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Macrophyte habitat selection by moulting mute swans and the effect of recreational disturbance in the largest Baltic Sea lagoon

Rasa Morkūnė [*], Martynas Bučas, Julius Morkūnas

Marine Research Institute, Klaipėda University, Klaipėda, Lithuania

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ABSTRACT

Moult, the process of replacing old feathers with new, is a critical event in the annual cycle of all bird species. In the Curonian Lagoon, situated in the south-eastern Baltic Sea, recreational activities and shipping lanes occur in close proximity to the staging areas of waterfowl. Knowledge on the habitat use of these birds however is scant. In this study, we combined visual observations, satellite telemetry and the distribution of macrophytes to study habitat use by moulting herbivorous mute swans (*Cygnus olor*) and analysed how the localities of the swans depended on the distribution of macrophyte habitats and anthropogenic activities. Our data highlighted the most important swan staging areas within the Lithuanian part of the Curonian Lagoon, this specifically being mostly shallow areas (<1-metre depth) with diverse and high-density coverage of submerged vegetation dominated by charophytes and pondweeds. The submerged macrophyte habitats in water depths of 1–2 m and stands of clasping-leaf pondweeds were considered less important for swans. Our results showed that mute swans exploited only half the most suitable habitat areas for feeding. Based on indirect assessment of the relationship between the abundance of swans and disturbance by kitesurfing and boating, we discuss possible impacts on their moulting grounds. Knowledge on both selection of moulting grounds and habitat use by waterbirds is necessary for effective management and biodiversity conservation.

1. Introduction

The Curonian Lagoon (south-eastern Baltic Sea) provides feeding habitats and shelter for a number of waterbird species. Most of the area in the lagoon is designated both as a European protected territory and as a national biosphere polygon focusing on the conservation of coastal habitats, waterbirds and the estuarine ecosystem. However, there are increasing pressures from recreational activities which are currently unrestricted in relation to waterbird protection in the Curonian Lagoon.

The mute swan (*Cygnus olor*) is one of the most abundant moulting waterbird species in the Curonian Lagoon (Morkūnė et al. 2020). At this location, the mute swan undergoes a complete moult during the post-breeding period (Ringelman 1990) and becomes flightless for 6–8 weeks in the period of mid-June to August (Ginn & Melville 1983). This species uses a wide range of shallow habitats overgrown with macrophytes. They primarily consume submerged aquatic vegetation with a few species dominating the diet (Sousa et al. 2008; Gayet et al. 2011). Many studies have reported the effect of grazing on macrophyte communities (Gayet et al. 2011; Gayet et al. 2013), but a lower number of studies have showed the importance of macrophyte species on waterfowl communities, including mute swans (Noordhuis et al. 2002).

In the estuarine part of the Curonian Lagoon, a significant spread of submerged macrophyte habitats has been recorded in the last decade (Sinkevičienė et al. 2017; Stragauskaitė et al. 2021), but the importance of these habitats as feeding grounds for mute swans has not been addressed yet. During the moulting period, the mute swans need suitable habitats that provide adequate food resources and ensure security from predators and human disturbance such as recreational water sports (Ringelman 1990; Clausen et al. 2020; Wieloch, 1991). However, the impact and characteristics of anthropogenic disturbance on moulting swans remains unstudied in the Curonian lagoon.

The negative effects on waterbirds of uncontrolled extreme sports such as kitesurfing have been described in coastal waters and on large lakes in other countries. However, as most studies on the effects of kitesurfing on birds are unpublished reports and only a few are available as scientific studies, more research is needed (Krüger 2016). The kites used for kitesurfing are large and brightly coloured, approximately 5–8 m^2 in area, and are flown at heights of around 30 m. They additionally

* Corresponding author.
E-mail address: rasa.morkune@apc.ku.lt (R. Morkūnė).

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make loud noises when hitting the water or being used at velocities from 24 to 100 km/h. Thus, birds can see and hear the kites from a great distance and, as a result, they can cause much more disturbance than simple boats or yachts (Davenport and Davenport 2006; Krüger 2016); this especially can become critical during bird moulting periods. A better understanding of the behaviour of moulting birds, their habitat selection and their reaction to disturbance sources is needed in order to establish suitable waterbird protection and regulations for recreational activities.

This study aimed to investigate preferred locations and habitat usage by mute swans during the moulting period in the Curonian Lagoon. Additional parameters such as water depths, structures of macrophyte communities and proximity to anthropogenic disturbance sources (kitesurfing and boating) were studied to determine their importance in habitat selection by the moulting swans in order to provide empirically based recommendations for the management of human activities in the shallow and densely vegetated waterbody. In the studied estuarine ecosystem, we hypothesized that moulting mute swans avoid navigation channels and areas in close proximity to kitesurfing and aggregate in less favourable habitats for feeding.

2. Methods

2.1. Swan abundance surveys and telemetry

The study was performed in the Lithuanian part of the Curonian Lagoon, which covers a 413 km^2 area of open water ecosystem. To estimate the abundance and distribution of mute swans in the study area, we used data from visual bird surveys performed monthly during March–November 2018. For this study, we extracted data covering the

Fig. 1. Study area with isobaths (m) and the sampling sites of submerged macrophytes (indicated by open circles) and the location where mute swans were captured (the white triangle) in 2019 (A) and a mute swan with a neck collar containing a solar powered GPS-GSM transmitter (B).

swan moulting period, i.e. June-September. All surveys were performed by two ornithologists from a vessel moving along the main navigation channel along the western coast of the Curonian Lagoon (methods described in Morkūnė et al. 2020). The monthly surveys were generally performed during the last two weeks of each month and each survey lasted 9–10 h and was conducted during daytime. During the surveys, the abundance and locations of mute swan aggregations were marked as polygons using the Arc Collector program.

For estimation of habitat use, moulting swans were caught and fitted with trackers at the beginning of the moult period (24 July – 1 August) in 2019 in the north-eastern part of the study area (N 55.581762˚, E 21.187591˚ WGS; Fig. 1). A motorboat and manual tools were used to catch the moulting individuals. In total, ten individuals (eight males and two females) were fitted with neck collars containing solar powered GPS-GSM trackers (OrniTrack-N57, Ornitela). All individuals were also ringed with metal and coloured plastic leg rings. All birds were released immediately.

On average, the transmitters equated to 1.5% of the body mass of the captured individuals. In the subsequent months, a total of 131,038 GPS data points were recorded, the data including both locations and speed of movements (Table 1). Permits to capture swans were obtained from the Environmental Protection Agency of Lithuania (EPA: permit 2019 No. 36 and No. 40). According to Lithuanian law, no other approval was required by the national animal welfare authorities to undertake this research.

The telemetry data used for this study was analysed from the period beginning two days after the tagging and continuing till the end of September 2019. GPS position points were collected each five minutes. Two data sets were used: (1) flightless period and (2) flying period. The first flight after moult was determined as being when the GPS points logged more than 10 km/h and the distance between GPS locations was more than 500 m.

2.2. Mapping of macrophyte habitats

Two types of macrophyte data were used: (1) submerged macrophytes and (2) emerged macrophytes. In August 2019, the relative coverage of submerged macrophytes was surveyed once at 166 sites (Fig. 1), these distributed according to earlier studies on macrophyte distribution in the study area (Bučas et al. 2019). At each site, the bottom was dredged from a boat with a double-headed rake (40 cm width) for a distance of at least 2 m and the relative coverage of macrophyte species on the rake was assessed. The relative coverage of all macrophytes and dominant species (maximum coverage of 100 %) was averaged at different depths (18) and then their distribution along the depth gradient was assessed by means of the generalized additive models (GAM) due to observed nonlinear patterns in the data. For each dependent variable (the relative coverage of all macrophytes and dominant species) in the GAM, the penalized cyclic cubic smoothing term was selected for the independent variable (depth) with 7 degrees of freedom. The GAM were performed with the "mgcv" package (Wood 2017) in R (R Core Team 2022). In each model, the assumptions of normality, homogeneity and autocorrelation of residuals were checked respectively by a plot of residuals vs fitted values and a residual autocorrelation plot by 'acf' function (Zuur et al. 2009). Based on the depth distribution patterns of the phytolittoral, the area of submerged macrophytes suitable for swan feeding was presented by the growth forms of the dominant macrophytes and bathymetry data ("Depth Information Data of the Republic of Lithuania on the Baltic Sea Coast") using vector data tools ('Lines to Polygons' and 'Vertex Tool') in QGIS 3.22.6 (QGIS Development Team 2022).

According to Sinkevičienė (2004), the emerged vegetation mainly (ca. 90 %) consisted of common reed (*Phragmites australis*), followed by lakeshore bulrush (*Schoenoplectus lacustris*), flowering rush (*Butomus umbellatus*), European bur-reed (*Sparganium emersum*), European water-plantain (*Alisma plantago-aquatica*), broadleaf cattail (*Typha latifolia*) and softstem bulrush (*Schoenoplectus tabernaemontani*). The area of emerged macrophytes was determined from the Copernicus products "Coastal Zones Land Cover/Land Use 2018" (available online: https://land.copernicus.eu/local/coastal-zones/coastal-zones-2018) and "CORINE Land Cover 2018" (available online: https://land.copernicus.eu/pan-european/corine-land-cover/clc2018). The polygons of inland marshes and salt marshes from both data were joined and the area of emerged macrophytes was derived over a 100 m inland buffer zone using vector data tools ('Union' and 'Buffer') in QGIS.

2.3. Analysis of habitat importance for mute swans

The data from visual surveys in 2018 and from satellite transmitters in 2019 on the habitat use by mute swans was analysed separately. The relative area exploited by swans in each habitat in relation to the total area available to swans was estimated using the data from visual surveys (in 2018) by vector tools ('intersection' and 'basic statistics for fields') in QGIS. While the relative duration of swans in each habitat was estimated using data from satellite transmitters (in 2019) by summing the time mute swans spent at a habitat and dividing from the total time. For this

Table 1
Information on ten moulting mute swans tagged with GPS satellite transmitters in the Curonian Lagoon.

ID	Sex	Age	Body mass, g	Wing, mm	Start of tracking period	End of tracking period	Duration of operational time, days	Number of GPS fixes	Date of the first flight
W-K05A/ 192439	M	2y+	11,150	472	24 July 2019	14 September 2019	53	10,473	6 August 2019
W-K01A/ 192436	F	2y+	8771	609	24 July 2019	14 October 2019	83	12,967	29 August 2019
W-K02A/ 192434	M	2y	9270	350	24 July 2019	19 September 2019	60	15,837	29 August 2019
W-K03A/ 192437	M	2y+	10,660	337	24 July 2019	22 August 2019	30	9387	11 August 2019
W-K04A/ 192438	M	2y+	11,350	294	24 July 2019	14 September 2019	53	12,887	10 September 2019
W-K06A/ 192440	M	2y+	11,460	328	24 July 2019	12 September 2019	51	14,198	25 August 2019
W-K07A/ 192441	M	2y+	10,530	383	24 July 2019	14 October 2019	74	14,456	11 August 2019
W-K08A/ 192442	M	2y+	11,450	356	24 July 2019	24 August 2019	32	9053	11 August 2019
W-K00A/ 192435	F	2y+	7700	470	1 August 2019	14 October 2019	75	18,845	23 August 2019
W-K09A/ 192443	M	3y	9370	312	1 August 2019	16 September 2019	47	12,934	4 August 2019

analysis, vector tools such as 'select by location' and 'basic statistics for fields' were used in QGIS. Additionally, the relative use of a habitat by mute swans was assessed using both data types, where the abundance and the time spent within each habitat were divided by their maximum values and expressed in percentages. The relative use by mute swans was then classified into three categories: not used (0 %), less than 50 % and more than 50 % of the maximum value.

2.4. Effect of anthropogenic activities on mute swan habitats

Kitesurfing and boating were considered as the most critical anthropogenic activities causing disturbance to mute swans in the study area. The impact of these activities was indirectly assessed in this study by calculating the minimum Euclidean distance from the main navigation channels and kitesurfing spots to the edges of the swan locations (polygons) using QGIS. Considering that most boats travel within 500 m either side of the main navigation channel, the Euclidean distance was determined for a 500 m buffer of the navigation channel. The kitesurfing areas were mapped according to descriptions provided by the representatives of kitesurfing sport bases. The relationships between the Euclidean distance from the anthropogenic activities and the abundance of mute swans during June–September 2018 were analysed with the GAM (the penalized cyclic cubic smoothing term for the independent variable with 5 degrees of freedom) due to observed non-linear patterns in the data.

3. Results

3.1. Distribution of mute swans

During the study period in 2018, the flocks of moulting mute swans were mainly present along the eastern coastline (Fig. 2), but the largest flocks (>100 individuals) were registered in the northern part (between Klaipeda and Dreverna settlements) and in the Nemunas Delta (to the south-east of Ventė settlement).

The distribution of mute swans differed according to moulting phase. In June, before the moult period, the birds were widely scattered in the northern part of the study area, whereas the birds kept close to the shore in the July-August period (moult period) when a high abundance (>100 individuals) was recorded in the Nemunas Delta (south-east of Ventė settlement). In September, after moulting, mute swans were distributed along almost the entire eastern coast of the study area, but there were no swans on the western coast of the lagoon.

3.2. Distribution of macrophyte habitats

At a 3 m depth, the mean coverage of macrophytes was relatively low (<5 %) (Fig. 3). Along the depth gradient, there were two peaks where the mean coverage of macrophytes exceeded 50 %, the first was at 1 m depth and the second was at 2.5 m. The mean coverage at the one-metre depth was the highest (ca. 80 %), where clasping-leaf pondweeds (*Potamogeton perfoliatus)* and sago pondweeds (*Stuckenia pectinata*) dominated. Both species were widely distributed in the study area (Fig. 4), especially along the western shore and to the south-east of Ventė settlement. The mean coverage of macrophytes at 2.2 m depth was ca. 60 %, where charophytes dominated. The charophyte stands were mainly along the eastern shore, especially between the northern and central parts of the study area. Based on the depth distribution patterns of the phytolittoral and the potential energy needed for swans to reach the submerged vegetation, the area of submerged macrophytes suitable for swan feeding was defined into two habitats: submerged macrophytes at 0–1 m depth (low energy to reach vegetation) and at 1–2 m depth (high energy to reach vegetation).

3.3. Habitat selection by moulting mute swans

Based on the visual surveys, the species distribution in the most suitable habitat (submerged macrophytes 0–1 m depth) accounted for

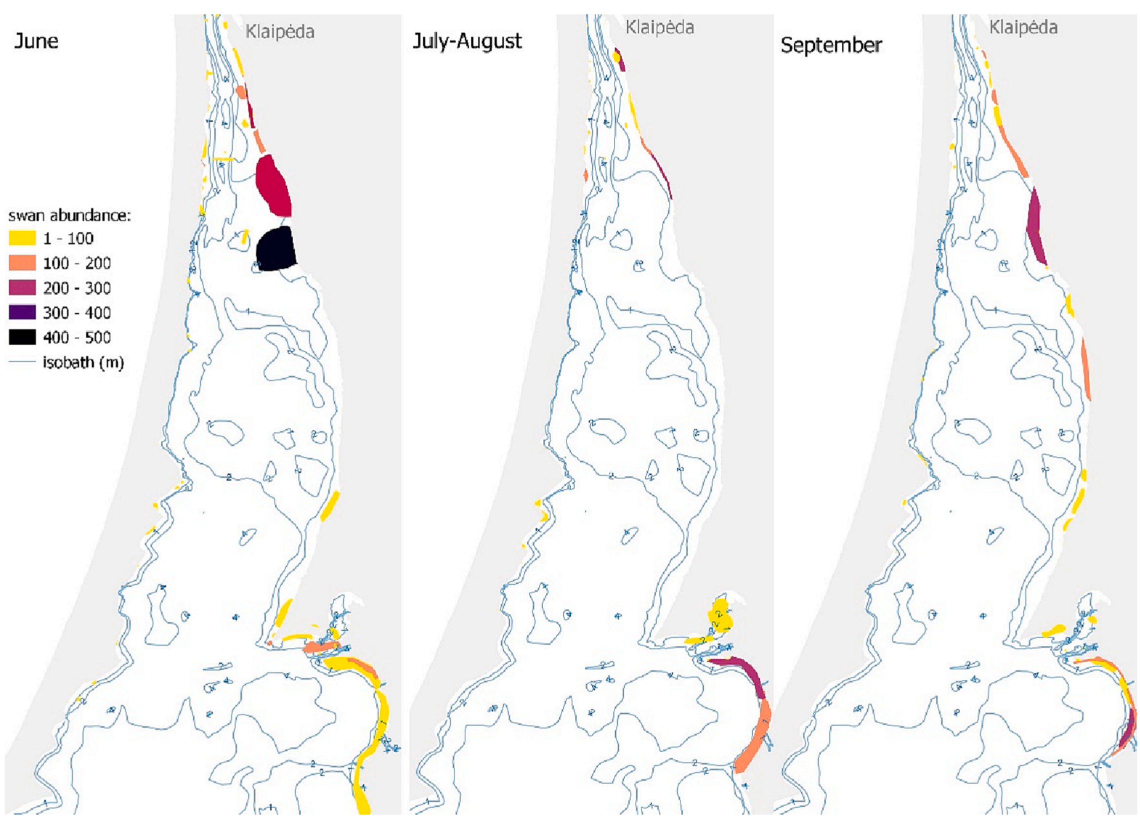

Fig. 2. Distribution of the abundance of mute swans in the northern part of the Curonian Lagoon during three periods in 2018.

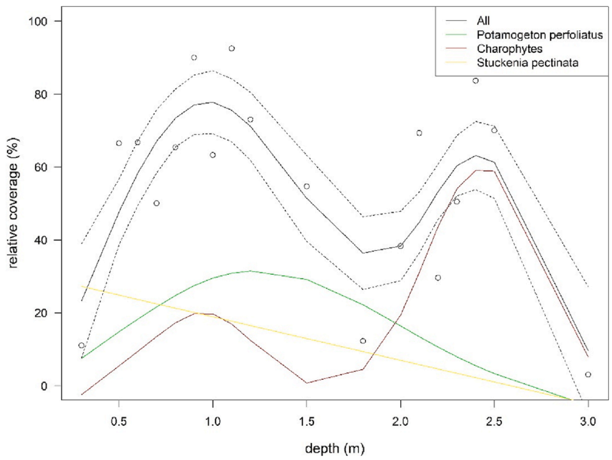

Fig. 3. Distribution of the mean coverage of all macrophytes and their dominant species along the depth gradient in the Curonian Lagoon. Points indicate the mean coverage of all macrophytes, where lines show predicted means by GAM and dotted lines indicate standard errors for the predicted mean.

more than half (58 %) of the total area exploited by mute swans (39 km^2). In less suitable habitat (submerged macrophytes 1–2 m depth), mute swans utilised 26 % from the total area (Fig. 4), and 9 % of even less suitable habitat at > 2 m depth, while only 7 % of reed habitats.

Considering the data from the satellite transmitters, the majority of mute swans (86 % of GPS locations) preferred to stay in depths<1 m with dense macrophyte coverage, while 13 % of locations were in reedbeds and only 1 % in the areas of > 2 m depth.

The most exploited habitat areas were in the northern parts (between Klaipeda and Dreverna settlements) and in the southern parts (near Ventė settlement) of the study area along the eastern shore of the lagoon (Fig. 5). The most unexploited areas of suitable habitat for mute swans were between Dreverna and Ventė settlements along the eastern shore and below Juodkrantė settlement along the western shore.

3.4. Disturbance effect of boating and kitesurfing on the distribution of mute swans

The main potential disturbance areas for mute swans from boating activities along the navigation channel were distributed along the western shore of the lagoon, where boats usually cruise from Klaipėda to Nida (Fig. 5). Areas of lower potential disturbance by boating activity were near the navigation channels from Juodkrantė to Dreverna and Nida to Ventė. The potential disturbance areas by kiteboarding were distributed only along the eastern shore of the lagoon between Dreverna and Ventė settlements. For human safety, these areas are usually located in shallow water (<1.5 m deep) and only up to 1 km distance from the shore.

There was a significant difference between the monthly abundance of mute swans and the distance to the areas with boating and kitesurfing activities (Fig. 6). In June and September, there was no significant relationship in the abundance of mute swans to the distance from the

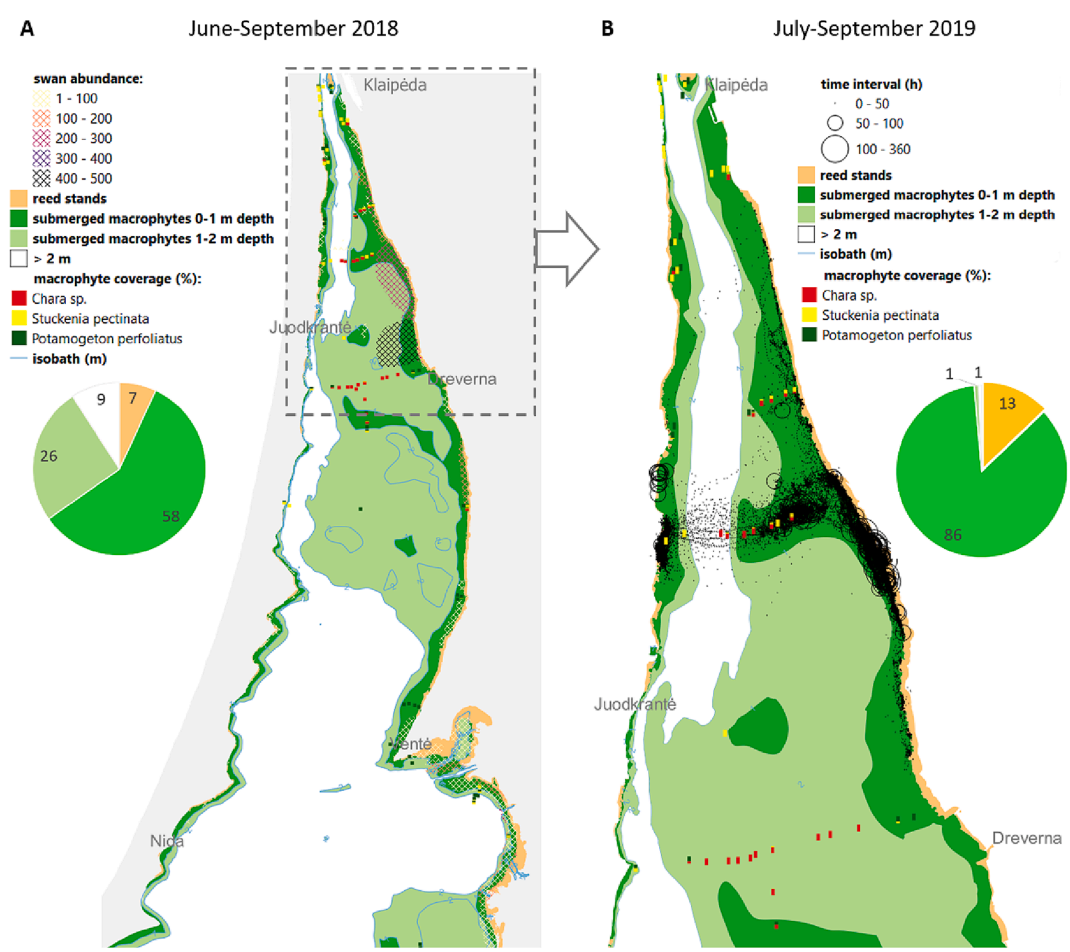

Fig. 4. Abundance and time spent duration of mute swans in different habitats in (A) the study area in June-September 2018 and (B) the northern part of the study area in July-September 2019. The pie charts represent relative abundance (visual observations in A) and the time spent (telemetry data in B) of swans in different habitats. The relative macrophyte coverage at the sampling sites is indicated by colour bars.

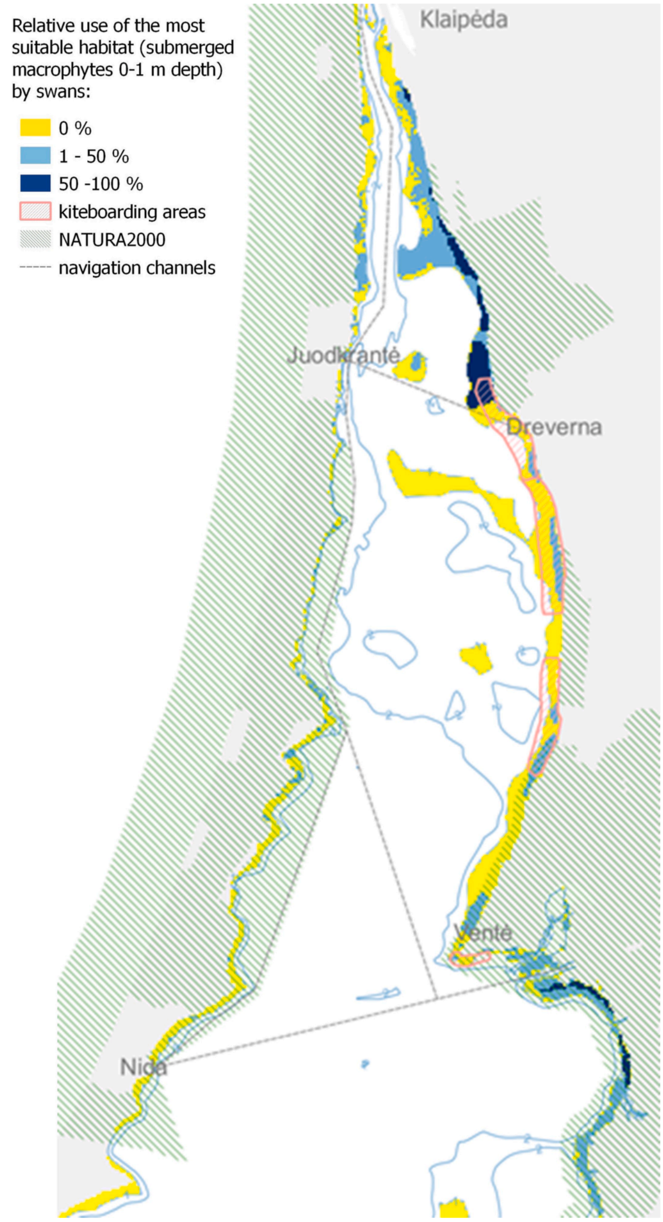

Fig. 5. Relative use of the most suitable habitat (submerged macrophytes at a depth of 0–1 m) by mute swans in the study area with a biosphere polygon in an open lagoonal area.

kitesurfing areas (respectively $F = 1.49$, $p = 0.24$ and $F = 1.40$, $p = 0.36$). Although the highest abundance in June (>400 individuals) and September (>200 individuals) were recorded respectively at ca. 2 and 4 km distances from the kiteboarding areas. In July-August, there was a significant non-linear relationship ($F = 5.19$, $p < 0.01$), where the maximum abundance of mute swans was at a distance of 6 km from the kitesurfing areas (Fig. 6).

A similar pattern was found between the abundance of mute swans and the distance to areas with boating (Fig. 6), where no significant relationship was found in June or September (respectively $F = 0.72$, $p = 0.50$ and $F = 1.58$, $p = 0.24$), while it was significant in July-August ($F = 3.28$, $p = 0.04$). The highest abundance in June (>400 individuals) was recorded at ca.1 km distance from the main navigation channels, while the abundance of mute swans increased to a distance of ca. 3 km from the main navigation channels in the latter period.

4. Discussion

4.1. Distribution and habitat use

In this study, the distribution of moulting mute swans and their use of macrophyte habitats was assessed for the first time in the Curonian Lagoon. Although the mute swan is easy to identify due its white colour and size, the detection of hiding individuals is complicated during the breeding period (Gayet et al. 2011) and moult. Moulting swans tend to have secretive behaviour and they need a safe habitat. Visual bird counts in this study revealed that during the period July-September, flocks of moulting mute swans were present along almost the whole eastern coastline, but the largest flocks were registered between Klaipėda and Dreverna and to the south-east of Ventė settlement. In the lagoon, the number of swans during the moulting period can reach 2200 individuals (Morkūnė et al. 2020).

Analysis of swan habitat selection using both visual observations in the Lithuanian part of the Curonian Lagoon and telemetry data from a part of the area revealed comparable results. As visual waterbird surveys were performed only in the daytime and included June (the month before moulting), the majority of swans seemed to use the most favourable low-depth and dense macrophyte habitats and were rarely registered in reeds (not possible to count birds in dense reedbeds). Swans spent a higher amount of time in reeds according to the telemetry data compared to the visual observations. Telemetry data additionally revealed habitat selection by swans in deeper areas with relatively dense macrophyte coverage, where some macrophyte species reach the surface (e.g. *Potamogeton perfoliatus*) and can be successfully grazed by swans. This study also shows how the results of the used methods complement each other and provide more information on swan behaviour.

Mute swans favour foraging methods that minimise energy expenditure and provide the most profitable food resources (Wood et al. 2013). In this study, the mute swans mostly fed in submerged macrophyte habitats up to 1 m in depth, which were more energetically efficient in terms of food quality (macrophyte types) and access. The most exposed feeding areas for mute swans were 0–1 m depth in the Limfjorden estuarine complex in Denmark (Balsby et al. 2017). The feeding depth of swans was also assessed using body measurements and feed by dipping at a depth of 79 cm and by upending to 103 cm in the Ouse Washes in England (Owen & Cadbury 1975). According to the map of relative use of habitats in the Curonian Lagoon, the widest exploited habitat by mute swans was located in the northern part (to the north of Dreverna settlement), which corresponded to the dominant charophyte stands. This is consistent with a strong positive correlation between mute swan abundance and charophyte biomass in the Lake Veluwemeer (Netherlands) (Noordhuis et al. 2002). Moreover, Noordhuis et al. (2022) reported that the abundance of swans increased after the colonization of Chara species. In the Curonian Lagoon, a significant spread of charophyte stands has been recorded in the last decade, which can be explained by changes in water quality (Sinkevičienė et al. 2017). Additionally, waterfowl may promote charophyte dominance by reducing pondweed species, which usually represent more eutrophic systems (Hidding et al. 2010).

In previous macrophyte surveys (in 2014–2015, Bučas et al. 2016) in the Curonian Lagoon, the charophyte stands corresponded to the locations of the mute swan flocks. Although the maximum depth of charophytes increased from 2 m in 2014–2015 to 3 m in 2019, the deeper charophyte habitats are barely reachable for swans since charophytes usually grow only to 20 cm above the bottom (Bučas et al. 2016). Usually mute swans avoid feeding grounds in deep areas and only forage in shallow waters near the shore (Holm 2002). In the deeper part (1–2 m depth) of the Curonian Lagoon, the leaves of clasping-leaf pondweed usually reach the surface and are available for swan feeding. However, a preference for clasping-leaf pondweed in the diet of swans has not been reported in a number of studies (e.g. Mathiasson 1973; Bailey et al. 2008; Hidding et al. 2010; Bakker et al. 2015) but swans affected

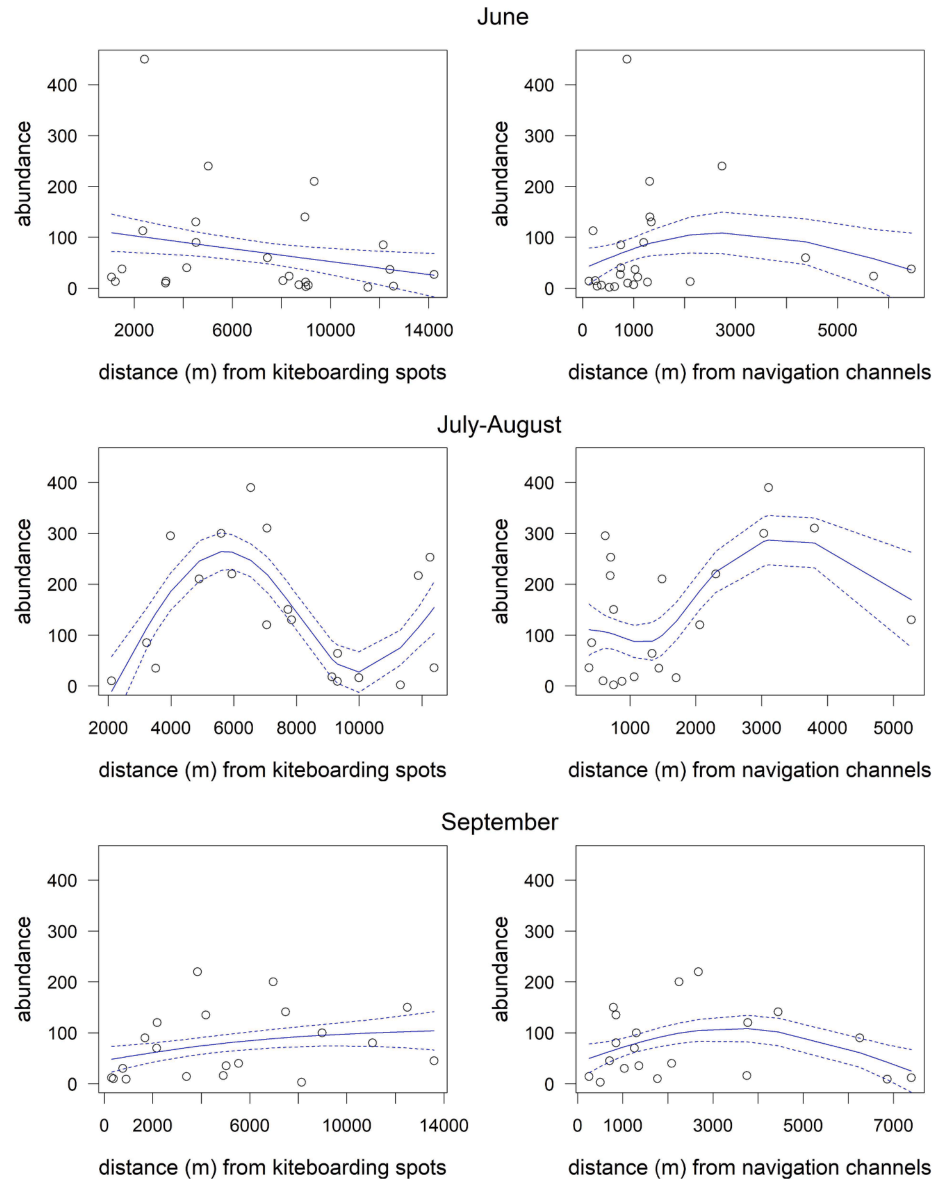

Fig. 6. Relationships between the abundance of mute swans and distance to areas with disturbance sources (kiteboarding spots and navigation channels) in different months. Solid lines show predicted means by GAM; dotted lines show standard errors.

distribution of clasping-leaf pondweeds in the Eastern Lake Ringsjon (Sandsten & Klaassen, 2008). Generally, the diet of mute swans consists of various submerged aquatic macrophytes, including both algae and vascular plants (Bailey et al. 2008; Kouzov et al. 2021). As the flightless period limits their capability to change habitats, moulting swans should choose reliable habitats which have capacities to maintain their populations during the moulting period (e.g. Holm 2002). The important characteristics for the moulting mute swans are a shallow water depth, a possibility to hide in wide reedbeds close to the suitable feeding grounds and historically low human disturbance. These characteristics were also determined in our study.

4.2. Recreational disturbance

The disturbing effects of coastal recreational activities have been already reported on many waterbird species (Krüger 2016), including ones associated with reedbed habitats (Jansen 2011). Visual observations and disturbance experiments have showed that the responses of waterbirds are highly variable and related to individual and environmental factors and types of disturbance (Davenport and Davenport 2006). We did not find any published study investigating relationships between moulting mute swans and kitesurfing, but the effect of disturbance on moulting birds such as eiders or shelducks by ship and kayak traffic have been reported (review in Krüger 2016) as well as the effect of kayaking on moulting mute swans (Clausen et al. 2020). Regarding the review of Krüger (2016), kitesurfing on all bird species has one of the strongest disturbance effects, similar to helicopters, water scooters, and speed boats. All other kinds of boats also cause disturbance to birds, especially during moult. According to Clausen et al. (2020), the effect of kayaking on moulting swans can be minimized by keeping a distance of > 300 m and banning kayaking in sheltered bays with shallow water. We suggest that these measures might be applied in the Curonian Lagoon.

This study determined that more than half of the suitable area in the Curonian Lagoon was unexploited by swans. Such unexploited habitat areas along the eastern shore corresponded to the areas of kiteboarding between Dreverna and Ventė settlements. This was indirectly determined by the non-linear regression between the abundance of swans and the distance (at least 6 km in July-August) from the kiteboarding spots. One unexploited habitat area to the north of Ventė settlement most likely was affected by small boat traffic from local small villages in this section. Swans did not use habitat areas along the western shore (especially to the south of Juodkrantė settlement), most likely due to the relatively narrow phytolittoral zone and close proximity to the main navigation channel between Klaipėda and Nida. The latter effect was indirectly confirmed by the non-linear regression between the abundance of swans and the distance (at least 3 km in July-August) from the main navigation channels.

Regarding disturbance response, the mean distance of flight initiation for various waterbird species varies between 200 and 2000 m. The flight initiation of tundra swan (*Cygnus columbianus*) in reaction to a kite surfer was 700 m, while its alert distance ranged from 1000 to 1400 m (Krüger 2016). Despite kitesurfing often being observed outside designated kitesurfing zones (if they are designated), observational studies report that a 500 m buffer zone is not effective to meet preservation goals for many waterbirds (Jansen 2011). Other studies suggest a buffer zone of 700 m which should be sufficient to minimize the disturbance effects of a kitesurfing zone. Beyond a distance of 700 m, the majority of the waterbird species would not be disturbed, but, for some species at particular locations that 700 m gap could potentially cause a reduction of foraging time (Verbeek and Krijgsveld 2013; Krüger 2016). Only a few studies on moulting birds have revealed much higher critical distances, e.g. > 1000 m for eiders (Krüger 2016). It is clear however that there is a lack of information on the behaviour of moulting waterbirds, especially regarding their sensitivity to various sources of disturbances and the needs to set an effective buffer zone. GPS tracking with observational or experimental data might be a useful method to quantify the effects of anthropogenic disturbance (e.g. Burger et al. 2019) on waterbirds during the moulting period. Regardless, it is obvious that buffer zones should be larger during the moulting season than other seasons.

Kite surfers may severely affect the distribution and abundance of swans, these forced to move to less favourable parts of waterbodies (this study) or to other waterbodies (e.g. in Veluwemeer, the Netherlands; Jansen 2008). Therefore, monitoring is essential for important bird areas and future studies on waterbird ecology and behaviour should be conducted. At the same time, the monitoring of disturbance sources and their effects on birds is necessary and could lead to regulations on disturbing recreational activities (according to Verbeek and Krijgsveld 2013). Additionally, results of studies or monitoring data can be used for communication to kite surfers to find common agreements how to reduce disturbance.

4.3. Management implications

Decision makers and managers should not only have information about the distribution of large bird flocks in an area, but also knowledge on species habitat use to ensure safe roosts and suitable foraging conditions and, from this, balance human needs and environmental protection (Gayet et al. 2013). This study attempts to provide valuable insights on habitat selection by moulting swans, the acquisition of which is needed for effective habitat management not only in the Baltic Sea lagoons, but also large waterbodies such as estuaries, lakes and wetlands.

The areas most frequently exploited by mute swans along the eastern shore of the Curonian Lagoon corresponded to the extent of the protected habitats by NATURA2000. The size and location of protected area seems to be adequate but there are protected areas where the potentially most suitable habitats are not exploited by swans probably due to recreational disturbance. The results of the visual bird surveys showed that before and after moulting, swans stayed more distributed and in larger flocks than during the moulting period. We assume that the number of swans during all months should be the same or similar in the lagoon, but that some moulting swans were hiding in reeds and thus avoided anthropogenic disturbance. This was confirmed using the telemetry data in this study. The visual observations of larger moulting flocks in the most remote areas of the littoral zone located south-east of Ventė settlement revealed it being the most important moulting ground for mute swans as it isa relatively calm area where swans could use open water habitats during the daytime.

Waterfowl usually coexist with human disturbance, but moulting swans are more vulnerable than individuals after moult (Döpfner et al. 2009). The significant impact of kiteboarding and boating was indirectly confirmed, especially during July-August by the negative relationship between the abundance of swans and the proximity to the kiteboarding spots and the main navigation channels. We speculate that the disturbance by kiteboarding was higher than by boating since the abundance of swans was > 100 individuals at 0.5 km from the main navigation channels, whereas this figure was only reached at 3 km from the kiteboarding spots. The spatial patterns of mute swans in this study were also confirmed during other surveys in 2021 and 2022 (pers. obs.), suggesting a rather stable distribution of swans across the study area. Moreover, we cannot identify any other factors that could account for swans not using potentially suitable habitats. Thus, we propose that recreational activities could be restricted at least in the vicinity of Dreverna settlement, where swans could use macrophyte habitats. We recommend setting restrictions for kiteboarding and boating in areas < 1 m in depth and in their proximity during July-August. Otherwise, displaced birds choose suboptimal habitats where they are less safe from predators or areas that are less suitable for feeding (Ringelman 1990; Dehnhard et al. 2020).

We studied only one of the most easily detected species; but a number of other waterbird species may experience a similar disturbance effect in the Curonian Lagoon. Other swan species, ducks Anas sp. and coots *Fulica atra* (Raudonikis 2004; Krüger 2016; Morkūnė et al. 2020) might also be disturbed and lose their moulting or staging habitats due to recreational activities.

5. Conclusions

Moulting mute swans mostly fed in the submerged macrophyte habitat (dominated by charophytes and pondweeds) in shallow areas (< 1 m depth) in the northern part of the Curonian Lagoon and the south-eastern area of the Lithuanian part of the lagoon. This habitat provided the most suitable feeding grounds for swans in terms of diversity and amount of available macrophytes. The habitat of submerged macrophytes at 1–2 m depth was considered of less importance for swans mainly due to the inefficiency of reaching the charophytes and sago pondweeds. Stands of clasping-leaf pondweed were presumed to be of low preference.

This study revealed that mute swans only exploited half of the most suitable habitat area for feeding, while the rest of the suitable habitat area remained unexploited due to disturbance by human recreational activities such as kiteboarding and boating. To enhance the use of the most suitable habitat for swans, it is recommended to restrict kiteboarding and boating activities in areas < 1 m deep during July-August.

Information about the behaviour of moulting swans is lacking, but preventive buffer zones between water sports areas and swan moulting habitats are needed. According to our analysis and available literature, the buffer zones should be larger during the moulting period than in other seasons. A combination of bird study methods, including telemetry, are effective in the collection of data which can be effectively used for bird behavior studies under growing human disturbance.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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