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Two of the most common crustacean zooplankton *Meganyctiphanes norvegica* and *Calanus* spp. produce sounds within the hearing range of their fish predators

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ABSTRACT



Sound is an effective channel for the transfer of information underwater. While it is known that fish and whales can use sound for communication, and as a cue to localise predators and prey, much less is known about sound production in invertebrates. Here we describe sounds produced by two of the most common marine crustacean zooplankton in the Northern hemisphere: Northern krill (*Meganyctiphanes norvegica*) and copepods (*Calanus* spp.). The recorded sounds were taxon-specific and within the hearing range of common planktivorous fish. We recorded similar sounds in the laboratory and in the field. In krill, the sound co-occurred with a tail flip, and the amplitude of the sound was correlated to the displacement distance of the animal, indicating a potential sound producing mechanism. Our findings highlight the possibility that zooplankton sounds could be used as a cue for their predators and for intraspecific communication.


ARTICLE HISTORY

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Introduction

Sound production in crustacean zooplankton has rarely been described (Giguère and Dill 1979) even though larger crustaceans are known to produce a variety of sounds during feeding (Meyer-Rochow and Penrose 1976; Tolstoganova 2002), during anti-predator behaviour (Henninger and Watson 2005; Bouwma and Herrnkind 2009; Staaterman et al. 2010; Hamilton et al. 2019) and for intraspecific communication (Buscaino et al. 2015; Jézéquel et al. 2019). Krill and copepods play a significant role in the ocean's carbon cycle, both as a key linkage between trophic levels, and as a carbon sink (Steinberg and Landry 2017; Cavan et al. 2019). They aggregate in large swarms that are exploited by fish, birds and marine mammals such as whales and seals, or penguins (Nicol and Rk 1985; Ritz 1994; Hamner and Hamner 2000; Tarling and Fielding 2016).

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Crustacean zooplankton are hard to locate visually, due to their small size, their transparent bodies and the limited visual range in water caused by light absorption, although a swarm of zooplankton is easier to spot than individual prey (Utne 1997; Utne-Palm 1999). Because light conditions are often far from optimal in the pelagic zone, it is an open question how predators locate zooplankton swarms at sea. Chemoreception has been shown to work on a shorter distance (Meagre et al. 2005), but sound has the potential to travel much further underwater than both light and chemical cues. Fish predators are known of being able to locate the direction of a sound source, which could be used to detect potential prey (reviewed in Popper and Hawkins 2019) and passive listening in cetaceans has been revealed to be one tool in the detection of prey fish (see review Gannon et al. 2005; Torres 2017). If zooplankton produce detectable sound it may explain how their swarms are located by predators. Further, there is a growing interest within fisheries to use passive acoustics to determine the presence and abundance of commercially relevant species (e.g. Rountree et al. 2006). Passive acoustics can also be used in management to monitor ecosystem health (Marques et al. 2013; Harris et al. 2015; Kaplan et al. 2015; Butler et al. 2016, 2017; Bolgan et al. 2018). Thus, detailed descriptions of taxon-specific sound characteristics are desired for the development of passive acoustic monitoring methods as a non-invasive way to determine the presence of a species below the sea surface.

Methods

Study location

All field and lab recordings were conducted at the Institute of Marine Research's fish farm facility in Smørdalen, Masfjorden, Norway (6052'0951"N; 533'0609"E), between 15 September and 31 October 2018. Masfjorden is a 20 km long fjord, divided into three basins with a maximum depth of 200 m. The study location is in the inner basin, here the fjord is 1 km wide and 150 metres deep.

Study species

The predominant krill and copepod species found in our study area is the Northern krill (*Meganyctiphanes norvegica*; Giske et al. 1990; Onsrud and Kaartvedt 1998) and *Calanus finmarchicus* (Calanoida, Copepoda), respectively (Giske et al. 1990; Balino and Aksnes 1993). Krill and copepods were caught using light traps (Figure 1) during dark hours (6 pm to 8 am). The light intensities of the diving torches used in the light traps were between 1,200 and 12,000 mW/m² (TriOS Ramses spektrometer, TriOS Mess- und Datentechnik GmbH, Rastede, Germany). The light traps were positioned at ca 340 m distance to shore towards the centre of the fjord (6052'0951"N; 533'0609"E) at ca 130 m depth. The light traps were pulled upwards at a speed of approximately 0.5 m s⁻¹ to avoid physical and physiological damage or behavioural effects due to a fast pressure change from the deep to the surface. In general, we did not expect an influence of the decreased pressure at the surface on the experimental animals because zooplankton exhibits diel vertical migration (Nicol

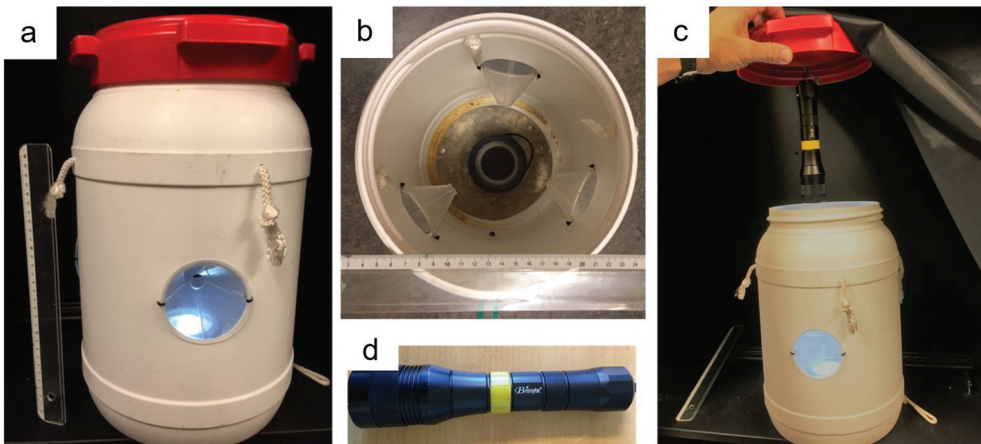


Figure 1. Light trap. a. Made from a 20-litre barrel of high density polyethylene (CurTec, 68 Lombard Street, London, EC3V 9LJ, UK), with three circular openings holding a transparent funnel (outer opening 75 mm, inner 16 mm). The transparency enhances light penetration and the organism's attraction to the funnel opening. Inside the barrel. b. We see the three funnels on the sidewalls. On the bottom there is a raised (50 mm above bottom) drainage pipe covered with plankton mesh (180 μm). The latter is raised 5 cm off the bottom to avoid full drainage of water when lifted out of water. Further, surrounding the drainage pipe there is an aluminium reflector that enhances the spreading of light from a diving torch fastened on the inside of the lid. c. Diving torch. d. a Brinyte DIV01 (Hongkong Yeguang Co., Ltd, Shenzhen, China). Trap designed by Sjur Blænes.

1986; Basedow et al. 2019) with measured swimming speeds of $\sim 0.1 \text{ m s}^{-1}$ towards the surface (Klevjer and Kaartvedt 2011). Animals caught in the trap were carefully poured from the light trap and into a holding tank (a 70-litre transparent plastic tank filled with seawater), where they were maintained (≤ 48 hours) at natural temperature ($10 \pm 2.5 \text{ }^\circ\text{C}$) at dim light until used in experiments. Salinity in the holding tank was checked daily and maintained at 30 ± 2 sal ppt. We observed that the mortality of the caught animals was less than 1%.

Recording sounds and behaviour in the laboratory

Experiments were conducted during the day (9 am to 4 pm) under natural and artificial light in Smørdalen station. *M. norvegica* individuals were carefully transferred to the experimental tank (a transparent plastic box of $17 \times 21 \times 11$ cm, 3.9 L) filled with seawater ($9.3\text{--}13.8^\circ\text{C}$ 30 ± 2 sal ppt). After 30 min acclimation, the krill's sound and behaviour were recorded for 5 minutes by the use of a hydrophone (HTI-96-Min Hydrophone, Wildlife Acoustics, Inc., Maynard MA, USA) (Max $-165 \text{ dB re } 1 \text{ V}/\mu\text{Pa}$) and a video camera (GoPro Hero 4, GoPro Inc, San Mateo, USA). The gain of the hydrophone was set to 36 dB or 24 dB, depending on the ambient noise level. Only recordings with 36 dB gain ($n = 22$) were used for the analysis of amplitudes of the dominant frequency, while the 24 dB gain ($n = 3$) recordings were additionally used for the frequency, sound pressure level and zero-to-peak sound level analysis. The video camera was placed above the

experimental tank. A 1×1 cm grid was placed underneath the transparent tank bottom to assess from the video recording the size of a sound producing krill, its behaviour distance and its distance to the hydrophone when a certain behaviour was initiated. The effect of krill numerical density on their sound production of krill was examined by stepwise adding conspecifics (range 14–109 individuals, equivalent to 4–30 ind/L) to the experimental tank. The same experimental setup was used for copepods as for krill. The experimental tank water temperature ranged from 12.8°C to 13.8°C. All sound recordings for copepods (estimated range 300 to 2,000 individuals, equivalent to 83 to 556 ind/L) were done with a gain of 36 dB.

Recording sounds in the field

To record krill and copepod sound in the field we used a metal frame equipped with three white light diving torches (each with an intensity of $12,000 \text{ mW/m}^2$) to attract krill and copepods, a hydrophone (HTI-96-Min Hydrophone) and a GoPro (Hero 4) camera to

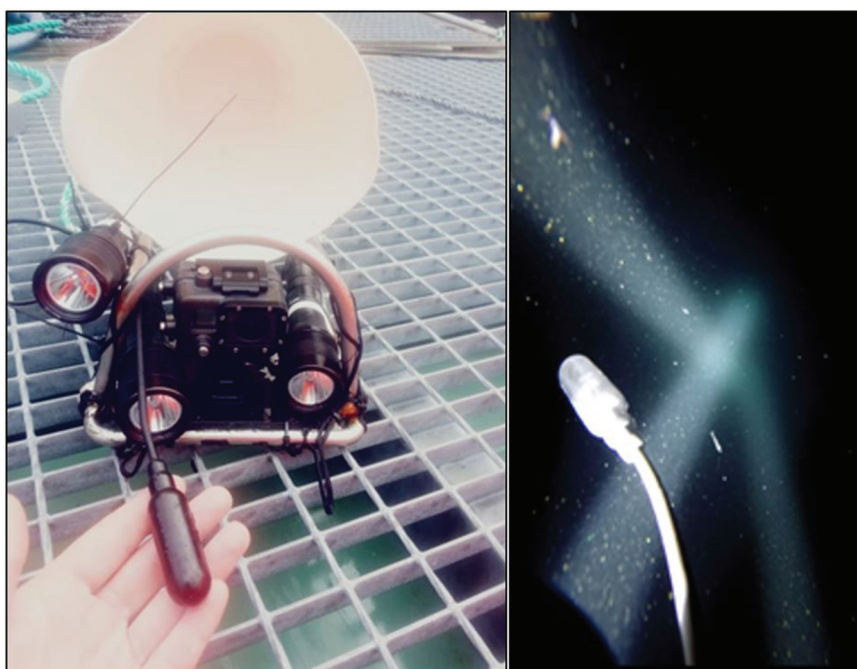


Figure 2. Field recording rig to record krill and copepod sound and behaviour/presence in the field. Left photo: the rig consists of a metal frame (19 x 29 x10 cm made of 10 mm diameter galvanic pipe), which was equipped with three white diving torches (of intensity $12,000 \text{ mW/m}^2$), a hydrophone (HTI-96-Min Hydrophone, Wildlife Acoustics, Inc., Maynard MA, USA) and a GoPro camera (Hero 4, GoPro Inc, San Mateo, USA). Right photo: video image during field recording, where one can see the hydrophone and some krill, copepods and other plankton in the light beam.

record individual krill and copepod sound and movement (Figure 2). The hydrophone had a 20-metre cable (Sensitivity: -165 dB re 1 V/ μ Pa, for more details see previous section), which enabled us to record during night when krill ascend to shallower water (ca. 15 m depth).

Analysis of sounds and behaviours

All sounds were analysed in *Praat* version 6.0.43 (Boersma and Weenink 2001). For the analysis of the laboratory and field recordings, we selected all sounds that had a signal-to-noise ratio (the ratio between the sound pressure of the signal towards the background noise) higher than 2 (Figure 3). Krill sounds were analysed from the unfiltered recordings (frequency range 5–24,000 Hz).

For krill, occurrences of behaviours (from video) and sounds (from sound recordings) were noted separately to avoid observer bias towards a link between certain sounds and behaviours. Afterwards the sound and video files were synchronised in *Blender* v2.79 (Output: FFmpeg, AC3 Audio Codec). For all sounds found in the recording we noted whether or not they overlapped with a specific behaviour, and vice versa, for all specific behaviours seen on the videos we noted whether or not it overlapped with a sound. Finally, all sounds that co-occurred with the

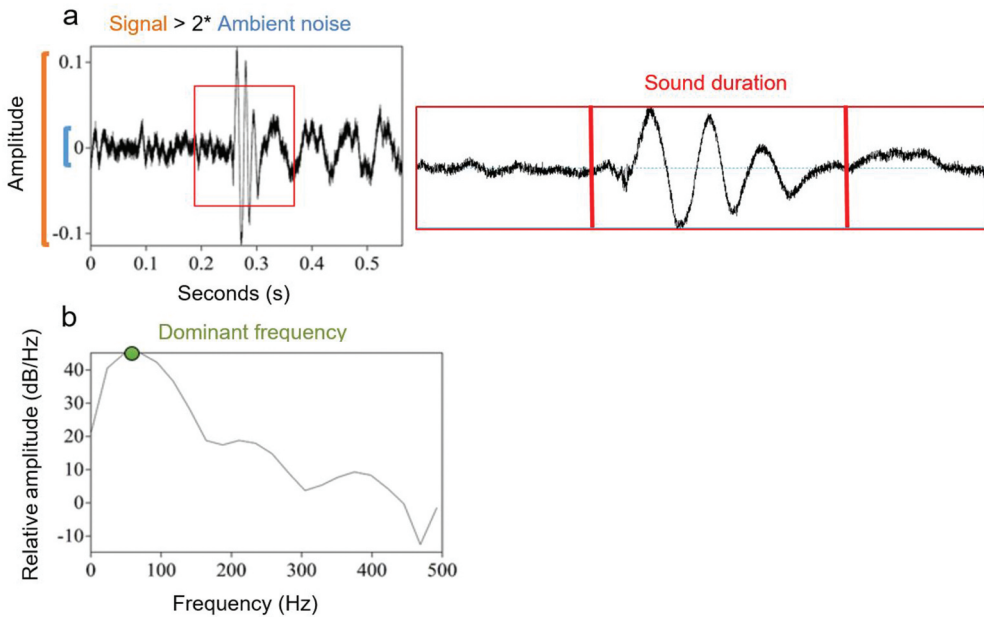


Figure 3. Extraction Sound characteristics. (a) Sound wave with the amplitude on the y-axis and the time in seconds on the x-axis. We selected all sounds that had a signal (orange bracket)-to-noise (blue bracket) ratio higher than 2. The red box shows how we extracted the duration of the sounds. Sound duration (red bracket) was measured from the first to the last zero crossing (red lines) of the sound. (b) Spectrum representing the energy at different frequencies with the relative amplitude (dB/Hz) on the y-axis and the frequency (Hz) on the x-axis. The green dot represents the dominant frequency, the frequency at the maximum amplitude.

behaviour of an individual krill were analysed. Additionally, the video was used to measure the length (mm, from the eyes to the end of the telson) of the krill that performed any behaviour, and the distance over which it performed its behaviour. Further, the distance (mm) between the centre of the hydrophone to the centre of the krill's carapax, was measured at the start of each behaviour.

The copepod sound recordings were filtered in the low frequency domain to reduce noise with an integrated Hann band-pass filter in *Praat* (Filter specifications: 250 Hz to 12,000 Hz; Smoothing = 10). We extracted the frequency range of each sound (signal/noise ratio of 2 or higher; [Figure 3a](#)) at 3 dB below the dominant frequency taken from the frequency spectrum (spectral slice; total width = 2 ms). Due to limitations in our video resolution, we could not relate copepod sounds to distinct behaviours in our videos.

We made seven field recordings (~2 hours). From each hydrophone recording we extracted 20 minutes that coincided with a high number of krill and copepods in the synchronised camera view. We extracted single krill and copepod sounds from the field recordings.

All krill and copepod laboratory and field sounds were further analysed for sound duration (s), energy (dB/Hz), the frequencies of all harmonics and the dominant frequency. Sound duration was measured from the first to the last zero crossing of the sound. The hydrophone's sensitivity was checked by a comparison with a calibrated B&K 8103 hydrophone and found to be within 3 dB from the factory specified sensitivity. Therefore, we used this sensitivity to calculate absolute sound levels (-165 dB re 1 V/ μ Pa).

Statistical analysis

All statistics were performed in R version 4.1.2 (R Development Core Team 2021). Plots and figures are based on the package *ggplot2* (Wickham 2016). Confidence Intervals of the median or the mean (95%) were calculated on the bootstrap-based function *MedianCI* and *MeanCI* from the package *DescTools* in R (Signorell 2021). We extracted the sounds from the recordings and calculated the sound pressure level (function 'rms' in package 'Seewave'; Sueur et al. 2008) and the zero-to-peak sound level. We used a linear regression model in R (function 'lm') to test for the relation between the relative number of behaviours per minute and the number of krill in the experimental tank. Here, a logarithmic transformation was applied to the response variable to obtain a normal distribution. We used a linear regression model to study the effects of the distance of the tail flip, krill size, distance to the hydrophone on the amplitude of the dominant frequency (function 'lmer' in package "lme4"; Bates et al. 2015). The model selection took place in a stepwise analysis suggested by Zuur et al. (2009). A random intercept model structure was chosen for each behaviour video (= trial). The optimal model was chosen based on the lowest Akaike's information criterion (AIC), and the fewest parameters if Δ AIC < 2 (Burnham and Anderson 2002). We included a null model for comparison in which all fixed x variables were excluded. The final model's assumptions were checked for normality, linearity, and homoscedasticity

(homogeneity of variances) by using residual plots and histograms. Because of non-normal distribution of the frequency and sound duration of *M. norvegica* and *Calanus* spp., a Mann-Whitney U test was applied to test differences of the two sampled populations. This was done with the function *wilcox.test* in R. Amplitudes were distributed normally. We analysed the differences in the zero-to-peak sound levels with the function *t.test* in R.

Results

Krill sounds and visual behaviours

We conducted 25 replicate tank experiments with krill, giving a total of 125 min with records of krill sound and behaviour. We recorded a low-amplitude *click*-sound that co-occurred simultaneously with a tail flip behaviour in krill. Tail flips consisted of a powerful straightening of the body leading to a displacement of the whole animal, which is known to be a common anti-predator or escape behaviour in krill (e.g. Kils 1981; O'Brien 1987; Abrahamsen et al. 2010). In our laboratory set-up, tail flips were performed by one individual at a time. In 125 minutes of video and sound recordings we observed a total of 971 individual krill (25 groups) that performed a total of 169 tail flips and produced 174 sounds. In the synchronised video and sound recordings, we found that 86% (145 of 169) of the tail flips co-occurred with a sound and 83% (145 of 174) of the sounds co-occurred with a tail flip that could

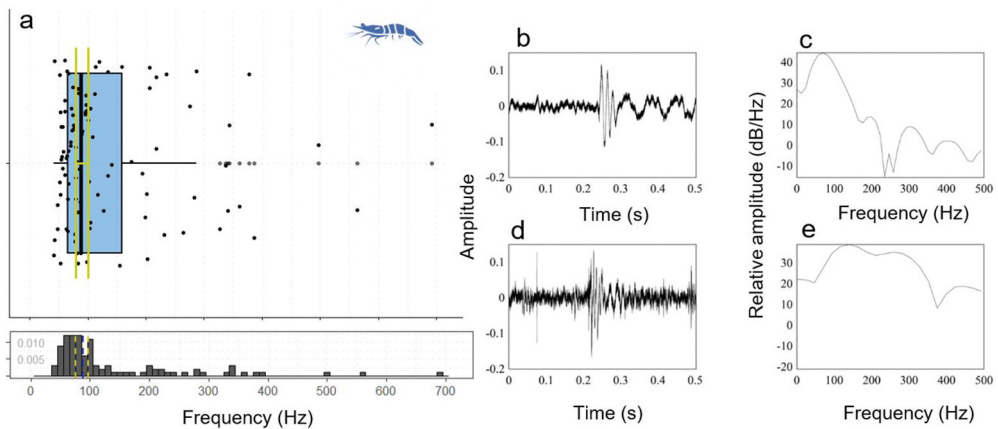


Figure 4. Krill sound characteristics recorded in the lab (a, b and c) and the field (d and e): a. Box plot of the dominant frequencies of the analysed sounds with frequency (Hz) on the x-axis. The box represents the interquartile distance, the black vertical line, the median and the jitter dots the original data. The yellow vertical lines show the limits of the 95% confidence intervals of the median. The histogram presents the distribution of the sounds over the frequencies, with the blue line at the median. b. Sound wave with the amplitude on the y-axis and the time in seconds on the x-axis. c. Spectrum representing the energy at different frequencies with the relative amplitude (dB/Hz) on the y-axis and the frequency (Hz) on the x-axis. d. An example of a sound wave, with the amplitude on the y-axis and the time in seconds on the x-axis. e. Its spectrum, representing the energy at different frequencies with the relative amplitude (dB/Hz) on the y-axis and the frequency (Hz) on the x-axis, extracted from the field recordings.

be attributed to an individual krill. Only these 145 attributed sounds were used for the analyses of sound characteristics. We excluded a further 44 sounds with a signal-to-noise ratio lower than 2:1, which left us with 101 sounds for the analyses. The median dominant frequency of the krill sounds was 87.92 Hz (95% CI 74.94–96.40 Hz; $n = 101$; [Figure 4a](#)) with most of the energy found at lower frequencies ([Figure 4a,c](#)). The median duration of a krill sound was 17 milliseconds ($n = 101$; [Figure 4b](#)). Ninety percent (91 out of 101 observations) of the sounds had their peak frequency at the first harmonic ([Figure 4c](#)). The energy of the dominant frequency decreased with distance to the hydrophone by 0.05 ± 0.015 dB (estimate \pm SE) per mm (LMM; $n = 79$; $t = > -3.174$; $p = 0.002$). The mean sound pressure level (SPL) of a single sound was 105 dB re 1 μ Pa (95% CI: 104–107 dB re 1 μ Pa; $n = 101$) and the zero-to-peak sound level was 114 dB re 1 μ Pa (95% CI: 113–115 dB re 1 μ Pa; $n = 83$) recorded in the laboratory at maximum distances of 23 mm to the hydrophone. The mean SPL of the ambient sound in the experimental tanks was 91 dB re 1 μ Pa (95% CI: 89–94 dB re 1 μ Pa; $n = 20$; frequency range 20–24,000 Hz). In our field recordings, we found sounds that were similar in frequency, waveform and amplitude (SPL 108 dB re 1 μ Pa; see sound presented in [Figure 4e-d](#)) to our laboratory recordings. The mean SPL of the ambient sound in the field was 95 dB re 1 μ Pa (95% CI: 94–96 dB re 1 μ Pa; $n = 10$; ambient field sound from [Figure 4e-d](#)).

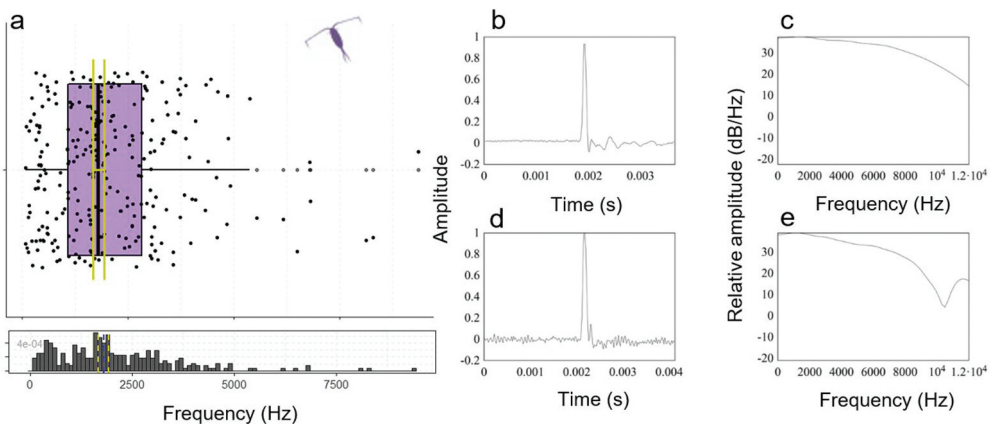


Figure 5. Copepod sound characteristics- recorded in the lab (a, b and c) and the field (d and e): a. Box plot of the dominant frequencies of the analysed sounds with frequency (Hz) on the x-axis. the box represents the interquartile distance, the black vertical line the median and the jitter dots the original data. the yellow vertical lines show the limits of the 95% confidence intervals of the median. the histogram presents the distribution of the sounds over the frequencies, with the blue line at the median and the yellow lines indicating the interquartile range. b. Sound wave with the amplitude on the y-axis and the time in seconds on the x-axis. c. Spectrum representing the energy at different frequencies with the relative amplitude (dB/hz) on the y-axis and the frequency (Hz) on the x-axis. d. an example of a sound wave, with the amplitude on the y-axis and the time in seconds on the x-axis, and e. its spectrum, representing the energy at different frequencies with the relative amplitude (dB/hz) on the y-axis and the frequency (Hz) on the x-axis, extracted from the field recordings.

Copepod sounds

In total, we conducted four replicate tank experiments with copepods, making up 20 min with records of copepod sounds. From these 20 minutes, 100 sounds were extracted. The sound recorded from copepods of the genus *Calanus* spp., was a low amplitude *cracking-click* sound. The median dominant frequency of the sound was 1657 Hz (95% CI: 1569 – 1735 Hz; n = 99), but the energy decreased gradually towards lower and higher frequencies rather than showing a clear peak. The dominant frequency range (upper 3 dB) ranged on average from 491 Hz to 3025 Hz (minimum: 95% CI: 385–549 Hz; n = 73; maximum: 95% CI: 2880–3229 Hz; n = 100; [Figure 5a,c](#)). The sounds had a median duration of 2.5 milliseconds (n = 100; [Figure 5b](#)). The mean SPL of a single sound was 104 dB re 1 μ Pa (95% CI: 103–105 dB re 1 μ Pa) and the zero-to-peak sound level was 118 dB re 1 μ Pa (95% CI: 116–119 dB re 1 μ Pa) recorded in the laboratory. The mean SPL of the ambient sound in the experimental tanks was 87 dB re 1 μ Pa (95% CI: 86–87 dB re 1 μ Pa; n = 10). We found copepod sounds in the field recordings that were similar in frequency, waveform and amplitude (SPL 115 dB re 1 μ Pa; see sound presented in [Figure 5e-d](#)) to the sounds recorded in the laboratory. The SPL of the ambient sound in the field was 99 dB re 1 μ Pa (95% CI: 98–101 dB re 1 μ Pa; n = 10; ambient field sound from [Figure 5e-d](#)). We did not control the exact number of copepods in the tank experiments nor in the field, thus we could not calculate the effect of density on the sound production.

Comparisons between krill and copepod sounds

Krill sounds were longer in duration (Wilcoxon signed rank test; n = 201; W = 213.5; p < .0001) and had a lower dominant frequency range (Wilcoxon signed rank test; n = 201; W = 10,096, p < .001) than copepod sounds. Copepods sounds had higher zero-to-peak SPL compared to krill sounds (Welch's *t*-test; n = 201; t = 5.4785; p < .001).

Details on the krill's tail flips

The optimal model chosen for the analysis is shown in [Table 1](#). Krill size ranged from 10 to 35 mm with a mean of 19 mm. The tail flip distance ranged from 10 to 38 mm (IQ) with a median of 20 mm. We found that larger krill performed tail flips over slightly longer distances (LM; n = 96; t = 2.043; p = 0.0439; [Figure 6a](#)). Tail flip distance had a weak positive linear relationship to sound amplitude (dB;

Table 1. Best fitting model. Response variable was the energy level of the dominant frequency. In this model comparison, we tested the effects of the distance to the hydrophone (DH), the krill size (KS) and the tail flip distance (TFD) on the energy level. The NULL model is shown for comparison without fixed variables. The best fitting model is shown in bold.

Model	Intercept	Df	LogLik	AIC
NULL	38.04	3	-292.08	590.2
~DH + KS + TFD	37.31	6	-268.63	549.26
~DH + KS * TFD	39.34	7	-268.50	551.00
~DH + TFD	40.38	5	-272.20	554.41

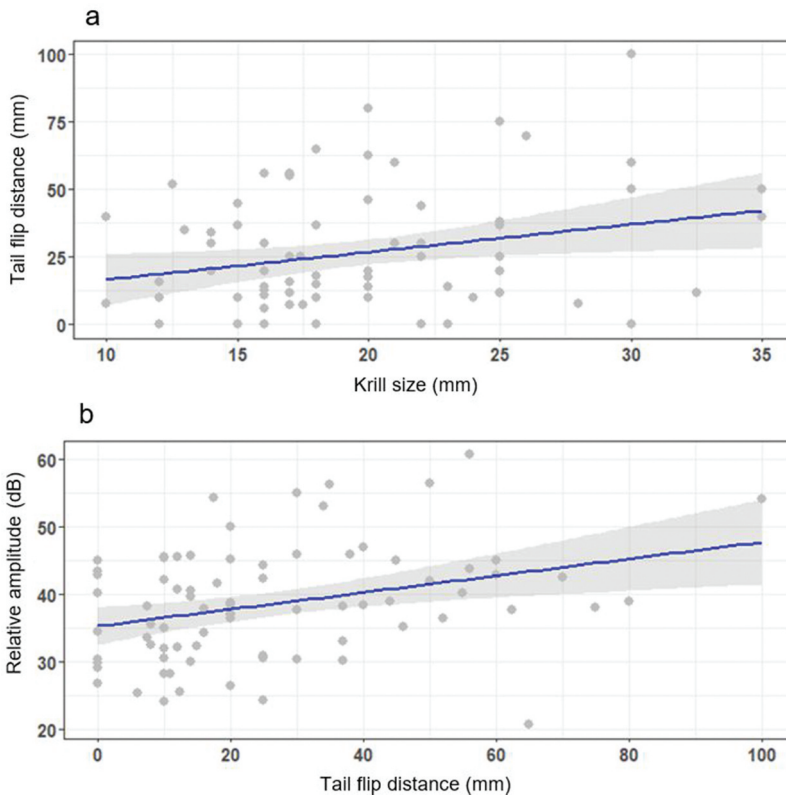


Figure 6. Relationship between tail flip and krill characteristics. a. Relationship between the tail flip distance and krill size. Adjusted R -squared: 0.032. b. Relationship between the relative amplitude of the dominant frequency and the tail flip distance. Adjusted R -squared: 0.333. The grey dots present single data points. The green area around the regression line represents the 95% confidence interval.

LMM; $n = 79$; $t = 2.591$; $p = 0.012$; [Figure 6b](#)). The distance to the hydrophone had a negative linear relationship to sound amplitude (dB; LMM; $n = 79$; $t = > -3.174$; $p = 0.002$).

Krill density and tail flips

The relative number of sound producing tail flips per minute increased with 0.37 tail flips per added individual krill in the range of 3.8 to 30.2 ind/L (LM; $n = 20$; $t = 2.743$; $p = 0.0134$). Most tail flips (69%) occurred after at least one conspecific directly touched the krill, while 31% of the tail flips occurred without any physical contact to a neighbouring krill. No tail-flips were observed at krill densities below 1.4 ind/L (SK, personal observations).

Discussion

From both field and laboratory studies we here present novel data on sounds produced by free-swimming krill and copepods, the two most numerous crustacean zooplankton taxa. We show that the sounds are taxon-specific and that they are recognisable in field

recordings. Nicol (1986) reported *M. norvegica* surface swarms with up to 41,000 individuals m^{-3} (~ 10 ind/L). In Norwegian waters we find large areas ($>1000 \text{ km}^2$) of swarming *Calanus spp.* at densities of 10,000 individuals m^{-3} (Basedow et al. 2019). The number of krill and copepods attracted towards the light was most likely less than observed swarm densities in literature. Further, these krill and copepod sounds fall within known hearing ranges of commercially important fish species (Popper and Hawkins 2019). In a following section we will further discuss zooplankton sound detection by fish.

Sound production and associated behaviour

Here we show that the anti-predator or escape tail flip behaviour is a likely sound producing mechanism in krill, because sounds predominately co-occurred with tail flips and vice versa ($\geq 83\%$ of the time). Tail flips only occurred at densities ≥ 1.4 ind/L and were most often (69% of the times) induced by physical contact with other individuals. Other studies show that tail flips can also be induced by the presence of predators (O'Brien 1987; Abrahamsen et al. 2010). Our measurements of sounds produced by free-swimming *Calanus spp.* are similar to Giguère and Dill (1979) findings for freshwater copepods, *Diaptomus spp.* Their study showed that copepods glued to a probe produced sounds with frequencies between a minimum of around 500 and a maximum of around 1200 Hz. We could not correlate copepod sounds to visual behaviour due to the small size of the copepods on our videos, however, leap or escape movements are also commonly observed in copepods (Strickler 1975; Abrahamsen et al. 2010). Yen and Strickler (1996) showed that copepods leave conspicuous hydrodynamic cues during such escape jumps. This suggests that the sounds recorded in the present study may have been produced by escape jumps in copepods as well as in krill.

Potential for detection by predatory fish

We recorded sounds in the field that had the same waveform as the sound produced by krill and copepods in the controlled lab recordings. Thus, the recorded zooplankton sounds are audible over the ambient sound in the sea at distances to the sound source as recorded in our laboratory setup. Copepods are the main prey of fish larvae. Krill and copepods are important prey to numerous fish species found in the northern hemisphere (e.g. cod (*Gadus morhua*), poor-cod (*Trisopterus minutus*), pollock (*Pollachius pollachius*), saithe (*Pollachius virens*); (Salvenes and Nordeide 1993); herring (*Clupea harengus*) and mackerel (*Scomber scombrus*; Darbyson et al. 2003). Field studies on teleost fish hearing capabilities have revealed highest sensitivity at low frequencies. For example, the hearing thresholds for cod and pollock are lowest below 400 Hz (Figure 7; Chapman 1973; Chapman and Hawkins 1973). Herring (*Clupea harengus*), also has a low hearing threshold at higher frequencies (Enger 1967). All these species may be capable of detecting the sounds emitted by *M. norvegica* and *Calanus spp.* For example, at night when vision is limited, sprat schools disperse and continue to

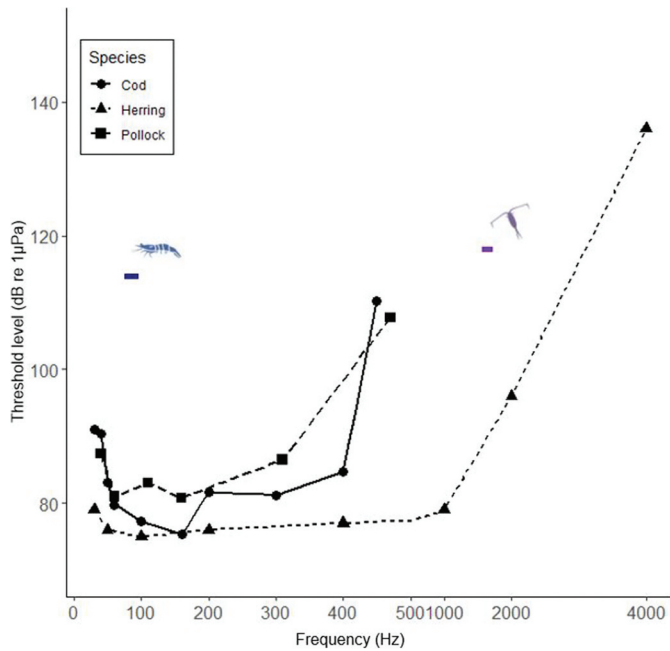


Figure 7. Audiograms for Cod ● (Chapman and Hawkins 1973), Herring ▲ (Enger 1967) and Pollock ■ (Chapman 1973). Threshold levels (dB re 1 μ Pa) are shown on the y-axis and the frequency (Hz) on the x-axis. The blue horizontal line shows the mean zero-to-peak sound level of a single krill sound (see Results krill) between the 95% CI 74.94 to 96.40 Hz. The purple horizontal line shows the mean zero-to-peak sound level of a single copepod sound between the peak frequency range 95% CI 1569.40 to 1735.51 Hz (see Results copepods).

prey on small invertebrates including calanoid copepods (Knudsen et al. 2009; Hawkins et al. 2012). Sprat hearing capabilities are known to be similar to that of herring (Allen et al. 1976) and behavioural reactions of sprat to sound are evident (Hawkins et al. 2014), which suggests sprat could also be a good candidate to use acoustic localisation of zooplankton swarms.

The sounds we recorded from individual zooplankton were above fish hearing thresholds, but of comparatively low amplitude (Figure 7). Therefore, it is unlikely that a single zooplankton can produce sufficient sound levels to be detected by predators over large distances. It remains to be tested whether sound levels will increase substantially due to additive effects when many sounds are produced in a swarm simultaneously.

Although most fish detect the particle motion of a sound wave, rather than sound pressure (e.g. Popper and Hawkins 2019), we measured sound pressure levels in our experimental setup, because there are currently no commercially available sensors to measure particle motion small enough for our zooplankton-recording set-up. Therefore, we only included audiograms for fish that are at least partly sensitive to sound pressure (Figure 7). However, future studies should focus on the sound production of zooplankton in the field and the propagation of particle motion with increasing distance from the source.

Potential for intraspecific communication

Even though the sounds we recorded may be an unintentional by-product of the anti-predator or escape behaviour in crustacean zooplankton, it could also act as signal for intraspecific communication. Sound is used for intraspecific communication in a large range of taxa, including crustaceans (e.g. Slabbekoorn et al. 2010; Radford et al. 2014; Sabet et al. 2015; Simpson et al. 2016). Crustacean zooplankton, and crustaceans in general, are thought to detect particle motion through mechanoreception by hair-like structures, the setae cells (Weatherby and Lenz 2000; Popper et al. 2001). The propulsion jets and jet-like flow fields by Antarctic Krill (*Euphausia superba*) and North Pacific Krill (*Euphausia pacifica*) are hypothesised to play a role in locating conspecifics (Wiese and Ebina 1995; Yen et al. 2003). Thus, jets from tail flips might give vital information to neighbouring individuals that may lead to coordinated escape responses that are found in swarming krill (O'Brien 1987). Interestingly, the frequency sensitivity of the appendages of *Calanus finmarchicus* (Newbury 1972) overlaps with present description of *Calanus* spp. sound. Thus, these sounds could as well be used for intra-specific communication in copepods.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

Data availability statement

All data are included in the supplementary material. Original recordings can be obtained from the authors.

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