Behavioral Ecology and Sociobiology (2021) 75: 14
https://doi.org/10.1007/s00265-020-02947-5

ORIGINAL ARTICLE

Predator presence affects activity patterns but not food consumption or growth of juvenile corkwing wrasse (*Symphodus melops*)

Tommy Norin[1] · Josefin Sundin[2,3] · Rachael Morgan[4] · Anna H. Andreassen[4] · Mirjam Amcoff[5] · Ben Speers-Roesch[6] · Fredrik Jutfelt[4] · Sandra A. Binning[7] · Dominique G. Roche[8,9] · Timothy D. Clark[10]

Received: 17 September 2020 / Revised: 3 December 2020 / Accepted: 9 December 2020 / Published online: 5 January 2021

Abstract

Indirect effects of predators can manifest themselves as changes in prey behaviour and physiology. Given that digestion requires energy, it has been suggested that prey will choose to eat smaller meals under predation risk to reserve a larger portion of the aerobic metabolic scope they have available for energetically demanding tasks more critical than digestion, such as escape. To test this prediction, we quantified food consumption and growth of juvenile corkwing wrasses (*Symphodus melops*) over 11 days in the presence or absence of a predator (Atlantic cod, *Gadus morhua*). We then quantified behaviour and food consumption of the same wrasses in behavioural arenas with a predator. All food consumption was examined in the context of the aerobic scope that would have been available during the digestive period. Overall, there was no effect of predator exposure on food consumption or growth, yet predator-exposed wrasses were more consistent in their daily food consumption, lending some support to our prediction of prey bet-hedging on meal size under predation risk. The lack of a clear pattern may have resulted from a relatively low percentage of aerobic scope (~ 20–27%) being occupied by digestion, such that fish retained ample capacity for activities other than digestion. In the subsequent behavioural trials, predator-exposed wrasses were more active and spent more time near the cod than predator-naïve wrasses, suggesting the former had habituated to predation threat and were more risk-taking. Our results highlight the complex and often counter-intuitive effects that predator presence can have on prey populations beyond direct consumption.

Significance statement

Predators affect the behaviour of prey species by simply being present in the environment. Such intimidation by predators can change activity patterns of prey and be as important as direct predation for ecosystem dynamics. However, compared to behavioural changes, we know little about how predators indirectly affect prey physiology. We investigated if fish deliberately eat less food when a predator is present, in order to retain sufficient physiological capacity for avoiding a potential attack, on top of the energetically costly process of digesting. While our study confirms that predator encounters reduce prey activity, prey fish appeared to rapidly habituate to predator presence and we did not see reduced food consumption in predator-exposed fish; these were, however, more consistent than unexposed fish in their daily food consumption, suggesting that fish may still be mindful about protecting their aerobic capacity under predation risk.

Communicated by J. Lindström

✉ Tommy Norin
tnor@aqua.dtu.dk

[1] DTU Aqua: National Institute of Aquatic Resources, Technical University of Denmark, Kgs. Lyngby, Denmark

[2] Department of Aquatic Resources, Swedish University of Agricultural Sciences, Drottningholm, Sweden

[3] Department of Neuroscience, Uppsala University, Uppsala, Sweden

[4] Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway

[5] Department of Zoology/Functional Zoomorphology, Stockholm University, Stockholm, Sweden

[6] Department of Biological Sciences, University of New Brunswick, Saint John, New Brunswick, Canada

[7] Département de sciences biologiques, Université de Montréal, Montréal, Québec, Canada

[8] Department of Biology, Carleton University, Ottawa, Ontario, Canada

[9] Institut de biologie, Université de Neuchâtel, Neuchâtel, Switzerland

[10] School of Life and Environmental Sciences, Deakin University, Geelong, Victoria, Australia

Keywords Fish · Behaviour · Digestion · Metabolic rate · Specific dynamic action · Predation risk

Introduction

Predators eat prey. Although this relationship sounds straightforward, the dynamics between animals higher up the food chain and the species they consume are, in fact, much more complicated. The mere presence of predators in an environment can have dramatic effects on the behaviour, physiology, and life history of potential prey (Preisser et al. 2005), including in fishes (Lima and Dill 1990; Dugatkin and Godin 1992; Hawlena and Schmitz 2010a; Gallagher et al. 2016; Hasenjager and Dugatkin 2017). Such non-consumptive effects of predators on prey are thought to be at least as strong as direct consumptive effects, especially in aquatic systems (Preisser et al. 2005), and can have cascading effects on prey demographics and ecosystem processes (Preisser et al. 2005; Hawlena and Schmitz 2010a). An example is the growth–predation risk trade-off, where the presence of predators reduces the foraging behaviour of prey species, resulting in reduced growth due to lost feeding opportunities (Lima and Dill 1990; Houston et al. 1993; Brown and Kotler 2004; McPeek 2004; Verdolin 2006). This cost is offset by increased survival as predators are less likely to detect potential prey when prey are less active and, similarly, prey are more likely to detect and respond early to the presence of a predator when they are not distracted by feeding. Although the growth–predation risk trade-off is generally supported by the available experimental evidence (Dugatkin and Godin 1992; Brown and Kotler 2004; Verdolin 2006), some studies have found that prey can maintain normal growth rates despite reduced foraging activity, due to compensatory changes in their underlying physiology (McPeek 2004; Thaler et al. 2012).

Predation risk affects the physiology of prey by inducing stress (Boonstra et al. 1998; Hawlena and Schmitz 2010a; Sheriff et al. 2009; Boonstra 2013), changing metabolic rate (Steiner and Van Buskirk 2009; Hall and Clark 2016; Lagos and Herberstein 2017), increasing oxidative damage (Janssens and Stoks 2013; Culler et al. 2014; Manzur et al. 2014; Jermacz et al. 2020), and altering the assimilation of nutrients (McPeek 2004; Hawlena and Schmitz 2010a, b; Thaler et al. 2012; Dalton and Flecker 2014). The latter is deemed an important mechanism through which prey may compensate for adverse impacts of predation risk (e.g. reduced foraging opportunities and food consumption; Hawlena and Schmitz 2010b; Thaler et al. 2012), including compensating for the (transient) increase in prey metabolic rate that is often observed in the presence of predators (Steiner and Van Buskirk 2009; Hawlena and Schmitz 2010b; Okuyama 2015; Hall and Clark 2016; Lagos and Herberstein 2017). Nonetheless, the consequences of predation risk on prey physiology can be complex and variable (Thaler et al. 2012; Handelsman et al. 2013; Tigreros et al. 2018), and the growth–predation risk trade-off may manifest itself via a range of different physiological pathways. For example, previous work has found that fish eating relatively large meals benefit from a higher digestion and growth efficiency, compared to fish eating smaller meals, but are disadvantaged by the metabolic cost of digestion (i.e. "specific dynamic action", SDA; Secor 2009) occupying a larger portion of the aerobic scope available for activities other than digestion (Norin and Clark 2017). Aerobic scope is the difference between an animal's aerobic maximum metabolic rate (MMR) and its standard (resting) metabolic rate (SMR), and represents the capacity to increase oxygen uptake rate above baseline levels to support energy-demanding activities (Clark et al. 2013). Therefore, animals should preferentially eat large meals in the absence of predators (i.e. in an environment perceived to be safe) to reap the associated growth benefits, but smaller meals in the presence of predators to conserve a portion of their aerobic scope in case energetically costly behaviours are abruptly required to avoid or escape predators.

Here, we tested these ideas in a laboratory setting using juvenile corkwing wrasses (*Symphodus melops*) exposed to a natural predator, the Atlantic cod (*Gadus morhua*). Wrasses, including *S. melops*, are common prey for cod (Nordeide and Salvanes 1991; Salvanes and Nordeide 1993). We conducted three sets of experiments, where we (1) fed wrasses meals of different sizes and quantified their metabolic cost of digestion (SDA) using respirometry in the absence of cod; (2) recorded growth and food consumption of wrasses kept in holding tanks with or without a cod for 11 days; and (3) transferred wrasses from their holding tanks to behavioural arenas and quantified their behaviour and food consumption with a cod present. We predicted that (1) SDA from larger meals would occupy a greater percentage of the wrasses' aerobic scope; (2) predator-exposed wrasses would eat smaller meals than wrasses held without predators; and (3) wrasses held without predators would display lower food consumption and activity when acutely confronted with a predator in a behavioural arena compared to wrasses that had been previously housed with a predator.

Methods

Fish collection and holding conditions

All experiments were performed at the Kristineberg Marine Research Station, University of Gothenburg, located on the west coast of Sweden, in June 2017. Juvenile corkwing wrasses (*Symphodus melops*) of unknown sex were collected on June 7–8 using a beach seine pulled by hand in bays of the Gullmar Fjord near Kristineberg (58° 15′ N, 11° 28′ E). Wrasses were initially housed in groups of ~ 10 individuals in laboratory holding aquaria (58 × 30 × 36 cm (length ×

width × height)) receiving flow-through, filtered seawater pumped into the station from a depth of 7 m (surface water supply). Artificial plastic plants were provided to all fish for shelter. Wrasses were fed live shrimp (*Crangon crangon* and *Palaemon adspersus*) and thawed chironomid larvae ("bloodworms") ad libitum once every second day. Temperature and salinity in the aquaria followed natural conditions in the area (means ± SDs: temperature, 14.9 ± 0.92 °C; salinity, 27.6 ± 2.15 PSU; data from the continuous monitoring system at the research station, June 7–30, 2017: http://www.weather.loven.gu.se/kristineberg/en/data.shtml). The photoperiod was set to 18 h light and 6 h darkness to mimic natural conditions, regulated by small lights on a timer from 06:00 to 24:00 in both holding and experimental rooms. Additional room lighting was manually switched on at ~ 08:00 and off at ~ 22:00.

Juvenile Atlantic cod (*Gadus morhua*) of unknown sex were cage-caught by local fishers in the waters off Lysekil, Sweden, in June 2017, and brought by boat to the research station. At the station, the cod were kept in four 1000-L tanks receiving thermoregulated, flow-through, filtered seawater pumped from a depth of 32 m (deep water supply). The water temperature was increased from 10.7 °C (the natural deep-water temperature at the time of capture) to a target temperature of ~ 14 °C over a period of 3 days (actual mean ± SD temperature during cod holding: 13.5 ± 1.15 °C). The cod were fed cooked blue mussels (*Mytilus edulis*) and shrimp (*Pandalus borealis*) once every second day. Artificial plastic plants and cut plastic pipes were provided in the tanks for shelter. The light cycle was the same as described for the wrasses.

Aerobic scope and metabolic cost of digestion

To understand how digestion affects the available aerobic scope of wrasses, the metabolic rate of 20 individuals (mean ± SD body mass: 3.92 ± 0.94 g) was estimated as the rate of oxygen uptake ($\dot{M}_{O_2}$) during and after the postprandial process (SDA), using intermittent-closed respirometry.

The respirometry setup consisted of eight 95-mL (total volume) glass respirometry chambers submerged in a 40-L (water volume) tank receiving flow-through normoxic surface seawater maintained at 15.4 ± 0.5 °C (mean ± range) and at a salinity following the natural conditions in the area (mean ± SD: 28.4 ± 1.71 PSU; June 20–30, 2017). Each respirometry chamber had an in-line pump (miniature DC pump; Loligo Systems, Viborg, Denmark) that continuously recirculated water through the chamber and past an optical oxygen probe (PyroScience GmbH, Aachen, Germany) in a closed loop of PVC tubing. The oxygen probe was connected to an oxygen meter (FireStingO_2; PyroScience GmbH, Aachen, Germany) that recorded the oxygen concentration of the water every 2 s. Another set of eight miniature DC pumps was controlled by a timer and was turned on for 3 min in every 7-min intermittent respirometry cycle to flush the chambers with clean and normoxic water from the ambient tank. The decrease in oxygen recorded over the other 4-min closed (sealed) period was used for calculating $\dot{M}_{O_2}$ by multiplying the slope for the decrease in oxygen concentration over time (mg O_2 L^{-1} s^{-1}) with the volume of the respirometry chamber after subtracting the volume of the fish (assuming a fish density of 1 g mL^{-1}).

The day before a respirometry experiment, wrasses were moved from their holding aquaria and placed in individual compartments (22 × 12 × 10 cm (length × width × height)) receiving flow-through water at the conditions described above. After ~ 24 h with no food available, wrasses were fed between 10 and 60 bloodworms and given about 30–45 min to eat. All fish were monitored with a webcam to determine precisely when they started eating. The wrasses were then gently moved (in a water-filled container) to the respirometry chambers, and $\dot{M}_{O_2}$ recordings were started between 38 and 54 min after the fish had started eating. Any uneaten worms were counted to calculate the final amount eaten by each individual, which ranged between two and 60 worms. The fish remained in the respirometry chambers for 38.5-43.2 h until $\dot{M}_{O_2}$ had plateaued at baseline values, yielding between 330 and 370 $\dot{M}_{O_2}$ recordings per fish. We used these recordings to quantify the wrasses' specific dynamic action (SDA) responses using a modified version of the SDA script provided by Chabot et al. (2016). Upon completion of these initial $\dot{M}_{O_2}$ recordings, the wrasses were gently removed from the respirometry chambers and placed in a tub with water at the same conditions as for the respirometry trials. The fish were then chased by hand for 2 min by an experimenter before being immediately reintroduced to the respirometry chambers for another 6–10 $\dot{M}_{O_2}$ recordings, of which the highest measurement (the first measurement for all but one fish) was taken to represent the MMR of the fish (cf. Norin and Clark 2016).

The entire respirometry setup was cleaned with a bleach solution (approximately 1 part bleach in 100 parts water) before each new respirometry trial (excluding the oxygen probes, which were cleaned in ethanol). Background (microbial) respiration was therefore near zero at the start of a trial. The mean of three background recordings taken at the end of a trial, after removal of the fish, was used to correct the $\dot{M}_{O_2}$ of the wrasses for the increase in background respiration during the trial by assuming a linear increase between zero at the start of a trial and the mean background value at the end of the trial.

The SDA script was used to calculate the SMR of the fish as the 0.05 quantile of all the $\dot{M}_{O_2}$ values for each fish (which always occurred towards the end of the respirometry trial once SDA was complete). The script was also used to calculate peak net SDA (the peak $\dot{M}_{O_2}$ during digestion, above SMR), time to peak SDA (the time to reach peak $\dot{M}_{O_2}$ from time of

feeding; corrections for handling effects outlined in the supplementary material), SDA duration (the time it took to complete the SDA response and reach SMR), and SDA magnitude (the total amount of oxygen used in digesting the meal, i.e. the area under the SDA curve but above SMR). Aerobic scope was calculated as the absolute difference between MMR and SMR.

Out of the 20 wrasses, two had to be excluded from the final dataset: one because the recirculation pump malfunctioned during the recording of MMR (meaning that aerobic scope could not be calculated), and another due to a loose connection to one of the oxygen probes that resulted in erratic oxygen recordings, as noted during the experiment. Final sample sizes are given in Fig. 1. Further details of the SDA analyses are given in the supplementary material along with all $\dot{M}_{O_2}$ profiles (graphs of $\dot{M}_{O_2}$ over time during digestion, annotated with SDA variables; Fig. S1).

The amount of food eaten by each fish was manually counted and thus not recorded blind at the time of the experiment; the subsequent calculations of each individual's $\dot{M}_{O_2}$ and SDA were done blinded (i.e. without knowing how much each fish had eaten until after the raw data analyses had been completed).

Food consumption and growth in holding tanks in the presence or absence of a predator

We quantified food consumption and growth of wrasses being held in the presence or absence of a predator (cod) for 11 days. Fish were fasted for 24 h before the experiment began.

On the first day of the experiment (June 12, 2017), 24 wrasses from the holding aquaria were weighed and transferred to individual, transparent plastic boxes (18 × 16 × 14 cm (length × width × height)). Four boxes were placed in each of six larger holding tanks (glass aquaria measuring 61 × 40 × 37 cm (length × width × height)) (Fig. S2), three of which contained a cod ("predator-habituated" treatment; mean ± SD wrasse body mass: 4.20 ± 0.39 g; mean ± SD cod body mass: 87.0 ± 6.46 g), and three of which did not ("predator-naïve" treatment; mean ± SD wrasse body mass: 4.04 ± 0.63 g). Each wrasse box had several ~ 5-mm holes on all sides (see photo in Fig. S2) to allow water exchange between the box and the surrounding holding tank. These boxes separated the wrasses physically from the cod but allowed for both chemical and visual cue exchange between predator and prey. Each of the six holding tanks received flow-through surface water and had an air stone for aeration and four artificial plastic plants. Each wrasse box also contained an opaque plastic tube for shelter (9.5 cm long, ∅3 cm). There was no significant difference in the initial mass of wrasses between the two treatments (t_{22} = 0.75, p = 0.463).

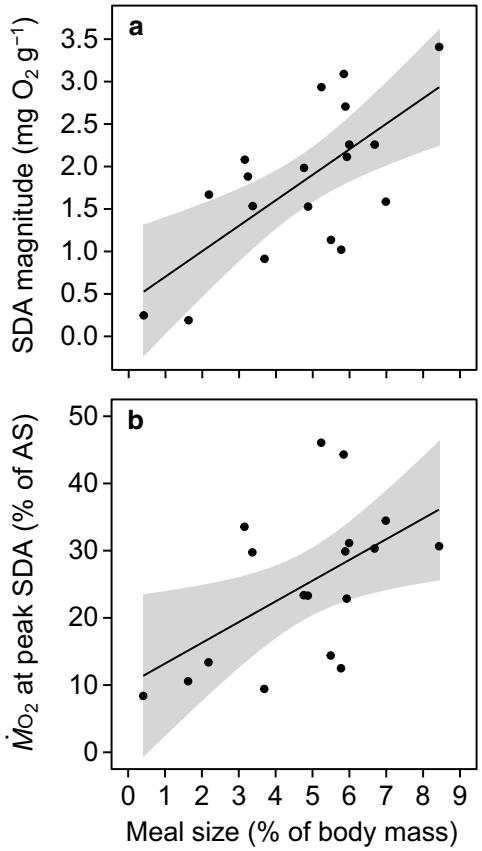

Fig. 1 Specific dynamic action (SDA) responses of juvenile corkwing wrasses fed different meal sizes of chironomid larvae ("bloodworms"). The overall cost of digestion per gram of fish (i.e. the SDA magnitude) increased with meal size (**a**; $F_{2,16}$ = 6.050, p = 0.011, r^2 = 0.431; n = 19), and so did the oxygen uptake rate ($\dot{M}_{O_2}$) at peak SDA, thus occupying a larger percentage of the fish's aerobic scope (AS) at the peak of the digestive response (**b**; $F_{1,16}$ = 6.716, p = 0.020, r^2 = 0.296; n = 18). Shaded areas are 95% confidence bands

To measure food consumption and growth, each wrasse was initially given 40 bloodworms in the afternoon of the first day of the experiment, followed by an additional maximum 40 bloodworms if the initial 40 were consumed within 1 h. The next morning, all remaining bloodworms were siphoned from each of the wrasse boxes into individual buckets and counted. This initial trial allowed us to establish 80 bloodworms as the satiation limit for wrasses of this size. We subsequently gave each wrasse a total of 80 bloodworms in the morning of each day. Uneaten bloodworms were siphoned and counted each morning before the fish were fed fresh bloodworms. Data from the first feeding event for three wrasses were excluded due to technical issues preventing us from accurately quantifying food consumption (e.g. we accidentally siphoned bloodworms onto the floor, preventing the data from being included, as some worms could have gone down the drain).

We also quantified the sheltering behaviour of the wrasses by noting whether individuals were sheltering or not (sheltering defined as more than ~ 90% of the fish being inside the

shelter) at the time of observation. Visual observations were made three times on the second day of the experiment (at approximately 09:00, 15:00, and 18:00), four times per day on the following 9 days (at approximately 09:00, 12:00, 15:00, and 18:00), and three times on the last day (at approximately 09:00, 15:00, and 18:00) before trials in the behavioural arenas commenced (see next section). The cod were fed cooked shrimp (*Pandalus borealis*) every second day. Temperature and salinity followed the natural conditions of surface seawater in the area (June 12–23, 2017, means ± SDs: temperature, 14.5 ± 0.97 °C; salinity, 28.0 ± 2.25 PSU).

Food consumption and sheltering were quantified directly from each transparent holding tank with the predator visible, and thus not recorded blind.

Behaviour and food consumption in behavioural arenas in the presence of a predator

To quantify whether being exposed to a predator or not had an effect on the behaviour and food consumption of wrasses in the presence of a predator, we conducted video-recorded behavioural trials in a novel behavioural arena.

Four glass aquaria measuring 60 × 38 × 35 cm (length × width × height; water depth ~ 20 cm) were used simultaneously as behavioural arenas (Fig. S3). Each arena was divided into two sections with a transparent glass plate glued (with silicone) to the sides of the aquaria with a small (3 mm) gap at the bottom, allowing for water exchange between sections. A predator (cod; different individuals than used previously) was placed in one section of the arena (40 × 38 cm (length × width)), with a wrasse placed in the other section (20 × 38 cm (length × width)). The walls of the aquaria were covered with a white waterproof paper to prevent fish in the four separate behavioural arenas from seeing each other. Each of the four cod had a shelter (opaque plastic pipe; 12.5 cm long, ∅7 cm) placed at the opposite end of the aquaria to the wrasse section. Each wrasse section also had a shelter (opaque plastic pipe; 8 cm long, ∅4.5 cm) placed on the opposite side relative to the cod section. Cod were housed in the behavioural arenas for the duration of the trials (2 days). Wrasses were placed in the arenas at the start of a trial and given ~ 6 min to settle (mean ± SD: 5.8 ± 0.8 min), during which time they were video recorded with a USB camera (Kurokesu C1; Kurokesu, Vilnius, Lithuania) mounted above the aquaria. After this habituation period, a dish containing 40 bloodworms was added to each wrasse section at the end opposite from the shelter (dish placement in all four arenas complete within 4 min; mean ± SD: 2.1 ± 1.2 min), and the wrasses were monitored for another ~ 30 min (mean ± SD: 31.2 ± 1.0 min) before the trial was ceased and any uneaten bloodworms were counted. Water temperature and salinity followed natural surface water conditions in the area (June 24–25, 2017, means ± SDs: temperature, 16.3 ± 0.14 °C; salinity, 27.0 ± 0.19 PSU).

The behavioural videos were analysed using tracking software (ZebraLab; ViewPoint, France). For the wrasses, we quantified time spent in four zones both before and after the food was added to the arena: zone 1, within proximity to food but away from the predator; zone 2, within proximity to food but close to the predator; zone 3, in or near the shelter but away from the predator; and zone 4, anywhere along the glass divider near the predator section but away from the food (Fig. S3). We also measured latency to inspect the food (defined as the fish being within ~ 1 cm of the food dish and facing the food), latency to feed (duration from food addition to consumption of first bloodworm), and percentage of bloodworms consumed (out of 40). In two instances, a wrasse never inspected the food and ate nothing; these fish were assigned the maximum run time of their respective trial after the addition of food (31.2 and 31.9 min) for both latency to inspect food and latency to feed. For both wrasses and cod, we quantified activity as swimming distance over time before and after the food was added. For the cod, time spent in two zones was analysed: zone 1, close to the wrasse; and zone 2, away from the wrasse (Fig. S3).

Three of the 24 wrasses (two from the predator-naïve treatment, one from the predator-habituated treatment) exhibited abnormal behaviour (constantly swimming in an atypical manner at the surface) after being transferred to the behavioural arenas and were therefore excluded from these trials. We had not observed any abnormal behaviour of these fish while in their holding tanks, and they do not stand out as outliers in the data analyses (see diagnostics in data analysis script). The fish were therefore kept in the analyses of the holding tank data.

Predator treatment history was known at the time of the trials; however, the trials were video recorded and the subsequent video analyses were done blinded using automated tracking software.

Calculation of bloodworm mass

To convert the number of bloodworms eaten by the wrasses into a percentage of the wrasses' body mass, we weighed 13 replicates of 80 bloodworms (i.e. 1040 bloodworms in total) on an analytical balance both before and after drying the worms for 26 h at 70 °C. From this, we calculated the overall mean mass of one bloodworm, which was 7.144 mg wet mass or 3.884 mg dry mass. Herein, we use wet bloodworm mass to express food consumption as a percentage of fish body mass.

Statistical analyses

All statistical analyses were performed in R v. 4.0.2 (R Core Team 2020).

The effect of digestion on metabolic rate was examined with two general linear models (LMs) with either the SDA

magnitude or the percentage of aerobic scope occupied at the peak of SDA as the response variable, and meal size (as percent of body mass) and wrasse body mass as predictor variables.

The effect of predator (cod) presence or absence on wrasse food consumption and sheltering in the holding tank was examined with two linear mixed-effects (LME) models using the package *lme4* (Bates et al. 2015). *p* values were estimated using *lmerTest* (Kuznetsova et al. 2017). These models included either the amount of bloodworms eaten (percent of body mass) or the percentage time spent sheltering as the response variable; treatment (predator present or absent), time (day of the experiment), and wrasse body mass were included as predictor variables; fish ID was nested within holding tank and included as a random effect.

The growth of wrasses was calculated as their specific growth rate (SGR; % day^{-1}) across their time in the holding tanks. This was determined as $SGR = [\ln(BM_f) - \ln(BM_i)] \times t^{-1} \times 100$, where BM_f is the final body mass, BM_i is the initial body mass, and t is the time (days) over which the fish were growing. These data were analysed with an LME with SGR as the response variable and treatment, mean daily food consumption, and mean wrasse body mass across the growth period as predictor variables; holding tank was included as a random effect. We calculated how consistent the fish were in the amount they ate across the experiment by computing the adjusted repeatability (R_{adj}, the repeatability after controlling for fixed effects; Nakagawa and Schielzeth 2010) of meal sizes using the same model structure as above in the package *rptR* (Stoffel et al. 2017). Adjusted repeatability was also calculated for each treatment group separately, without treatment as a predictor variable. Uncertainty in the repeatability estimates was evaluated by running 1000 parametric bootstraps.

For the behavioural arena trials, the effect of predator treatment (predator-habituated vs. predator-naïve wrasses) on wrasse activity (distance moved over time), time spent near vs. far from food and/or predator (i.e. time spent in each of the four zones of the behavioural arena), and food consumption in the presence of a predator were analysed with six LMEs. These models had percentage time spent in a given zone, activity, or amount of bloodworms eaten in the behavioural arena as a response variable; treatment, presence of food (before vs. after food was added to the arena), wrasse body mass, and cod behaviour (time spent close to the wrasse) were included as predictor variables in all models; behavioural arena number was specified as a random effect.

Latency to inspect food and latency to feed in the behavioural arenas were analysed using two mixed-effects Cox proportional hazards models (COXME) with the package *coxme* (Therneau 2020): Latency either to inspect food or to feed was included as the response variable; treatment, wrasse body mass, and cod behaviour were included as predictor variables; behavioural arena number was specified as a random effect. Individual fish were censored in these models if they never inspected the food or never fed.

Model simplification was performed by dropping non-significant ($p > 0.05$) variables sequentially and, at each step, comparing models using likelihood ratio tests to identify the best-fit model. Results presented in the text below are model-predicted estimates for each treatment (predator present or absent in holding tanks), evaluated at the means of the other predictor variables in the models using ggpredict in the package *ggeffects* (Lüdecke 2018). Associated uncertainties are ± SEs or, for repeatability estimates (R_{adj}), 95% CIs in square brackets. Graphs show the raw data.

Results

Aerobic scope and metabolic cost of digestion

The total increase in metabolic rate during digestion of a meal (the SDA magnitude) increased with meal size (LM, effect of meal size: $F_{1,16} = 8.973$, $p = 0.0086$) (Fig. 1a). Similarly, the amount of aerobic scope occupied at the peak of the SDA response increased with meal size (LM, effect of meal size: $F_{1,16} = 6.716$, $p = 0.0197$), with wrasses fed between 0.4 and 8.4% of their body mass having, on average, between 11.4 and 36.1% of their aerobic scope occupied by the postprandial process (Fig. 1b).

Food consumption and growth in holding tanks in the presence or absence of a predator

In the holding tank trials, an average-sized (4.2 g) wrasse ate a model-predicted meal of 4.4 ± 0.7% of its body mass (predator present) or 5.5 ± 0.7% of its body mass (predator absent) (26 ± 4.0 or 33 ± 4.0 bloodworms, respectively) on the first day of the 11-day trial (Fig. 2). If the bloodworms had been consumed as one meal, digestion would have occupied an average 23.6 or 27.1% of the fish's aerobic scope, respectively, at the peak of the SDA response (based on the relationship established between meal size and $\dot{M}_{O_2}$ at peak SDA; Fig. 1b). Food consumption tended to increase slightly by 0.1% of the wrasses' body mass (0.6 worms) per day throughout the experiment (LME, effect of day: $t_{236.2} = 1.905$, $p = 0.058$), with no difference between treatments in this increase (supported by the non-significant and dropped interaction; LME, day × treatment: $t_{233.0} = 0.348$, $p = 0.728$) (Fig. 2a). The overall difference in food consumption between treatment groups across the 11 days was not significant (LME, effect of treatment: $t_{22.05} = -1.322$, $p = 0.200$). Specific growth rates also did not differ between predator treatments (LME, effect of treatment: $t_{20.00} = 0.487$, $p = 0.632$) (Fig. 2b).

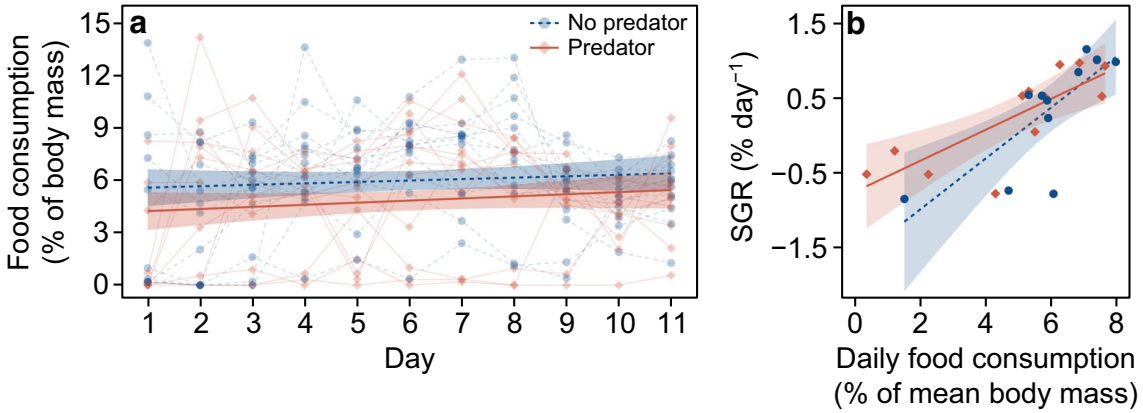

Fig. 2 Daily food consumption (**a**) and resulting specific growth rates (SGR; **b**) of juvenile corkwing wrasses being held in the presence (red) or absence (blue) of a predator (cod) in their holding tanks for 11 days. Diamonds (predator) and circles (no predator) represent data for individual fish. Shaded areas are 95% confidence bands

Individual wrasses were consistent in their food consumption throughout the experiment and across treatments (R_{adj} = 0.360 [95% CI = 0.186–0.519], $p < 0.0001$). Interestingly, within treatments, wrasses being held with predators were more than twice as consistent (repeatable) in the amount of food they ate each day ($R_{adj} = 0.480$ [0.226–0.674], $p < 0.0001$) compared to wrasses not exposed to predators ($R_{adj} = 0.227$ [0.046–0.408], $p < 0.0001$).

An average-sized wrasse held in the presence or absence of a predator spent a model-predicted 60 ± 8.1% or 48 ± 8.1% of its time sheltering on the first day of the 11-day experiment, respectively. Time spent sheltering decreased significantly thereafter by 3.9% per day (LME, effect of day: $t_{239.0}$ = 8.502, $p < 0.0001$), with no difference between treatments in this decrease (supported by the non-significant and dropped interaction; LME, day × treatment: $t_{238.3} = -1.062$, p = 0.289). The overall difference in sheltering between treatments was not significant (LME, effect of treatment: $t_{4.000}$ = 1.172, $p = 0.306$).

Behaviour and food consumption in behavioural arenas in the presence of a predator

In the behavioural arena trials, the predator treatment (predator-habituated vs. predator-naïve wrasses) had no effect on the time wrasses spent near the food, regardless of whether the wrasses were directly adjacent to the predator section (time in zone 2; LME, effect of treatment: $t_{38.00} = -1.548$, $p = 0.130$) or on the far side of the food dish (time in zone 1; LME, effect of treatment: $t_{35.76} = 0.523$, $p = 0.604$) (Table 1). However, the predator-habituated wrasses spent less time in or near the shelter (time in zone 3; LME, effect of treatment: $t_{38.00} = 2.023$, $p = 0.050$) and more time closer to the predator but away from the food (time in zone 4; LME, effect of treatment: $t_{37.11} = -2.294$, $p = 0.028$) compared to the predator-naïve wrasses (Table 1).

Predator-habituated wrasses were most active in the behavioural trials (LME, effect of treatment: $t_{40.00} = -2.734$, p = 0.0093), swimming 252 ± 18.6 cm min^{-1} compared to 179 ± 19.5 cm min^{-1} for predator-naïve wrasses (Fig. 3).

Predator-habituated and predator-naïve wrasses did not differ significantly in the time they took to inspect the food (COXME, effect of treatment: $z = 1.49$, $p = 0.14$) (Fig. 4a) or to feed (COXME, effect of treatment: $z = 1.01$, $p = 0.31$) (Fig. 4b).

Food consumption in the behavioural arenas also did not differ between treatments (LME, effect of treatment: $t_{19.00}$ = 1.100, $p = 0.285$), with predator-habituated wrasses eating 3.3 ± 0.6% of their body mass, while predator-naïve wrasses ate 4.3 ± 0.6% of their body mass. Digestion of this food would have occupied an average 20.3 or 23.2% of the wrasses' aerobic scope at the peak of their SDA, respectively (cf. Fig. 1b).

Discussion

Corkwing wrasses exposed to a predator (Atlantic cod) for 11 days ate 20% less than wrasses being held without a predator, but this difference was not statistically significant (p = 0.200) and therefore does not support our prediction that predator-exposed fish would significantly reduce food consumption compared to fish being held in the absence of predators. We also predicted that a reduction in food consumption would occur in the presence of predators as a mechanism used by prey to reserve a larger portion of their aerobic scope for energetically costly behaviours associated with predator avoidance and recovery from a possible predator attack. However, a 20% lower food consumption would only have reduced the portion of aerobic scope occupied by digestion from, on average, 27.1 to 23.6% at the peak of the digestive (SDA) response if the food was eaten as one meal. This suggests that the wrasses would have gained little by reducing their food consumption, possibly explaining why we did not

Table 1 Time spent by wrasses in different zones of the behavioural arenas (means ± SEs). "Predator-habituated" and "predator-naïve" refer to the two treatments (wrasses being previously exposed to cod or not in the holding tanks); there was always a cod present in the behavioural arenas. The combined values for zones 1, 2, 3, and 4 do not necessarily sum up to 100%, as these are model-predicted values. Significant differences ($p \leq 0.05$) between treatments are indicated with an asterisk

Zone of behavioural arena	Time spent in zone (% of total)		
	Predator-habituated		Predator-naïve
Zone 1 (near food, far from predator)	3.9 ± 0.6		4.7 ± 0.6
Zone 2 (near food, near predator)	11.5 ± 0.4		6.7 ± 0.4
Zone 3 (in or near shelter, far from predator)	55.6 ± 4.7	*	69.5 ± 5.0
Zone 4 (far from food and shelter, near predator)	24.4 ± 4.3	*	14.1 ± 4.4

observe a stronger response to the presence of a predator. While reduced food consumption under perceived predation risk is often reported (Dugatkin and Godin 1992; Benard 2004; Thaler et al. 2012), there are also reports that foraging does not decrease under predation risk (McPeek 2004). Similarly, some studies have found that the effects of predators on prey foraging and food consumption are highly context-dependent, for instance, occurring only at certain (high) temperatures (Culler et al. 2014) or for certain prey sizes (Veldhuis et al. 2020). Since the SDA response is expected to be completed faster but has a higher peak at warmer temperatures, thus occupying an increasing portion of aerobic scope with increasing temperature (Jutfelt et al. 2020), it is possible that our results would have been different had we performed the experiment at higher temperatures. Another possibility is that our prediction of differential feeding in predator-exposed vs. unexposed fish might hold more strongly in prey fishes that tend to eat large meals rapidly (e.g. juvenile carnivores) rather than species that graze on smaller food items, such as the wrasses used here.

Some studies have found that food consumption and growth can be decoupled in prey when exposed to predators (McPeek 2004; Steiner 2007; Thaler et al. 2012), because predator exposure induces a change in the intake, storage, and/or use of nutrients (Hawlena and Schmitz 2010a, b; Thaler et al. 2012). However, we found no differences in growth rate between wrasses being held with or without predators, in line with our results for food consumption. The relatively short duration of our experiments (11 days) may not have been long enough to detect differences in growth between treatments in this species, although the lack of such

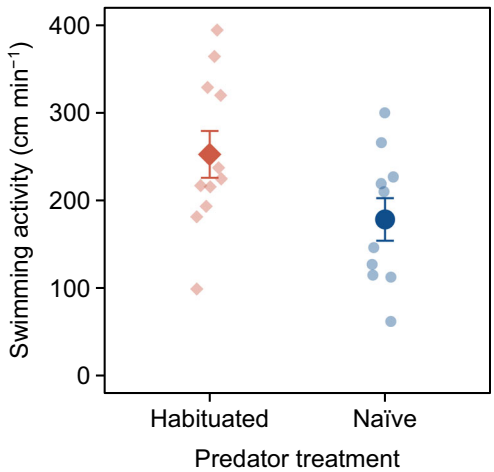

Fig. 3 Swimming activity of juvenile corkwing wrasses in behavioural arenas with a predator present (behind a glass wall). Larger symbols with error bars are means ± SEs, while smaller and semi-transparent symbols represent individual fish. Predator treatments (habituated ($n = 11$) or naïve ($n = 10$)) refer to the two treatments (wrasses being previously exposed to cod or not in the holding tanks); there was always a cod present in the behavioural arenas

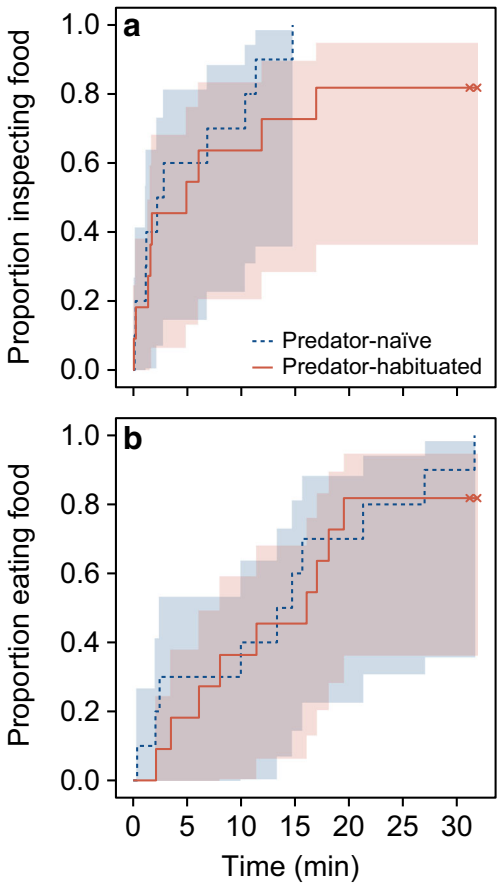

Fig. 4 Latency to inspect food and to start feeding by juvenile corkwing wrasses in behavioural arenas with a predator present (behind a glass wall). The data are shown as the proportion of fish inspecting food (**a**) or eating food (**b**) at a given time since food was introduced to the arena. "Predator-habituated" ($n = 11$) and "predator-naïve" ($n = 10$) refer to the two treatments (wrasses being previously exposed to cod or not in the holding tanks); there was always a cod present in the behavioural arenas. A cross indicates censoring (two fish never inspected and never ate any food). Shaded areas are 95% confidence bands

an effect of predators on prey growth rates has also been reported in several other studies, particularly in experiments lasting more than only a couple of days (Benard 2004; Van Dievel et al. 2016). These results suggest that, even if food consumption and growth are initially reduced under predation risk, animals, including fishes, often have the capacity for compensatory growth later on (Maclean and Metcalfe 2001; Metcalfe and Monaghan 2001), although this may eventually trade off with lifespan (Inness and Metcalfe 2008; Lee et al. 2013).

We found that wrasses exposed to predators in their holding tanks were more than twice as consistent in how much food they ate each day, compared to wrasses not exposed to predators ($R_{adj} = 0.480$ vs. 0.227, respectively). This interesting result lends some support to our prediction that prey will adjust meal size to protect their aerobic scope, as inconsistent meal sizes, including eating a very large meal on a given day, could compromise aerobic scope on that day; the largest amount of food eaten in 1 day by an individual wrasse was 14% of the wrasse's body mass, which would have occupied an estimated 53% of aerobic scope if eaten as one meal (cf. Fig. 1b). In comparison, southern catfish (*Silurus meridionalis*) require ~ 44% of their aerobic scope at the peak of SDA to digest a meal corresponding to 16% of the fish's body mass; this energetic cost caused a significant reduction in the catfish's maximum swimming speed by 14% (Fu et al. 2011; non-fasted treatment group), which could impair escape from predators (Billerbeck et al. 2001; Lankford et al. 2001). Temporal consistency in the size of a meal eaten in predator presence may be an important behavioural adjustment in prey that warrants further investigation.

In the behavioural arena trials with predators present, predator-habituated wrasses were more active (Fig. 3) and spent more time away from the shelter and near the predator than predator-naïve conspecifics (Table 1). The lower activity of predator-naïve fish when exposed to a predator is in general agreement with the findings of other studies. For example, Trinidadian guppies (*Poecilia reticulata*) and killifish (Hart's rivulus, *Rivulus hartii*) that infrequently experience predators in their natural stream habitats decrease activity and hide more when presented with both live and model predators (Fraser and Gilliam 1987). Reduced activity under predation risk is also a common response in many other animal species (reviewed in Lima and Dill 1990; Laurila 2000; Takahara et al. 2012). Although lower activity levels are sometimes associated with reduced foraging opportunities, we did not observe any measurable cost to reduced activity in terms of food consumption. In fact, although the difference was not statistically significant, the more active predator-habituated wrasses consumed 23% less food than the less active fish from the predator-naïve treatment during the ~ 30-min behavioural arena trials. Other predator–prey studies have also shown that activity levels are unrelated to food consumption, suggesting that cautious individuals may gain from being risk-averse while also not suffering from lost foraging opportunities (McPeek 2004; Steiner 2007).

Predator-habituated fish also spent more time away from the shelter and near the predator than predator-naïve individuals. Although predator inspection is common in fishes as a way for to assess predation risk (Pitcher et al. 1986; Lima and Dill 1990; Dugatkin and Godin 1992), and may lead to increased mortality in the prey species (Dugatkin 1992), our results rather suggest that more time spent out of a shelter and near a predator reflects habituation to a predator threat rather than risk assessment. Increased risk-taking behaviour and boldness in predator-experienced fish is a common observation (Fraser and Gilliam 1987; Kelley and Magurran 2003; Brown et al. 2005, 2007; Riesch et al. 2009; Sommer-Trembo et al. 2016). However, displaying more risky behaviours may be costly to the individual as the extra time spent near the predator may result in a greater mortality risk. Increased activity also elevates metabolic rate (Speers-Roesch et al. 2018), which, in the absence of compensatory food consumption, points to the more active predator-habituated wrasses being at an energetic disadvantage.

Why, then, did the wrasses behave as they did? Fish and other animals have the ability to gauge when a predator is likely to attack (rather than simply pass by) and respond accordingly by adjusting their behaviour (e.g. freezing) or initiating escape (Stankowich and Blumstein 2005; McGhee et al. 2013; Lagos et al. 2014). Since the wrasses in the present study were always separated from the cod by a transparent divider, the prey was never in direct contact with the predator. The predator-habituated wrasses may have learned this, thus no longer perceiving the cod as an immediate threat. Such habituation to the presence of a predator has previously been found to reduce the perception of fear in prey (Stankowich and Blumstein 2005). Our results are also consistent with the idea that prey continuously living in the presence of predators simply have to accept the greater risk, as being chronically scared and hiding would trade off with foraging and mating opportunities (Lima and Bednekoff 1999; Brown et al. 2005), with resulting fitness consequences if prey over-respond to predator presence. Overall, our results add to a growing body of literature suggesting that non-consumptive (indirect) effects of predators on prey are complex, sometimes counter-intuitive, and important to consider in the context of behavioural and eco-physiological research.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-020-02947-5.

Acknowledgements We thank Bengt Lundve and the Royson family for the fish collection, and the staff at the University of Gothenburg's Kristineberg Marine Research Station for the technical assistance. We also thank the editor and two anonymous reviewers for their comments.

Author contributions TN, TDC, and JS conceived and designed the study; all authors performed the experiments; TN, JS, TDC, RM, and AHA analysed the data; TN, JS, and TDC drafted the manuscript; all authors revised the manuscript.

Funding This work was funded by the Royal Swedish Academy of Sciences (JS: grant no. FOA14SLC027; JS, FJ, BSR, DGR, SAB, MA, TDC: grant no. FOA17SLC), the Swedish Research Council VR (MA: grant no. 637-2014-449), the Swedish Research Council Formas (JS: grant no. 2013-947), the Natural Sciences and Engineering Research Council of Canada (BSR, SAB), the Danish Council for Independent Research (TN: grant no. DFF-4181-00297), the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement (TN: grant no. 713683), the Carl Trygger Foundation (Carl Tryggers Stiftelse för Vetenskaplig Forskning; MA: grant no. 14:15), and the Australian Research Council Future Fellowship programme (TDC: grant no. FT180100154) funded by the Australian Government.

Data availability The data and analysis script for this study are archived in the repository figshare and were made available to editors and reviewers upon initial submission: https://doi.org/10.6084/m9.figshare.13180616 (Norin et al. 2020).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval All experiments were conducted in accordance with licence Dnr103-2014 (held by FJ) from the Swedish Board of Agriculture. All applicable international, national, and/or institutional guidelines for the use of animals were followed.

Consent for publication All authors approve of the publication of this work.

References

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Benard MF (2004) Predator-induced phenotypic plasticity in organisms with complex life histories. Annu Rev Ecol Evol Syst 35:651–673

Billerbeck JM, Lankford TE Jr, Conover DO (2001) Evolution of intrinsic growth and energy acquisition rates. I. Trade-offs with swimming performance in *Menidia menidia*. Evolution 55:1863–1872

Boonstra R, Hik D, Singleton GR, Tinnikov A (1998) The impact of predator-induced stress on the snowshoe hare cycle. Ecol Monogr 79:371–394

Boonstra R (2013) Reality as the leading cause of stress: rethinking the impact of chronic stress in nature. Funct Ecol 27:11–23

Brown JS, Kotler BP (2004) Hazardous duty pay and foraging cost of predation. Ecol Lett 7:999–1014

Brown C, Jones F, Braithwaite V (2005) In situ examination of boldness–shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. Anim Behav 70:1003–1009

Brown C, Jones F, Braithwaite VA (2007) Correlation between boldness and body mass in natural populations of the poeciliid *Brachyraphis episcopi*. J Fish Biol 71:1590–1601

Chabot D, Koenker R, Farrell AP (2016) The measurement of specific dynamic action in fishes. J Fish Biol 88:152–172

Clark TD, Sandblom E, Jutfelt F (2013) Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. J Exp Biol 216:2771–2782

Culler LE, McPeek MA, Ayres MP (2014) Predation risk shapes thermal physiology of a predaceous damselfly. Oecologia 176:653–660

Dalton CM, Flecker AS (2014) Metabolic stoichiometry and the ecology of fear in Trinidadian guppies: consequences for life histories and stream ecosystems. Oecologia 176:691–701

Dugatkin LA (1992) Tendency to inspect predators predicts mortality risk in the guppy (*Poecilia reticulata*). Behav Ecol 3:124–127

Dugatkin LA, Godin JGJ (1992) Predator inspection, shoaling and foraging under predation hazard in the Trinidadian guppy, *Poecilia reticulata*. Environ Biol Fish 34:265–276

Fraser DF, Gilliam JF (1987) Feeding under predation hazard: response of the guppy and Hart's rivulus from sites with contrasting predation hazard. Behav Ecol Sociobiol 21:203–209

Fu S-J, Pang X, Cao Z-D, Peng J-L, Yan G (2011) The effects of fasting on the metabolic interaction between digestion and locomotion in juvenile southern catfish (*Silurus meridionalis*). Comp Biochem Physiol A 158:498–505

Gallagher AJ, Lawrence MJ, Jain-Schlaepfer MR, Wilson DM, Cooke SJ (2016) Avian predators transmit fear along the air-water interface influencing prey and their parental care. Can J Zool 94:863–870

Hall AE, Clark TD (2016) Seeing is believing: metabolism provides insight into threat perception for a prey species of coral reef fish. Anim Behav 115:117–126

Handelsman CA, Broder ED, Dalton CM, Ruell EW, Myrick CA, Reznick DN, Ghalambor CK (2013) Predator-induced phenotypic plasticity in metabolism and rate of growth: rapid adaptation to a novel environment. Integr Comp Biol 53:975–988

Hasenjager MJ, Dugatkin LA (2017) Fear of predation shapes social network structure and the acquisition of foraging information in guppy shoals. Proc R Soc B 284:20172020

Hawlena D, Schmitz OJ (2010a) Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. Am Nat 176:537–556

Hawlena D, Schmitz OJ (2010b) Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. Proc Natl Acad Sci U S A 107:15503–15507

Houston AI, McNamara JM, Hutchinson JMC (1993) General results concerning the trade-off between gaining energy and avoiding predators. Phil Trans R Soc B 341:375–397

Inness CLW, Metcalfe NB (2008) The impact of dietary restriction, intermittent feeding and compensatory growth on reproductive investment and lifespan in a short-lived fish. Proc R Soc B 275:1703–1708

Janssens L, Stoks R (2013) Predation risk causes oxidative damage in prey. Biol Lett 9:20130350

Jermacz Ł, Nowakowska A, Kletkiewicz H, Kobak J (2020) Experimental evidence for the adaptive response of aquatic invertebrates to chronic predation risk. Oecologia 192:341–350

Jutfelt F, Norin T, Åsheim ER, Rowsey LE, Andreassen AH, Morgan R, Clark TD, Speers-Roesch B (2020) Aerobic scope protection reduces ectotherm growth under warming. Preprint: EcoEvoRxiv. https://doi.org/10.32942/osf.io/zc3bm

Kelley JL, Magurran AE (2003) Learned predator recognition and antipredator responses in fishes. Fish Fish 4:216–226

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest package: tests in linear mixed effects models. J Stat Softw 82:1–26

Lagos PA, Ebensperger LA, Herberstein ME (2014) A quantitative test of the 'economic' and 'optimal' models of escape behaviour. Anim Behav 97:221–227

Lagos PA, Herberstein ME (2017) Are males more scared of predators? Differential change in metabolic rate between males and females under predation risk. Physiol Behav 173:110–115

Lankford TE Jr, Billerbeck JM, Conover DO (2001) Evolution of intrinsic growth and energy acquisition rates. II. Trade-offs with vulnerability to predation in *Menidia menidia*. Evolution 55:1873–1881

Laurila A (2000) Behavioural responses to predator chemical cues and local variation in antipredator performance in *Rana temporaria* tadpoles. Oikos 88:159–168

Lee W-S, Monaghan P, Metcalfe NB (2013) Experimental demonstration of the growth rate–lifespan trade-off. Proc R Soc B 280:20122370

Lima SL, Dill LM (1990) Behavioural decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Lima SL, Bednekoff PA (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. Am Nat 153:649–659

Lüdecke D (2018) Ggeffects: tidy data frames of marginal effects from regression models. J Open Source Softw 3:772

Maclean A, Metcalfe NB (2001) Social status, access to food, and compensatory growth in juvenile Atlantic salmon. J Fish Biol 58:1331–1346

Manzur T, Vidal F, Pantoja JF, Fernández M, Navarrete SA (2014) Behavioural and physiological responses of limpet prey to a seastar predator and their transmission to basal trophic levels. J Anim Ecol 83:923–933

McGhee KE, Pintor LM, Bell AM (2013) Reciprocal behavioral plasticity and behavioral types during predator-prey interactions. Am Nat 182:704–717

McPeek MA (2004) The growth/predation risk trade-off: so what is the mechanism? Am Nat 163:E88–E111

Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? Trends Ecol Evol 16:254–260

Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol Rev 85:935–956

Nordeide JT, Salvanes AGV (1991) Observations on reared newly released and wild cod (*Gadus morhua* L.) and their potential predators. ICES Mar Sci Symp 192:139–146

Norin T, Clark TD (2016) Measurement and relevance of maximum metabolic rate in fishes. J Fish Biol 88:122–151

Norin T, Clark TD (2017) Fish face a trade-off between 'eating big' for growth efficiency and 'eating small' to retain aerobic capacity. Biol Lett 13:20170298

Norin T, Sundin J, Morgan R, Andreassen AH, Amcoff M, Speers-Roesch B, Jutfelt F, Binning SA, Roche DG, Clark TD (2020) Data and R script for: predator presence affects activity patterns but not food consumption or growth of juvenile corkwing wrasse (*Symphodus melops*). https://doi.org/10.6084/m9.figshare.13180616

Okuyama T (2015) Metabolic responses to predation risk in a jumping spider. J Zool 297:9–14

Pitcher TJ, Green DA, Magurran AE (1986) Dicing with death: predator inspection behaviour in minnow shoals. J Fish Biol 28:439–448

Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology 86:501–509

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R.project.org/

Riesch R, Duwe V, Herrmann N, Padur L, Ramm A, Scharnweber K, Schulte M, Schulz-Mirbach T, Ziege M, Plath M (2009) Variation along the shy–bold continuum in extremophile fishes (*Poecilia mexicana*, *Poecilia sulphuraria*). Behav Ecol Sociobiol 63:1515–1526

Salvanes AGV, Nordeide JT (1993) Dominating sublittoral fish species in a west Norwegian fjord and their trophic links to cod (*Gadus morhua* L.). Sarsia 78:221–234

Secor SM (2009) Specific dynamic action: a review of the postprandial metabolic response. J Comp Physiol B 179:1–56

Sheriff MJ, Krebs CJ, Boonstra R (2009) The sensitive hare: sublethal effects of predator stress on reproduction in showshoe hares. J Anim Ecol 78:1249–1258

Sommer-Trembo C, Zimmer C, Jourdan J, Bierbach D, Plath M (2016) Predator experience homogenizes consistent individual differences in predator avoidance. J Ethol 34:155–165

Speers-Roesch B, Norin T, Driedzic WR (2018) The benefit of being still: energy savings during winter dormancy in fish come from inactivity and the cold, not from metabolic rate depression. Proc R Soc B 285:20181593

Stankowich T, Blumstein DT (2005) Fear in animals: a meta-analysis and review of risk assessment. Proc R Soc B 272:2627–2634

Steiner UK (2007) Linking antipredator behaviour, ingestion, gut evacuation and costs of predator-induced responses in tadpoles. Anim Behav 74:1473–1479

Steiner UK, Van Buskirk J (2009) Predator-induced changes in metabolism cannot explain the growth/predation risk tradeoff. PLoS One 4:e6160

Stoffel MA, Nakagawa S, Schielzeth H (2017) rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods Ecol Evol 8:1639–1644

Takahara T, Kohmatsu Y, Maruyama A, Doi H, Yamanaka H, Yamaoka R (2012) Inducible defence behaviour of an anuran tadpole: cue-detection range and cue types used against predator. Behav Ecol 23:863–868

Thaler JS, McArt SH, Kaplan I (2012) Compensatory mechanisms for ameliorating the fundamental trade-off between predator avoidance and foraging. Proc Natl Acad Sci U S A 109:12075–12080

Therneau TM (2020) Coxme: mixed effects Cox models. R package version 2.2–16. https://CRAN.R-project.org/package=coxme

Tigreros N, Wang EH, Thaler JS (2018) Prey nutritional state drives divergent behavioural and physiological responses to predation risk. Funct Ecol 32:982–989

Van Dievel M, Janssens L, Stoks R (2016) Short- and long-term behavioural, physiological and stoichiometric responses to predation risk indicate chronic stress and compensatory mechanisms. Oecologia 181:347–357

Veldhuis MP, Hofmeester TR, Balme G, Druce DJ, Pitman RT, Cromsigt JPGM (2020) Predation risk constrains herbivores' adaptive capacity to warming. Nat Ecol Evol 4:1069–1074

Verdolin JL (2006) Meta-analysis of foraging and predation risk tradeoffs in terrestrial systems. Behav Ecol Sociobiol 60:457–464