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Diel patterns of fish activity in the Vistula Lagoon's littoral zone: integrating acoustic and net fishing methods

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Abstract

The study investigated summer diel variability in fish abundance and movement within a highly eutrophic Baltic lagoon, with a focus on horizontal migrations between reed beds and open water. A combination of multibeam ARIS sonar and traditional net fishing was employed, allowing for continuous, non-invasive monitoring of fish behaviour alongside assessments of species composition and size structure. The dominant species caught included roach, bleak, silver bream, and juvenile perch. Acoustic recordings revealed consistently higher fish activity during the day compared to the night, with activity elevated during the full moon relative to the new moon. Morning migrations to open water were observed, whereas mass evening migrations back to the reed beds occurred only once. The study suggests the presence of reverse migration patterns, potentially driven by improved visibility at night and predation pressure from sander.

Keywords

Vistula Lagoon; Sonar ARIS; Horizontal fish migrations

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1. Introduction

Diel horizontal migration (DHM) of fish is commonly observed in shallow aquatic ecosystems (Gliwicz and Jachner, 1992; Muska et al., 2013). These migrations primarily involve planktivorous and predatory fish, driven by the need to find food and avoid predation. Generally, the offshore zone is considered the most attractive in terms of food availability but also entails the highest predation risk (Gliwicz et al., 2006). To minimize this risk, filter-feeding crustaceans migrate toward the pelagic zone at dusk. They are followed by schools of planktivorous fish, and subsequently by predatory fish that hunt them. At dawn, the direction of these movements reverses, with most migrants heading toward the littoral zone. The near-shore, vegetated area offers poorer food conditions but better shelter from predators. While this general pattern is widely recognized, exceptions occur depending on species, developmental stage (Gliwicz and Jachner, 1992; Vasek and Kubecka, 2004; Järvalt et al., 2005), water transparency (Jeppesen et al., 2006; Horppila et al., 2018), habitat complexity (Pekcan-Hekim et al., 2010), lunar phases, seasonal changes, water temperature, and atmospheric pressure (Imbrock et al., 1996; Gaudreau and Boisclair, 2000), all of which influence the metabolic rate of ectothermic fish.

These factors make diel fish migrations unique to each water body. Although fish migration mechanisms are relatively well understood in lakes, they remain poorly studied in brackish temperate coastal lagoons, which provide a range of ecosystem services that support both biodiversity and local communities. The low salinity in these lagoons primarily supports fish typical of both lakes and estuarine river sections. However, salinity levels are sufficient to negatively affect some freshwater cladocerans (Moss, 1994; Kornijów et al., 2020; Karpowicz et al., 2023). Consequently, zooplankton – the primary food source for planktivorous fish – is often dominated by the dominant copepod species in coastal lagoons, which tend to exhibit vertical rather than horizontal migrations. The study of these migration patterns in temperate climate lagoons is still poorly understood (Bollens et al., 1992, Cervetto et al., 1995, Wasserman et al., 2014), and in the littoral zone, due to shallow depths and strong wind-driven water mixing, it is even more difficult to assess.

Since copepods are much smaller than cladocerans, fish require more light to detect their prey. Therefore, we hypothesize that:

1. Fish will be more active during the day than at night.
2. Fish activity will be higher during the full moon than the new moon.
3. Predator-prey interactions under variable light conditions drive synchronized diel horizontal migrations, with organisms shifting toward the pelagic zone at sunset and the littoral zone at sunrise.

To test these hypotheses, we studied diel fish activity in the Baltic Vistula Lagoon, focusing on horizontal migration between the littoral reed beds and open water under different lunar phases. We used gillnets alongside multibeam sonar ARIS (Adaptive Resolution Imaging Sonar), an acoustic camera capable of producing high-resolution images that visualize fish swimming behaviour (Morsund et al., 2003; Martignac et al., 2015). Because ARIS relies on sound, it is well-suited for turbid environments and night observations. However, like other acoustic devices, its species identification capacity is limited, so we supplemented acoustic data with net catches to determine species composition. This combined approach allowed continuous, non-intrusive monitoring of fish behaviour by means of sonar, while nets provided species, size structure, and movement direction data.

Understanding the DHM mechanisms within brackish lagoons is crucial, as they serve as nurseries, feeding grounds, and migratory corridors for numerous fish species. Insights into how factors like light, salinity, food availability, and predation pressure influence fish migrations enable more effective population management and conservation of these dynamic habitats.

2. Material and methods

2.1 Study area

The Vistula Lagoon is a shallow coastal water body located in the southeastern part of the Baltic Sea. The lagoon has a strongly elongated shape with the NE-SW orientation and is separated from the Baltic Sea by a narrow sandy spit. The total area of the lagoon is 838 km^2, with an average depth of 2.5 metres (maximum 5.2 metres). During the period of our study, the exchange of water between the lagoon and the Baltic Sea was possible only through the Piława Strait located in the northern part of the Vistula Spit. The salinity of the water varies spatially from approximately 6.5 PSU to less than 1 PSU, increasing towards the east. In the south-central part of the lagoon studied in this publication, salinity most often ranges between 1.4 and 3 PSU (Pawlikowski and Kornijów, 2019). The lagoon's expansive surface area and shallow bathymetry drive persistent sediment resuspension, maintaining turbidity levels that limit Secchi depth visibility to 40 cm. This light-limited environment shapes distinct vegetation patterns: emergent species form extensive but fragmented belts along margins, while submerged macrophytes are sparse, appearing only as isolated patches in shallow areas approximately 1 metre deep (Kornijów, 2018; Pawlikowski and Kornijów, 2019). The ichthyofauna of the lagoon is composed mostly of freshwater species, with dominance of roach (*Rutilus rutilus*), bream (*Abramis brama*), perch (*Perca fluviatilis*), and sander (*Sander lucioperca*). Typical marine species such as flounder (*Platichthys flesus*), turbot (*Scophthalmus maximus*), and Atlantic herring (*Clupea harengus*) are found in the lagoon only occasionally, as a result of irregular food migrations or spawning (Psuty-Lipska and Borowski, 2003; Psuty and Wilkońska, 2009; Kornijów, 2018).

The research covered the reed bed in the southwestern part of the Vistula Lagoon (54.33°N, 19.54°E, Figure 1). The patch of dense reed vegetation had a width of about 100 metres. Adjacent reed patches were located several metres apart, with the space between consisting of sandy, vegetation-free bottom.

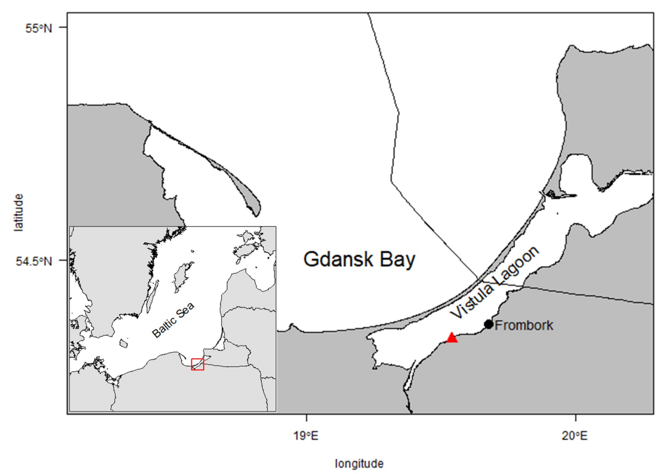

Figure 1. Map of the study area, with the location site indicated by a red triangle.

2.2 Sampling and analyses

The study was conducted in August 2017 during two sessions: from August 7 to August 10, during the full moon, and from August 21 to August 24, during the new moon. Acoustic and net sampling sites were situated near adjacent reed patches located on opposite sides of a vegetation-free corridor, with approximately 50 metres separating them. The sampling locations remained consistent throughout all sessions.

2.2.1 Gillnet catches

During each session, two net exposures were conducted at dawn and two at dusk, each lasting 4 and a half hours. Each net sampling session began 2 hours and 15 minutes before sunrise or sunset and ended 2 hours and 15 minutes after sunrise or sunset (see Table 1). We utilised NORDIC

Table 1. Schedule of conducted catches. The listed times correspond to the local times of civil sunrise and civil sunset hours.

Session	No. of net sampling	Data	Time of net exposure	Time of sunrise/sunset
full moon	1	07.08.2017	18:47–23:00	04:18/21:16
	2	08.08.2017	02:30–07:00	04:20/21:14
	3	09.08.2017	18:30–23:00	04:22/21:11
	4	10.08.2017	02:30–07:00	04:24/21:09
new moon	5	21.08.2017	18:35–23:00	04:46/20:42
	6	22.08.2017	02:30–07:00	04:48/20:40
	7	22.08.2017	18:35–23:00	04:48/20:40
	8	23.08.2017	02:40–07:10	04:50/20:37

multimesh gillnets, measuring 30 m in length and 1.5 m in height. The gillnet comprised 12 panels, each 2.5 m long, with mesh sizes ranging from 5 mm to 55 mm from knot to knot (Appelberg et al., 1995). The sequence of these panels was initially randomised. The gillnet was positioned parallel to the shoreline at a distance of approximately 1.5 metres from the edge of the reeds bordering the open water. After each net exposure, the net was stretched on poles, and the fish were identified to species, measured, and weighed. Additionally, the fish's swimming direction was determined based on its position in the net.

2.2.2 Acoustic recording

The multibeam sonar ARIS was equipped with the AR2 rotator (a motorised rotary system) that was mounted on a special steel structure and then submerged in water (see Figure 2). The water depth at the measurement site was approximately 1 m, with the transducer positioned 20 cm below the surface. The acoustic beam was directed slightly below horizontal and parallel to the edge of the reed bed, and oriented in the opposite direction from the location of the net catches. The ARIS operated in low-frequency mode (1.1 MHz) with a horizontal field of view of 29 degrees and a vertical field of view of 14 degrees. The range was set to 12 m, starting from 0.7 m in front of the transducer, with a resolution of 8.7 mm. The frame rate was 3.7 frames per second. The sonar was activated at the beginning of each session, and recording was conducted continuously throughout the session, with data saved in separate files for each half hour of recording. During operation, the sonar was powered by a generator located on the shore.

ARIS recordings were processed using the Sonar 5-Pro post-processing system (Lindem Data Acquisition, Oslo, Norway, ver. 6.0.3). Analysis of ARIS recordings relied on manually tracking each fish in consecutive frames, allowing for the determination of its trajectory and size. Subsequently, based on the characteristics of their movement, the fish were classified as migrating fish or milling fish. Fish exhibiting direct movements toward the reeds or open water were classified as migrating to the reed bed or open water, respectively. A movement was considered a migration process only when more than 50% of the observed fish moved in the same direction. All other fish displaying chaotic swimming in multiple directions, including sudden changes in direction due to, for example, interactions with other fish, were classified as milling. In the analysis of the ARIS recordings, all traces that appeared as uniform linear movements without the visible elongated shape of a fish were disregarded, as they were assumed to be non-fish entities, such as crabs moving along the bottom.

Due to the vast amount of acoustic data, over 120 hours of acoustic recordings were captured, and due to the extensive time required for data analysis, only the first 5 minutes of each half-hour recording were analysed. Additionally, the analysis covered the entire recording corresponding to the period of net 2 exposure, on August 8, 2017, between 2:30 and 7:00 LT. To avoid any differences due to subjective assessment, all the videos (recordings) were analysed by the same person. For further analysis, only fish longer

Figure 2. Sonar ARIS with AR2 rotator mounted on the steel structure, showing its positioning within the water.

than 5 cm were considered to avoid including smaller, less significant entities. Additionally, fish that appeared at a distance smaller than 1.8 m were not included in the analysis due to the narrow beam width and short observation time for such fish.

In this study, "fish number" refers to the number of fish detected within the portion of the sonar's field of view between 1.8 m and 12 m from the device, during a given time interval. The insonified water volume analysed within this range was approximately 28.6 m^3 and remained constant across both sessions.

2.2.3 Water temperature and meteorological measurements

Continuous water temperature measurements were carried out using an automatic temperature logger, the HOBO 8K Pendant® UA-001-08 (ONSET Computer Corporation, USA). Meteorological data, including air temperature, atmospheric pressure, wind direction, and wind speed, were obtained from a weather station in Frombork, operated by the National Marine Fisheries Research Institute. This station is located approximately 12 km northeast of the measurement site. Although quantitative light measurements were not available, nighttime luminosity during both the full moon and new moon sessions was assessed based on observations of the moon's visibility and cloud cover.

2.2.4 Statistical analysis

In the statistical analysis, non-parametric tests were used, as the data did not meet the assumption of normal distribution (Shapiro–Wilk test, $p < 0.05$). To compare fish length distributions between the full moon and new moon sessions, as well as between morning and evening migration periods, we applied the two-sample Kolmogorov–Smirnov test and the Mann–Whitney U test, using data from both gillnets and ARIS recordings. Fish lengths obtained from ARIS recordings for different behavioural categories (movement towards reed beds, movement towards open water, and milling) during day and night (excluding twilight hours i.e., 4:30–5:29 and 20:00–20:59 during the full moon session, and 5:00–5:59 and 19:30–20:29 during the new moon session) were compared using the Kruskal–Wallis test. Differences in fish activity between day and night, as well as between sessions, were evaluated using the Mann–Whitney U test applied to mean fish numbers averaged over 5-minute sampling intervals, with twilight hours excluded. The Mann–Whitney U test was also used to compare gillnet catches between the two sessions.

3. Results

3.1 Gillnet catches

In the course of 8 gillnet fishing efforts, a total of 653 fish were caught, belonging to 13 species. The most abundant were silver bream (*Blicca bjoerkna*), roach, bleak (*Alburnus alburnus*), perch, and sander, which together accounted for 96% of the fish caught (Figure 3).

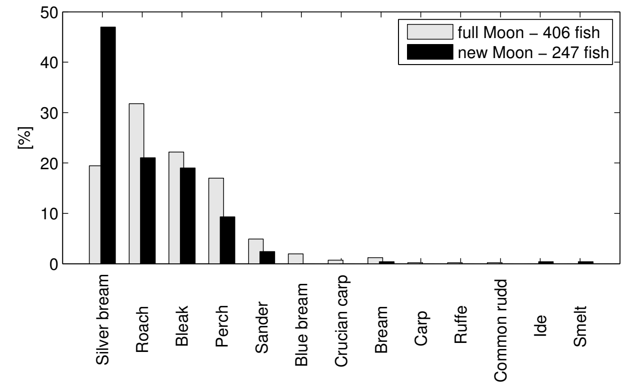

Figure 3. Percentage of fish captured by gillnets during the full moon and new moon phases.

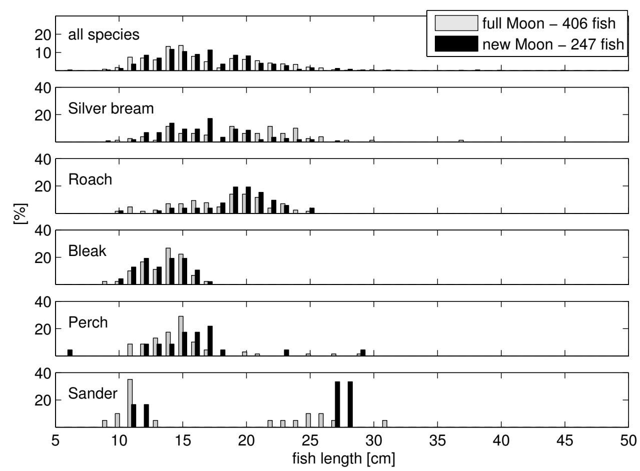

Figure 4. Length distribution of fish captured by gillnets during the full moon and new moon phases.

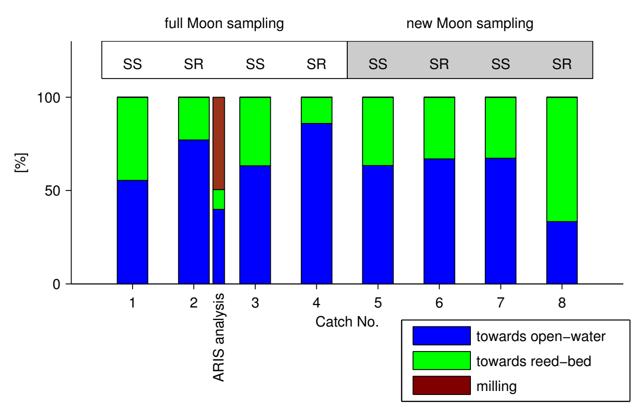

Figure 5. Positioning of fish in the nets (wide bars), indicating movement toward either open water or reed beds at sunrise (SR) and sunset (SS). The narrow bar shows the results of the detailed analysis of the ARIS recording corresponding to the time of net 2 exposure.

In terms of fish length, silver bream and roach (the two dominant species) had a bimodal distribution: silver bream ranged from 9 to 37 cm, and roach from 10 to 25 cm (Figure 4). Bleak and perch exhibited a unimodal distribution (10 to 17 cm). Sander occurred in two length intervals: 9–12 cm and 22–31 cm. The largest fish caught was a bream (45 cm). No significant differences were found in the length distributions or median lengths of dominant fish species between full moon and new moon sessions, as well as between morning and evening catches (two-sided Kolmogorov–Smirnov and Mann–Whitney U tests, all $p > 0.5$).

The number of fish caught during the new moon was 40% lower than during the full moon. However, the Mann-Whitney U test did not confirm statistically significant differences between the results ($n1 = 4$, $n2 = 4$, $U = 2$, $Z = 1.58$, $p = 0.11$). The effect of moon phase on dominance structure was noticeable only for silver bream, whose proportion was more than twice as high during the new moon (Figure 3).

The orientation of the fish caught in the nets indicated that in the studied littoral zone, most were moving toward open water, regardless of the time of day. This tendency was particularly noticeable at dawn during the full moon. Only in the final catch during the new moon was a dominant movement in the opposite direction observed (Figure 5).

3.2 Acoustic recording

The recordings from ARIS showed diel variability in fish number but did not allow for determining the species composition. The length distribution of fish recorded by the echosounder was unimodal (Figure 6), with smaller fish dominating during the full moon (mean length 12.2 cm) compared to the new moon (15.5 cm) (Kolmogorov–Smirnov test, $p < 0.001$; Mann–Whitney U test, $p < 0.001$). The Kruskal–Wallis test revealed significant differences in median fish size among behavioural groups and daytime periods only during the night period of the full moon (Kruskal–Wallis test, $p < 0.05$), with milling fish being smaller than those migrating towards open water (Mann–Whitney U test, $p < 0.001$) (Figure S1). The number of observed fish was significantly higher during daytime than during night, regardless of the moon phase (Mann–Whitney U test, $p < 0.001$) (Figure 7).

During the night, fish numbers stayed at a low level, with an average of 1 fish/min, whereas during the day it was 3 fish/min. The highest daytime fish numbers were observed in the afternoon (16:00–18:30) on August 8 and 9, reaching above 10 fish/min. During the new moon, however, the maximum observed fish number did not exceed 4 fish/min.

In addition to the diel pattern, the observed fish number also varied with the lunar phase. During the full moon, significantly higher numbers were recorded both during

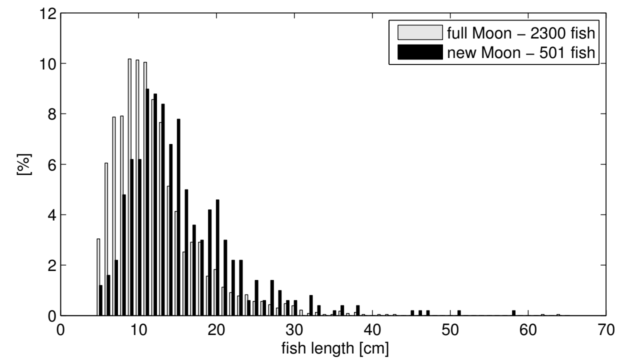

Figure 6. Length distribution of fish observed by the ARIS sonar during the full moon and new moon phases.

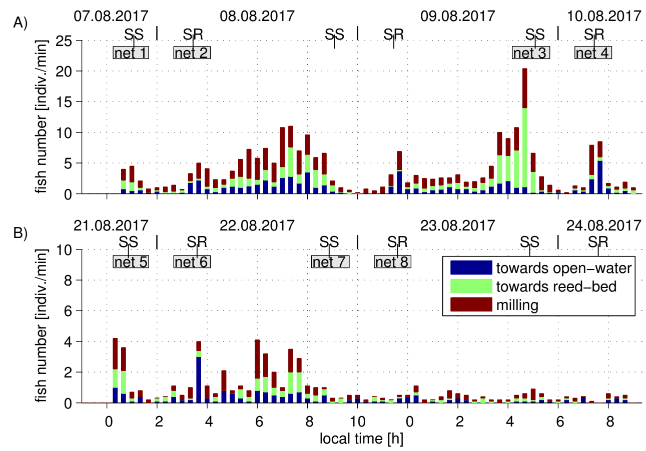

Figure 7. Fish number based on ARIS recordings at hourly intervals during the full moon (A) and new moon (B). Note the differing y-axis scales for each session. The periods of net exposure are indicated by grey boxes.

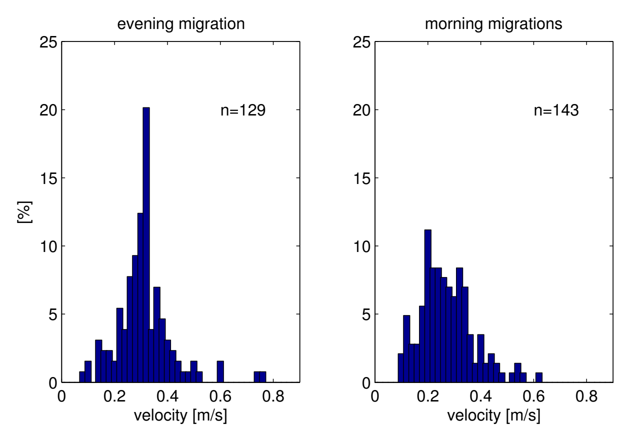

Figure 8. Histograms of fish movement speeds classified as migrating toward the reeds on August 9, 2017, at 20:00 (left panel) and those migrating toward open water on August 8, 9, 10, and 22, 2017, at 05:00 (right panel).

the day (5.2 fish/min on average) and at night (1.4 fish/min), compared to the new moon period, when average counts dropped to 1.2 and 0.5 fish/min, respectively (Mann–Whitney U test, $p < 0.001$). Also in the transition periods, around sunrise and sunset, higher fish numbers were observed. Especially in the evening of August 9 when the number of fish reached the highest value of 20 fish/min.

During both the full moon and new moon phases, milling behaviour – characterized by chaotic swimming in multiple directions – was predominant, observed in 50% of fish during the new moon and 41% during the full moon. A detailed analysis of the sonar recording corresponding to the deployment period of net 2 revealed that milling was consistently present throughout that timeframe, accounting for 50% of all observed behaviour (Figure 5). In the mornings of both moon phases, migrations toward open water were observed, involving over 60% of the fish. Evening migrations toward the reeds occurred only once (on August 9) but were significantly more intense than the morning migrations, comprising 63% of the fish. The migrations were dominated by fish measuring less than 15 cm (average: 10–12 cm), which accounted for over 85% of individuals. Fish size distributions and medians did not differ significantly between morning and evening migrations (Kolmogorov-Smirnov test, $p > 0.05$; Mann-Whitney U test, $p > 0.05$). Their average movement speed was 0.3 m/s (Figure 8).

3.3 Meteorological conditions

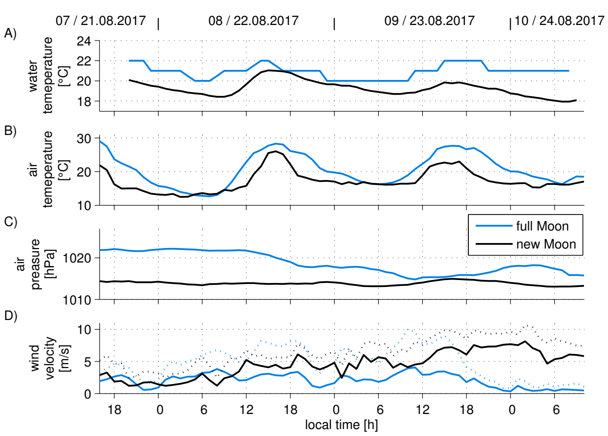

Figure 9. Water temperature A), air temperature B), atmospheric pressure C), and wind speed D) measured during the full moon (light blue lines) and new moon (black lines) sessions. * solid line presents mean wind speed; dotted line – max wind speed.

Both water and air temperatures fluctuated in a diel cycle, reaching their maximum in the early afternoon hours (13:00–15:00) and their minimum in the early morning hours (5:00–6:00) (Figure 9). During the studies conducted at full moon, the pressure ranged from 1022 to 1015 hPa, while during the new moon, it remained at 1014 hPa. Wind speed during the full moon increased throughout the day, reaching average values of up to 3 m/s (with gusts up to 8 m/s) on August 8 and up to 4 m/s (with gusts up to 10 m/s) on August 9, tapering off to no more than 1 m/s by the end of the research session. In contrast, during the studies conducted at new moon, wind speed gradually increased from 2–3 m/s at the beginning of the measurements to 7 m/s during the second half of the session, reaching maximum values of 8–10 m/s. The wind direction during the full moon period was mainly offshore (southerly wind), whereas during the strong wind event in the new moon period, it was onshore (northerly wind). During the full moon session, the moon was clearly visible, with no cloud cover.

4. Discussion

The conducted research aimed to investigate the diel fish activity pattern in the coastal zone of the Vistula Lagoon, with particular emphasis on horizontal migrations between reed beds and open water. The results indicate a clear diel variation in fish activity, with a higher number of fish observed during the day than at night, regardless of the moon phase (Figure 7), thus supporting our first hypothesis. The catches were dominated by diurnally active species such as roach, bleak, silver bream, and perch, which explains the generally low level of fish activity observed at night. This low nighttime activity is consistent with previous findings in the literature, which report reduced fish movement under low-light conditions (e.g., Peckan-Hekim et al. 2010).

However, both diurnal and nocturnal fish activities were lower during the new moon compared to the full moon, supporting our second hypothesis. The reduced nighttime activity may be attributed to the further decrease in ambient light levels during the new moon. Interestingly, a lower number of fish was also observed during the day under new moon conditions. This could be related to weather factors – specifically, high wind speeds recorded during the new moon sessions, which may have caused sediment resuspension and reduced underwater visibility, thereby negatively affecting diurnal fish activity.

An important part of the results was the observed fish migration pattern, which appeared to be the reverse of what is commonly reported – namely, an evening movement toward the pelagic zone followed by a return to the littoral zone at dawn – and contrary to our expectations (third hypothesis). Morning migrations toward open water were consistent, occurring every morning during the study sessions. However, the fish involved did not always move in just one direction, which may be attributed to the presence of predators, such as perch, hunting at dawn. The evening migration toward the reeds was recorded only once but exhibited an intense and more organised character (Figure 8). This suggests an escape response from predators, aligning with theories regarding mass fish migrations in response to predator pressure (Benndorf, 1990). The dominance of smaller fish (< 15 cm) during these migrations may indicate the prevalence of species such as bleak, juvenile perch, and roach.

The observed reverse DHM in species such as perch, roach, and silver bream are particularly interesting. The literature presents various migration patterns. Peckan-Hekim et al. (2010) described reverse DHM in perch (both small < 8 cm, primarily zooplanktivorous, and larger, piscivorous individuals) that spent the day in open water and the night in the coastal zone. Muska et al. (2013) observed a complete absence of perch in open water at night and reverse DHM among adult roach (80% of the population) in the Rimov reservoir. Jacobsen et al. (2004) demonstrated that in turbid waters, roach remain dispersed throughout the reservoir during the day but aggregate in the coastal zone at night, whereas in clear lakes, they exhibit classic DHM. This reverse migration has been attributed to the presence of sander, which hunts in open water after dark, during twilight, and at night, favouring turbid water, and is also present in the Vistula Lagoon. A similar pattern of migration in bream in the presence of sander was observed by Brabrand and Faafeng (1993) and Hölker et al. (2002). In contrast, planktivorous bleak is typically cited in the literature as exhibiting classic DHM, spending the day in the littoral zone and foraging in open water at night (Gliwicz et al., 2006; Musk et al., 2013). Generally, species such as perch, roach, and silver bream, which dominated in our catches during both sessions (Figure 3), prefer to stay in the coastal zone at night and move to open water at dawn (Muska et al., 2013; Walter and Freyhof, 2004).

In our study, the high abundance of sander – an active nocturnal predator in open water – may have influenced the observed pattern of fish movement in the opposite direction to the classic DHM pattern. Additionally, the observation of more intense migrations toward the reeds during the full moon may suggest that better lighting conditions increase predation pressure and affect migratory patterns. This aligns with research by Gaudreau and Boisclair (2000) regarding the influence of moon phases on fish migrations. In particular, during the full moon, the lower wind speed and consequently less pronounced resuspension, along with better lighting conditions in the water, may have facilitated mass migrations of fish toward the reeds, as observed on August 9 (Figure 7).

In summary, morning migrations towards open water were observed almost daily, regardless of whether an evening migration had occurred the previous day. This suggests that a specific group of fish resides in the reed beds overnight and consistently leaves them at dawn, likely in response to predator activity. This migration pattern may indicate an adaptive behaviour of fish in response to variable environmental conditions, such as water transparency and predation pressure. A comprehensive understanding of these relationships requires further research, including diel changes in zooplankton distribution.

Our research highlights the utility of combining direct fish catches with advanced sonar technology in studies of horizontal migrations. However, it is important to note that each method used has its limitations. Caution should be exercised when inferring the direction of migration based on the positioning of fish in the nets, as demonstrated by the intense evening migration recorded by the ARIS sonar on August 9. The absence of this migration reflected in the arrangement of fish in catch number 3 could have been due to the nets being filled before the 'actual' migration began (resulting in too long an exposure period) (Olin et al., 2004). Additionally, nets cannot differentiate between milling fish, which made up a significant portion of the observed catch and may have 'masked' the true direction of migration. Nets may also exhibit selectivity, preferentially capturing larger individuals (Ravn et al., 2018). In our study, the majority of captured fish were individuals over 10 cm in length, while the ARIS sonar recorded the full range of fish lengths, including those below 10 cm. Furthermore, the fish number determined from acoustic recordings may be overestimated, particularly in the case of milling, where the same individual may be recorded multiple times within the sonar beam. Therefore, further studies are needed to enhance the complementarity of results obtained through netting and acoustic methods.

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Supplementary materials

Supplementary data associated with this article can be found online. Please follow this link to see the supplementary data associated with this article.

Conflict of interest

None declared.

References

Appelberg, M., Berger, H.M., Hesthagen, T., Kleiven, E., Kurkilahti, M., Raitaniemi, J., Rask, M., 1995. *Development and intercalibration of methods in Nordic freshwater fish monitoring*. Water Air Soil Pollut. 85, 401–406. https://doi.org/10.1007/BF00476862

Benndorf, J., 1990. *Conditions for effective biomanipulation: conclusions derived from whole-lake experiments in Europe*. Hydrobiologia 200/201, 187–203. https://doi.org/10.1007/BF02530339

Bollens, S.M., Frost, B.W., Thoreson, D.S., Watts, S.J., 1992. *Diel vertical migration in zooplankton: field evidence in support of the predator avoidance hypothesis*. Hydrobiologia 234, 33–39.

Brabrand, Å., Faafeng, B., 1993. *Habitat shift in roach (Rutilus rutilus) induced by pikeperch (Stizostedion lucioperca) introduction: predation risk versus pelagic behaviour*. Oecologia 95, 38–46. https://doi.org/10.1007/BF00649504

Cervetto, G., Pagano, M., Gaudy, R., 1995. *Feeding behaviour and migrations in a natural population of the copepod Acartia tonsa*. Hydrobiologia 300, 237–248. https://doi.org/10.1007/BF00024464

Gaudreau, N., Boisclair, D., 2000. *Influence of moon phase on acoustic estimates of the abundance of fish performing daily horizontal migration in a small oligotrophic lake*. Can. J. Fish. Aquat. Sci. 57, 581–590. https://doi.org/10.1139/f99-277

Gliwicz, Z.M., Jachner, A., 1992. *Diel migrations of juvenile fish – a ghost of predation past or present*. Arch. Hydrobiol. 124, 385–410. https://doi.org/10.1127/archiv-hydrobiol/124/1992/385

Gliwicz, Z.M., Slon, J., Szynkarczyk, I., 2006. *Trading safety for food: evidence from gut contents in roach and bleak captured at different distances offshore from their daytime littoral refuge*. Fresh. Biol. 51, 823–839. https://doi.org/10.1111/j.1365-2427.2006.01530.x

Horppila, J., Liljendahl, A., Estlander, S., Nurminen, L., 2018. *The role of visual and physiological refuges in humic lakes: Effects of oxygen, light quantity, and spectral composition on daytime depth of chaoborids*. Int. Rev. Hydrobiol. 103, 63–70. https://doi.org/10.1002/iroh.201801933

Hölker, F., Haertel, S. S., Steiner, S., Mehner, T., 2002. *Effects of piscivore-mediated habitat use on growth, diet and zooplankton consumption of roach: an individual-based modelling approach*. Freshw. Biol. 47, 2345–2358. https://doi.org/10.1046/j.1365-2427.2002.01002.x

Imbrock, F., Appenzeller, A., Eckmann, R., 1996. *Diel and seasonal distribution of perch in Lake Constance: A hydroacoustic study and in situ observations*. J. Fish Biol. 49, 1–13. https://doi.org/10.1111/j.1095-8649.1996.tb00001.x

Jacobsen, L., Berg, S., Jepsen, N., Skov, C., 2004. *Does roach behaviour differ between shallow lakes of different environmental state?* J. Fish Biol. 65, 135–147. https://doi.org/10.1111/j.0022-1112.2004.00436.x

Järvalt, A., Krause, T., Palm, A., 2005. *Diel migration and spatial distribution of fish in a small stratified lake*. Hydrobiologi 547, 197–203. https://doi.org/10.1007/s10750-005-4160-z

Jeppesen, E., Pekcan-Hekim, Z., Lauridsen, T.L., Søndergaard, M., Jensen, J.P., 2006. *Habitat distribution of fish in late summer: changes along a nutrient gradient in Danish lakes*. Ecol. Freshw. Fish 15, 180–190. https://doi.org/10.1111/j.1600-0633.2006.00142.x

Karpowicz, M., Kornijów, R., Ejsmont-Karabin, J., 2023. *Not a good place to live for most, excellent for a few - diversity of zooplankton in a shallow coastal ecosystem*. Sustainability 15(3), 2345. https://doi.org/10.3390/su15032345

Kornijów, R., 2018. *Ecosystem of the Polish part of the Vistula Lagoon from the perspective of alternative stable states concept, with implications for management issues*. Oceanologia 60(3), 390–404. https://doi.org/10.1016/j.oceano.2018.02.004

Kornijów, R., Karpowicz, M., Ejsmont-Karabin, J., Nawrocka, L., de Eyto, E., Grzonkowski, K., Magnuszewski, A., Jakubowska, A., Wodzinowski, T., Woźniczka, A., 2020. *Patchy distribution of phyto- and zooplankton in large and shallow lagoon under ice cover and resulting trophic interactions*. Mar. Freshwater Res. 71, 1327–1341. https://doi.org/10.1071/MF19259

Martignac, F., Daroux, A., Bagliniere, J.L., Ombredane, D., Guillard, J., 2015. *The use of acoustic cameras in shallow waters: New hydroacoustic tools for monitoring migratory fish population. A review of DIDSON technology*. Fish Fish. 16, 486–510. https://doi.org/10.1111/faf.12071

Moss, B., 1994. *Brackish and freshwater shallow lakes – different systems or variations on the same theme?* Hydrobiologia 275, 1–14. https://doi.org/10.1007/BF00026695

Moursund R.A., Carlson T.J., Peters R.D., 2003. *A fisheries application of dual-frequency identification sonar acoustic camera*, ICES J. Mar. Sci. 60, 678–683. https://doi.org/10.1016/S1054-3139(03)00036-5

Muška, M., Tušer, M., Frouzová, J. Drastík, V., Cech, M., Juza, T., Kratochvíl, M., Mrkvicka, T., Peterka, J., Prchalová, M., Ríha, M., Vasek, M., Kubecka, J., 2013. *To migrate, or not to migrate: partial diel horizontal migration of fish in a temperate freshwater reservoir*. Hydrobiologia 707, 17–28. https://doi.org/10.1007/s10750-012-1401-9

Olin, M., Kurkilahti, M., Peitola, P., Ruuhijärvi, J., 2004. *The effects of fish accumulation on the catchability of multimesh gillnet*. Fish. Res. 68: 135–147. https://doi.org/10.1016/j.fishres.2004.01.005

Pawlikowski, K., Kornijów, R., 2019. *Role of macrophytes in structuring littoral habitats in the Vistula Lagoon (southern Baltic Sea)*. Oceanologia 61(1), 26–37. https://doi.org/10.1016/j.oceano.2018.05.003

Pekcan-Hekim, Z., Nurminen, L., Ojala, T., Olin, M., Ruuhijärvi, J., Horppila, J., 2010. *Reversed Diel Horizontal*

Migration of Fish: Turbidity Versus Plant Structural Complexity as Refuge. J. Freshw. Ecol., 25(4), 649–656. https://doi.org/10.1080/02705060.2010.9664414

Psuty-Lipska, I., Borowski, W., 2003. *Factors affecting fish assemblages in the Vistula Lagoon*. Arch. Fish. Mar. Res. 50(3), 253–270.

Psuty, I., Wilkońska, H., 2009. *The stability of fish assemblages under unstable conditions: A ten-year series from the Polish part of the Vistula Lagoon*. Arch. Pol. Fisheries 17. https://doi.org/10.2478/v10086-009-0004-1

Ravn, H.D., Lauridsen, T.L., Jepsen, N., Jeppesen, E., Hansen, P.G., Hansen, J.G., Berg, S., 2019. *A comparative study of three different methods for assessing fish communities in a small eutrophic lake*. Ecol. Freshw. Fish 28, 341–352. https://doi.org/10.1111/eff.12457

Vasek, M., Kubecka, J., 2004. *In situ diel patterns of zooplankton consumption by subadult/adult roach Rutilus rutilus, bream Abramis brama, and bleak Alburnus alburnus*. Folia Zool. 53, 203–214.

Wasserman, R.J., Vink, T.J.F., Kramer, R., Froneman, P.W., 2014. *Hyperbenthic and pelagic predators regulate alternate key planktonic copepods in shallow temperate estuaries*. Mar. Freshw. Res. 65, 791–801. https://doi.org/10.1071/MF13233

Wolter C., Freyhof J., 2004. *Diel distribution patterns of fishes in a temperate large lowland river*. J. Fish Biol. 64, 632–642. https://doi.org/10.1111/j.1095-8649.2004.00327.x