was twice the daytime acoustic estimate, but this difference was not significant due to the low number of observations (Table 2). Using the strobe during daytime increased the catch estimate by a factor of seven to nine (212.6/29.8, 212.6/24.4; Table 2).

4. Discussion

DVM behaviour of krill modulated the S_v from a vertically looking echosounder and catches from an efficient krill sampling net, but in opposite ways. One explanation is that the krill migrated into the top 10 m at night-time and were therefore missed by the acoustic observations starting at 10 m (Demer and Hewitt, 1995). However, the relatively high S_v at 120 kHz in the 10-20 m layer indicated that at least some of the krill near the surface were ensonified. If much less than 50% of the night-time dense SL was observed in the 10-20 m layer, then catches differences with the acoustic estimates in the 10-20 m samples would be systematically higher than in the other layers. This was not the case. Rather, the night-time catch estimates in the 10-20 m samples were as randomly distributed relative to the regression line (Figure 4b) as the deeper night-time samples.

The response of krill to the strobe light was significant only during daytime. At night-time, krill did not avoid the net, possibly because of: a) their inability to visually or otherwise detect and efficiently avoid it (e.g. when densely swarming); or b) a night-time-behaviour, such as feeding, which might affect their alertness and ability to avoid the net. In the first case, a strobe light will have no effect if the net is already fishing efficiently during night-time. Also, while high packing densities were observed during night-time, dense, deep SLs were observed during daytime when strong avoidance was observed. In the second case, the krill may not react to the strobe when they are feeding in the surface layer. After krill returned to the deep SL at night-time, the ratios of catch-to-acoustic densities with the strobe light were similar to those during daytime (Figure 4b,d). This observation supports the second hypothesis. Also, because the catch estimate during daytime was double the acoustic estimate and seven to nine fold greater than the catches without the strobe light, there remains a possibility that the strobe light acts as a lure during the daytime.

Daytime net samples in a krill SL are significantly biased. Catch effort should be concentrated at night-time, when the animals are feeding or swimming between the upper and lower parts of the water column (Sourisseau *et al.*, 2008). At this time, they do not appear to react to the net, possibly because cohesion between individuals requires daylight cues, as suggested by Blaxter *et al.,* (1964), as cited in Wiebe *et al.,* (2004). Another possibility supported by the results is that cohesion cannot occur when the animals are feeding, but can resume, even during night-time, when this behavior is stopped and the animals have reformed their deep SL. Avoidance may be triggered by flashes of bioluminescence from krill hitting the net (Wiebe *at al.*, 2004), but the results of this study and those of Sameoto *et al.* (1993) suggest that this would not be efficient when krill is feeding during night-time. The exact action of the strobe light on krill behaviour during daytime and night-time still needs much further investigation.

The average biases of the catch and acoustic estimates were equivalent, resulting in similar three-day average estimates. This result suggests relative biomass estimates can be derived using data from either sampling method, provided that sampling is uniformly conducted 24-hrs day^{-1}. This result also depends on the spatial sampling relative to the geographical distribution of krill; otherwise the diel variability will contribute time-varying biases to the relative biomass estimates. To effectively combine daytime and night-time data for biomass estimation over a survey area, a model must be employed which correctly accounts for spatio-temporal aliasing (e.g. Demer and Hewitt, 1995).

Accurate estimates of biomass from measurements of S_v 24-hrs day^{-1} depend on the exact distribution of krill θ during the diel cycle. It is generally incorrect to assume a constant distribution of θ for all phases of DVM. Even a simple two-phases daytime/night-time model could not account for the continuous changes occurring over the 24-hr cycle. Large diel changes in the distributions of krill θ are clearly evident from the time-series of differences in the distributions of $\Delta S_{v\ 120\text{-}38}$. Stronger contribution of the 38 kHz S_v to $\Delta S_{v\ 120\text{-}38}$ during night-time is indicative of larger θ (Stanton and Chu, 2000). The $\Delta S_{v\ 120\text{-}38}$ distributions at different S_v thresholds suggest that distributions of krill θ also depend on their packing density. At their densest daytime concentrations, krill appear to be oriented close to N(mean=11°, s.d.=4°) used in the SDWBA model. At lower densities, their orientation distribution is likely different and more variable. The observed diel change and wide $\Delta S_{v\ 120\text{-}38}$ distributions are in accord with the diel change and large variability of *in situ* krill θ measured by Sameoto (1980).

Inversions of accurate *TS* models using multi-frequency measurements of S_v for known krill length distributions could provide estimates of *in situ* krill θ distributions at different depths, and spanning the diel cycle (e.g. Cochrane and Sameoto, 1991; Sameoto *et al.*, 1993; Demer and Conti, 2005). Such data could further characterize the DVM behaviour of krill, although information from only two frequencies may be insufficient for such determinations (Chu *et al.*, 1993). Estimating distributions of both θ and krill length from inversions of a *TS* model with multifrequency measurements is even more challenging.

Because multi-frequency measurements of S_v from krill exhibit large diel variations, *TS* models must be parameterized with distributions of θ that are accurate for each phase of the diel cycle. Also, because $\Delta S_{v\ 120\text{-}38}$ varies throughout the diel cycle, thresholding of S_v before estimating krill biomass may introduce large biases.

In situ θ could be estimated from backscattering measurements from beams projecting in multiple directions (e.g. see Cutter and Demer, this volume). Such data could feed an adaptive *TS* model and thus account for the diel fluctuations encountered in surveys.

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Tables

Table 1. Mean ± s.d. (no. of samples) krill biomass (wet g m^{-3}) for daytime, night-time, and with or without strobe lighting, ascent and descent samples excluded, for the whole three-day series and separately for the third-day period of alternating strobe/no-strobe tows (see Figure 5).

	Acoustic		Catch	
	Daytime	Night-time	Daytime	Night-time
No strobe 3-day				
10-20 m	0.02 ± 0.04 (17)	0.40 ± 0.25 (28)	0.00 ± 0.00 (17)	6.18 ± 7.40 (28)
20-40 m	0.02 ± 0.01 (17)	0.10 ± 0.14 (29)	0.00 ± 0.01 (17)	1.03 ± 1.01 (29)
40-100 m	0.52 ± 0.99 (17)	0.05 ± 0.03 (29)	0.08 ± 0.10 (17)	0.33 ± 0.29 (29)
100-150 m	2.11 ± 2.27 (17)	0.11 ± 0.04 (29)	0.43 ± 0.52 (17)	0.18 ± 0.26 (29)
10 -150 m	0.68 ± 1.51 (68)	0.16 ± 0.20 (115)	0.28 ± 1.05 (68)	1.77 ± 4.13 (115)
No strobe 3rd day				
10-20 m		0.42 ± 0.26 (6)	0.00 ± 0.02 (5)	10.85 ± 14.17 (6)
20-40 m	0.05 ± 0.09 (5)	0.15 ± 0.28 (7)	0.01 ± 0.02 (5)	0.42 ± 0.45 (7)
40-100 m	0.01 ± 0.01 (5)	0.04 ± 0.01 (7)	0.02 ± 0.02 (5)	0.21 ± 0.25 (7)
100-150 m	0.17 ± 0.11 (5)	0.11 ± 0.05 (7)	0.59 ± 0.60 (4)	0.14 ± 0.20 (7)
10 -150 m	1.69 ± 1.66 (4) 0.42 ±0.96 (19)	0.17 ± 0.23 (27)	0.12 ± 0.33 (19)	2.61 ± 7.67 (27)
Strobe 3rd day				
10-20 m	0.01 ± 0.01 (4)	0.52 ± 0.47 (5)	0.00 ± 0.00 (4)	8.21 ± 3.20 (5)
20-40 m	0.01 ± 0.00 (4)	0.03 ± 0.01 (5)	0.01 ± 0.00 (4)	0.50 ± 0.17 (5)
40-100 m	0.03 ± 0.01 (4)	0.04 ± 0.01 (5)	0.06 ± 0.03 (4)	0.45 ± 0.35 (5)
100-150 m	2.29 ± 1.43 (4)	0.12 ± 0.03 (5)	5.01 ± 1.45 (4)	0.22 ± 0.16 (5)
10 -150 m	0.58 ± 1.20 (16)	0.18 ± 0.30 (20)	1.27 ± 2.32(16)	2.35 ± 3.78 (20)

Table 2. Mean [95% C.I.] catch and acoustic krill biomass paired estimates (wet g m^{-2}) integrated from 10 m to bottom for different sample subsets. Night-time includes the ascent and descent samples. Significant differences from K-S test (p <=0.01) are in bold.

	Acoustic	Catch	*n.*
No-strobe 3-day	51.9 [28.3, 75.4]	67.6 [47.4, 87.8]	55
No-strobe 3-day, daytime	**121.0** [55.0, 187.0]	**24.4** [10.9, 38.0]	17
No-strobe 3-day, night-time	**20.9** [11.8, 30.0]	**86.8** [60.1, 113.6]	38
No strobe 3rd day, daytime	81.1 [12.1, 150.1]	29.8 [1.6, 58.0]	6
No-strobe 3rd day, night-time	**15.0** [11.0, 19.1]	**110.7** [4.2, 217.3]	8
Strobe 3rd day, daytime	98.5 [5.2, 191.7]	212.6 [91.3, 333.9]	5
Strobe 3rd day, night-time	**13.7** [8.3, 19.0]	**126.0** [81.5, 170.5]	5

Figures

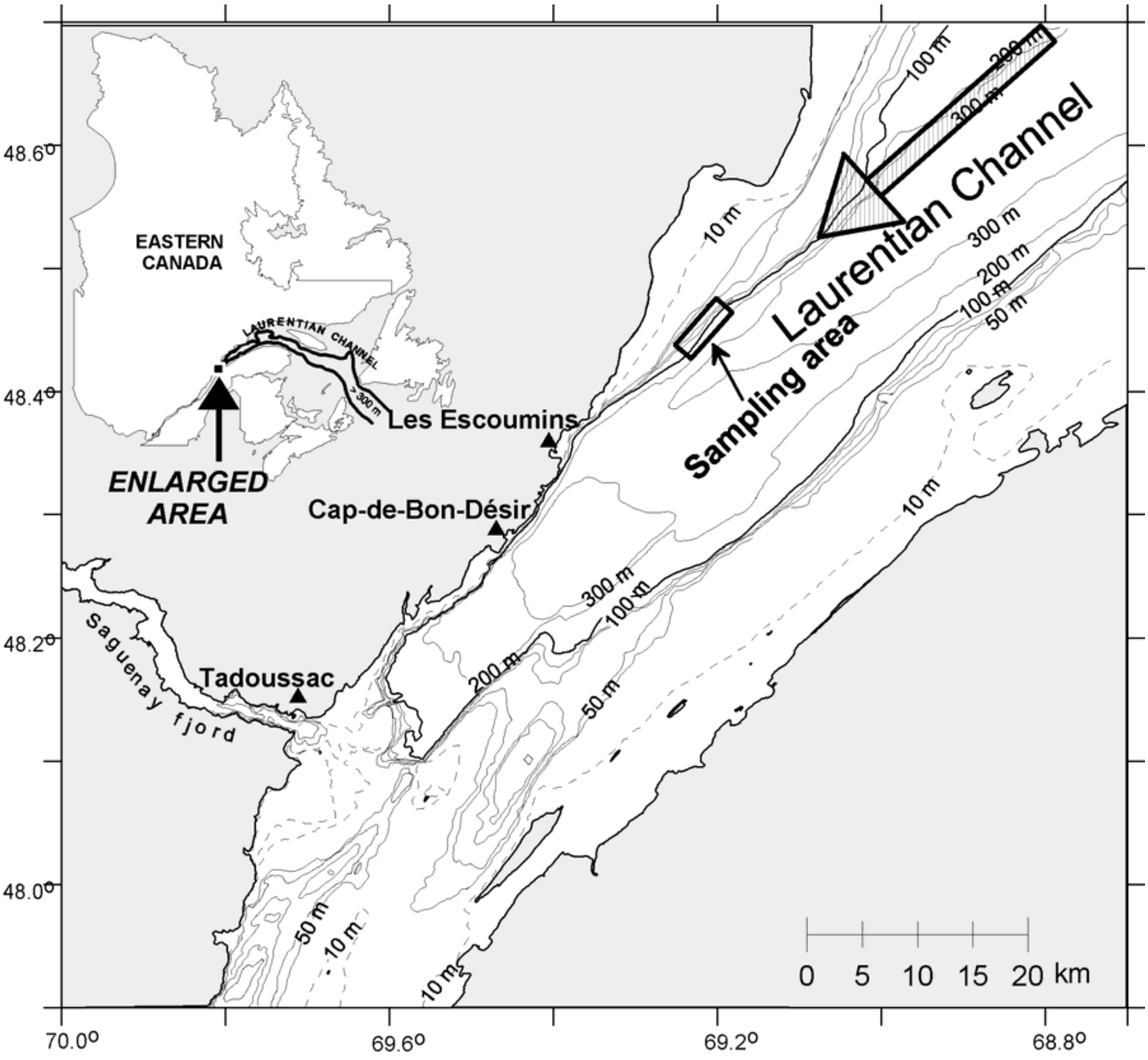

Figure 1. Map of the head of the Laurentian Channel in the Lower St. Lawrence Estuary, showing the sampling location where the slope current feeds the local krill aggregation (hatched arrow).

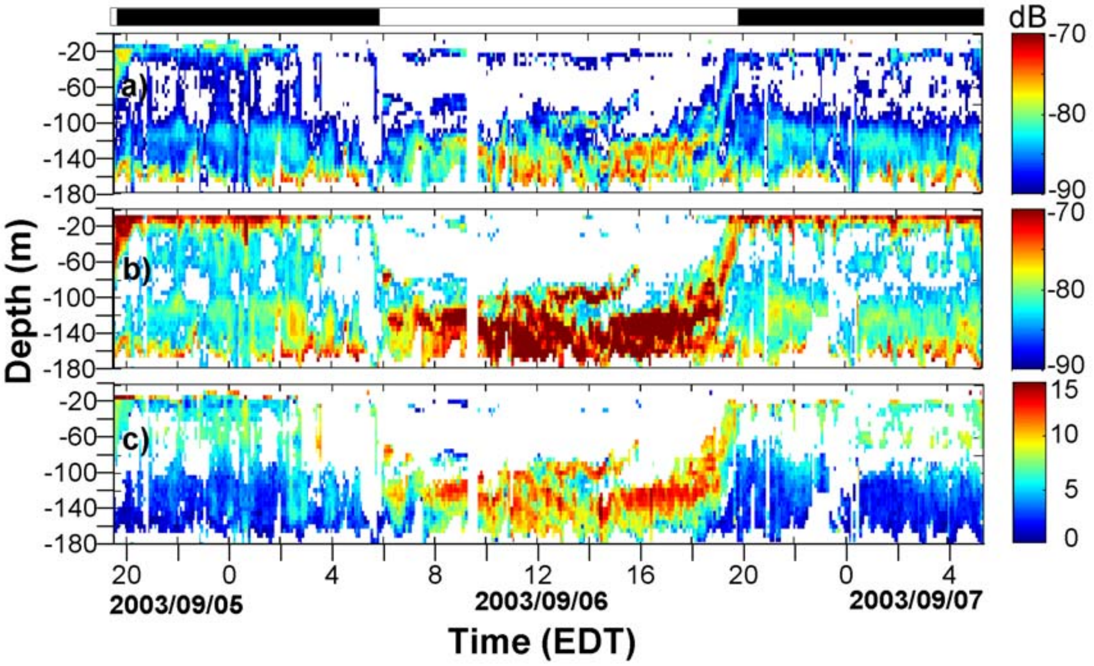

Figure 2. Echograms of krill DVM from half of the time-series. The 38 (a) and 120 kHz (b) volume backscattering strength (S_v, dB re 1 m^{-1}), and their difference ($\Delta S_{v\ 120\text{-}38}$) (c), correspond to the Bioness tows,. S_v < -90 dB at 38 kHz and <-85 dB at 120 kHz are blanked. Night-times from civil twilight time are indicated by the thick black line on top. (Note: This figure corrects a 5-dB palette error in Figure 5b-c of Sourisseau *et al.*, 2008.)

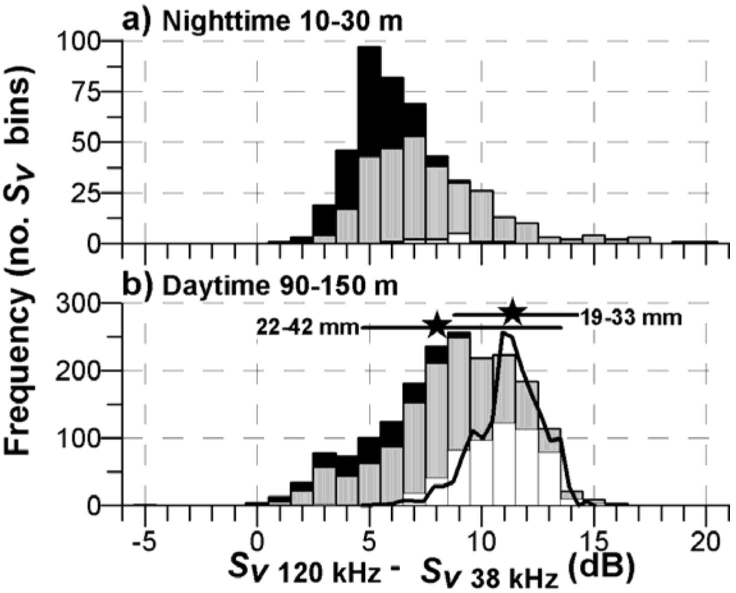

Figure 3. $\Delta S_{v120-38}$ distributions in the krill SL from 4 m by 5 min bins corresponding to Figure 2 for the 10–30 m depth layer during night-time (a), and the 90–150 m layer during daytime (b). S_v thresholds at 120 and 38 kHz increase from –90 and –85 dB (black), –90 and –80 dB (grey), and –80 and –70 dB (white), respectively. The bold line in (b) indicates the $\Delta S_{v120-38}$ predicted from the simplified SDWBA *TS* model with θ= N(11°, 4°) and krill total length distribution, scaled to the observed $\Delta S_{v120-38}$ peak. The ranges corresponding to *T*. *raschi* and *M*. *norvegica* are indicated with superposed horizontal lines with stars for the mean total lengths.

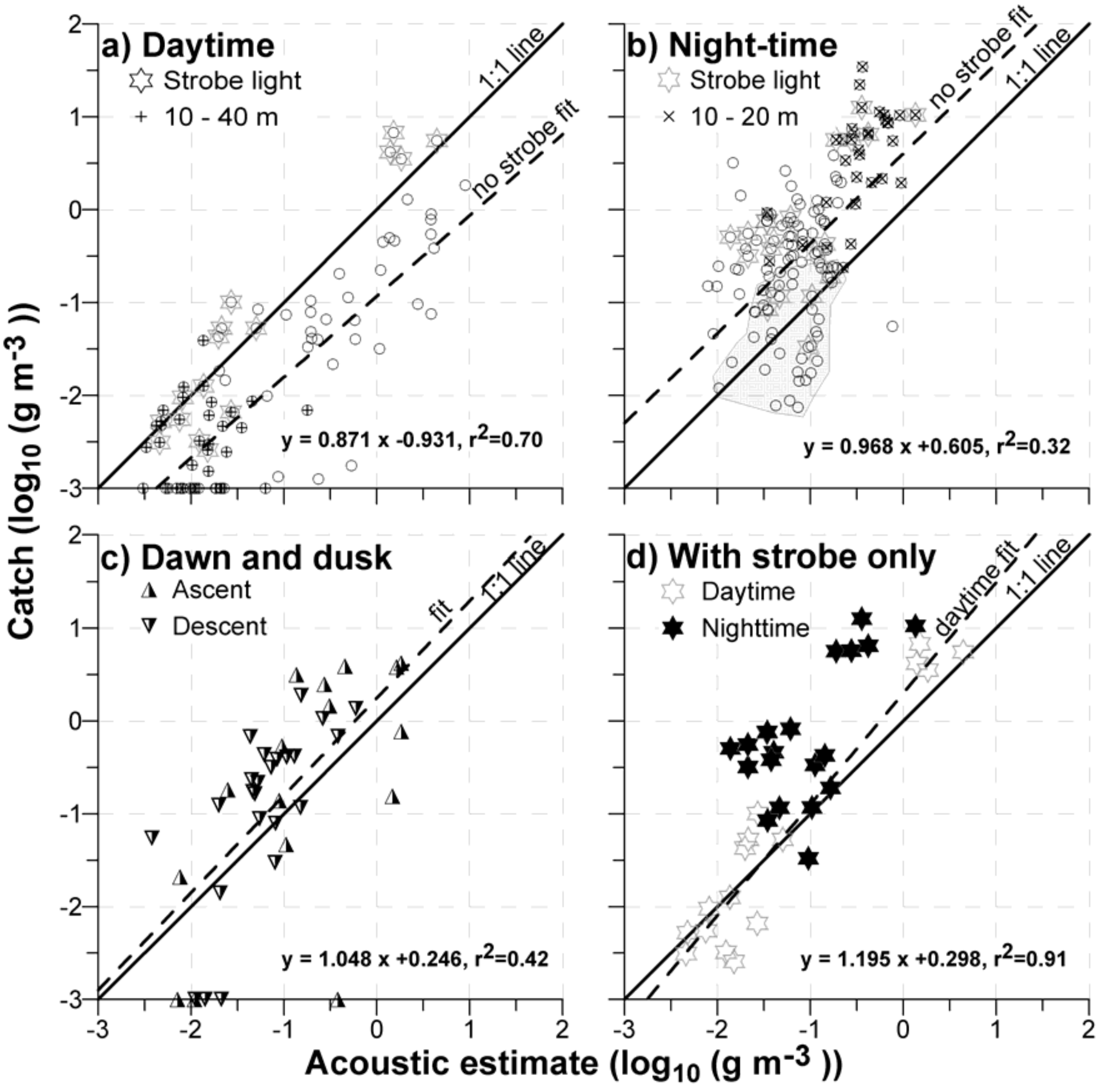

Figure 4. Log-log scatter plot of the krill biomass per m^3 from Bioness catches and 120-kHz echo-integration. Zero catches are plotted on the abscissa.

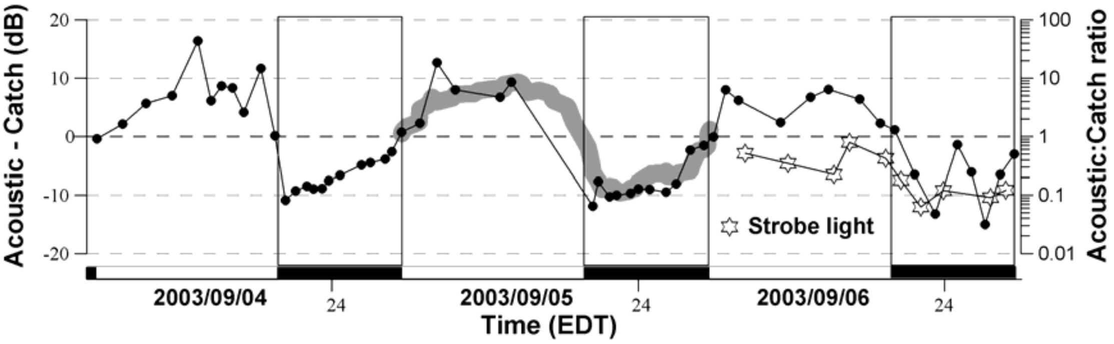

Figure 5. Time series of the difference in krill biomass per m^2 from 120-kHz echo-integration and Bioness catches in dB (10log(acoustic–Bioness biomasses)). The thick grey line in the middle of the time-series is the average of the three-day series, strobe light samples excluded. Night-times from civil twilight time are indicated by the thick black line on the bottom.