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Improved agreement of net and acoustical methods for surveying euphausiids by mitigating avoidance using a net-based LED strobe light system

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Euphausiids are known for their ability to avoid capture by standard plankton nets. Repeat sampling was conducted in the Gulf of Maine with a 1 m^2 MOCNESS equipped with a light-emitting diode (LED)-based strobe light concurrent to multifrequency acoustic data collection. On cruise one, the strobe light's efficacy in reducing euphausiid net avoidance was evaluated on two horizontal tows where four of the eight nets were sampled with the strobe flashing and four with the strobe off. With the strobe light on, there was a significant increase in euphausiid abundance by a factor of 4.5 at night and by a factor of 11.0 during the day. There was also a significant increase in biovolume catch of zooplankton when the strobe light was on by factors of 2.2 at night and 5.5 during the day due to a higher abundance of 10 and 35 mm euphausiids. Euphausiids caught with the strobe light on accounted for most of the observed backscattering, and acoustic and net estimates of their abundance agreed. Similar results were obtained on cruise two. Agreement of acoustic and net estimates when using the strobe light suggests that reduced avoidance enhanced the efficiency of catching euphausiids.

Keywords: acoustics, avoidance, euphausiids, krill, strobe light, zooplankton.

Introduction

Euphausiids are a well known and important global component of marine macrozooplankton/micronekton (Mauchline and Fisher, 1969). They are "... fundamentally different from the 'small drifting animals' of the plankton ..." (Nicol, 2000) by virtue of their larger size, visual acuity, and complex behaviour in aggregations. Euphausiids are also an important component in the economy of the sea by providing an essential link between primary producers and higher trophic levels (fish, squid, whales, seabirds, etc.; Robinson, 2000; Letsessier *et al.*, 2009) and through export of carbon into the deep sea (Schnack-Schiel and Isla, 2005; Swadling, 2006). Thus, quantitative sampling of their distribution and abundance is key to providing assessments of their impact on the marine ecosystem.

Euphausiids are also well known for their ability to avoid capture by standard oceanographic plankton nets (Brinton, 1967; Cochrane *et al.*, 1991; Sameoto *et al.*, 1993; Wiebe *et al.*, 1982, 2004). Traditional methods to reduce avoidance of nets have been to increase the towing speed or to increase the cross-sectional area of the net opening (Clutter and Anraku, 1968). Both methods have serious shortcomings: high tow speeds cause significant extrusion of animals through the net mesh (Vannucci, 1968), and large nets that may reduce avoidance are difficult to handle on most oceanographic research vessels. Since most strong net avoiders have good visual acuity (e.g. fish, squid, and euphausiids) and can use this to detect the approach of the net, recent efforts to reduce avoidance have been to use bright continuous or flashing lights to create a blinding effect so that individuals cannot see the net (Herman *et al.*, 1993; Sameoto *et al.*, 1993; Wiebe *et al.*, 2004; Simard and Sourisseau, 2009).

A new light-emitting diode (LED)-based strobe light system has recently been developed specifically for use on the Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS; Wiebe *et al*., 1985). In contrast to previous strobe systems (e.g. Wiebe *et al*., 2004; Simard and Sourisseau, 2009), the new system is fully integrated with the MOCNESS software, allowing the system to be turned on and off at the user's discretion, and various other parameters (e.g. flash duration and interval) to be controlled. The use of LEDs allows for low power consumption, and the strobe system is run off the standard MOCNESS battery pack. The LEDs emit light at a wavelength chosen to overlap with peak euphausiid spectral sensitivity (Frank and Widder, 1999; Myslinski *et al*., 2005). The objective of this study was to test the efficacy of this strobe light system to reduce the net avoidance of euphausiids in the Gulf of Maine. Comparisons of net samples were thus made with the strobe on vs. off and with independent information derived from a multifrequency acoustic system.

Methods

During a study of euphausiid–herring interactions in Franklin Basin (Gulf of Maine; 42°12′N 67°44'W), two cruises were carried out aboard the R/V "Endeavor" in the autumn of 2010 (Figure 1). MOCNESS tows were performed at night and during daylight to collect zooplankton in order to determine the taxonomic composition of the zooplankton in the study region and to provide ground-truth for acoustic surveying. The standard 1 m^2 MOCNESS was equipped with nine nets with a 335 μm mesh, Sea Bird temperature and conductivity probes, and the newly designed strobe light to reduce the net avoidance by the euphausiids (Figure 2a). Incidental to the ecological objectives, these cruises also provided opportunities to evaluate the strobe light efficacy in reducing euphausiid avoidance of the net.

The strobe system consisted of two LED strips, each with 12 LED sets (LUXEON Rebel LED), that were mounted on the top portion of the forward-projecting MOCNESS fenders (Figure 2b). Peak output of the LEDs was between 490 and 520 nm, and the light produced is in a Lambertian pattern, a

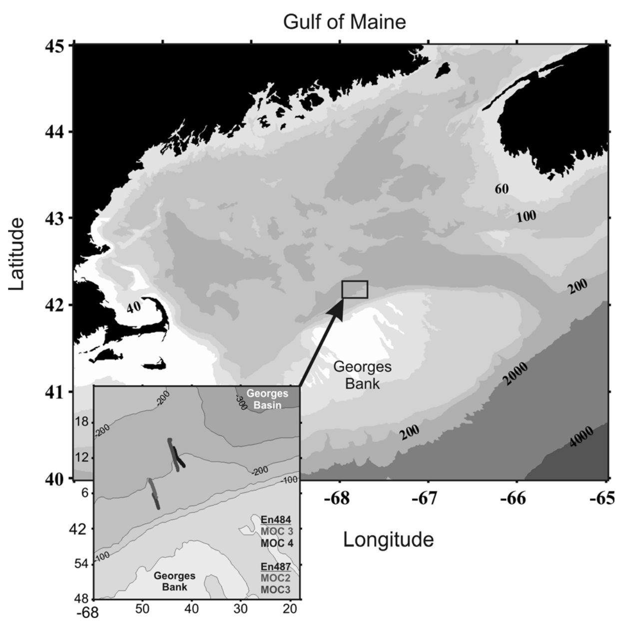

Figure 1. MOCNESS LED strobe light experiment tow positions taken on R/V "Endeavor" cruise 484 (September 2010) and R/V "Endeavor" cruise 487 (October/November 2010).

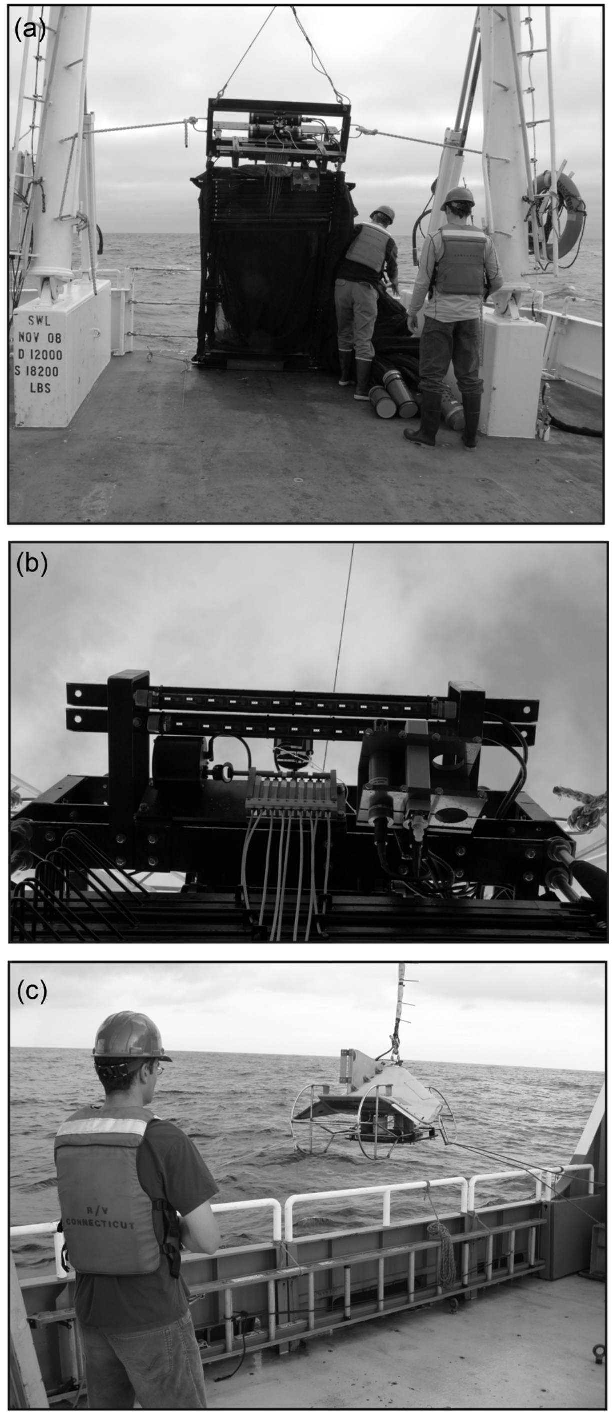

Figure 2. (a) The 1 m^2 MOCNESS on the R/V "Endeavor" cruise 484 ready for a tow. (b) Close-up showing the two LED arrays positioned to illuminate the area in front of the net mouth opening. (c) The "Greene Bomber" towed v-fin being launched. It carried a Hydroacoustic Technologies Inc. four-frequency acoustic system (43, 120, 200, and 420 kHz) and provided collocated acoustic data during MOCNESS tows.

radiation pattern that approximates a sphere. A region in front of the net is filled with light several orders of magnitude higher than ambient, such that at 2 m range the intensity is ~ 50 μW cm^{-2}. The LEDs are powered by the MOCNESS battery, and their pulse width, flash rate period, and on/off are controlled by the MOCNESS software. The amplitude of the flash relative to maximum was fixed at 99%. In this system, the minimum flash rate interval is 100 ms and the maximum pulse width is the interval/8, to allow the capacitors powering the LEDs to recharge. On the first cruise (EN484; 22 September to 1 October), the pulse width was 2 ms and the flash interval was the minimum 100 ms; the light was on for 2% of the time interval. On the second cruise (EN487; 27 October to 5 November) the pulse width was increased to 40 ms to provide more light per flash interval and the flash interval was increased to 1000 ms; the light was on for 4% of the time interval. As noted below, the difference did not seem to affect the catch efficiency.

Concurrent acoustic data were collected with the "Greene Bomber" surface-towed v-fin equipped with a four-frequency acoustic system (43, 120, 200, and 420 kHz) manufactured by Hydroacoustic Technologies Inc. (HTI), Seattle, WA, USA (Figure 2c). The transducers were split-beam and had full beam widths (−3 dB to −3 dB) of 7° for 43 kHz and 3° for 120–420 kHz. A 10 kHz bandwidth, linear frequency-modulated (chirp) signal was used at a repetition rate of 0.5 pings s^{-1}. Echo integration was performed every 6 s to obtain volume backscattering strength, S_v. Measurements of S_v [$S_v = 10\log_{10}(s_v)$ in units of decibels relative to 1 m^{-1}, and s_v is the volume scattering coefficient] were collected from sequential transmissions from all four transducers in 1 m depth intervals to a range of 300 m at 43 and 120 kHz, 150 m at 200 kHz, and 100 m at 420 kHz.

To evaluate the strobe light efficacy in reducing euphausiid avoidance of the net, on EN484 two horizontal tows (tow numbers 3 and 4, conducted during the night and day, respectively) were taken at a site where euphausiids (mostly *Meganyctiphanes norvegica*, but also *Euphausia krohnii* and *Thysanoessa gregaria*) were present. Each tow consisted of a sequential series of down and up oblique casts through a set depth interval (60–75 m at night; 160–190 m during daylight; Figure 3). The strobe light was set to either "on" or "off", with four of the eight nets sampling with the strobe flashing and four sampling with the strobe off, in a random sequence. For both tows, volumes filtered by each net ranged from 463 to 741 m^3. A second opportunity to test the strobe light efficacy occurred on EN487 (Figure 4). A MOCNESS night tow (MOC2) from ~ 190 m to the surface, sampling 25 m intervals, occurred with the strobe light on. A second night tow (MOC3) was taken in the same place a day later at about the same time at night, but with the strobe off. This latter tow also sampled from about 190 m to the surface, but nets 5, 6, and 7 were towed between 55 and 30 m, so sampling intervals are not directly comparable net for net (Figure 4). In carrying out the analysis, the samples were therefore pooled so that the same depth intervals were being compared between the tows; as a result, in this analysis, there are five depth intervals of nominally 190–150, 150–100, 100–45, 45–25, and 25–0 m.

Sample processing

Samples were preserved in a 4% formalin solution buffered above pH 8.0 with sodium tetraborate decahydrate. Two sets of data were developed from the samples: (i) total zooplankton displacement volume, henceforth referred to as biovolume, was measured using the techniques of Alhstrom and Thrailkill (1963) and Wiebe *et al.* (1975); and (ii) a silhouette technique modified from those of Davis and Wiebe (1985) and Foote (2000) was used to determine the abundance and size frequencies of zooplankton taxa in the samples. Generally, a sample was split using a Folsom splitter, modified to blow air gently into the main compartment for better mixing (Longhurst and Seibert, 1967), to reduce the sample so as to allow all the euphausiids to lie in a photo tray with little overlap. A silhouette photo was taken of the animals in the tray and then the photo was scanned with an Epson Expression 1600 scanner in black and white (8 bit) at 1200 DPI (Supplementary material, Figure S1).

The photos were analysed using a MATLAB-based digitizing program, the WHOI Silhouette DIGITIZER (version 1.12; Little and Copley, 2003). Organisms were identified to taxonomic and/or size category, and lengths were measured either on a random sample of very abundant taxa or, in the case of the euphausiids, on all individuals of all species in the image using standard length 3 (i.e. base of the eye-stalk to the posterior margin of the sixth abdominal segment; Mauchline, 1980). The euphausiid silhouette lengths were multiplied by 1.095 to produce an "acoustic length" for use in the model used to estimate their target strength (Lawson *et al.*, 2006). This length adjustment was based on measurements on a subset of euphausiids from the samples on both EN484 and EN487. Wet weights (WW) of all the taxa were estimated from allometric equations relating length to WW. In the case of the euphausiids, the equation used was $WW = 0.0055 \times length^{3.2059}$. Counts of the taxa were standardized to numbers per m^3 and biomass to mg WW m^{-3} taking into account sample aliquot size and volume filtered by a net.

Data analysis

Comparisons were made of the biovolumes and the abundance and size distribution estimates of euphausiids in each net relative to whether the strobe light was off or on. In addition, the silhouette data were used in a procedure referred to as the "Forward Problem" that enabled comparison of observed volume backscattering levels vs. those predicted on the basis of net catches (Wiebe *et al.*, 1997; Lavery *et al.*, 2007). Specifically, the backscattering cross-section σ_{bs} was calculated for each individual organism measured in the silhouette images using models of acoustic scattering appropriate to the individual's taxonomic group (Stanton *et al.*, 1994, 1998; Stanton and Chu, 2000) and parameterized using the values presented in Lavery *et al.* (2007), except for the euphausiids as explained below and for the shrimp where the length to width ratio (L/W) was changed based on measurements on the samples to 10.3. Estimates of expected backscattering cross-sections for each individual were summed over all individuals in each taxon and then over all taxa to yield an estimate of the total expected volume backscattering strength (S_v, in dB) in the volume defined by the depth range sampled by each net. For comparison with these predictions, the observed median volume backscattering coefficient was determined from the collocated acoustics data for the same time intervals and range of depths as were sampled by each of the MOCNESS nets in a tow, taking into account the setback between the net system and the acoustic transducers. The median was used instead of the mean S_v to exclude the influence of rare, large outliers.

To compare the nets further relative to the acoustics, inversions of volume backscattering measurements at 120 kHz were performed to estimate the numerical density of euphausiids in each

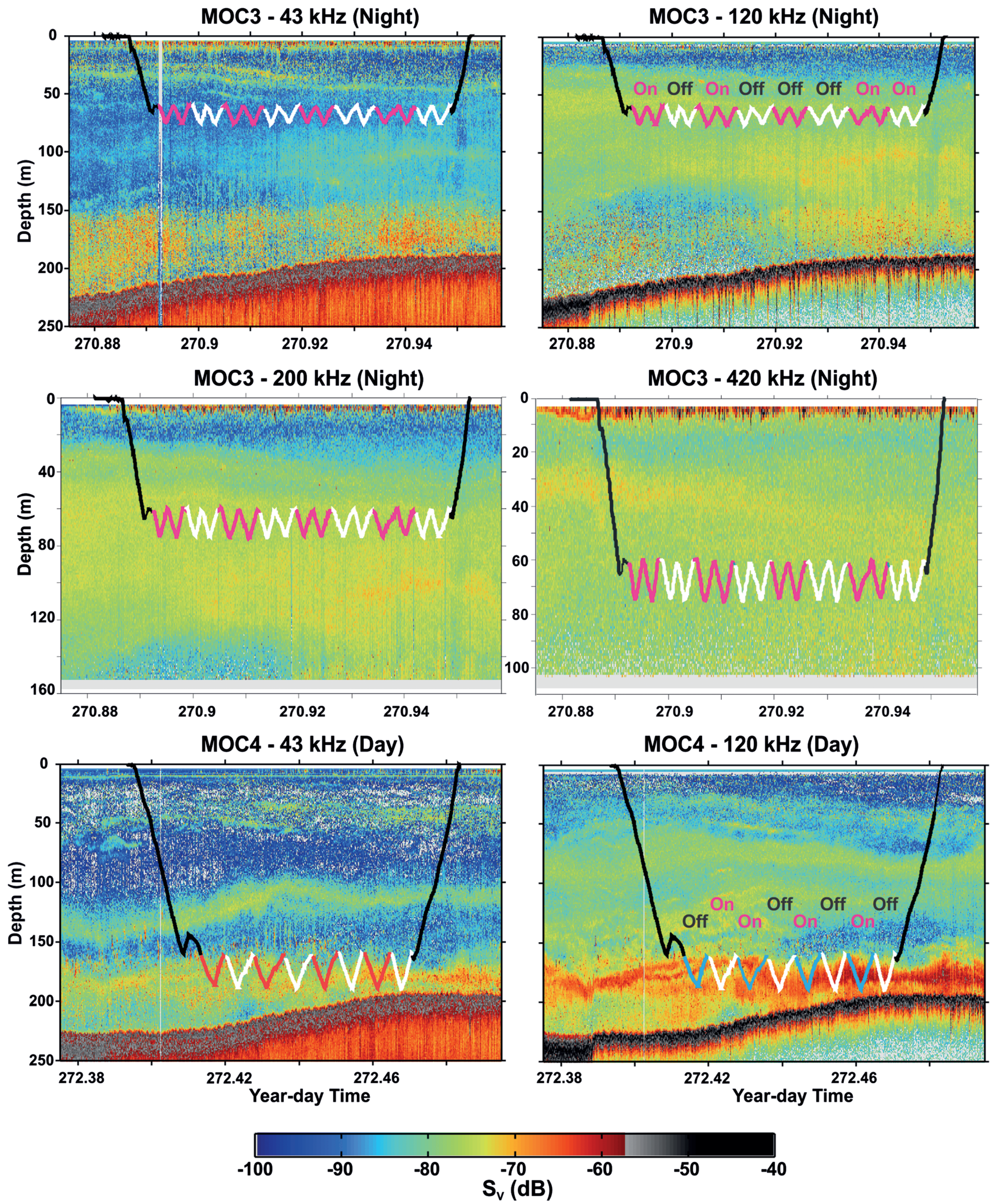

Figure 3. Upper panels: the path of the night-time MOCNESS (MOC3) tow taken on 27 September 2010 during cruise EN484 displayed on 43 and 120, 200 and 420 kHz echograms. Colour change marks change of nets. Each net was cycled twice between 60 and 75 m. Lower panels: the path of the daytime tow (MOC4) taken on 29 September 2010 displayed on 43 and 120 kHz echograms; no data are shown for 200 and 420 kHz because the sampled layer was beyond the range of those frequencies. Each net was cycled once between 160 and 190 m. Nets were randomly selected for strobe on or off, with four on and four off on both tows, and the sequence is noted on one of the echograms for each tow.

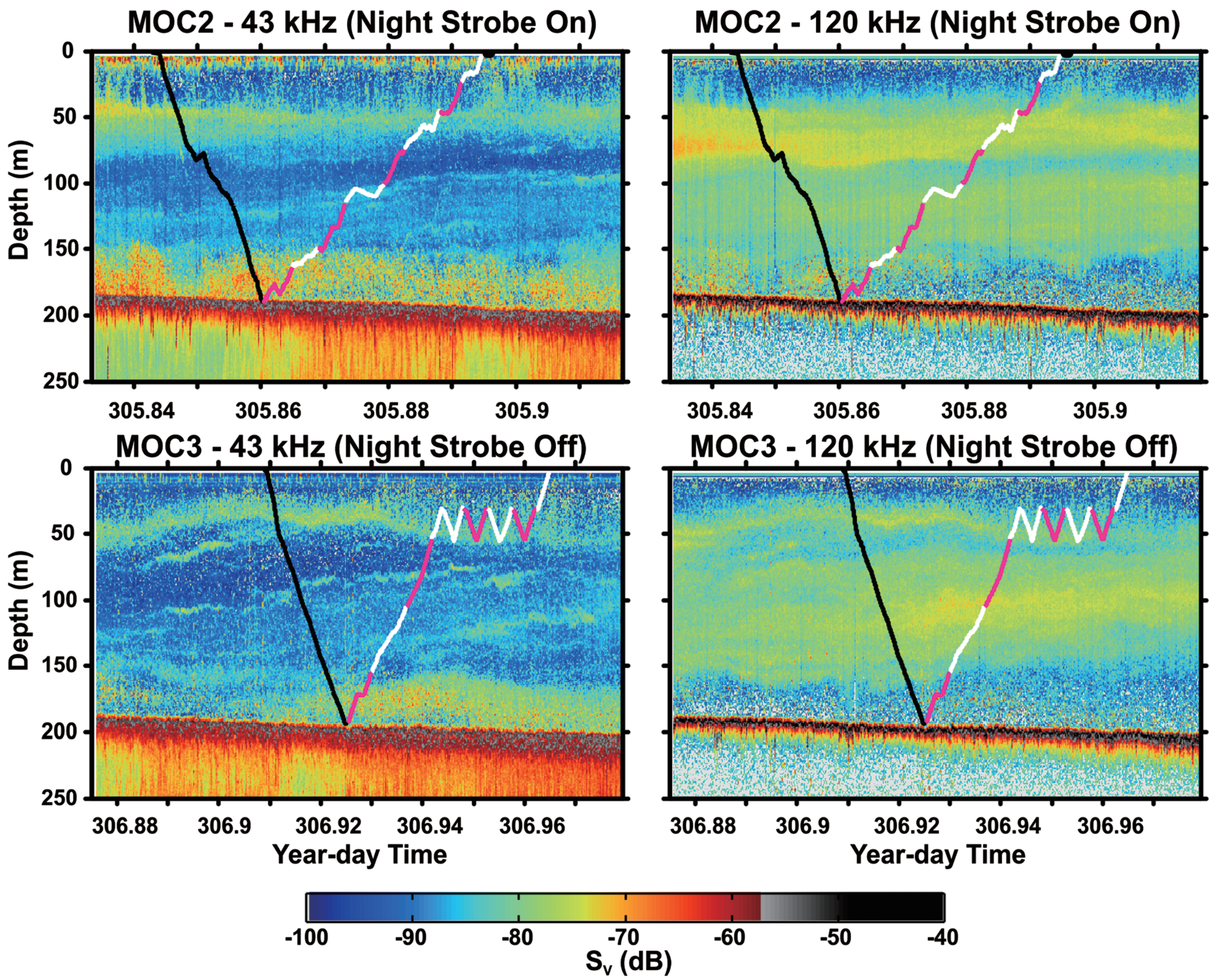

Figure 4. The path of the night-time MOCNESS tows taken on 2 November 2010 (MOC2) and 3 November (MOC3) during cruise EN487 displayed on 43 and 120 kHz echograms. Colour change marks change of nets. MOC2 had the strobe light on; MOC3 had the strobe light off.

net. The number of individuals per m^3 was calculated using the equation $N = s_v / < \sigma_{bs} >$, where s_v is the observed median volume backscattering coefficient for each net, and $<\sigma_{bs}>$ is the predicted average backscattering cross-section for all euphausiids in each net (Greene and Wiebe, 1990; Cochrane *et al.*, 1991). The acoustic scattering model used to calculate the scattering cross-section of each individual euphausiid in each net is given by Lawson *et al.* (2006), re-parameterized with parameter values suitable for *M. norvegica* [i.e. $g = 1.039$, $h = 1.038$ (Calise, 2009); $L/W = 9.10$). These individual scattering cross-sections were then averaged, as a weighted average over the observed length distribution, to obtain $<\sigma_{bs}>$. The resulting acoustic estimates of euphausiid numbers were compared with the abundance measured in the corresponding net samples.

Results

Environmental conditions

Water column temperatures and salinities were typical of the Gulf of Maine in the autumn. Temperatures ranged from 5.9 to ~16°C, and salinities from 31.96 to 34.98 PSU on EN484 (Supplementary material, Figure S2a). The warmest temperatures were in the surface mixed layer and minimum temperatures occurred between 50 and 100 m. Salinities were lowest at the surface and increased with depth. The shallow night tow (60–75 m) had temperatures between 5.97 and 8.48°C, and salinities between 32.32 and 32.76 PSU. The deep day tow (160–190 m) had temperatures between 8.80 and 9.25°C, and salinities between 33.95 and 34.94 PSU. On EN487, the water column temperatures where the MOCNESS tows were taken were between 6.7 and 12.27°C, and salinities were between 32.14 and 34.97 PSU (Supplementary material, Figure S2b). Wind-driven mixing lowered the temperature and increased the depth of the surface mixed layer from ~ 30 m to 50 m between the two cruises; otherwise the water column structure was similar to that observed on EN484.

Biovolumes

On EN484, biovolumes in the night tow ranged from 74 to 223 ml 1000 m^{-3} (Figure 5a) and in the deeper daytime tow from 129 to 1664 ml 1000 m^{-3} (Figure 5b). There was a significant ($p < 0.05$) increase in biovolume catch of zooplankton when the strobe light

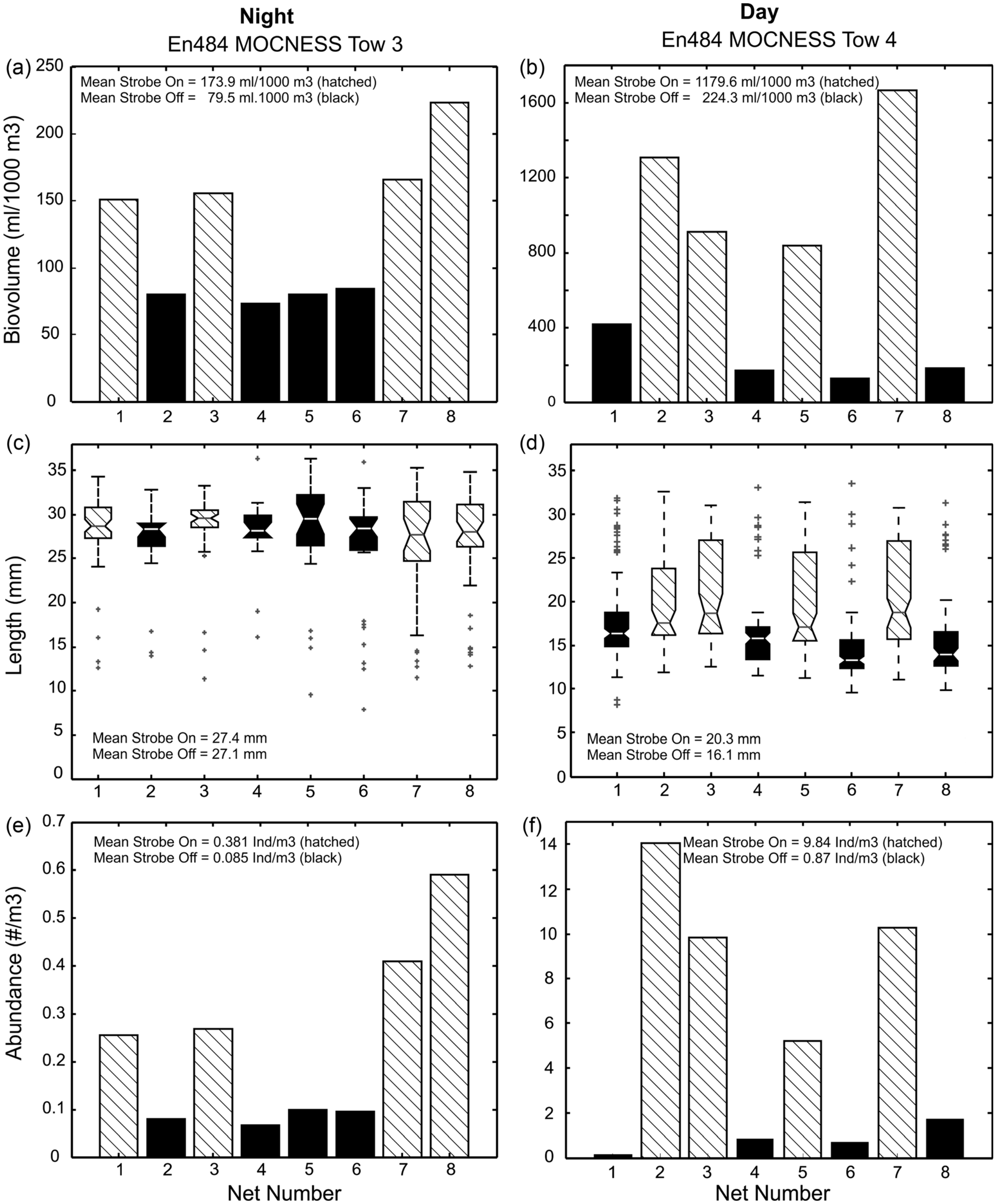

Figure 5. "Endeavor" cruise 484 results for the night (MOC3) and day (MOC4) tows. (a and b) Biovolumes for each net. (c and d) Euphausiid size distribution box plot for each net. (e and f) Euphausiid abundance for each net. Cross-hatched bars represent nets with the strobe light on and black bars represent nets with the strobe light off.

was activated, with total biovolume increased by a factor of 2.2 at night (mean of 174 vs. 80 ml 1000 m^{-3}) and by a factor of 5.5 during the day (mean of 1180 vs. 224 ml 1000 m^{-3}).

On EN487, biovolumes in the night tow with the strobe on ranged from 262 to 911 ml 1000 m^{-3} and were significantly higher ($p < 0.05$) by a factor of 1.8 than on the night tow with

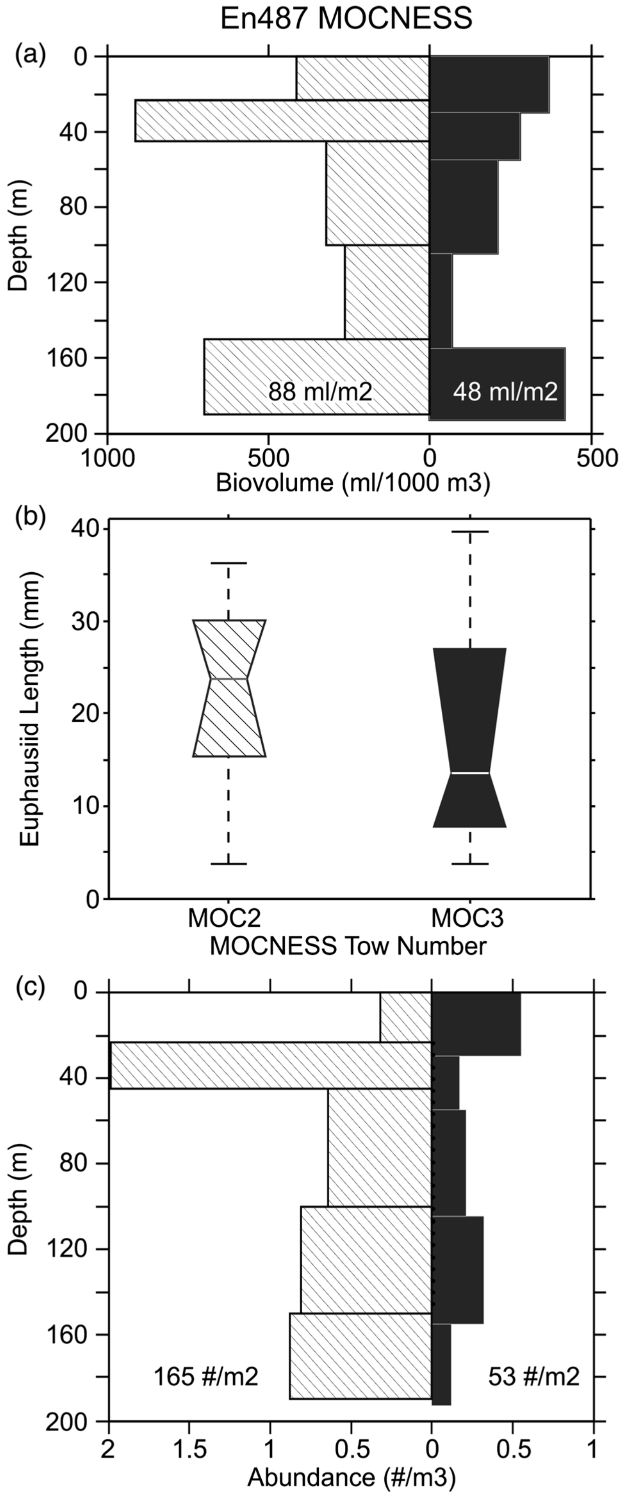

Figure 6. "Endeavor" cruise 487 results for the two night tows (MOC2, strobe light on; MOC3, strobe light off). (a) Vertical distribution of biovolume; total vertically integrated biovolumes (ml m^{-2}) are also shown. (b) Euphausiid size distribution box plot for the water column as a whole. (c) Vertical distribution of euphausiid abundance. Data for MOC2 face left and are cross-hatched; data for MOC3 face right and are solid.

the strobe off, where they ranged from 69 to 418 ml 1000 m^{-3} (Figure 6a).

Species composition of the tows

Based on the silhouette analyses, samples from both cruises were dominated numerically by copepods. On EN484 MOC3, they accounted for $\geq$95% of the individuals present in the samples (Table 1). Salps and euphausiids were ranked second and third in abundance, but had low abundances relative to the copepods. Other taxa were even less abundant. On EN484 MOC4, copepods accounted for $>$90% of the individuals, with one exception (for MOC4 net 7 the value was 75%; Table 1). Euphausiids were second most abundant, especially when the strobe light was on. On EN487, copepods accounted for 94–99% of the individuals present on both MOC2 and MOC3 (Table 2). Euphausiids and the other taxa generally accounted for $<$ 1% of the individuals in the samples.

Euphausiids generally dominated the biomass of the EN484 MOC3 and MOC4 samples, accounting for $>$80% of the biomass with the strobe light on and, with one exception (MOC4, net 1 = 8%), $>$ 50% of the biomass with the strobe light off (Table 1). Copepods ranked second in the biomass composition. In the EN487 MOC2, euphausiids dominated the biomass in the depth intervals 150–100 m, 100–45 m, and 45–23 m, but copepods were dominant in the deepest (190–150 m) and shallowest depth (25–0 m) intervals (Table 2).

Euphausiid abundance and size

The euphausiids were between 10 and 35 mm length on EN484 tows MOC3 and MOC4 (Figure 5c and d). The distribution was bimodal; in the night tow, the large mode ($\geq$ 20 mm) was dominant in both abundance and biomass (Figure 7a–d) whereas during the day tow, the small mode ($<$20 mm) was dominant in abundance (Figure 7f–i), but the large mode still contributed most to the euphausiid biomass. The abundance of all euphausiids in the night tow ranged from 66 to 591 individuals 1000 m^{-3} and during the day tow ranged from 168 to 14 038 individuals 1000 m^{-3} (Figure 5e and f). The mean catch with the strobe off during the night was 85 individuals 1000 m^{-3}, and with it on it was significantly higher ($p < 0.01$) at 381 individuals 1000 m^{-3}. There was no difference ($p = 0.76$) in the mean size of individuals caught with the strobe off (27.1 mm) vs. strobe on (27.4 mm). Thus, at night, the nets with strobe on caught significantly more euphausiid individuals than nets with the strobe off, by a factor of 4.5. The mean catch with the strobe off during the day was 867 individuals 1000 m^{-3} and with it on it was significantly higher ($p < 0.01$) at 9839 individuals 1000 m^{-3}. In this case, there was a significant difference ($p < 0.01$) in the mean size of the euphausiids with strobe off (16.1 mm) vs. strobe on (20.3 mm). Many more small individuals were present in the day tow (Figure 7g and i). The nets with strobe on during the day caught significantly more euphausiids than nets with the strobe off, by a factor of 11.3.

The euphausiids were between 3 and 37 mm length on EN487 tows MOC2 and MOC3 (Figure 6b). The distributions were unimodal on both tows, but large euphausiids in the 20– 30 mm range were most abundant in the tow with the strobe on (mean

Table 1. Abundance and biomass composition of the zooplankton in EN484 MOCNESS samples based on silhouette analysis.

Cruise/tow	Taxa	Net no.								Net no.							
		1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
		Percentage abundance composition								Percentage biomass composition							
	Copepods	95.64	98.37	96.90	98.63	95.49	97.43	96.86	96.62	8.96	24.65	12.04	39.49	24.79	40.72	13.97	11.58
	Euphausiids	1.58	0.34	1.24	0.26	0.40	0.24	0.91	0.94	82.93	49.34	86.87	58.92	73.40	56.43	85.77	88.19
EN484	Amphipods	0.08	0.10	0.03	0.10	0.06	0.09	0.03	0.02	0.29	0.28	0.08	1.18	0.00	2.11	0.00	0.00
MOC3	Chaetognaths	0.21	0.20	0.09	0.15	0.11	0.20	0.21	0.24	0.07	0.31	0.16	0.36	0.34	0.47	0.26	0.23
	Siphonophores	0.05	X	X	0.14	0.06	X	X	0.02	0.03	X	X	0.05	0.00	X	X	0.00
	Salps	1.26	0.88	1.05	0.47	2.97	1.20	0.86	1.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Others	1.18	0.10	0.69	0.25	0.91	0.84	1.13	0.68	7.73	23.06	0.85	0.00	1.58	0.00	0.00	0.00
		Abundance composition (no. m^{-3})								Biomass composition (mg m^{-3})							
	Copepods	15.44	23.13	21.06	26.23	23.86	38.51	43.47	60.97	11.47	14.59	16.16	17.76	15.05	24.51	24.50	30.23
	Euphausiids	0.25	0.08	0.27	0.07	0.10	0.10	0.41	0.59	106.20	29.21	116.65	26.50	44.55	33.97	150.35	230.18
EN484	Amphipods	0.01	0.02	0.01	0.03	0.01	0.04	0.01	0.01	0.37	0.18	0.11	0.53	0.00	1.41	0.00	0.01
MOC3	Chaetognaths	0.04	0.05	0.02	0.04	0.03	0.08	0.10	0.15	0.08	0.20	0.22	0.16	0.19	0.31	0.45	0.60
	Siphonophores	0.01	X	X	0.04	0.01	X	X	0.01	0.03	X	X	0.02	0.00	X	X	0.00
	Salps	0.20	0.21	0.23	0.13	0.74	0.47	0.39	0.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Others	0.19	0.02	0.15	0.07	0.23	0.33	0.51	0.43	9.90	15.02	1.15	0.00	0.90	0.00	0.00	0.00
	Total	16.14	23.52	21.74	26.59	25.01	39.53	44.88	63.10	128.05	65.13	134.29	44.98	56.98	66.55	175.30	261.01
		Percentage abundance composition								Percentage biomass composition							
	Copepods	99.92	96.52	96.66	98.88	94.44	97.29	75.60	93.62	91.96	10.74	9.53	44.17	7.02	33.62	1.30	35.48
EN484	Euphausiids	0.05	3.39	3.12	0.86	5.35	2.23	19.78	1.16	8.04	89.26	90.47	55.78	92.98	65.56	98.69	61.56
MOC4	Others	0.03	0.09	0.22	0.26	0.21	0.48	4.62	5.22	0.00	0.00	0.00	0.05	0.00	0.82	0.01	2.96
		Abundance composition (no. m^{-3})								Biomass composition (mg m^{-3})							
	Copepods	357.61	399.25	305.01	98.35	91.90	31.31	39.24	139.58	235.70	261.95	202.21	66.34	65.34	23.34	27.58	92.38
EN484	Euphausiids	0.17	14.04	9.85	0.86	5.21	0.72	10.27	1.73	20.60	2177.70	1920.30	83.78	865.03	45.50	2091.30	160.30
MOC4	Others	0.11	0.37	0.69	0.26	0.20	0.16	2.40	7.78	0.01	0.02	0.04	0.07	0.01	0.57	0.14	7.71
	Total	357.89	413.66	315.54	99.46	97.31	32.18	51.91	149.08	256.31	2439.67	2122.55	150.18	930.38	69.40	2119.01	260.39

Taxa not present in a sample are marked by X; zeros indicate an abundance or biomass <0.01. Shaded columns indicate samples collected with the strobe light on.

Table 2. Abundance and biomass composition of the zooplankton in EN487 MOCNESS samples based on silhouette analysis.

Cruise	Taxa	Depths (m)					Depths (m)				
		190–150	**150–100**	**100–45**	**45–23**	**23–0**	**190–150**	**150–100**	**100–45**	**45–23**	**23–0**
		Percentage abundance composition					Percentage biomass composition				
	Copepods	99.38	96.37	99.45	99.55	99.66	66.83	6.64	29.83	40.21	86.96
	Euphausiids	0.25	2.18	0.16	0.12	0.03	31.38	92.98	68.70	58.07	9.93
EN487	Amphipods	0.04	0.13	0.02	X	0.05	0.22	0.34	0.84	X	0.69
MOC2	Ostracods	0.06	0.09	0.00	X	X	0.03	0.01	0.00	X	X
	Crustacea larvae	0.00	0.17	0.07	0.10	0.12	0.00	0.00	0.00	0.01	0.01
	Peteropods	X	X	0.02	0.08	0.03	X	X	0.05	0.27	0.07
	Chaetognaths	0.21	0.05	0.03	0.05	0.04	0.99	0.02	0.44	1.04	1.68
	Siphonophores	X	X	0.02	0.06	0.04	X	0.00	0.09	0.40	0.65
	Others	0.06	1.02	0.23	0.04	0.04	0.56	0.02	0.05	0.00	0.00
		Abundance composition (no. m^{-3})					Biomass composition (mg m^{-3})				
	Copepods	347.39	35.90	395.97	1581.80	933.32	251.73	16.12	60.95	223.68	144.67
	Euphausiids	0.87	0.81	0.64	1.98	0.32	118.21	225.86	140.35	323.00	16.52
EN487	Amphipods	0.13	0.05	0.07	X	0.44	0.83	0.81	1.71	0.00	1.15
MOC2	Ostracods	0.22	0.03	0.01	X	X	0.10	0.02	0.01	0.00	0.00
	Crustacea larvae	0.02	0.06	0.29	1.61	1.11	0.00	0.00	0.00	0.03	0.02
	Peteropods	X	X	0.07	1.24	0.28	X	X	0.10	1.50	0.11
	Chaetognaths	0.72	0.02	0.14	0.74	0.39	3.72	0.04	0.90	5.77	2.80
	Siphonophores	X	X	0.07	0.99	0.33	X	X	0.19	2.24	1.08
	Others	0.21	0.38	0.92	0.62	0.33	2.10	0.05	0.10	0.01	0.01
	Total	349.56	37.25	398.17	1588.99	936.52	376.69	242.90	204.30	556.24	166.36
		Depths (m)					Depths (m)				
		193–155	155–105	105–55	55–30	30–0	193–155	155–105	105–55	55–30	30–0
		Percentage abundance composition					Percentage biomass composition				
	Copepods	99.79	94.11	97.07	99.31	99.19	92.36	18.28	24.45	70.23	80.80
	Euphausiids	0.04	1.09	0.45	0.03	0.08	7.45	79.05	72.35	21.13	12.27
EN487	Amphipods	0.09	0.14	0.08	0.05	0.02	0.17	1.07	1.66	0.56	0.24
MOC3	Ostracods	0.06	0.02	X	X	X	0.03	0.00	X	X	X
	Crustacea larvae	X	0.05	0.12	0.02	0.01	X	0.00	0.00	0.00	0.00
	Peteropods	X	0.02	0.02	0.02	0.01	X	0.01	0.01	0.05	0.14
	Chaetognaths	X	0.05	0.14	0.08	0.08	X	0.17	1.38	2.58	2.72
	Siphonophores	X	X	0.10	0.13	0.22	X	X	0.12	1.76	3.70
	Others	0.02	4.52	2.02	0.35	0.39	0.00	1.43	0.04	3.70	0.13
		Abundance composition (no. m^{-3})					Biomass composition (mg m^{-3})				
	Copepods	341.32	27.64	45.34	494.17	649.12	243.94	11.28	11.32	89.63	126.90
	Euphausiids	0.12	0.32	0.21	0.17	0.55	19.67	48.77	33.49	26.97	19.27
EN487	Amphipods	0.31	0.04	0.04	0.26	0.13	0.44	0.66	0.77	0.71	0.38
MOC3	Ostracods	0.20	0.01	X	X	X	0.07	0.00	X	X	X
	Crustacea larvae	X	0.01	0.06	0.12	0.07	X	0.00	0.00	0.00	0.00
	Peteropods	X	0.01	0.01	0.08	0.07	X	0.00	0.00	0.07	0.21
	Chaetognaths	X	0.01	0.07	0.41	0.52	X	0.11	0.64	3.29	4.27
	Siphonophores	X	X	0.05	0.65	1.43	X	X	0.05	2.24	5.81
	Others	0.08	1.33	0.94	1.76	2.54	0.00	0.88	0.02	4.73	0.20
	Total	342.03	29.37	46.71	497.61	654.42	264.13	61.69	46.28	127.63	157.05

Taxa not present in a sample are marked by X; zeros indicate an abundance or biomass <0.01. MOC2 had the strobe light on; MOC3 had the strobe light off.

length = 22.1 mm; Figure 8b), while individuals in the <20 mm range were most abundant in the tow with the strobe off (mean length = 15.6 mm; Figure 8d). The total abundance of euphausiids ranged from 306 to 1984 individuals 1000 m^{-3} on the first tow, with a total water column catch of 165.5 individuals m^{-2} (Figure 6c). On the second night tow, the abundances ranged from 81 to 549 individuals 1000 m^{-3}, with a total water column catch of 52.6 individuals m^{-2}. Thus, both the numbers caught and the size ranges of the individuals were significantly larger on the tow with the strobe on ($p < 0.05$). As a result, the night tow with the strobe on caught 3.1 times more euphausiids. It is important to recognize that although the same location was sampled on successive nights on EN487, it is unlikely the same populations were sampled, and some of the differences in the abundance of the euphausiids and other taxa were due to spatial variability in the population's densities and species composition.

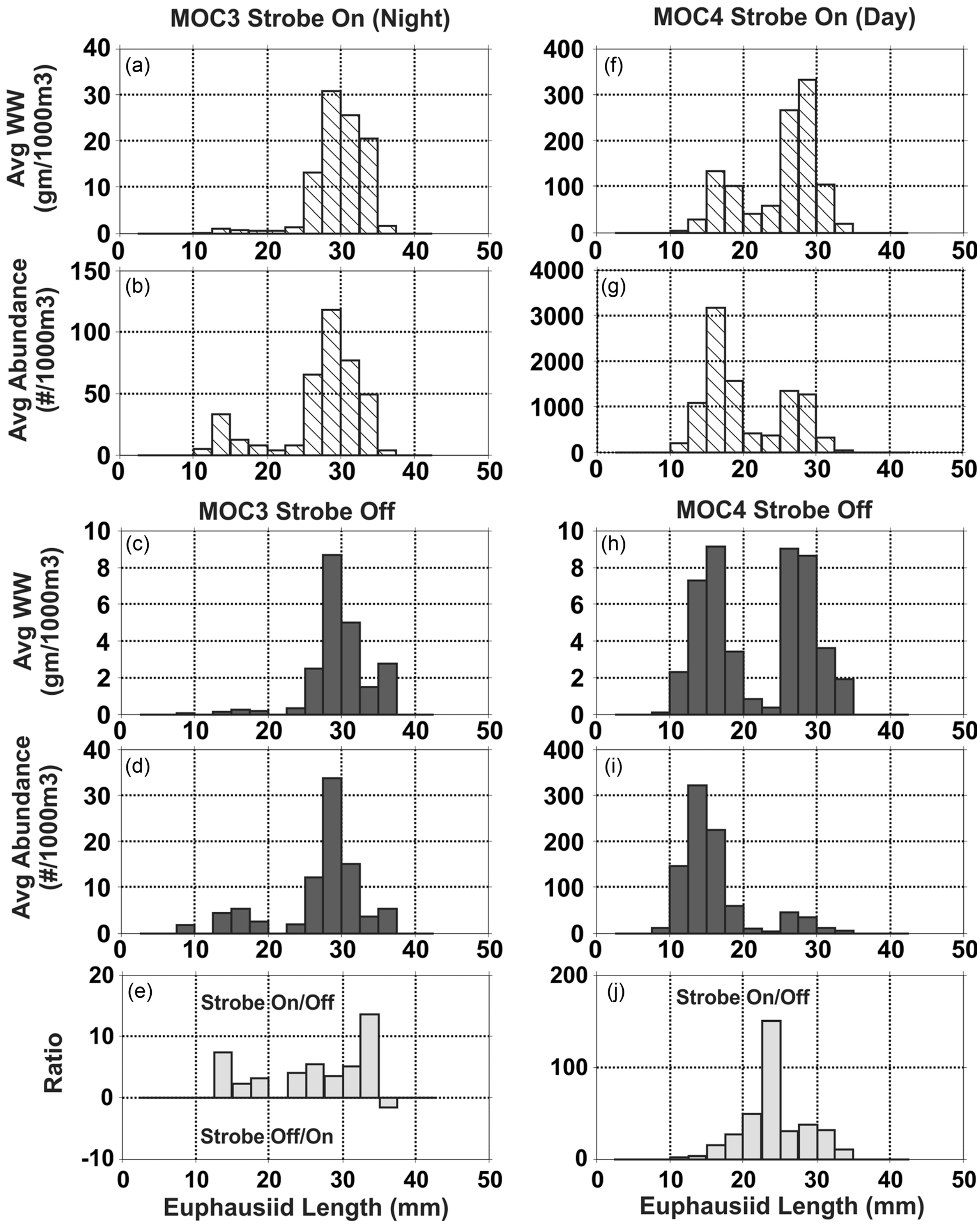

Figure 7. "Endeavor" 484 average size frequency distribution of euphausiid wet weight and abundance determined from the silhouette analysis of the four samples for the night tow (MOC3) with the strobe on (a and b) and four with the strobe off (c and d), and the four samples for the day tow (MOC4) with the strobe on (f and g) and four with the strobe off (h and i). Where the abundance was higher with the strobe on than off, the abundance for a given size euphausiid category with strobe on was divided by catch for the same size category with the strobe off; where abundance was higher with the strobe off, abundance with strobe off was divided by that with strobe on and made negative, to facilitate graphing (e and j).

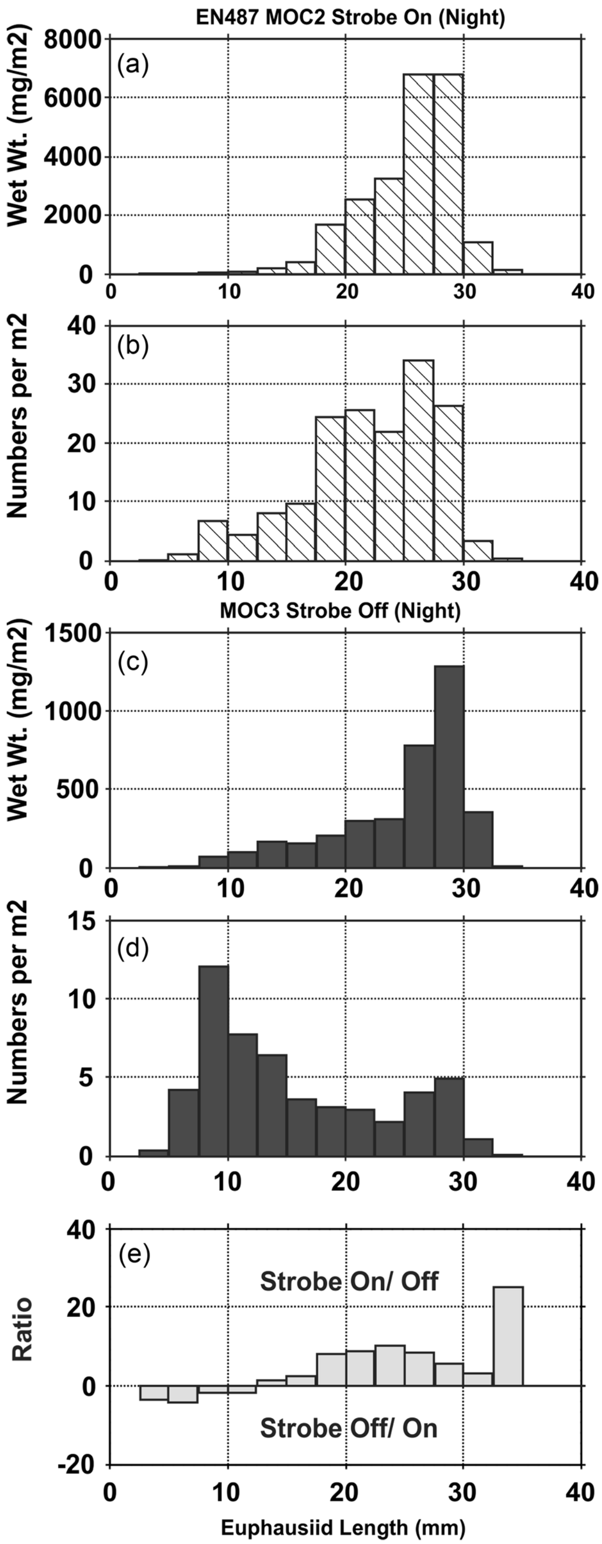

Figure 8. "Endeavor" 487 water column integrated size frequency distribution of euphausiid wet weight and abundance determined from the silhouette analysis of the stratified vertical samples for the two night tows (MOC2 and MOC3) with the strobe on (a and b) and with the strobe off (c and d). The abundance for a given size euphausiid category with strobe on was divided by catch for the same size category with the strobe off when the strobe on abundance was higher than the strobe off, and vice versa (e).

To examine the effect of the strobe on the distribution of euphausiid lengths, the distribution of abundance relative to length sampled with the strobe on was normalized to that sampled with the strobe off (Figures 7e and j, and 8e). The ratio above 1.0 indicates where individuals were caught more effectively. For both EN484 tows, individuals larger than 12.5 mm were caught more effectively with the strobe on. On EN487, individuals larger than 15 mm were caught more effectively with the strobe on.

Comparison with acoustics

Forward computations were done to predict the volume backscattering from the size and abundance data for each taxon determined from the silhouette analysis of net catches for comparison with the collocated estimates of backscattering as a function of frequency in the region sampled by each MOCNESS net (Figure 9). In the EN484 tows, euphausiids accounted for >90% of the estimated backscattering at 43, 120, and 200 kHz when the strobe light was on for both tows, and also for MOC4 with the strobe light off (Table 3). They accounted for > 70% for MOC3 with the strobe light off. There was very good correspondence between the observed volume backscattering and the predicted backscattering based only on the euphausiids when the strobe light was on for both tows on EN484 (Figure 9). The average deviation between predicted S_v and median observed S_v was −2.03 dB for 43 kHz and −0.34 dB for 120 kHz. When the strobe was off, there was poor correspondence: the average deviation was −11.31 dB for 43 kHz and −9.55 dB for 120 kHz. Accounting for the contributions of all the other taxa in addition to the euphausiids reduced the difference between predicted and observed volume backscattering negligibly (<0.5 dB).

On EN487, euphausiids also accounted for an average of 91% of the volume backscattering at 43, 120, and 200 kHz when the strobe light was on (MOC2), except in the upper 25 m, where fewer euphausiids occurred (Table 4). With the strobe light off, euphausiids accounted for ∼76% of the backscattering at these three frequencies, with the exception of the surface layer. With the strobe on, the depth intervals where euphausiids dominated the backscattering showed good correspondence between the estimated s_v and the observed s_v (Figure 10), especially for nets 2 and 3 which sampled within a layer of enhanced scattering (Figure 4). With the strobe off, there was poorer correspondence.

In nets where most of the backscattering was due to euphausiids, inverse acoustic estimates of the euphausiid abundance were determined by dividing the median measured s_v by the mean euphausiid $<\alpha_{bs}>$ for each net (Greene and Wiebe, 1990; Cochrane *et al.*, 1991). For the tows on EN484, the numbers of individuals estimated acoustically in this way ranged from 398 to 16 369 individuals 1000 m $^{-3}$ with the strobe on and 381 to 47 712 individuals 1000 m^{-3} with the strobe off. For the strobe on, the estimated numbers were on average 1.1 times higher than observed in the nets, and for the strobe off they were 23.8 times higher than the net estimates (Figure 11a). On EN487 with the strobe on (MOC2), the inverse acoustics estimates ranged from 235 to 782 individuals 1000 m^{-3} and with it off, from 325 to 1200 individuals 1000 m^{-3}. In this case, with the strobe on, the net estimated numbers were on average ∼ 3.0 times higher than the acoustic estimates, while, with the strobe off, the acoustic estimated numbers were on average 2.3 times higher that the net estimates (Figure 11b). Agreement was best within the layer of high scattering sampled by nets 2 and 3, whereas outside of this layer

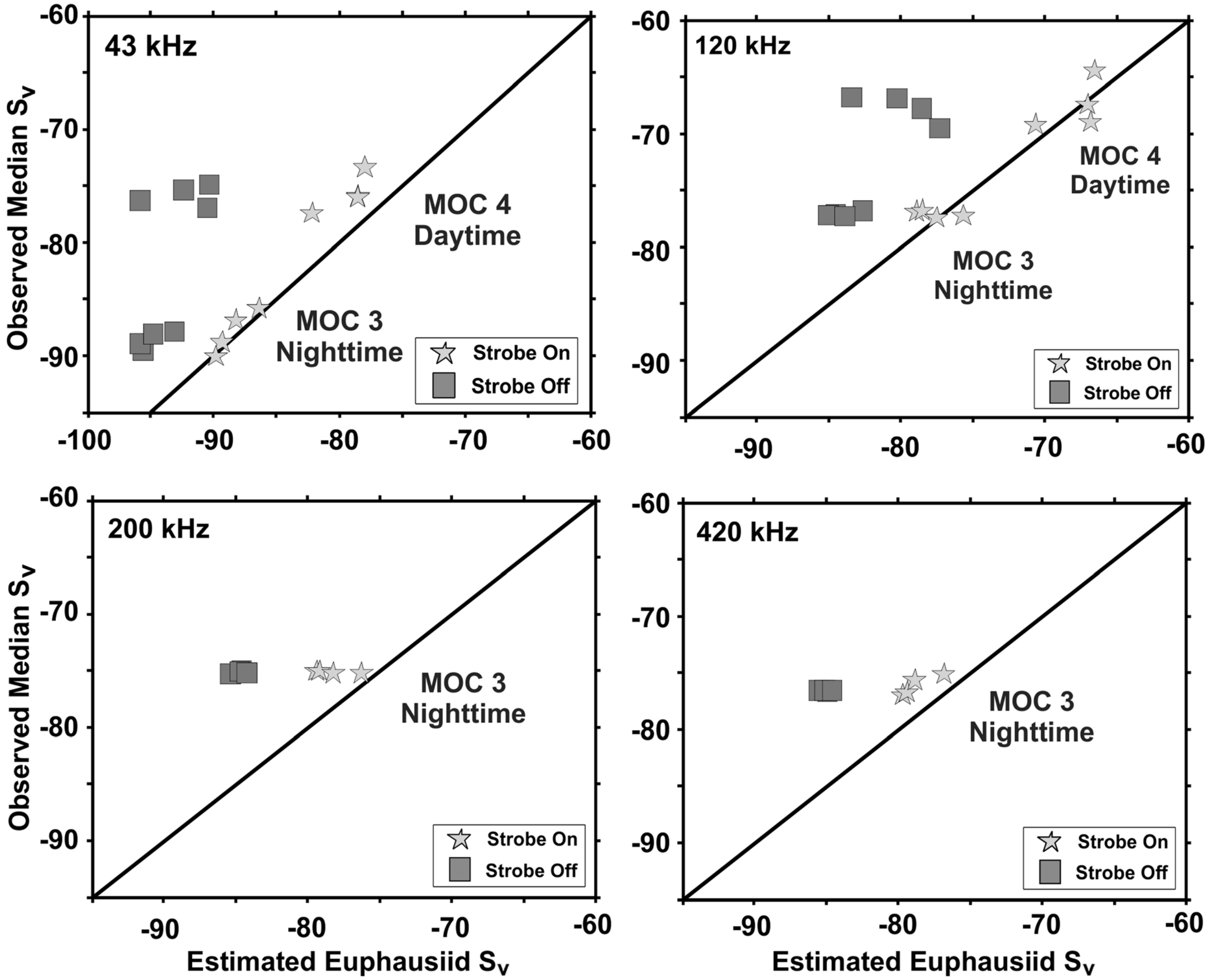

Figure 9. Results from the forward computations: comparison of the predicted volume backscattering strength, S_V (dB), based on the euphausiids caught in the "Endeavor" 484 MOCNESS night and day tows with median observed volume backscattering strength S_V from the collocated acoustics data for the same time intervals and range of depths of each net. Stars are for nets with the strobe on; squares are for nets with the strobe off. Data were not available at 200 and 420 kHz for MOC3 as the net sampling was conducted at depths beyond the range of these frequencies.

Table 3. Average percentage contribution of euphausiids to the estimated volume backscattering on EN484 tows.

Frequency (kHz)	MOC3		MOC4	
	Strobe on	Strobe off	Strobe on	Strobe off
43	95.95	72.98	98.55	96.93
120	96.57	79.06	96.45	96.95
200	93.53	76.09	92.49	93.41
420	85.52	59.76	80.71	83.95

Each average is based on four nets.

in regions of lower background scattering the discrepancy between acoustic and net estimates of abundance was greater.

Discussion

There have been a number of studies of net avoidance over the past 100 years. As noted by Brinton (1967), one of the earliest studies was by Holt and Tattersall (1905) who observed what was interpreted as avoidance of nets by *Nematoscelis megalops*. Most of these studies (see reviews in Wiebe *et al*., 1982, 2004; Sameoto *et al*., 1993) were based on differences between day and night net collections, with night catches exceeding the day catches by factors of 2–10 for some species, especially euphausiids. Brinton (1967), in a classic paper on euphausiid vertical migration and avoidance behaviour at a sampling site offshore of California, found that avoidance of nets was variable amongst the seven genera and 22 species that were in sufficient abundance to evaluate. Eight species showed no evidence of day/night avoidance and 12 showed moderate to strong avoidance. Both non-migrators and migrators were capable of avoiding capture. Offshore species were weaker avoiders than nearshore species.

As Brinton (1967) pointed out, however, without independent information about the abundance of species such as euphausiids in the water column, the differences in abundance between day and night vertical distributions that usually favoured night catches could only provide a relative indicator of avoidance. Night-time avoidance could not be evaluated. With the development of collocated net, acoustic, and optical techniques to study zooplankton

Table 4. Average percentage contribution of euphausiids to the estimated volume backscattering on EN487 oblique tows by depth stratum.

Depth	MOC2 on	MOC3 off
43 kHz		
190 – 150	96.64	86.40
150 – 100	96.64	87.63
100 – 50	81.35	79.55
50 – 25	89.82	53.71
25 – 0	46.11	52.59
120 kHz		
190 – 150	92.80	68.45
150 – 100	95.28	84.90
100 – 50	84.45	75.83
50 – 25	93.43	76.32
25 – 0	67.60	77.02
200 kHz		
190 – 150	81.44	47.71
150 – 100	95.73	85.93
100 – 50	94.62	79.10
50 – 25	90.98	86.02
25 – 0	67.87	87.19
420 kHz		
190 – 150	56.97	30.71
150 – 100	93.33	82.75
100 – 50	70.37	69.94
50 – 25	48.40	47.30
25 – 0	35.62	74.66

and nekton, independent qualitative, and in some cases with proper calibration, quantitative estimates of zooplankton abundance and biomass have become possible (Sameoto *et al.*, 1993; Simard and Sourisseau, 2009), so that both day and night net avoidance can be evaluated.

Previous studies of euphausiid net avoidance in the Gulf of St. Lawerence and Scotian Shelf have resulted in broadly similar findings to those found here. Simard and Sourisseau (2009) conducted a study in the Gulf of St. Lawrence of the diel changes in euphausiid abundance as estimated by acoustics and net collections, the latter augmented for some tows with a flashing strobe light. They did see euphausiids avoid the Bedford Institute of Oceanography Net and Environmental Sensing System (BIONESS; Sameoto *et al.*, 1980) during the daytime tows, as evidenced by the 120 kHz acoustic estimates of euphausiids, which were 3–6 times higher than the day net catches with no strobe. With a strobe light mounted on BIONESS turned on, the catches were increased by a factor of 10 and matched or exceeded the daytime acoustic estimates. Their findings differ from those of the present study for the night period in that the night-time BIONESS tow estimates were 15 times higher than the night-time acoustic estimates without the strobe on and, when turned on, the strobe light did not enhance the night-time net catches. In contrast, working on the Scotian Shelf, Sameoto *et al.*, (1993) found that BIONESS equipped with a light system caught 2–3 times more euphausiids during the night and 10–20 times more during the day when the light was on continuously.

The results of the present experiments described above demonstrate that the use of an LED-based strobe light causes a significant increase in biovolume of zooplankton caught in both the day and the night when large euphausiids dominate the biovolume. Total biovolume was significantly increased when the strobe light was

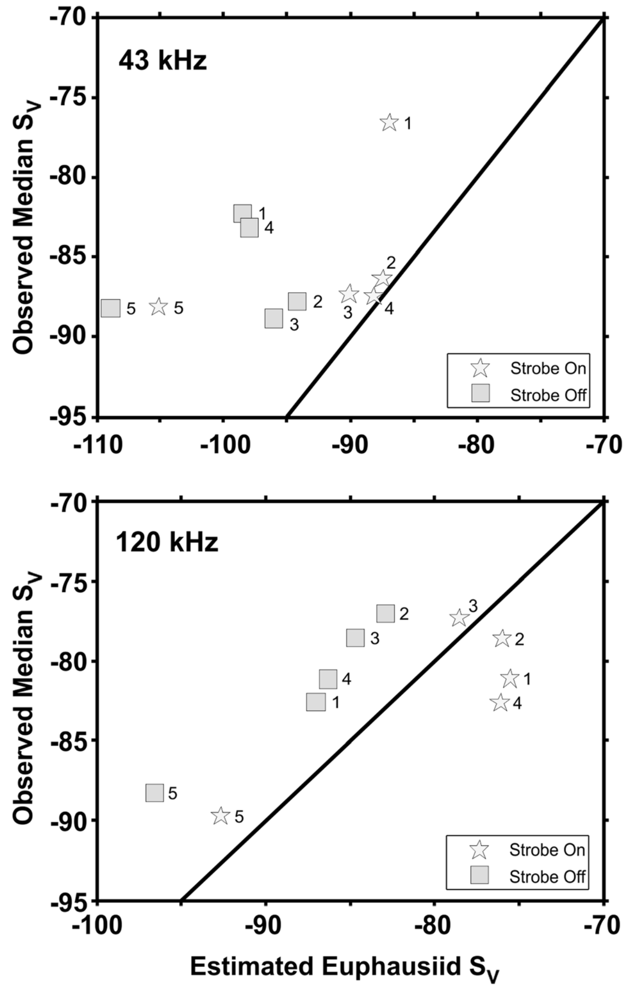

Figure 10. Results from the forward computations: comparison of the predicted volume backscattering strength, S_V, based on the euphausiids caught in the two "Endeavor" 487 MOCNESS night tows with median volume backscattering strength S_V from the collocated acoustics data for the same time intervals and range of depths of each net. Stars are for nets with the strobe on; squares are for nets with the strobe off. The numbers indicate the nominal depth strata sampled: 1, 190 – 150 m; 2, 150 – 100 m; 3, 100 – 50 m; 4, 50 – 25m; 5, 25 – 0 m.

being used, and this was due largely to the enhanced catch of euphausiids of size between 10 and 35 mm. Similar to Sameoto *et al.* (1993), the enhancement in catch of euphausiids was substantially higher during the daytime.

The tows on EN484 deliberately targeted acoustic layers for the experiments that were known from earlier net tows to have euphausiids present. The layers were dominated numerically by copepods, but the biomass was dominated by the euphausiids. The two oblique night tows made on EN487 were also dominated numerically by copepods, but euphausiids accounted for much of the biomass in all strata except the upper 25 m of the water column. While these two tows were separated by ~ 24 h and there was spatial variability in species abundance, the zooplankton community composition remained quite similar, and the results support the overall findings of the EN484 tows.

The collocated acoustic data enabled an evaluation of the extent to which animals might have been attracted to the light, thus

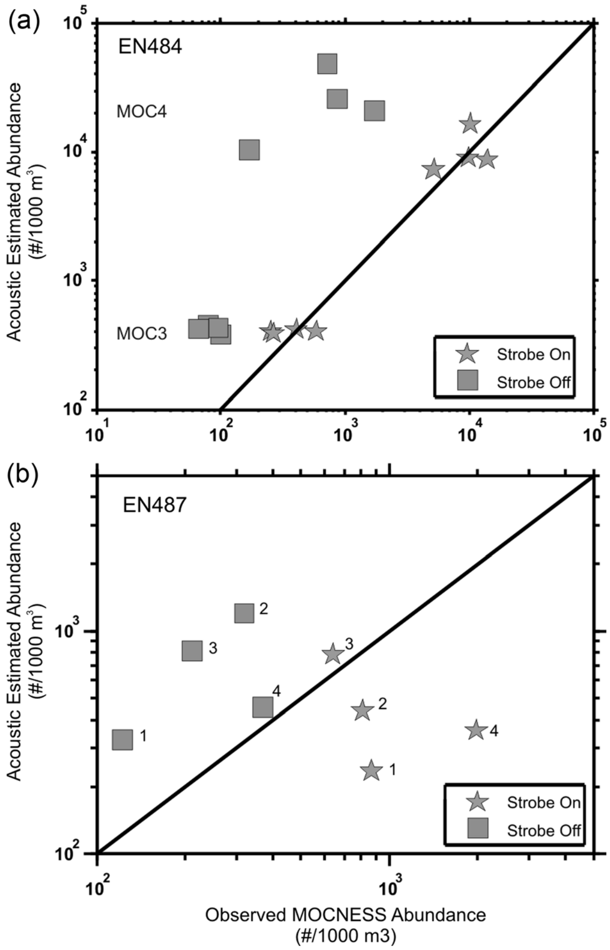

Figure 11. Results from the inverse computations: comparison of net measurements of abundance with the predicted number of euphausiids in each net based on the average individual target strength divided into the collocated measurements of volume backscattering at 120 kHz. (a) "Endeavor" 484 results from the night (MOC3) and day (MOC4) tows; (b) "Endeavor" 487 results for the two oblique night tows (MOC2 and 3); stars are for nets with the strobe on; squares are for nets with the strobe off. The numbers indicate the nominal depth strata sampled: 1, 190–150 m; 2, 150–100 m; 3, 100–50 m; 4, 50–25 m. Note the 25–0 m depth interval is absent from this plot because, on both tows, it did not have enough euphausiids to make a prediction.

enhancing their abundance when the strobe was on. The forward problem computations based on the MOCNESS collections demonstrated that euphausiids accounted for most of the volume backscattering, and, when the strobe was on, the acoustically measured backscattering closely matched the predicted values. In addition, using the average target strength of the euphausiids caught by the MOCNESS, inverse computations showed that with the strobe on, the acoustically predicted abundance values matched estimates based on the net catches. Were the strobe light attracting euphausiids, the net measurements of abundance would be expected to be higher than the acoustics, and hence both the forward problem and the inverse acoustic computations provide strong evidence that the euphausiids are not being attracted to the MOCNESS with the strobe light flashing. Additional support for the conclusion that a flashing or constant light on a moving net is not causing attraction is provided in Wiebe *et al*., (2004).

The cruises examined here represented a first opportunity to test the efficacy of this new strobe system, incidental to a larger study examining euphausiid ecology. Pulse width and flash interval differed between the two cruises examined and appeared to have little effect on catch efficiency, but these settings should be examined in more detail. Future targeted studies might also explore questions such as the impact on the strobe's enhancement of catches of net size and mode of towing (i.e. oblique vs. vertical), flash intensity, and the density of euphausiids present.

Additional support for the present findings comes from a 1/4 m^2 MOCNESS tow equipped with the LED strobe light that was taken in Saanich Inlet (Vancouver Island, Canada) in the afternoon on 28 June 2011 aboard the R/V "Centennial" during a Friday Harbor bioacoustics summer course field trip. On a horizontal tow between 80 and 100 m, nets were opened/closed with the strobe light on and off in random sequence. *Euphausia pacifica* was the dominant euphausiid present. The four nets with the strobe on caught an average of 3.1 times more biovolume and 4.5 times more euphausiids than did the four nets with the strobe off. These findings suggest that the strobe system can increase catch efficiency even for a net system with a much smaller mouth opening.

Together, the results from these different tests suggest that the new MOCNESS strobe light system significantly reduces the effects of net avoidance for the euphausiid species studied and reaffirms the results of earlier studies. The very good agreement between the net and acoustic measurements when the strobe light was on suggests that the euphausiids were caught in higher numbers not because they were attracted by the light to the net, but because the strobe light mitigates their avoidance reaction, probably because they were blinded by the bright light and thus could not see the net and avoid capture. The distribution and abundance of euphausiids that form aggregations or dense layers that are studied with standard nets without a strobe light system may be seriously underestimated.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of the paper. Supplementary Figure 1 is a silhouette photo of an aliquot of the sample from net 3 of EN484 MOCNESS tow 3 (strobe on). The sample is dominated by *Meganyctiphanes norvegica* and *Calanus finmarchicus*. The red lines indicate typical length measurements made on each individual (Standard length 3; Mauchline, 1980). Supplementary Figure 2 shows the vertical distributions of temperature and salinity where the strobe light experiments were conducted based on (a) EN484 MOC2 (26 September 2010) and (b) EN487 MOC2 (2 November 2010). The solid line is temperature; the dotted line is salinity.

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Inlet study mentioned in the Discussion of this paper was conducted as part of the summer 2011 Marine Bioacoustics course taught at the University of Washington's Friday Harbor Laboratories. Ship time and other logistics associated with the course were supported by a grant from the Office of Naval Research's Marine Mammals and Biology Program. Finally we thank the three anonymous reviewers for the positive and constructive reviews.

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