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Research Article

Round gobies in the third dimension – use of vertical walls as habitat enables vector contact in a bottom-dwelling invasive fish

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Abstract

Sessile invasive species often efficiently exploit anthropogenic structures, such as harbour walls and pontoons, which can lead to increased vector contact (i.e. contact with boats), and therefore spread rate. The round goby (*Neogobius melanostomus*) is a bottom-dwelling invasive fish species which was never documented on boats or habitats near the water surface. In this study, we wanted to find out if this fish makes use boat hulls and other vertical anthropogenic structures, which could act as invasion beachheads. We inspected boats close to harbour walls in the river Rhine in Basel, Switzerland, to search for gobies on them and documented the position of the boat and the ways the gobies could have reached the hull. We observed round goby presence on three different boats, with up to 28 goby sightings on one boat hull in the course of 45 minutes. Additionally, we recorded gobies on walls between one and five meters above the ground. Based on these observations, we investigated the behaviour of round gobies using vertical walls as habitat and compared the observed behaviours to those exhibited by gobies on the bottom. Gobies used the habitat along a wall in a generally similar fashion to the habitat on the bottom. However, they sat still for less time and moved more on walls than on the bottom, while feeding activity was similar in both habitats. The results raise questions about the drivers for using vertical structures as habitat in the usually bottom-dwelling round gobies and the plasticity of this behaviour. Our study documents round gobies in direct contact with boats for the first time. Potentially, gobies could find hiding places or suitable structures to nest on boats. This study therefore provides support for the theory that boat hulls are potential vectors for the translocation of round gobies. Our observations should lead to an increased awareness about fish and their eggs on boat hulls and stimulate efforts to implement measures like the check-clean-dry routine for commercial as well as private boats.

Key words: *Neogobius melanostomus*, non-indigenous species, translocation, boat, anthropogenic habitat, behaviour

Introduction

Anthropogenic structures can form novel niches in an ecosystem (Connell 2000; Chapman and Bulleri 2003; Bulleri and Chapman 2010). In invasion biology, research focuses on how and by which species these niches are occupied (Tyrrell and Byers 2007; Ruiz et al. 2009; Albano and Obenat 2019). In aquatic environments, anthropogenic structures like walls or pontoons are common in harbor areas, which are the entry point for many invasive species (Connell and Glasby 1999; Airoldi and Bulleri 2011; Foster et al. 2016). Sessile non-indigenous species (NIS) colonize anthropogenic structures easily, where they often outnumber native species (Bulleri and Airoldi 2005; Glasby et al. 2007; Dafforn et al. 2009). Anthropogenic structures may therefore act as critical beachheads, increasing success of establishment and subsequent spread of NIS (Bulleri and Airoldi 2005; Ruiz et al. 2009; Lacoursière-Roussel et al. 2016). Research about the use of anthropogenic structures as habitat mainly focuses on sessile species, while less is known about how mobile species like fish interact with anthropogenic habitats. Studies comparing fish communities between anthropogenic and natural habitats find results ranging from no observable effects, over seasonal differences, up to pronounced effects on species composition and abundance, as well as dependence on type of structure, exposure, or associated epibiota (Rooker et al. 1997; Able et al. 1998; Clynick et al. 2007; Burt et al. 2013; Davis and Smith 2017; Mercader et al. 2018). Little work considered species-specific habitat use and adaptations associated with anthropogenic structures, although the new habitat can cause novel selective pressures. For example, Franssen (2011) showed that anthropogenic habitat alteration can cause persistent population-level differences in body shape of the red shiner (*Cyprinella lutrensis* Baird and Girard, 1853).

Recently, the availability of cheap off-the-shelf underwater cameras has paved a way for direct observations without humans intruding the habitat via e.g. SCUBA diving. Direct observation techniques are among the most effective means for unobtrusively obtaining accurate information about aquatic organisms in their natural surroundings (Sagarin and Pauchard 2010; Thurow et al. 2012; Mallet and Pelletier 2014). Here, we present a case that exemplifies how the application of hand-held and underwater cameras can aid with the detection of conservation-relevant behaviours in an invasive fish species.

The round goby *Neogobius melanostomus* Pallas, 1814 is one of the most notorious invasive fish species throughout Europe and North America (Vilà et al. 2009; Kornis et al. 2012). Round gobies do not possess swim-bladders and are therefore primarily demersal fish. They are especially abundant in harbour areas and readily use artificial materials at the bottom as nesting sites (Corkum et al. 1998; MacInnis and Corkum 2000; Johnson et al. 2005). Together with a single anecdotal observation of round gobies sitting on vertical walls (Hensler and Jude 2007), it seems plausible that they could use pipes, grates and crevices on boat hulls to hide or spawn in spite of their benthic lifestyle (Hoese 1973; Wonham et al. 2000; Johansson et al. 2018). Gobies or their eggs could subsequently be translocated via waterways or even over-land transport (Hirsch et al. 2016). However, the actual observation of how and when this association between propagule and vector occurs is hardly ever made due to a number of limitations, mainly the rareness of the occasion and the impossibility of researchers constantly spending their time in the field to monitor propagule behaviour near vectors. Hence, there is no confirmation of invasive gobies or their eggs on boat hulls published in the peer-reviewed literature until today (Adrian-Kalchhauser et al. 2017).

The main objective of this study was to confirm this postulated, but never documented association: we aimed to find first observational evidence of the presence of round gobies on boat hulls using underwater and hand-held cameras. Additionally, we explored the research question if round gobies show higher activity on vertical habitats than on the bottom by analysing and comparing their movement behaviours on the ground and on concrete walls. Our results document a not yet investigated use of anthropogenic habitat in the round goby, which establishes a connection to potential vectors for translocation.

Materials and methods

Field observations

We visited the industrial harbour Port of Switzerland in Kleinhüningen, Basel, two to three times a week between June and August 2019 (total number of visits: 30) and searched boat hulls for round goby presence in Basel harbour. On each visit, there were between one and three container ships mooring in the harbor that we could investigate. We carried an Olympus Tough TG5 colour video camera (Olympus Corporation, Shinjuku, Tokyo, Japan) to document any round goby presence on boat hulls. We carefully searched for gobies on boats lying at an observable distance to the harbour walkways. To do so, we slowly walked along the side of the boat that was facing the harbour walkway, looking out for gobies moving on the boat hulls. Observations of round gobies on the harbour walls in short distance (20–40 cm) to the boat hulls confirmed the presence of round gobies at the respective mooring sites and our ability to detect them with bare eyes from our position. We took pictures or videos whenever we found round gobies on a boat hull.

We observed a round goby on a boat hull for the first time on 05 July 2019 (Location A, Figure 1). As the boat on which we observed the goby stayed in its position for weeks (private sailing yacht mooring for maintenance), we aimed to repeat the observation and document it on camera. To do so, we carefully searched the boat for a similar event twice a week for *ca*. 15 minutes (total: 24 times) and took photos or videos every time we detected a goby on the boat. Additionally, we installed GoPro Hero 7 black cameras (GoPro, San Mateo CA, USA) at the stern of the boat on five days to film the rudder and stern area for 10–30 minutes (Table 1). We subsequently checked the recorded videos for the presence of round gobies. Differences in recording times arises from the conditions in the harbour. The bottom in the harbour is muddy to sandy, so commercial boat

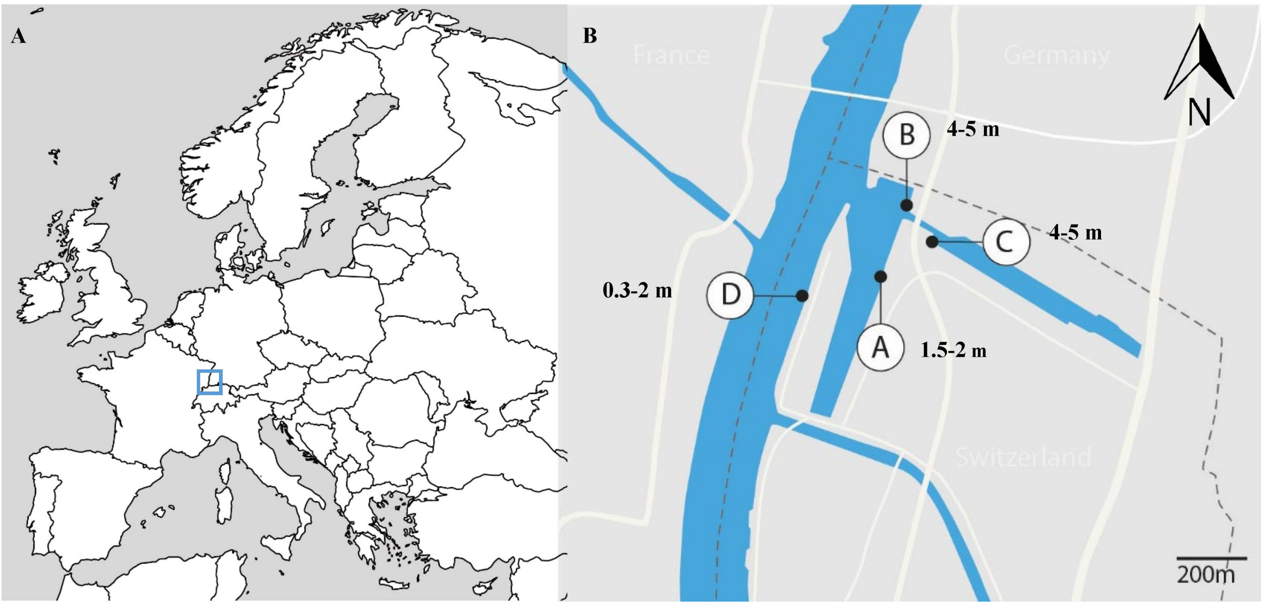

Figure 1. A. Political map of Europe. Blue square indicates the position of Basel, Switzerland; B. Map of the Rhine harbour Port of Switzerland, Basel-Kleinhüningen. Letters indicate the positions of the video recordings of gobies on walls and the bottom below. Numbers next to the letters indicate water depth at the sites. Gobies on boat hulls were present at A, C and D. Videos for behavioural analysis of round gobies on walls and the bottom below were taken at A, B and C.

Table 1. Details of the observations of round gobies on boat hulls. Only observations documented on camera are reported here.

	Date of Record (number of observations)	Location of Record (Figure 1)	Harbour conditions	Boat type	Boat hull
Boat 1 Figure 2	13.08.19 (28)	D	Marina, current (river), no waves, water depth = 0.3–2 m	Commercial ship	Hull entirely covered in biofilm, small patches of macrofouling (algae and mussels). Closest distance to bottom *ca.* 15 cm, hull not moving
Boat 2	10.07.19 (1), 12.07.19 (1), 05.08.19 (5), 09.08.19 (2), 12.08.19 (5), 14.08.19 (2)	A	Industrial harbour, no current, small waves, water depth = 1.5–2 m	Sailboat	Hull almost entirely covered in biofilm, small patches of macrofouling (algae and mussels). Distance rudder-bottom *ca.* 5 cm, hull moving with water motion
Boat 3	17.07.19 (1)	C	Industrial harbour, no current, no waves, water depth = 4–5 m	Container ship	Extensive hull fouling, covered entirely in biofilm and macrofouling, hull in contact with harbour wall, hull not moving

traffic increases turbidity to a point of no visibility at all. Any time a ship entered or exited the harbour, we therefore had to stop recording.

For all three boats on which we found round gobies we recorded characteristics of the boat, location and circumstances under which the observation was made. Specifically, we recorded:

- Boat type
- Hull biofouling presence and composition, based on Floerl et al. (2005)
- Distance of boat to bottom or next harbour wall
- Water depth: estimated based on Port of Switzerland water level particulars

Figure 2. A round goby on the hull of a commercial ship with a layer of biofouling (Boat 1, s. Table 3). The goby was observed to feed and move along the boat hull with as well as against the current.

- Presence of waves and current at time of observation (qualitatively)
- Movement of boat at time of observation

From these observations we developed plausible scenarios, which elucidate how round gobies could have reached the boat hull.

Video recording for behavioural analysis

After observing round gobies sitting on boat hulls we wanted to find out what kind of behaviours they exhibit on these vertical surfaces and if these behaviours are different from the behaviours shown on the bottom. The presence of round gobies on boat hulls was, however, not predictable enough to achieve enough observations of their behaviour. We therefore decided to make use of closely related locations instead, i.e. vertical harbour walls. Gobies on walls were present every time we visited the harbour in our study period between June and August. We collected video material for a behavioural comparison of round gobies on the wall and on the bottom below the wall on four days in July and August 2019 at three different locations in the harbour (Figure 1, Table 2).

The video set-up for the comparative observations of behaviours on walls and the bottom consisted of GoPro Hero 7 black cameras mounted on a concrete block with a 1 m long metal pole protruding in direction of the camera lens, marked with cable straps every 20 cm (Figure S1). We used strings to lower the set-up to the bottom of the harbour, or to the wall close to the water surface. On each site, we placed one camera on the bottom and at the same time one camera on the wall as close as possible to the position of the camera on the bottom. In total, we recorded 16 videos (bottom: 8 videos, wall: 8 videos) suitable for further analysis. We aimed for paired observations, however, on one occasion our set-up for the bottom camera did not reach the ground, so that we could only analyse the

Table 2. Parameters of the videos used for the comparison of behaviours between round gobies observed on either the harbour bottom or vertical harbour walls. Differences in duration of time analysed are due to hindering external conditions (boats in the harbor causing high turbidity). Total N: total number of observations of gobies. Analysed N: Gobies that were in view for > 10 s and therefore part of the statistical analysis. Max N: maximum number of observed gobies in a frame at the same time.

Video Nr.	Habitat	Date	Location	Time Start (hh:mm)	Total time (mm:ss)	Time analysed (mm:ss)	Total N	Analysed N	Max N
1	Bottom	26.07.19	B	12:06	04:38	03:51	15	7	4
2	Wall	26.07.19	B	12:07	04:08	03:32	2	1	1
3	Wall	26.07.19	C	13:24	15:12	11:44	19	14	3
4	Bottom	29.07.19	B	12:09	06:33	05:38	7	3	2
5	Wall	29.07.19	B	11:36	06:58	05:45	20	15	7
6	Bottom	29.07.19	C	11:43	15:28	12:58	50	43	7
7	Wall	29.07.19	C	11:44	13:32	11:14	12	7	3
8	Bottom	05.08.19	A	12:01	18:22	16:22	32	21	4
9	Bottom	05.08.19	A	12:20	17:16	14:41	49	37	5
10	Wall	05.08.19	A	11:59	34:47	34:20	118	85	6
11	Bottom	05.08.19	C	12:01	09:32	08:44	49	40	8
12	Wall	05.08.19	C	11:38	18:09	17:48	6	3	2
13	Bottom	08.08.19	A	12:36	07:23	06:41	2	1	2
14	Wall	08.08.19	A	12:37	06:41	06:00	25	13	4
15	Bottom	08.08.19	B	12:19	09:59	08:50	31	16	4
16	Wall	08.08.19	B	12:22	07:25	07:03	0	0	0

Table 3. Description of the round goby behaviours considered for the analysis of videos taken at the bottom or walls in the harbor. N = number, T = time (s).

Behaviour name	Behaviour type	Description	Variable derived for statistical comparisons
Sitting	State event	Goby sits on one place, with or without fin beats	Percent of time sitting: $\frac{T_{Sitting\ total} \times 100}{T_{in\ view}}$
Fin beat (while sitting)	Point event	Goby moves his pectoral fins: for analysis we only counted fin beats on one side of the body.	Fin beat frequency: $\frac{N_{Fin\ beats}}{T_{Sitting}}$
Hop	Point event	Goby moves forward close to ground, short distance, ≤ 1 pectoral fin stroke	Number of hops per minute: $\frac{N_{Hops} \times 60}{T_{in\ view}}$
Picking food	Point event	Goby picks some food from the bottom/the wall	Number of feeding events per minute: $\frac{N_{Picking\ food} \times 60}{T_{in\ view}}$
Swimming	State event	Goby swims: whole body of goby leaves the bottom, > 1 fin strokes	Percent of time swimming: $\frac{T_{Swimming} \times 100}{T_{in\ view}}$

recording of the wall. On another occasion, we had to relocate the bottom camera amidst the recording, resulting in two videos on the bottom. Table 2 provides details on the videos and the respective circumstances under water. The analysed video sequences were between 4 and 34 minutes long after subtracting camera handling time and time after placement of camera, during which the water was turbid. The difference in times result from increased turbidity due to boat traffic, as described above.

Video analysis

We quantified basic movement and activity parameters that correlate to oxygen consumption and therefore energy expenditure in fish (Trudel and Boisclair 1996; Steinhausen et al. 2005; Tudorache et al. 2008; Table 3). We considered the behaviours of every round goby that stayed within the field of view of the camera for more than 10 seconds. We recorded the duration of the behaviours "sitting" and "swimming" and the number of the behaviours "hop", "pectoral fin beats while sitting" and "picking food". We were able to clearly identify the behaviours irrespective of the turbidity of the water with an exception of pectoral fin beats. In videos with a high turbidity we therefore did not count fin beats for gobies of which we could not clearly see the fins. For the quantification of the behaviours we used the program BORIS V.7.9 (Friard and Gamba 2016).

Once an individual left the field of view, it was impossible to decide whether the next individual entering was the same individual or a different one. We therefore counted every round goby entering the field of view as a new observation. The total number of round goby observations was 235 on the bottom and 202 on the wall. Considering only gobies that were in the field of view for more than ten seconds, we ended up with a sample size of 167 for the bottom and 138 for the wall.

We also determined the maximum number (MaxN) of observed gobies in the frame at the same time for every video. MaxN is a widely used, conservative estimate of abundance of a species in video censuses (Whitmarsh et al. 2017). The metal pole that was part of the set-up allowed us to estimate the visibility. With this information we estimated the respective round goby abundance standardized by visibility (MaxN/m).

Statistical analysis

To allow a comparison of the behaviours recorded in the videos on walls and the bottom, we standardized the data gained from the behavioural quantification of a single goby with the time each observation lasted (Table 2). To confirm that there is no difference in the investigated behaviours depending on the duration of the videos, we plotted every behavioural variable against the duration of the video. We did not observe any trends in these plots. Additionally, we took the four videos with a duration of more than twelve minutes and selected the seven first and last individuals that entered the field of view. We conducted t-tests on all considered behavioural variables between gobies observed early and late in the video. There were no significant differences for any of the behavioural variables considered. In total, we recorded 89 minutes of video material on the bottom and 90 minutes on walls.

We inspected each of the derived variables for normal distribution and equal variances visually using histograms and QQ-plots. If the distribution was approximately normal, we used two-tailed student`s t-tests (if variances were equal) or Welch's t-tests (if variances were not equal) to compare the behaviours that round gobies exhibited on the wall and on the bottom. If the data did not follow a normal distribution, we log-transformed the data before applying *t*-tests. If transforming the data did not result in normal distribution, we used Mann-Whitney *U* tests for the comparisons. We rejected or assumed null hypotheses using a significance level of $\alpha = 0.05$. All statistical analyses were conducted using the stats package in R version 3.5.1 (R Core Team 2019) in RStudio (RStudio Team 2019). Graphs were produced using the package ggplot2 (Wickham 2016).

We are aware that we cannot guarantee complete independence of data for the statistical tests used, as some of the observed gobies could easily have entered the field of view of the camera more than once or could even have been filmed both on the wall and on the bottom. However, this being an exploratory study, we only aimed to quantify observable differences in some basic behaviours that round gobies display on walls as well as the bottom. Therefore, we decided to neglect potential individual pseudo-replication. Considering the high number of observations ($N_{Bottom} = 235$, $N_{Wall} = 202$), and the high goby abundance in the harbour (Bottom: MaxN/m ± SD = 15.67 ± 13.6, Wall: MaxN/m = 9.42 ± 10.0), it is unlikely that behavioural differences between individuals drive major variation in our data. We considered potential site-bias in the data by visually examining all variables separately for each sampling site (Figure S2). We could not fit linear mixed models with sampling site as random factor to quantify the potential site-effect, because with < 5 levels the among-population variance cannot be estimated accurately, and models can be unstable if sample sizes across groups are unbalanced (Harrison et al. 2018). The chosen statistical tests should be able to detect prominent patterns in the data while not taking into account any variability caused by individual or environmental differences.

Results

Round goby observations on boat hulls

Of the *ca*. 40 boats that we inspected, we detected and documented round gobies on three boats mooring in different conditions (Table 1). On boat 1, we documented 28 goby sightings on the hull in the course of 45 minutes. We recorded photos or videos of the hull of boat 2 on eight occasions (Video S3), because it stayed on its position for the entire study period (Table 1). This resulted in six documented instances of goby presence on boat 2 with a total of 16 goby sightings. An initial observation of a goby on the same boat was not documented with a camera. We documented the presence of one goby on the hull of boat 3. All boats had a layer of biofouling on their hulls (Table 1, Figure 2). Round gobies close to the water surface on walls were present every time in varying numbers.

Quantification of behaviours the bottom and on walls

Visual examination of the investigated behaviours for every sampling site separately revealed similar patterns of differences between bottom and wall at every sampling site as in the pooled data, validating the consistency of the measured differences (Figure S2). The only exception to this was mean

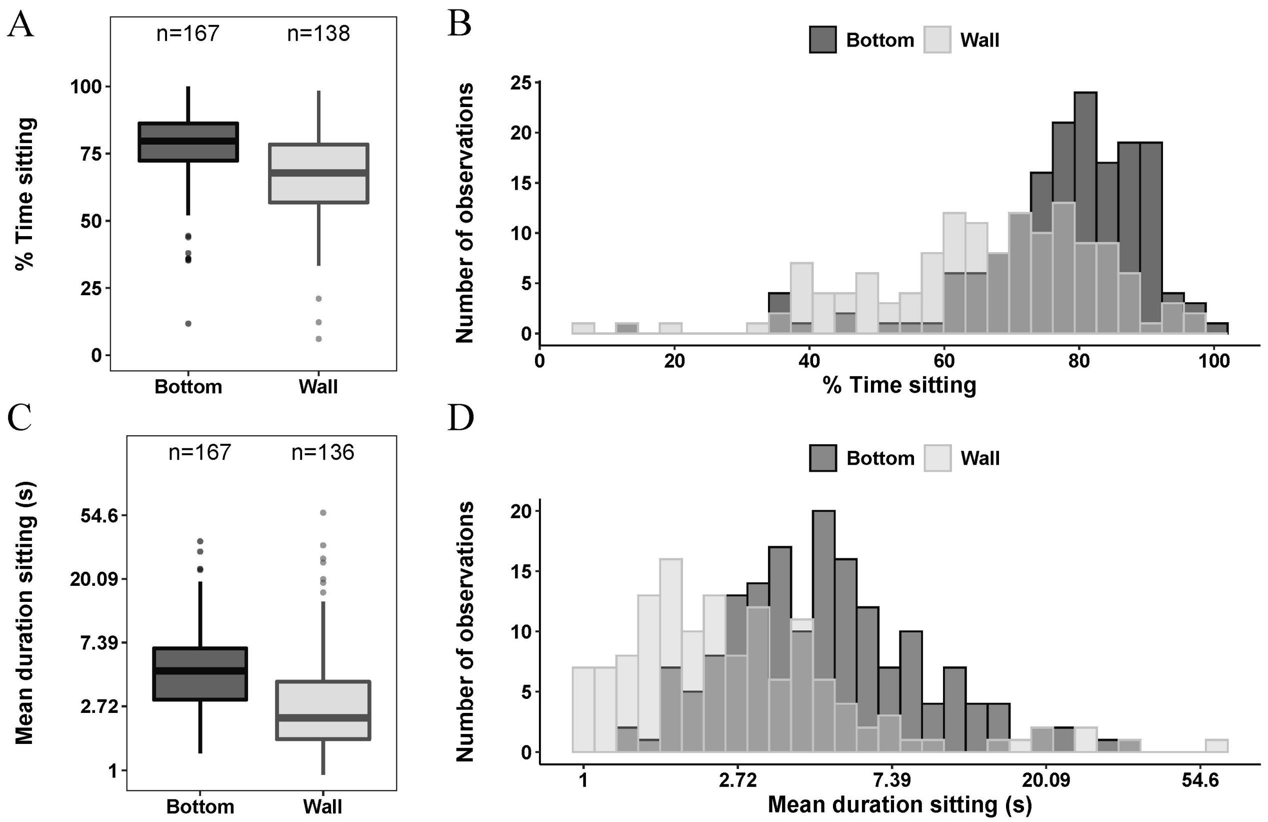

Figure 3. Comparison of time spent sitting still by round gobies on the bottom and on walls. A. Comparison of time spent sitting still (percentage of the total time in view) between gobies observed on the bottom and gobies observed on walls; B. Histograms of the percentage time spent sitting still by gobies on the bottom and on walls; C. Comparison of the mean duration of sitting events between gobies on the bottom and gobies on walls; D. Histograms of the mean duration of sitting events of gobies on the bottom and on walls. Note logarithmic scale in C and D. A, C: Central horizontal lines = median. Boxes = interquartile range. Whiskers = smallest/largest value within 1.5 times interquartile range. Points = outliers. B, D: Overlapping data appears medium grey in histograms.

duration sitting, where no difference in mean duration on walls was visible at sampling site C, whereas the duration was shorter at the other two sites.

Round gobies spent significantly less time sitting still on the wall than on the bottom ($Mean_{Bottom} \pm SD = 77.54 \pm 13.3$, $Mean_{Wall} \pm SD = 66.01 \pm 17.4$, *t*-test: $T_{252.18} = 6.39$, $P < 0.0001$. Most of the observed gobies on the bottom spent around 80 percent of the time sitting still, while gobies on the wall spent on average 66 percent of time sitting (Figure 3A, B). The variance in time sitting still was higher for gobies on the wall. Additionally, single sitting events had a significantly lower mean duration on walls than on the bottom ($Mean_{Bottom} \pm SD = 5.98 \pm 4.9$, $Mean_{Wall} \pm SD = 4.17 \pm 6.7$, *t*-test: $T_{260.03} = 7.01$, $P < 0.0001$, Figure 3C, D). While sitting still, fin beat frequency was significantly higher on the walls ($Mean_{Bottom} \pm SD = 0.01 \pm 0.04$, $Median_{Bottom} = 0.00$; $Mean_{Wall} \pm SD = 1.68 \pm 0.57$, $Median_{Wall} = 1.78$; Mann-Whitney *U* test: $U = 109.5$, $P < 0.0001$, Figure 4A, B). Additionally, gobies hopped significantly more often on walls compared to on the bottom ($Mean_{Bottom} \pm SD = 22.18 \pm 11.9$, $Mean_{Wall} \pm SD = 43.47 \pm 19.3$, *t*-test: $T_{219.01} = -11.31$, $P < 0.0001$, Figure 4C, D).

Round gobies did not feed significantly more often ($Mean_{Bottom} \pm SD = 1.81 \pm 4.9$, $Median_{Bottom} = 0.00$; $Mean_{Wall} \pm SD = 1.86 \pm 5.3$, $Median_{Wall} = 0.00$;

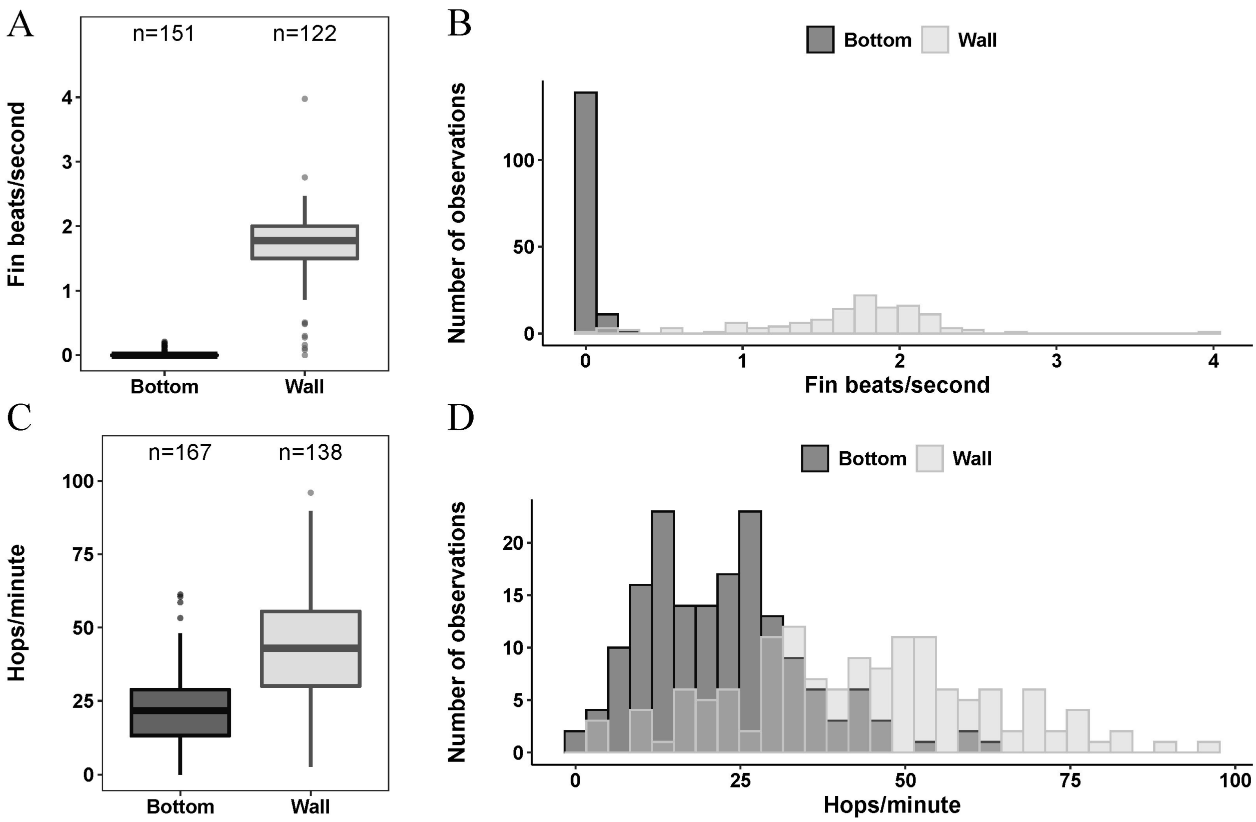

Figure 4. Comparison of activity parameters of round gobies on the bottom and on walls. A. Comparison of fin beat frequency between gobies observed on the bottom and gobies observed on walls; B. Histograms of the fin beat frequency of gobies on the bottom and on walls; C. Comparison of the number of hops per minute between gobies observed on the bottom and gobies observed on walls; D. Histograms of number of hops of gobies on the bottom and on walls. A, C: Central horizontal lines: median. Boxes = interquartile range. Whiskers = smallest/largest value within 1.5 times interquartile range. Points = outliers. B, D: Overlapping data appears medium grey in histograms.

Mann-Whitney *U* test: $U = 11918$, $P = 0.54$), and did not spend significantly more time swimming ($\text{Mean}_{\text{Bottom}} \pm \text{SD} = 1.23 \pm 11.9$, $\text{Median}_{\text{Bottom}} = 0.00$; $\text{Mean}_{\text{Wall}} \pm \text{SD} = 1.27 \pm 2.43$, $\text{Median}_{\text{Wall}} = 0.00$; Mann-Whitney *U* test: $U = 11918$, $P = 0.54$) in any of the habitats.

Further documented behaviours on walls

Apart from the behaviours that we quantified, we also made noteworthy observations of goby behaviours in our videos and in the field. The following list names behaviours that might prove important to understand the use of walls as habitat and for further studies:

Males in spawning colouration: We observed male round gobies with black colouration on few occasions on the bottom as well as on walls. Black colouration is a sign of reproductive activity in nest-guarding male round gobies.

Sitting in holes in walls: We observed round gobies entering holes in harbour walls during fieldwork and in one video. In that video it seems like the hole is used as a nest by a goby, however, due to high turbidity and bad lighting we cannot confirm this without doubt.

Catching insects or feeding above water surface: We observed round gobies sticking their head out of the water or even jumping out of the water on several occasions during fieldwork (partly documented on photo or video). One of these observations included clearly the capture of an insect that was sitting above the water surface (not documented).

Accumulation of round gobies on walls in boat shadow: On very sunny days, we observed round gobies on walls accumulating in the shadows of boats, while we rarely observed any gobies sitting in the open sun.

Sitting upside down: On locations B and C the harbour walls consisted of a concrete wall and an overhanging sheet pile wall 20 cm in front of the concrete wall. In videos that filmed walls sideways, we observed gobies sitting completely upside down on these overhanging sheet pile walls. Gobies also regularly swam up and down between both wall parts.

Holding on to structural elements using the ventral fin: We observed gobies sitting down on the metal pole that was part of the camera set-up, and on structural elements on the walls (e.g. zebra mussels, *Dreissena polymorpha* Pallas, 1771). Thereby, gobies wrapped their fused ventral fin around the respective structure and held on to it for some seconds before moving on.

Bighead gobies (*Ponticola kessleri* Günther, 1861) on walls: Although this study only considers round gobies, we also observed bighead gobies on walls. We did not consider bighead gobies in a similar level of detail here, because the number of observations was much lower.

Discussion

Round goby presence on boat hulls

Here, we present the first photographic and video documentation of round gobies on boat hulls. Our study thereby provides support for the hypothesis that gobies can be translocated by boats via mechanisms other than ballast water intake (Hirsch et al. 2016). On a boat, gobies can feed, hide and possibly even lay eggs if they find suitable structures like holes, pipes or other openings. This holds the potential of the unwanted translocation of hidden gobies or attached eggs, like proposed by several authors (Hoese 1973; Moskal'kova 1996; Wonham et al. 2000; Johansson et al. 2018). This mechanism is especially important in areas without commercial shipping, because wherever commercial ships exchange ballast water, this is likely the most important vector for invasive fish (Wonham et al. 2000; Kotta et al. 2016; Johansson et al. 2018). Recreational boats are known as a major vector for a wide range of invasive species, specifically those occurring in biofouling communities (Minchin et al. 2006; Rothlisberger et al. 2010; Murray et al. 2011). However, fish have rarely been associated with this dispersal mechanism. Our data stresses that there are ways in which the invasive round goby can get in contact with recreational boats.

Combining our observations of round goby presence on boats and the characteristics of the boats and their positions, we developed four plausible scenarios how round gobies could have reached the boats:

1. Swimming up a short distance to reach a boat mooring close to the ground. Like this, gobies can reach boats in shallow water. Our observations show that gobies swim upwards short distances also in a moderate current.
2. Using a part of a boat that is close to the bottom to reach the hull (e.g. ascending the rudder). Gobies can reach boats mooring in medium water depths like this. Our observations show that gobies ascend boat parts also when the boat is moving due to wave action.
3. Ascending a wall and moving onto a boat that is in direct contact to that wall. Like this, gobies can reach boats mooring far from the bottom.
4. Ascending walls and swimming to a boat without direct contact to the wall from there. We did not directly observe gobies on a boat in such a position. However, we consider this way to reach a boat plausible, because we observed round gobies swimming small distances side- and upwards to overhanging sections of walls.

We only observed round gobies on boats that were close to the ground or a wall. Walls can therefore indeed be considered as beachheads for vector contact, drastically reducing the distance that gobies have to overcome to reach boat hulls in deeper water. Importantly, this does not exclude the possibility of round gobies reaching boats that are further away from bottom or walls. In the presented work, we were limited to observations from shore. We therefore cannot make statements about boats that were outside of our visible range.

We detected round gobies on only three out of *ca*. 40 investigated boats. However, the high repeatability of the observations on a boat that stayed stationary for more than two months and the high number of round gobies on the boat that was closest to the ground indicate that this behaviour is nothing out of the ordinary if the conditions are right. Limitations for the observations of container ships that can interfere with detailed investigation include for example the limited time they spend in one place, ongoing unloading and loading of goods, or maintenance work on the hull. It is therefore possible that round goby presence is more common than we were able to document. Our data shows that boats that are moored close to the substrate, remain at one place for a while, and show at least patches of biofouling are readily used as habitat by round gobies.

The ubiquity and practicality of nowadays cameras will enable further discoveries and documentation of conservation-relevant behaviours and instances like the herein described ones (Sagarin and Pauchard 2010; Thurow et al. 2012). An increasing interest of volunteers from the general public in observing nature, e.g. in citizen science projects, can also lead to more frequent documentation of infrequent and unpredictable behaviours researchers struggle to detect (Beckmann et al. 2015; McKinley et al. 2017).

Round goby behaviour on walls and the bottom

The use of artificial vertical structures like concrete walls and boat hulls by the round goby is a largely neglected aspect of their behaviour. Apart from a side-note in Hensler and Jude (2007), we are not aware of any literature describing round gobies on vertical walls – Ghedotti et al. (1995) even found that round gobies left any mussels or snails above 20 cm off the bottom untouched in feeding experiments. However, the two mainly bottom-dwelling genera gobies and blennies are worldwide among the most commonly translocated fish families (Wonham et al. 2000). Their high success in establishing populations in their arrival areas has been attributed to their creviculous nature and their resulting ability to make use of harbour habitats (Wonham et al. 2000).

The quantified movement behaviours indicate that using walls as habitat is likely more energy consuming than staying on the bottom for round gobies. Without a swim bladder, moving up several meters and staying there while constantly having to work against sinking down causes gobies to sit still for less time, hop more often, and exhibit an increased fin beat frequency while staying on walls compared to on the bottom. Increased number of movements and increased fin beat frequency are correlated to oxygen consumption and therefore metabolic costs in other fish (Trudel and Boisclair 1996; Steinhausen et al. 2005; Tudorache et al. 2008). Although we did not have the data to calculate bioenergetics models for the determination of the actual metabolic costs in the round goby, it is reasonable to assume a correlation between the measured behaviours and energy expenditure similar to other fish.

If a behaviour takes up more energy than an alternative behaviour, it should be compensated by other advantages like access to more food or more valuable food resources, or higher security from predators, according to optimal foraging theory (McNamara and Houston 1985; Bartumeus and Catalan 2009; Mikheev et al. 2010). We did not observe an increased feeding frequency in gobies on walls compared to gobies on the bottom. This could be due to the short time we got to observe individual gobies before they left the field of view again, or that we recorded them during day time instead of night time, when feeding activities peak in round gobies (Johnson et al. 2008). Another possibility is that there are more energy rich food organisms, or that food organisms are easier accessible on the wall compared to on the bottom. The bottom at all sites was sandy to muddy, while the walls were covered with biofouling, probably harbouring differing invertebrate communities. Zebra mussels, a known major food source for round gobies (Diggins et al. 2002; Lederer et al. 2008; Angradi 2018), were present in both habitats.

Round gobies on walls are seemingly more exposed to predators than round gobies on the bottom due to a lack of refugia and proximity to the water surface, which makes them visible e.g. to fish-eating birds. Although we did see native fish in our videos (e.g. European perch *Perca fluviatilis* Linneaus, 1758, a known predator of round gobies: Liversage et al. 2017), we did not observe any predatory interactions between species in any of the videos. It hence remains unclear whether using walls as habitat actually exposes round gobies to a higher predation risk.

Another reason for using walls as habitat could be high competition at the bottom. If there are not enough resources for the whole population on the bottom of the harbour, individuals could try to migrate out of the area (Chuang and Peterson 2016), or alternatively make use of an unoccupied niche dimension: the harbour walls. For example, food competition is suggested to cause the spread of populations lead by migrating adult round gobies (Gutowsky and Fox 2011; Azour et al. 2015; Brandner et al. 2018). In other regions, juveniles are reportedly more common at the invasion front (Ray and Corkum 2001; Brownscombe and Fox 2012). Similarly, either large, strong gobies could be the ones primarily moving up walls, or rather young and light ones, who might be outcompeted on the bottom. Investigating the distribution of individuals between the two habitats would help to evaluate the ecological and behavioural significance of wall climbing for the respective individuals and populations. Further studies using controlled experimental set-ups should investigate the influence of demographic and environmental variables on the use of walls as habitat. Understanding the use of vertical anthropogenic structures could add important knowledge about behavioural repertoire, population dynamics and invasion progression of the round goby (Mikheev et al. 2010; Wright et al. 2010; Chuang and Peterson 2016).

Conclusions

Round gobies regularly use vertical anthropogenic structures including boat hulls as habitat. Although their energy consumption is likely higher on vertical structures, round gobies display the same behaviours there as on the bottom. Round gobies are therefore likely to use walls and boats as equivalent habitat to the bottom, including behaviours like foraging and possibly nesting. The hypothesis that round gobies or their eggs are translocated on boat hulls gains additional relevance with the herein presented observations. Measures to prevent the spread of round gobies by boats should hence not only consider ballast water, but also the control and cleaning of boat hulls including hard-to-reach areas like pipes and grates.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. Camera set-up for the observation of round gobies on harbor walls.
Figure S2. Results of the behavioural comparisons of gobies observed at the bottom and gobies observed on walls separated by sampling site.
Figure S3. Video of a round goby on the rudder of a recreational sailing boat.

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