Opposite selection on behavioural types by active and passive fishing gears in a simulated guppy fishery

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Running headline: Fishing gear selection on behavioural types

Abstract

The present study assessed whether fishing gear was selective on behavioural traits, such as boldness and activity, and how this was related with a productivity trait, growth. Female guppies *Poecilia reticulata* were screened for their behaviour on the shy–bold axis and activity, then tested whether they were captured differently by passive and active fishing gear, here represented by a trap and a trawl. Both gears were selective on boldness; bold individuals were caught faster by the trap, but escaped more often the trawl. Boldness and gear vulnerability showed weak correlations with activity and growth. The results draw attention to the importance of the behavioural dimension of fishing: selective fishing on behavioural traits will change the trait composition of the population, and might eventually impact resilience and fishery productivity.

Keywords: activity; boldness; fishing; gear avoidance; *Poecilia reticulata*.

INTRODUCTION

Humans have profound effects on natural ecosystems. In particular, humans exploit natural populations in a selective manner, so that the most desirable individuals are removed first. Evidence is accumulating that such selective harvesting is having ecological and evolutionary impacts in a wide range of fish (reviewed by Law 2000; Palumbi, 2001; Heino & Dieckmann, 2008). However, most of the studies have focused on life-history and morphological traits.

A behavioural change is the key first response to human-induced environmental changes; such behavioural responses allow coping with novel habitats, resources, enemies, etc. (Sih *et al.*, 2011; Tuomainen & Candolin, 2011). Fishing is unlikely to be an exception in triggering behavioural responses: fishing activities may cause avoidance of certain areas (e.g., passive gear led to avoidance of diel vertical migration in cod *Gadus morhua* L. 1758; Olsen *et al.*, 2012), increased vigilance behaviour (Walsh *et al.*, 2006), gear avoidance (Beukema, 1969), and modified social interactions and reproductive behaviour (Suski & Philipp, 2004; Sutter *et al.,* 2012). Capture process itself may depend on behavioural responses triggered by the fishing gear, such as the herding effect in trawling (Wardle, 1993). Not surprisingly, knowledge on fish behaviour is utilized in the improvement of fishing gears, reducing by-catch of non-target species and under-sized individuals (Engås, 1994).

It is expected that behaviour affects differently capture efficiency of different fishing gears and methods. Passive gear (that is, static gears such as traps and gillnets) relies on fish movement and exploratory behaviours in both components of the catching process, encounter with the gear and retention by the gear (Rudstam *et al.*, 1984). Passive gear might be selective for behavioural types as bold individuals are associated with more exploratory and active behaviours (Heino & Godø, 2002; Biro

& Post, 2008; Uusi-Heikkilä *et al.*, 2008; Wilson *et al.*, 2011; Olsen *et al.*, 2012). In contrast, the catchability of active gears (that is, mobile gears such as trawls, dredges and seines) is less straightforward as these gears are based on chasing the fish. In this case, innate predator-avoidance reactions influence the capture, and it is possible that shy fish are more easily frightened by the approaching vessel and gear (Ona & Godø, 1990; Heino & Godø, 2002). Thus, shy individuals might be caught less if they freeze behind boulders on the seabed or dive under the path of an approaching mid-water trawl, but more if their reaction response is slower and they do not swim away from the approaching trawl in time. However, little is known on how fishing gear affects behavioural traits and this effect might be contrary to initially expected (e.g., angling caught more often timid, rather than bold, bluegill sunfish *Lepomis macrochirus* Rafinesque 1819; Wilson *et al.*, 2011).

Behaviours that could be linked to vulnerability (e.g., boldness, activity and exploration) show consistent inter-individual variation (Réale *et al.*, 2010) and are heritable (Philipp *et al.*, 2009; Chervet *et al.*, 2011; Arimoyo *et al.*, 2013), thus selectivity on them has potentially evolutionary consequences. In addition, behaviour-linked vulnerability might be related to other traits such as physiological and life-history ones (Uusi-Heikkilä *et al.*, 2008). It has been shown that vulnerability to fishing gear can be related to growth (Biro & Post, 2008; Redpath *et al.*, 2009) and metabolic rate (Redpath *et al.*, 2010). In addition, vulnerability can be related to other behaviours such as boldness (Biro & Post, 2008), activity (Olsen *et al.*, 2012), and parental care (Cooke *et al.*, 2007). Therefore, selective removal of one behavioural type by fishing might have a profound effect on the diversity of traits in a population.

Behavioural changes towards gear can be adaptive: avoiding being caught obviously increases survival, a key fitness component. However, correlated changes in other traits or in other situations may be maladaptive. An individual hiding under a rock or being very passive may be safe from predators (including fishing), but it will not have many chances for foraging (Walters, 2000; Killen & Brown, 2006; Jørgensen & Holt, 2013). Adaptive or not, these behavioural and correlated trait responses are likely to have an impact on the profitability of the fishery. If a fishery systematically removes highly vulnerable individuals, only those more difficult to catch will remain in the population (Miller, 1957; Philipp *et al.*, 2009). If these changes are at least partly heritable (Philipp *et al.*, 2009), such practices will over time reduce the value of a fish stock for commercial and recreational fishers alike. Thus, increased knowledge on effects of fishing on behaviour can be crucial for conservation of interspecific diversity and biology—and for the efficiency and profitability of fisheries.

The aim of this paper was to study whether fishing gear are selective on certain behaviours and whether such vulnerability and behavioural traits are correlated with each other and with growth. The Trinidadian guppy *Poecilia reticulata* Peters 1859 was used a model species, due to its amenability to laboratory testing and the availability of established protocols for studying their behaviour and other traits. In particular, the study focused on vulnerability of behavioural types along the shy–bold axis, which is heritable in fish (Arimoyo *et al.*, 2013). While fishing gears are not purposely selective on boldness, this behaviour has been extensively studied and is correlated with many other behavioural, life-history and physiological traits in fish, including guppies and important capture fisheries species such as cod. In addition, boldness, activity and exploration are thought to play a role in cod escaping trawls and nets (Hansen *et al.*, 2009; Olsen *et al.*, 2012). It was tested whether female guppies were captured differently according to their boldness behavioural type (i.e., shy or bold), which is a consistent behaviour in guppies (Burns, 2008). Female *P.*

reticulata screened for this behavioural trait were tested with two types of fishing gear, passive and passive gear, here represented by a trap and a trawl. Additionally, to look for possible relations between boldness and other traits, experimental fish were assessed for growth and activity/exploration behaviour. Studying selection toward boldness and the indirect selection towards other, more directly ecologically relevant traits (growth, exploration, etc.) in guppies can bring insights on the selectivity of fishing towards behaviour in commercially relevant species and its consequences for the fishery.

MATERIALS AND METHODS

This study was performed at the University of Bergen, Norway, with first generation offspring of wild-caught *P. reticulata* from the Yarra River in Trinidad, the West Indies. The wild individuals were caught with active (hand nets) and passive fishing gears (minnow traps) both in the edges and in the centre of the river, to reduce any bias in the sampling. In addition, individuals were caught both in areas with current and still water. Sixteen wild-caught females were used to breed sixteen families. Females had mated in the wild, likely with multiple males, and individuals within each family were half-siblings or full-siblings. Wild-caught females were housed individually in 2-litre aquaria and fed ad-lib newly hatched brine shrimp, *Artemia salina* (Silver Star Artemia), in the morning, and fish flakes (TetraMin, Tetra) in the afternoon. Females were checked twice a day for offspring, which were removed from the mother aquaria by hand netting as soon as they were found. Offspring of a single female were kept together in broods until sexing was possible, then males and females were separated. Six virgin mature F1-females from each of the 16 families were chosen for this study. We only chose virgin females to eliminate possible differences of sex and gestation stage. They were further reared isolated in 2-litre aquaria (42 days before the beginning of the experiments) under the same light (12:12) and temperature (25 ± 0.5 ºC) conditions and fed the same amount of food (20 µl of concentrate brine shrimp per day per female). All aquaria, including those with wild-caught females, were placed in the same circulation system with constant flow-through water (12:12 light and 25 ± 0.5 ºC temperature).

Each individual was used once, in a randomized order, in each of the four different tests (see details below): 1) boldness, 2) vulnerability to being capture by a trap, 3) vulnerability to being capture by a trawl, and 4) activity. The different experimental arenas were cleaned and water was renewed between individual tests. Growth rate was estimated as change in length per day from beginning to the end of the study. The values obtained in the present study (mean ± SE: 0.37 ± 0.07 mm day^{-1}) is comparable to other studies on *P. reticulata* maintained in similar conditions (0.25 mm day^{-1}; Auer, 2010). Thus, there is no evidence to suggest that the testing and handling negatively affected individual growth.

All females were dissected at the end of the study and found to be mature but virgin, except one individual that was pregnant; this female was dismissed from the study. Therefore, a total of 95 individuals were considered in this study. Females were killed by an overdose of MS222 (Metacaine) and their heads were cut off to ensure brain death prior dissection.

BOLDNESS

Here boldness in fish is considered sensu Gosling, (1998) and Toms *et al.* (2010), i.e., responses to novel events and environments (for a contrasting definition see Réale *et al.*, 2007). Boldness is considered a behavioural personality trait as in a population there are individual differences that are consistent in time and/or across contexts (Budaev, 1997; Dall *et al.*, 2004; Gosling, 1998; Réale *et al.*, 2007). In *P. reticulata* boldness is most reliably measured as susceptibility to a novel environment in an Open Field Test (OFT; Burns, 2008).

OFT was conducted by introducing a fish in an experimental arena (a round plastic tub of 24 cm diameter and 4 cm of water depth), unknown to that individual, and recording its behaviour, from the time of release, with a digital video camera (Sanyo-VPC-WH1). The fish was first placed inside a black plastic pipe (7 cm diameter) in the middle of the arena to acclimatize for 60 s; once the pipe was lifted the fish could swim freely for three minutes. *Freezing time* was defined as the total time the individual was immobile for a period longer than two seconds during the three minutes of the test; shorter breaks were considered part of normal swimming behaviour. The estimation was done from the video file using Etholog 2.2 (Ottoni, 2000). Freezing time is considered the best measurement of boldness in *P. reticulata* (Burns, 2008) and is commonly used for other fish (Toms *et al.,* 2010). Fish with a relatively long freezing time were considered shy, while those with a relatively short freezing time were bold.

Measurement of the freezing time in *P. reticulata* has been shown to be repeatable in different populations and between sexes (Burns, 2008), and this was confirmed for the population in our lab too. A pilot OFT study with 155 individuals tested twice showed that 48.5% of the variance was explained by inter-individual differences being maintained between tests (Linear Mixed Model based-Repeatability, $R = 0.49$, 95% C.I. = 0.35–0.60, $P = 0.0001$ statistical significance based on 10000 permutations; Nakagawa & Schielzeth, 2010). Some of the residual variance was explained by mean-level changes in behaviour between the two tests. Once this residual variance was controlled for 51% of the variance was explained by individual differences (R_{adj} = 0.51, 95% C.I. = 0.38–0.62; P = 0.0001). A different coloured arena was used in each of the two trials (similar to the alternate form of OFT in Burns; 2008), thus the measurement of boldness was consistent over time and context. Similar values of R and R_{adj} were found in brown trout *Salmo trutta* L. 1758 and were interpreted as behavioural consistency (Adriaenssens & Johnsson, 2012) and are above average repeatability values for behavioural traits (Bell *et al.*, 2009; Wolak *et al.*, 2011).

VULNERABILITY TO TRAP

The trap consisted of a transparent plastic bottle (a 75 cm^2 cell culture flask) where the top was cut off and reversed (9.5 x 7.8 x 3.5 cm), mimicking a small minnow trap with one opening, typically used for catching small freshwater fish. The inlet of the bottle was reduced to 1.4 cm diameter with a plastic film shaped as a funnel glued to the inlet. This way the fish were unable to escape once inside the trap. The trap was placed inside a white round plastic tank (60 cm diameter and 4 cm water depth). It was set 10 cm from the edge of the tank with the inlet oriented anticlockwise and parallel to the edge. Each fish was singly placed with a hand net in the experimental arena, in the opposite side of the tank relative to the trap. Each fish was given 100 min in the experimental arena. The time until trapping was recorded. Fish that did not get trapped were given a notional score of 100 min. The experimental arena was checked every five minutes and trapped fish were released immediately when found inside the trap.

VULNERABILITY TO TRAWL

The experimental ‘trawl’ consisted of a vertical net moving along the horizontal axis of a glass aquarium (90 x 20 x 17.5 cm) with 5 cm water depth (Fig. 1; similar to the trawl apparatus of Brown & Warburton, 1999*a*). The trawl consisted of a vertical green plastic net of approximately 2.5 x 2.5 mm mesh size (made of two superimposed garden meshes of 5 x 5 mm mesh size), mounted in an aluminium frame, and pulled along rails on the aquarium sidewalls. A constant velocity of 5 cm s^{-1} was maintained by winching the net frame with an electrical motor (Multifix constant). The net covered the whole transverse section of the tank, without allowing the fish to pass through, except through four escape holes at the bottom of the trawl: one in each corner (1 x 1 cm) and two holes (2 x 1 cm) 3 cm from the corners (see Fig. 1). This experimental trawl tries to imitate a bottom trawl where fish can escape under the footrope because of stones and other irregularities of the sea floor.

Each fish was tested alone. The fish were allowed 60 min to acclimatize inside the tank, with the trawl at 14 cm from the wall of the tank and with the holes of the trawl covered. It took 15 s for the trawl to move from one end of the tank to the other. The trawl stopped 1 cm before the end of the tank to avoid damaging the fish. Here the trawl was held immobile and the fish was given 60 extra seconds to escape the trawl through the holes. Fish that did not escape the trawl were given a notional score of 75 s. Afterwards, the trawl was returned to the starting position and, after an interval of two minutes for fish acclimation, the net was pulled again. This procedure was repeated five times, in order to assess whether the escaping behaviour differed between trials, and thus, to determine learning or habituation in the fish. The whole procedure was recorded with a video camera and time to escape the trawl was noted for each trial.

The trap and the trawl were designed in such a manner that the stress during the catching process was minimized. Caught fish were in a limited space, but they could still swim freely; no signs of high stress were observed. The fish were not inside the trap and trawl longer than five minutes and one minute, respectively.

LOCOMOTION

Locomotion or activity refers to the general activity of an unstressed individual, i.e., in a non-novel, non-risky environment (Réale *et al.*, 2007; Burns, 2008). The effect of activity was assessed in order to disentangle whether vulnerability to fishing gear was associated with activity rather than boldness. Locomotion was determined from video recordings of the trap test. Therefore, the experimental arena was the same as explained above, a white round plastic tank of 60 cm diameter and 4 cm water depth. Fish movement was recorded for five minutes, starting ten minutes after the fish was introduced to the arena. This time frame was chosen to allow some acclimatizing; none of the fish got trapped by this time.

The videos were analyzed for trajectories of movement with the software LabTrack 2.3 (Bioras Aps, Denmark). Fish position was assessed every fifth frame of the video recorded at 31.3 frames s^{-1}. Thus, over the five minutes recorded we assessed the position of the fish in 1878 frames. Eighteen individuals are missing from the activity assessment, as their videos could not be analyzed with the standard settings, in a comparable manner with the rest. From the coordinates of each position of the fish, we obtained the total *distance moved* and the total *area covered* by movements.

These measurements of movement are considered as general fish activity in the present study because movement was measured after an acclimation of ten minutes in the experimental arena. It is assumed that at the time of measuring the arena was no longer a novel and stressful environment, but acknowledged that the presence of the trap might have played a role as a novel object and affected the measurement. In such case activity might be confounded with exploratory behaviour. Exploration is an individual's behaviour to collect information about a new environment and object (Réale *et al.,* 2007; Burns, 2008). Burns (2008) found that activity and exploration are correlated and thereby confounded in novel object tests for *P. reticulata*. In such tests, general locomotion is associated with activity in a known environment, while exploration could only be measured as inspecting behaviour oriented to the novel object within few centimetres (Burns, 2008). Therefore, in the present study the measurement of movement can be interpreted as activity.

STATISTICAL ANALYSIS

Statistical analyses were performed with software R 2.14.1 (R Development Core Team 2012). A principal component analysis was performed to assess covariability between the different behavioural variables: freezing time, distance moved, area covered, trapping time and trawl escapement time. All the time variables were square root transformed, while the activity ones were untransformed. These variables were reduced to three principal components, which were then each tested for an effect of growth with a linear mixed model (LME). Each LME performed had one principal component as response variable, growth as a fixed effect, and family as random intercept. In addition, pair-wise correlations between all the variables were calculated. Time until trapping and time until escaping the trawl were assessed with survival analysis with censoring (trapped/not trapped and escaped/not escaped, respectively). These survival analyses not only consider how long it takes the fish to get caught, but also whether it gets caught or not. Time until trapping was tested with a parametric survival analysis (PSA; R package “survival”; Therneau, 2012*a*) for the effect of freezing time as a proxy for boldness, with family as random effect (frailty). Time until escaping the trawl was tested for personality and trial number (repetitions of the trawling test) effects with a non-parametric survival analysis (NPSA; R package “coxme”; Therneau, 2012*b*), with individual identity nested within family as a random effect. A Tukey’s HSD posthoc test was performed to assess differences between trials (R package “multcomp”; Hothorn *et al.*, 2008). The same NPSA model was performed with the factor boldness type (shy or bold), characterized by freezing times higher and lower than the median time (28.9 s) to further understand the effect of trial in each of the behavioural types (shy or bold). Similar survival analyses with censoring were performed to test the effect of activity on trapping (PSA with family as random effect) and trawling (NPSA with individual identity nested within family as a random effect). In both survival analyses total distance moved and area covered were the covariates included as proxies of activity.

We found that in a linear mixed effect model with family as random factor the freezing time (square root-transformed) was affected by the weight at the end of the study and by when the open field test took place in the sequence of tests. Therefore, these factors were included as covariates in all survival analyses mentioned above. Neither of the activity measurements was affected by those factors in a linear mixed effect model with family as random factor and area covered or distance moved as response variables.

In all tests freezing time was considered as a continuous variable. However, we additionally classified individuals with freezing time under or equal to the median (28.9 s) as bold (N = 48), while those with freezing time larger than the median were classified as shy ($N = 47$) for illustration purposes. In addition, we used the shy and bold categories in a second NPSA (boldness type as factor) model for trawling time to be able to interpret the results of the first NPSA model (freezing time as covariate; see results for details). We repeated this test only considering the 30 shyest and the 30 boldest individuals.

In addition, intra-class (linear mixed model based-) correlation coefficients were calculated as estimates of repeatability of trawling time among the five trawling trials (R package rptR; Nakagawa & Schielzeth, 2010).

RESULTS

BOLDNESS

Freezing time in the open field test (OFT) was highly variable (Fig. 2). Interpreted as a proxy for boldness, this result suggests high variability along the bold–shy axis. Freezing time was not affected by differences in age (LME: $t_{27} = -0.11$, $P = 0.90$), length at the beginning ($t_{27} = -0.90$, $P = 0.37$) or at the end of the experiment ($t_{27} = 0.90$, $P = 0.37$), weight at the beginning of the experiment ($t_{27} = -0.89$, $P = 0.37$), growth ($t_{27} = -0.90$, $P = 0.37$; see also Table I), nor any of the activity variables (distance: $t_{27} = -1.47$, $P = 0.15$; area: $t_{27} = -0.88$, $P = 0.38$). However, freezing time was positively associated with when in the sequence of behavioural tests the open-field test was performed: individuals tested for boldness after being tested for trawling and trapping froze for a shorter time than those first tested for boldness (LME: $t_{71} = -3.06$, $P = 0.003$). Individuals assessed in OFT in the second place did not differ from those assessed in the third or first place.

LOCOMOTION

The total distance moved varied between 183 cm and 1780 cm (mean ± SD: 676 ± 4314 cm, N = 77) and the total area covered between 85 cm^2 and 885 cm^2 (mean ± SD: 539 ± 112 cm^2, N = 77); these variables were positively correlated ($r_p = 0.43$, $t_{75} = 4.18$, $P = 0.00007$). Neither of these activity variables was correlated with freezing time. Growth rate was weakly correlated with distance (Pearson's correlation: $r_p = 0.27$, $t_{72} = 2.4$, $P = 0.01$) but not with area (Table I).

BEHAVIOURAL ASSOCIATIONS

Principal Component Analysis (PCA) of the behavioural traits (excluding area covered due to its strong correlation with distance) resulted in the first two principal components (PC1, PC2) explaining 65% of the variance. The loadings of PC1 were high and positive for distance, showing positive association between them, and negative for time to be trapped, suggesting that active fish were trapped fastest. For PC2 the loadings were high and positive for trawl escape time, and high and positive for freezing time (Table II). These results suggest that vulnerability to trap/activity, vulnerability to trawl/freezing time represent two, partly independent aspects of behavioural diversity in guppies.

Growth was not correlated with PC1, but it was correlated with PC2 ($r_p = 0.32$, $t_{53} = -2.49$, $P = 0.01$), indirectly suggesting a positive association between growth and freezing/trawl time.

VULNERABILITY TO TRAP

Only 28.4% of individuals got trapped, from those the time to get trapped ranged between 16 to 94 min (mean ± SD: 55.7 ± 23.8 min, N = 27) was affected by freezing time (PSA: $X^2_1 = 3.61$, $P = 0.05$), when being controlled for the effect of test order

(PSA: $X^2_1 = 0.01$, $P = 0.93$). Moreover, freezing and trapping times were positively correlated (Pearson's correlation: $r_p = 0.20$, $t_{96} = 2.03$, $P = 0.04$; Table I). Shy individuals, i.e., those with longer freezing times, had longer capture times than bold individuals (Fig. 3a). Time to get trapped was not affected by total distance moved (PSA: $X^2_1 = 0.03$, $P = 0.86$) or by area covered (PSA: $X^2_1 = 1.37$, $P = 0.24$).

VULNERABILITY TO TRAWL

In 87% of trials the individual managed to escape the trawl ($N = 475$, 5 trials per individual), and all the individuals managed to escape the trawl at least once. Time to escape from trawl was negatively affected by freezing time (NPSA: $z = -1.99$, $P = 0.04$) and trial, even after controlled by the effect testing order (NPSA: $z = 0.50$, $P = 0.62$). Time to escape the trawl was not affected by activity (NPSA, area covered: $z = -0.19$, $P = 0.85$; total distance: $z = -0.55$, $P = 0.58$). Shy individuals needed more time to escape (Fig. 3b), however, this time also depended on the trial number (Fig. 4). Fourth and fifth trial resulted in a longer escape time than the first trial (Tukey HSD: $z = -2.8$, $P = 0.03$ and $z = -3.01$, $P = 0.02$, for respectively 4th and 5th trial).

The time to escape the trawl was also assessed using boldness type as a binary explanatory variable (bold vs. shy, categories divided by the median freezing time, see methods for details). The significant interaction between boldness type and trial number showed that the difference in time to escape the trawl between shy and bold fish depended on trial number. Bold fish were not affected by trial number in their time to escape the trawl (Fig. 4). Shy fish did not differ from bold ones in the first trial, but in trials 2 to 4 shy individuals had longer escaping time than bold ones (NPSA: trial 2: $z = -2.71$, $P = 0.006$; trial 3: $z = -2.46$, $P = 0.01$; trial 4: $z = -2.41$, $P = 0.01$). In the fifth trial the difference was no longer significant (Fig. 4). The trawl escaping behaviour was repeatable among trials, but the variation explained by individual differences was low (*R* = 0.25, 95% C.I. = 0.16–0.35; *P* = 0.0001).

DISCUSSION

In the present study, Trinidadian guppies *Poecilia reticulata* exhibited a large variation in their behavioural traits, and this variability was linked to their vulnerability to being captured by "fishing" gear. This experiment illustrates that both passive and active fishing methods are selective with respect to boldness, a trait known to be heritable in fish (Arimoyo *et al.*, 2013), and therefore, have the potential to drive evolutionary change in behavioural traits.

The experimental trawl caught more often shy individuals with long freezing times than bold ones, which were better at finding their way out of the trawl. This effect of boldness on ability to escape the trawl was apparent despite the fact that trawl escape behaviour presented a high variation within individuals. Thus, the present study shows the potential selectivity of trawl-like fishing gear on fish boldness. The differential vulnerability of boldness types to trawls has previously been suggested not to be strong enough to be relevant (Biro & Post, 2008). However, Wilson *et al.* (2011) showed that catchability by active and passive fishing gears depends on fish boldness: *L. macrochirus* caught by seine were bolder (measured as shorter latency to exit a refuge to a novel environment) than individuals caught by angling.

The escape time of shy individuals differed between trials, while this was not the case for bold fish confronted with the trawl, suggesting learning behaviour. However, in our experiment time to escape increased over time for the shy fish, which is the opposite of what is expected if avoidance is a learned skill, as a number of earlier studies suggest. A tendency of faster escape was found over repeated trials in an experimental study rainbowfish *Melanotaenia duboulayi* (Castelnau 1878) were fished with an experimental trawl similar to the one used here (Brown & Warburton, 1999*a*). On the other hand, haddock *Melanogrammus aeglefinus* (Linnaeus 1758) initially avoided penetrating a mesh curtain, but the time of later penetrations was reduced as a result of previous experience (Özbilgin & Glass, 2004). These studies, together with the present experiment, show that fish learn to cope with trawl-like gear. However, in the present experiment, the shy fish apparently learned that it was safe to remain in the trawl. This is an artefact caused by the experimental set-up where being retained by the trawl had no negative consequences: the trawl stopped one centimetre before the wall of the tank to avoid harming the fish.

Bold fish with short freezing times were captured faster with a passive gear (trap) than shy fish with long freezing times. In experimental situations similar results have previously been shown for rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) fished with gillnets (Biro & Post, 2008) and for angled *L. macrochirus* (Wilson *et al.*, 2011). However, angling seemed to catch more shy fish in wild habitats, as angling took place close to dense, covered areas with refuges where shy individuals were more abundant (Wilson *et al.*, 2011). Using acoustically tagged wild *G. morhua* Olsen *et al.* (2012) showed that fish with consistently strong vertical migration behaviour were more at risk being caught in the fishery using a range of passive gears (traps, gillnets, and hand lines).

It has been suggested that personality traits are correlated with life history and physiological traits. The common framework considers bold and active individuals to grow faster (Biro & Stamps, 2008; Réale *et al.*, 2010). However, no general rule has emerged yet, as the association might depend on the context, the exact definition of boldness, or be very variable in the wild (Adriaenssens & Johnsson, 2009; Réale *et al.*, 2010). In the present study there was a positive correlation between growth rate and activity (measured as the distance moved) and a positive relationship between growth and the second principal component, which was related to freezing time and time to escape the trawl, suggesting that shy fish that took longer to escape the trawl have higher growth. Braithwaite & Salvanes (2005) and Adriaenssens & Johnsson (2011) also showed that shy individuals grew faster for *G. morhua* and *S. trutta*, respectively. Our results point that shy fish grew more in a situation where there was no need to search or compete for food, as the test fish were reared isolated. The results showed here point to that a trap that selectively removes bolder individuals, could indirectly also remove slow growing individuals, while a trawl would selectively remove shy and fast growing individuals.

Independently of whether personality traits are related to productivity traits (e.g. growth rate) or not, selective fishing on personality most probably has consequences for the population and for the productivity of the fisheries. In *P. reticulata*, exploratory behaviour is related to schooling, boldness, aggressiveness (Budaev, 1997) and longer resistance to stress (Budaev & Zhuikov, 1998). In addition, bold individuals are faster at escaping a predator and are preferred by females (Godin & Dugatkin, 1996). Thus, removal of certain behavioural types might interfere with population structure and viability. For example, mixed-personality shoals of guppies fed more than shy- and bold-only shoals; mixed shoals also resumed swimming faster than shy-only and bold-only shoals after a fright stimulus (Dyer *et al.*, 2008). A mixed-behavioural types population seems more resilient relative to a single-behavioural type one (Dyer *et al.*, 2008).

A limitation of the experiments presented here is that they mostly relate to the second part of the capture process, retention by the gear. The first part is encounter with gear (Rudstam *et al.*, 1984), which was unavoidable with the trawl and relatively immediate for the trap placed on a small arena. The effect of freezing time and activity on encounter rate (measured as 1/ time to first touch the trap with snout and 2/ time to inter the trap inlet for the first time) was tested for a sample of our data (N = 23). Both trap encounter measurements were affected by area covered, but not freezing time or distance move. Thus, from the small subsample of the data it could be concluded that encountering the trap seems to be related to fish activity, while the fact of actually entering the trap and being retained was affected by activity and freezing time (similar to the analysis with the whole dataset). Thus, something else than passing by the trap determined whether the fish was trapped or not. Allowing for a more complex capture process could yield different insights to the role of behavioural traits on vulnerability to fishing gears. While logistically challenging, this is an important avenue for future studies to follow.

Another drawback from the present study is that single fish being tested for vulnerability to fishing gear does not represent most fishing situations nor normal fish behaviour. The present experimental design compromised the applicability of the results to real situations in order to assess clearly the effect of behavioural types on the selectivity of fishing gears. Thus, it is acknowledged that the conclusion might vary when more complexity is added. Future experiments should test how groups of fish performed in the different vulnerability tests compare to individual fish. Of particular interest would be testing how different fishing gears select groups with dissimilar average boldness and sociability scores, whether the presence of a experience individual would improve the performance of the group, and whether groups with different sex ratio would performed differently. Brown & Warburton, (1999*b*) found that larger groups performed better in an experimental trawl similar to ours. It is difficult to predict what would happen if mixed-personality guppy shoals are tested for vulnerability to traps and trawls. Intuitively one could say that bold individuals would lead the rest of the group to the trap, increasing the efficacy of the trap, but reducing its selective towards boldness. However, bold individuals might benefit from the vigilance and careful exploration of shy individuals (as seen for foraging behaviour; Dyer *et al.*, 2008) reducing the efficacy of the trap. A group might be less vulnerable to a trawl if the shy individuals follow the bold ones escaping the trawl or more vulnerable if the shoaling behaviour increase the herding and the efficiency of trawl.

The selective removal of certain behavioural types by different fishing gears has a number of practical consequences. First, it can lead to sampling bias in behavioural studies (Biro & Dingemanse, 2009). Second, it affects the population structure, which in turn can have consequences for the population viability and the profitability of the fishery. Although *P. reticulata* is not an important fisheries species, it can provide valuable lessons for understanding evolutionary consequences of fishing in commercially fished species. The particular novelty of this study is including active gears, here a trawl, whose selectivity with respect to behavioural is still poorly known. There are similarities between the escape behaviour of gadoids (Engås & Godø, 1989; Ona & Godø, 1990) and guppies as both tend to escape by diving deeper. The present results suggest that active gear such as trawls favour fish with bold personalities. On the other hand, more active fish were more vulnerable to passive gears in our study, similarly as in yellow perch *Perca flavescens* (Mitchill 1814) with higher feeding activities or feeding on more active prey (Engås & Løkkeborg, 1994). Moreover, this selection on behaviour can in turn select for other important traits such as growth. Largemouth bass *Micropterus salmoides* (Lacepède 1802) illustrates another example of adverse effect of inadvertent selection on behaviour: it has been shown that more aggressive individuals are more likely to be caught by angling, but these are also found to be better at parental care and have higher reproductive fitness (Suski & Philipp, 2004; Cooke *et al.*, 2007; Sutter *et al.*, 2012). Selective fishing on *M. salmoides* may thus be interfering with population productivity and with sustainability of the recreational fishery (Sutter *et al.*, 2014).

This study stresses the need to consider the many facets of fish population responses to fishing. Trapping is advocated as an environmentally friendly way of catching fish (FAO, 2003), but our results highlight that this may inflict selection against bold, exploratory fish. When vulnerability is heritable, removal of more vulnerable fish will reduce the future profitability of the fishery (Philipp *et al.*, 2009). In conclusion, establishing how fisheries or other human-induced selectivity affect behavioural traits is crucial to understand how populations respond to human-induced environmental change.

ACKNOWLEDGEMENTS

The authors would like to thank S. Killen, an anonymous reviewer, and the associate editor for comments that helped to improve this manuscript, H. Savolainen, C. Nissanka and J. Sala Coromina for their great help in the lab, J. V. Helvik and O. Moberg for access to their technical supplies, K. H. Jensen for statistical advice, D. Reznick and his group for assistance with obtaining the fish, and Bergen Research Foundation and the Research Council of Norway (project number 214189) for funding.

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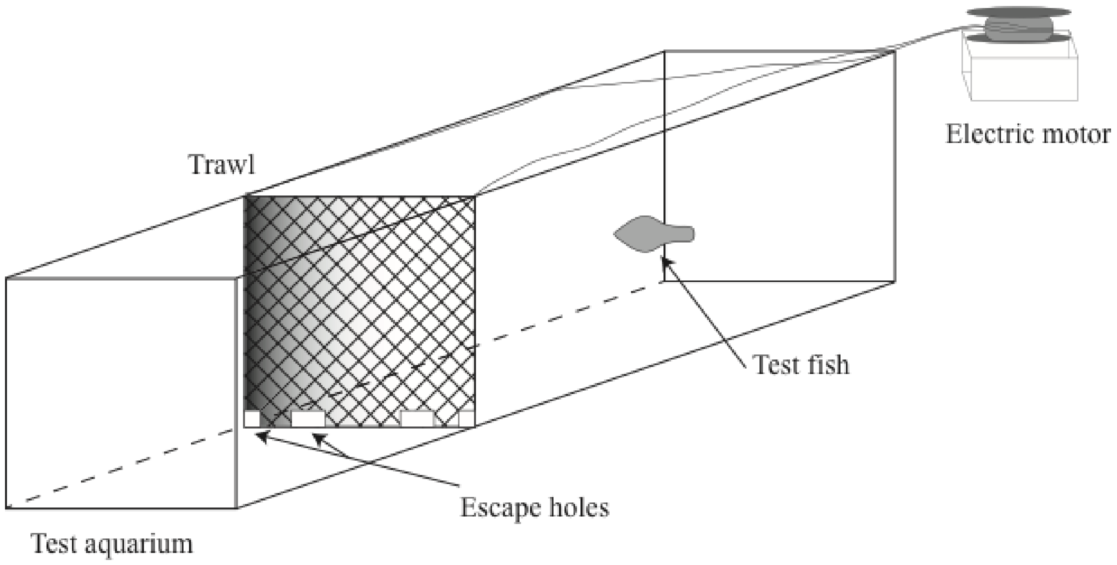
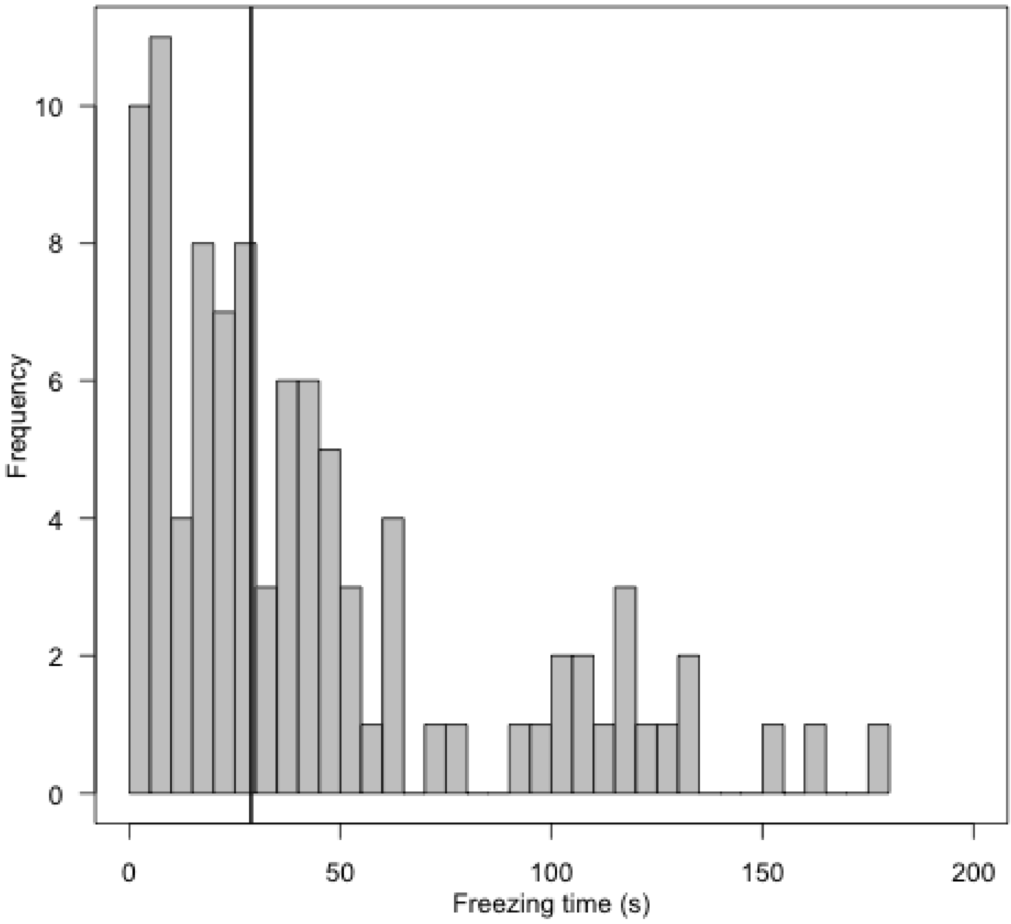
Table I. Pair-wise correlation matrix. Pearson's correlation coefficients, r_p, for all variables. Coefficients in italics represent those correlations whose P value is lower than 0.05, for these cases, degrees of freedom and t statistic can be found in the text. *The time variables were squared-root transformed.

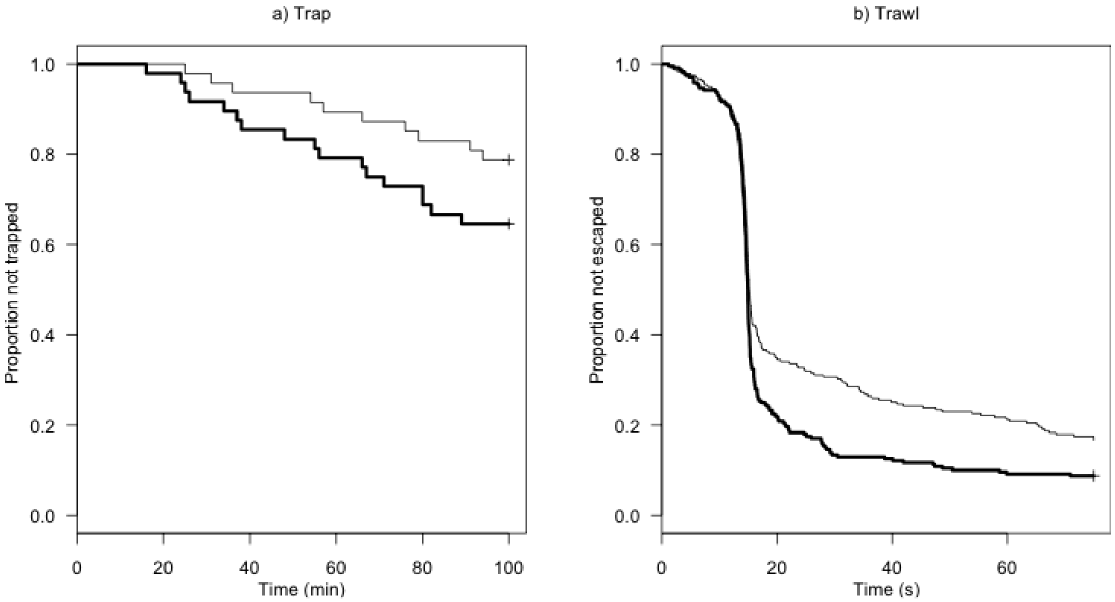
	Time until being trapped*	Time until escaping the trawl*	Distance	Area	Growth rate
Freezing time*	*0.20*	-0.05	-0.06	-0.07	0.13
Time until being trapped*		-0.09	-0.12	-0.17	-0.07
Time until escaping the trawl*			0.21	0.02	0.16
Distance				*0.43*	*0.27*
Area					0.08

Table II. Loadings of each behaviour from the principal component analysis (PCA) for the first two principal components: PC1, PC2. Eigenvalues and proportion of variance explained by each of them. Highest loadings per PC highlighted in italics. *The time variables were squared-root transformed.

	PC1	PC2
Freezing time*	-0.42	*0.57*
Time until being trapped*	*-0.56*	0.36
Time until escaping the trawl*	0.40	*0.65*
Distance	*0.57*	0.31
Variance explained	39.1%	64.5%
Eigenvalues	1.56	1.02

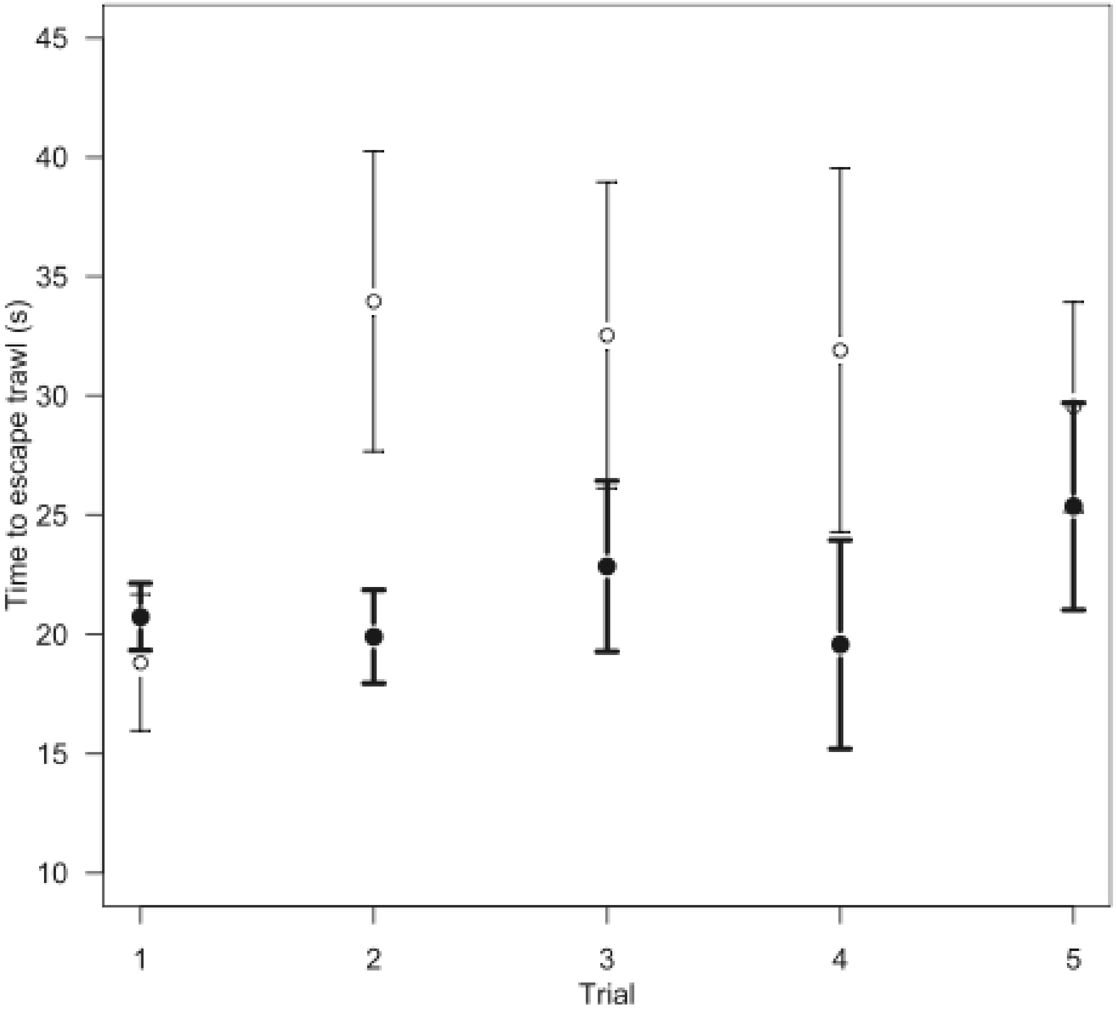

Electric motor
Trawl
Test fish
Escape holes
Test aquarium


Frequency
0
2
4
6
8
10
0
50
100
150
200
Freezing time (s)


a) Trap
b) Trawl
Proportion not trapped
Proportion not escaped
1.0
0.8
0.6
0.4
0.2
0.0
0
20
40
60
80
100
Time (min)
Time (s)

726

727


Time to escape trawl (s)
45
40
35
30
25
20
15
10
1
2
3
4
5
Trial

728