



Short communication

Chasing the light: Positive bias in camera-based surveys of groundfish examined as risk-foraging trade-offs

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ABSTRACT

Unbiased survey data are important for understanding the effects of fisheries and environmental change on fish communities. We applied predation risk and life history theories to examine how parallel laser beams, which provide a scale for estimating transect width and the sizes of fish and habitat features, might bias groundfish counts during visual surveys conducted with a towed video camera. The laser beams project forward as “dots” onto the benthos, and species differ in their propensity to chase them. We hypothesized that fish perceive the laser dots as potential food and the camera, which lags behind the dots while moving forward, as a generalized threat. Analyses accounted for species primary diet and tested the prediction that shorter-lived species are more likely to chase the laser dots than longer-lived species, but these differences should weaken in the perceived safety of larger groups. Consistent with our predictions, the probability that fish would chase the laser dots decreased with the maximum age of species and increased with group size, although these effects were independent of each other. Also, chase probabilities were ≈ 20 to 25 times greater for species known to include benthic mobile prey in their diet than for species that feed primarily on pelagic, sessile or low-mobility prey. Our results suggest that risk-foraging trade-offs are inherent to fish behaviors that might bias surveys counts. While further insight into species differences is still needed, we illustrate how group size- and species-specific chase probabilities can generate bias correction factors to improve surveys counts.

1. Introduction

Antipredator behaviors—fleeing, hiding, vigilance and others—have the benefit of increasing immediate survival in the face of predation risk, and the cost of diverting time and energy from foraging or other resource acquisition. Given these tradeoffs, prey responses to predators are thought to optimize short-term risk-taking and longer-term reproductive success (Lima and Dill, 1990; Clark, 1994). Consequently, animals may approach resources associated with greater danger (e.g., in the vicinity of a predator) when fitness benefits are perceived to outweigh the risk (Abrahams and Dill, 1989), as influenced by food availability (Anholt and Werner, 1995), body condition (Heithaus et al., 2007), life-history characteristics (Clark, 1994), and other factors (Lima and Dill, 1990).

For example, starving prey may be more likely to take greater risks to access food than better-fed prey, because the former is attempting to avoid an imminent loss of condition-dependent reproductive potential (Clark, 1994; Heithaus et al., 2007). Similarly, if prey belong to species

with a fast life-history (i.e., rapid growth, early reproduction, and short lifespan), individuals may be less likely to stop feeding and engage in antipredator behaviour than individuals of species with slower life histories and the potential for more reproductive bouts over a longer lifespan (Clark, 1994; Frid et al., 2012). Also, an increase in group size dilutes the predation risk experienced by individuals (Hamilton, 1971), potentially allowing increased foraging rates or access to resources associated with greater danger (Elgar, 1989; Lima and Dill, 1990).

According to the risk-disturbance hypothesis, human-made objects that move and create a visual stimulus may create trade-offs that resemble those associated with predation risk. For instance, animals may perceive direct approaches by aircraft, powerboats or other vehicles as generalized threatening stimuli from which they may escape when the object's proximity crosses a context-specific threshold (Frid and Dill, 2002).

These parallels between human disturbance and predation risk have potential applications to marine conservation (Dill, 2017). For example, assessment of fish populations and communities requires survey data,

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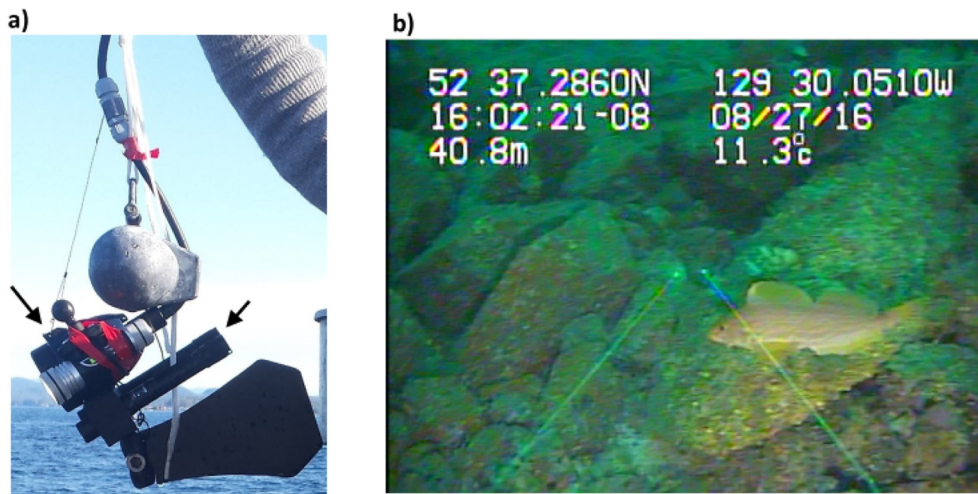


Fig. 1. Components of survey equipment hypothesized to create a tradeoff for fish during visual surveys. a) Towed video camera system, which is assumed to create a generalized threatening stimulus while moving. Left arrow points to the camera, while right arrow points to the parallel laser lights. Laser lights project forward onto the benthos as the camera system lags behind while simultaneously moving forward. b) Video frame of a female Kelp Greenling (*Hexagrammos decagrammus*) chasing the laser dots, which are assumed to be perceived as food.

which often are obtained via destructive sampling with longline or trawl fishing gear that may further damage declining stocks or be prohibited within protected areas. Additionally, trawl gear cannot be used to survey structurally complex rocky habitats preferred by rockfish (*Sebastes* spp.) and other groundfish (Jagiello et al., 2003). Alternatively, visual surveys conducted with video cameras, either towed from a surface vessel or contained within a remotely operated vehicle (ROV) or crewed submersible, do not cause fish mortality (e.g. Haggarty et al., 2016). One potential trade-off inherent to camera-based surveys, however, is that fish may respond behaviourally to the camera and its surrounding apparatus and associated lights, either fleeing or approaching it, which could bias fish counts (Ryer et al., 2009; Laidig et al., 2013; Rooper et al., 2015). Predation risk and life history theories have the potential to provide insight into this problem.

In this study, we applied the risk-disturbance hypothesis to examine potential bias in camera-based surveys of marine fish. Camera systems used for this work generally are equipped with one or more pairs of parallel laser beams (10 or 20 cm apart) and external illumination. The laser beams project forward as “dots” onto the benthos or other objects (Fig. 1b), providing a scale for estimating the sizes of fish or habitat features and to measure the field of view (Laidig et al., 2013; Rooper et al., 2015; Haggarty et al., 2016). We hypothesized that fish perceive the laser dots as a potential prey items, but also perceive the camera and its surrounding apparatus—which lag behind the lasers dots while simultaneously moving towards them—as a generalized threatening stimulus (Frid and Dill, 2002). Because the proportional cost of foregoing feeding increases as an organism’s reproductive window decreases (Clark, 1994), we predicted that species with shorter lifespans (i.e. faster life histories) would be more likely to chase the laser dots than species with longer lifespans (i.e., slower life histories) (Frid et al., 2012), but these differences would weaken as group size increased (Elgar, 1989). Because benthic predators of mobile prey might be more likely to follow laser dots along the bottom than species that feed primarily on pelagic, sessile or low-mobility prey, tests of this prediction accounted for species differences in primary diet.

2. Methods

2.1. Field data

Field data were collected as previously reported by Frid et al. (2018). Briefly, fieldwork took place in the Central Coast of British Columbia, Canada (see map in Appendix S1 of Frid et al., 2018), during late winter (early March) or summer (late May–August) of 2015–2017 (Appendix S1). A video camera (Fig. 1a: Deep Blue Pro: diameter = 7.6 cm, length = 8.9 cm) was connected to 240 m of cable and

towed from small vessels (≤ 8 m-long) at approximate speeds of 0.9 to 1.8 km/h. The cable transmitted video signals in real-time to a laptop computer that displayed and recorded images. The vessel’s GPS and depth sounder were connected to the laptop, which recorded geographic coordinates and water depth into a text file approximately every 2 s while overlaying that information onto the video image.

The camera system included parallel laser beams (10-cm apart) as a horizontal scale, and external illumination in the visible light spectrum (Fig. 1). Only green laser beams were used throughout our study. The ratio of horizontal distance captured by the frame to the distance from the camera to the object in the frame was 1.2. We aimed to tow the camera approximately 1–3 m above the substrate, which yielded images with sufficient detail for benthic species identification and a relatively wide field of view (i.e., horizontal distance between the frame’s boundaries), which had a median distance of 1.9 m.

Although they encompassed some shallow sites, video transects primarily sampled depths > 50 m (max. depth = 230 m). Individual transects covered 100–1200 m².

2.2. Literature data

Data on maximum known age and primary diet of different species were gathered from the literature (Appendix S2). Given that diets shift ontogenetically, diet information was specific to subadults and adults. Based on their diets, species were classified as: BPMP = benthic predator of mobile prey (e.g. crabs, fish); BSS = benthic predator of sessile (e.g. barnacles) or low-mobility prey (e.g. bivalves, polychaetes); Pelagic = planktivore or piscivore of pelagic prey; M1 = Mixed, both sessile/low-mobility and mobile benthic prey consumed frequently; M2 = Mixed, both pelagic and benthic mobile prey consumed frequently. From these classifications, we created a categorical variable depicting the relative extent to which species prey on benthic mobile prey: 3 = BPMP, 2 = M1 or M2, and 1 = BSS or Pelagic. Species lacking data on diet or maximum known age were excluded from analysis.

2.3. Analyses

We analyzed 85 video transects (71% of those reported by Frid et al., 2018), which yielded 1035 fish encounters of species for which we could access data on maximum age and primary diet. Both lasers were operational in 811 cases (78.4%), but only one laser worked in 124 cases (12.0%). Preliminary analyses showed no difference in fish responses to one vs. two lasers, and both cases were pooled for analyses. Both lasers malfunctioned in 100 cases (9.7%), which we excluded from analyses (Appendix S3).

Table 1

Statistical models describing variation in chase probabilities. Model 1 is the binomial GLMM best-supported by AIC model selection (Appendix S5), which included all observations and used species as a random effect; partial predators of benthic mobile prey (M1 and M2 species combined) are the reference for coefficients describing primary diet (see Appendix S2). Model 2 is the best-supported binomial GLM (Appendix S6) limited to 14 species with ≥ 10 observations; Black Rockfish is the reference species. Late winter is the reference season for both models. Appendix S2 provides scientific names of species.

Model	Predictor	Estimate	Standard error
Model 1	Intercept	-0.7484	0.5980
	^a Benthic predators of mobile prey	-0.0593	0.6361
	^b Non-consumers of benthic mobile prey	-3.3755	0.9087
	Depth	-0.0225	0.0070
	Group size	0.2537	0.1077
	Max. Age	-0.5641	0.3330
	Season	0.6324	0.2774
	Model 2	Intercept	-3.8968
Depth		-0.0217	0.0076
Canary rockfish		4.1170	1.3258
China rockfish		1.9444	1.2345
Copper rockfish		2.7373	1.3305
Deacon rockfish		-14.1808	1050.1813
Greenstriped rockfish		2.3913	1.6096
Kelp Greenling		4.4549	1.1773
Lingcod		4.5414	1.1868
Puget sound rockfish		0.1969	1.3256
Quillback rockfish		1.3209	1.1776
Spotted ratfish		-12.7903	632.9641
Tiger rockfish		1.4047	1.5563
Yelloweye rockfish		3.3898	1.2055
Yellowtail rockfish		1.3372	1.2022
Group size		0.0848	0.0349
Season		0.6145	0.2888

^a BPMP species.

^b BSS and Pelagic species combined.

We scored, by species and group size, whether fish chose to “chase” or “not chase” the laser dots (or single dot). “Chases” were defined operationally as fish moving directly (headfirst) towards the laser dots on the benthos and continuing to move with that general orientation for a minimum of 5 s. Fish that did “not chase” either maintained the same position as first observed, swam away at an angle of $\geq 45^\circ$ relative to the path of the lasers, or followed the laser dots for < 5 s before stopping or veering in a different direction.

These criteria were chosen because they are repeatable and, we assumed, likely to demarcate intentional chasing behaviour from other movement types (e.g. swimming in front of the camera without chasing the laser dots). Consistent with that assumption, the median duration of fish movements towards the laser dots was 12 s during chases ($N = 152$; Appendix S4) but 0 s when fish did not chase ($N = 779$). Also, fish first appeared in the camera frame already moving headfirst towards the laser dots in 90.1% of chases, but only 2.2% of non-chases. Further, rush-stop movement sequences directed at the laser dots, often involving sharp directional changes to maintain headfirst orientation and suggesting an attack, occurred in 51.3% of chases, but only once (0.13%) during non-chases. After the initial ≥ 5 s head-first movement towards the laser dots, fish moved ahead of the laser dots in 6.6% of chases; fish that did not chase moved ahead of the laser dots in only 0.39% of cases.

Cases involving groups (i.e. ≥ 2 individuals of the same species together) contributed a single data point to the analyses. In most cases, group members behaved synchronously. In the few cases when only a subset of the group could be seen throughout the entire duration of the chase (i.e., within the restricted field of view of the camera), the event was scored as a chase.

We tested our a priori prediction with data from all species (Appendix S2) and a generalized linear mixed model (GLMM) with a binomial distribution implemented in R (Bates et al., 2015). The

response variable was “chase” vs “not chase” (coded as 1 or 0, respectively). The predictors (i.e. fixed effects) of a priori interest were primary diet, maximum known age, group size and the interaction of the latter two factors. To account for other potential sources of variability, we also included depth (which correlates with ambient light) and season as fixed effects. Season consisted of a two-level categorical variable: late winter (early March), when Lingcod (*Ophiodon elongatus*) and Kelp Greenling (*Hexagrammos decagrammus*) are likely to be guarding eggs, vs. summer (late May–August), when no species are expected to be egg guarding. From these variables we generated 36 competing models (Appendix S5), each including a random effect for species to control for additional variation. AIC model selection was then used to select the model that best traded-off likelihood and parsimony (Burnham and Anderson, 2002). For this analysis, five observations of Yellowtail Rockfish (*Sebastes flavidus*) in groups of 40, 50, 60, 70 and 140 were excluded because these were extreme cases, each with a sample size of one, which led to very poor model diagnostics.

In addition to testing the a priori prediction, we used a general linear model (GLM) with a binomial distribution (McCullagh and Nelder, 1989) to further assess species differences in their probabilities of chasing the laser dots, using species and group size as predictors. This analysis was restricted to species with ≥ 10 observations (see Appendix S2). To control for other sources of variability, we included depth, season and group size as additional predictors, generating 16 competing models subject to AIC model selection procedures (Appendix S6).

For both analyses, visual inspection of quantile-quantile plots and plots of residual versus fitted values were examined to verify model assumptions. Raw data and R code are provided as electronic Supplementary material.

3. Results

Towed video transects recorded 29 fish species with maximum known lifespans ranging from 10 to 118 years (Appendix S2). Based on the literature, we classified 8 species as primarily benthic predators of mobile (BPMP), 10 as mixed feeders that included benthic mobile prey in their diet (M1 or M2) and 9 as non-consumers of benthic mobile prey (BSS or Pelagic). Diet data were unavailable for two species (Appendix S2). Fish encounters occurred at a median depth of 42 m (range 7–155 m, Appendix S7).

According to the best-supported GLMM (i.e., lowest AIC value: Appendix S5), the probability that fish would chase the laser dots decreased with the maximum age of species, increased with group size, and depended on primary diet (Model 1 in Table 1; Figs. 2, 3). For instance, a single individual of a species with a maximum lifespan of 30 years is estimated, depending on primary diet, to be 35% to 48% and 1.9 to 2.2 times more likely to chase than species with maximum lifespans of 55 or 80 years, respectively (Fig. 2). Also, a species with a maximum lifespan of 55 years in groups of 3 or 5 is estimated, depending on primary diet, to be 13%–17% or 27%–37% more likely to chase, respectively, than single individuals (Fig. 3). For single individuals, average chase probabilities were, depending on age, ≈ 20 to 25 times greater for species known to consume benthic mobile prey (BPMP, M1 and M2) than for species that do not (BSS-Pelagic combined) (Fig. 2). Additionally, chase probabilities were greater in summer than during late winter and decreased slightly with depth (Model 1 in Table 1).

Of 14 species with adequate sample sizes for analysis of species effects, group size-corrected probabilities of chasing the laser dots were highest for two relatively short-lived species, Kelp Greenling (max. Known lifespan, $Age_{max} = 18$ yrs) and Lingcod ($Age_{max} = 25$ yrs), and intermediate for two long-lived rockfishes, Canary (*Sebastes pinniger*, $Age_{max} = 84$ yrs) and Yelloweye Rockfish (*S. ruberrimus*, $Age_{max} = 118$ yrs) (Model 2 of Table 1; Fig. 4). Responses by the two rockfishes, however, were more variable than for Kelp Greenling and Lingcod. The remainder of species either did not chase laser dots or did

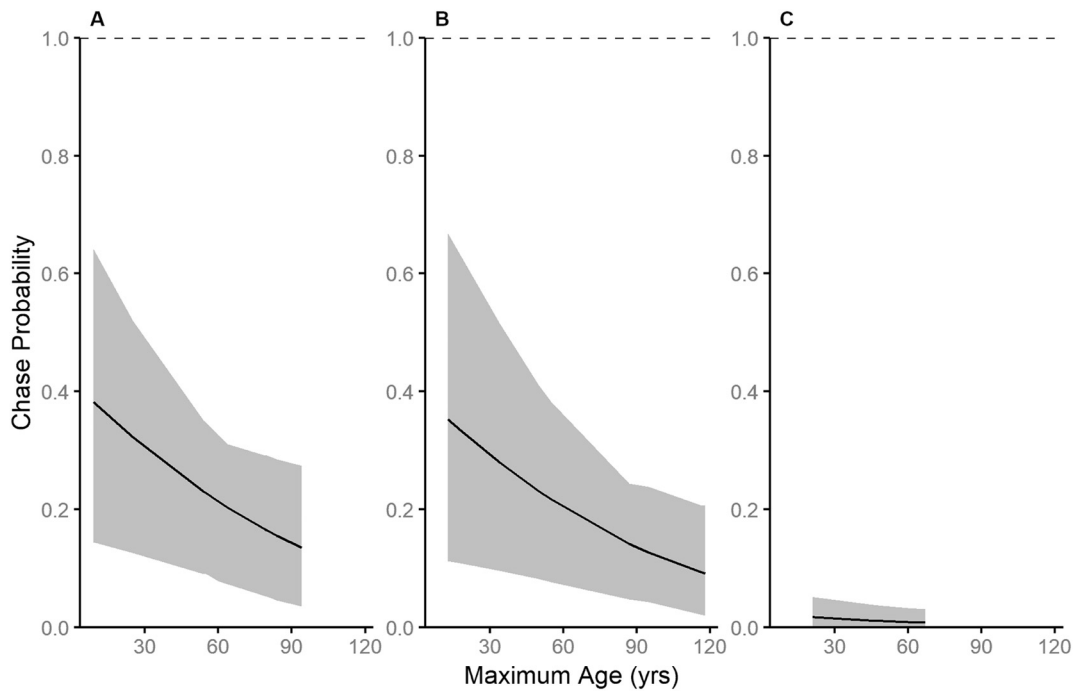


Fig. 2. Probability of chasing the laser dots, as estimated by Model 1 of Table 1, in response to the maximum age and primary diet of different species: A) partial predators of benthic mobile prey (M1 and M2 species), B) primary predators of benthic mobile prey (BPMP species), and C) non-consumers of benthic mobile prey (Pelagic and BSS species). The band is the bootstrapped 95% confidence interval based on 500 iterations. Estimates are for depths of 50 m during summer and single individuals. For each panel, the range of maximum ages corresponds to that of species in the given diet group.

so infrequently (Model 2 of Table 1; Fig. 3).

4. Discussion

Understanding biases in survey methodologies is important when assessing the status of fish populations. Previous studies have analyzed

potential biases caused by factors such as visible light used for illumination during camera-based surveys (Ryer et al., 2009; Rooper et al., 2015), movement of ROVs and their associated noise, electrical and mechanical signals (Stoner et al., 2008), catchability associated with different fishing gear types (Fraser et al., 2007) and survey timing (Ryer and Barnett, 2006). To our knowledge, our study is the first to address

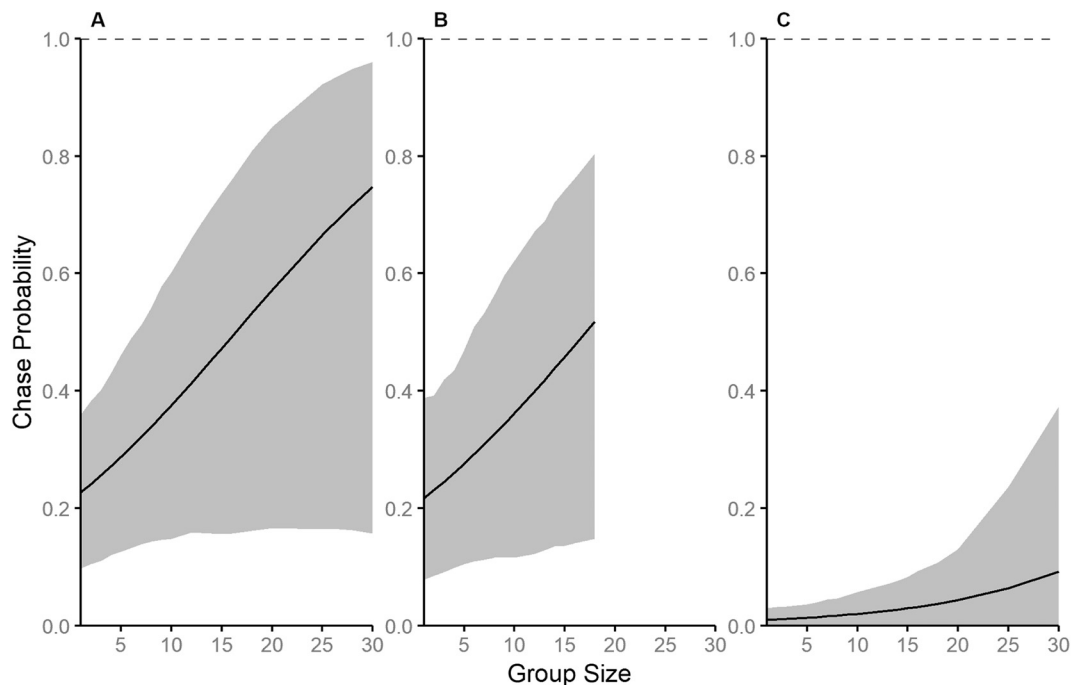


Fig. 3. Probability of chasing the laser dots, as estimated by Model 1 of Table 1, in response to group size and primary diet (see Appendix S1): A) partial predators of benthic mobile prey (M1 and M2 species), B) primary predators of benthic mobile prey (BPMP species), and C) non-consumers of benthic mobile prey (Pelagic and BSS species). The band is the bootstrapped 95% confidence interval based on 500 iterations. Estimates are for depths of 50 m during summer and a species with maximum age of 55 years. For each panel, the range of group sizes corresponds to those commonly observed for those species.

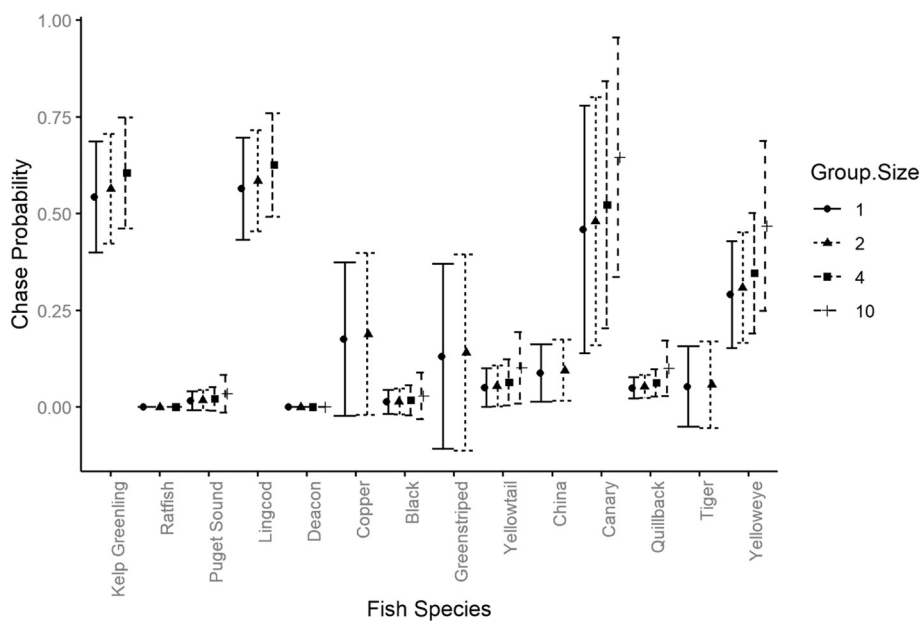


Fig. 4. Group-size corrected probabilities of chasing the laser dots by species with ≥ 10 observations (Model 2 of Table 1). Whiskers are 95% confidence intervals. Species are ordered, left to right, from shortest to longest maximum known lifespan (Appendix S2). Group sizes shown for a given species are constrained to those generally observed during our study. Estimates are for depths of 50 m during summer. Appendix S2 provides scientific names of species.

how parallel laser beams used as distance scalers and projected from a towed video camera might bias the rate at which visual surveys record different species.

Our approach was to seek generality by applying predation risk and life history theories (Clark, 1994; Frid and Dill, 2002) to predict that species characterized by shorter lifespans would be more likely to chase the laser dots than species characterized by longer lifespans, but these differences would weaken for larger groups. The results essentially supported this prediction: chase probabilities decreased with maximum age and increased with group size, although we did not find support for an interaction between group size and maximum age.

Additional variability was explained by depth, season and species differences in primary diet. In particular, species known to consume benthic mobile prey were ≈ 20 to 25 times more likely to chase laser dots moving along the benthos than species that feed primarily on pelagic or sessile or low-mobility prey. This finding is consistent with our assumption that fish perceive the laser dots as potential food. It is plausible that species that do not consume benthic mobile prey were choosing to avoid energetic and/or perceived risk costs that would not yield a net fitness benefit.

We acknowledge, however, that two long-lived species, Canary and Yelloweye rockfishes had, on average, the third and fourth highest chase probabilities out of 14 species in the species-specific model (Fig. 4), which suggests that our analyses did not account for some important sources of variability. Predation risk factors unaccounted for by our analyses that may have influenced our results include body size. Smaller individuals are more vulnerable to predation (Nilsson and Brönmark, 2003) and invest more in antipredator behaviour (Rizzari et al., 2014). Perhaps the decision to chase the laser dots responds to an interaction between body size and expected lifespan or other key life-history characteristics. That is, large individuals of a given species may be more likely to chase the laser dots than smaller individuals, but the effect of body size should be stronger in longer-lived species. To account for intraspecific variation in size (i.e. due to variation in age and growth rates), tests of this prediction require data on the body sizes of individuals (i.e., estimated with the scale provided by parallel laser) encountered during the camera survey, for which we obtained too few observations.

Other unexplained variability in our data may relate to variation in speed and the vertical and horizontal angles of approach of the camera system, which may affect responses to generalized threatening stimuli (Frid and Dill, 2002). Additionally, lower food availability may lead to

greater risk-taking; it is plausible that chase probabilities may vary intraspecifically and across time and space according to variation in food supply and the energy state of individuals (Anholt and Werner, 1995; Heithaus et al., 2007). While the application of this concept may not be always practical, perhaps broad indices of variation in temporal and spatial variability in biological productivity could eventually be used to adjust survey bias.

Fish responses may also vary with different types of equipment (Stoner et al., 2008). Laidig et al. (2013), for instance, recorded a greater frequency of escape reactions to a tethered ROV (1.0 m tall, 1.4 m wide, and 2 m long) than to a crewed submersible (1.8 m tall, 1.1 m wide but tapering to 0.4 m at front port, and 4.6 m long). More research is needed to understand how the characteristics of different gear types used for visual surveys contribute to how fish perceive generalized threatening stimuli (Laidig et al., 2013).

Our evidence that chase probabilities decrease with a species' maximum lifespan, increase with group size and are highest for species that include benthic mobile prey in their diets is consistent with the hypothesis that risk-foraging trade-offs are inherent to fish behaviors that might bias surveys counts when parallel laser beams are used (Frid and Dill, 2002; Frid et al., 2012). While further insight into the underlying mechanisms that lead to species differences is still needed, our results already provide a basis for bias correction in fish surveys that use equipment similar to ours.

Specifically, let $Pr_{sp, g, d, s}$ be the species-, group size-, depth- and season-specific probability of chasing the laser dots. Next, assume that, within the constraints of the field of view of the camera, an unbiased count, C_u , occurs if $Pr_{sp, g, d, s} = 0$ while a biased count, C_b , if $Pr_{sp, g, d, s} > 0$ and that inflation of count data is directly proportional to $Pr_{sp, g, d, s}$. Under these assumptions, biased counts can be corrected such that:

$$C_u = C_b \times (1 - Pr_{sp, g, d, s}) \quad (1)$$

If a species of interest is included in the species-specific model (Model 2 of Table 1; Fig. 4), then $Pr_{sp, g, d, s}$ can be estimated from that model. For instance, if a total of four Kelp Greenling are observed during a transect conducted in summer at a 50 m-depth, then corrected counts would be 1.83 ± 0.57 if fish were encountered as single individuals, or 1.58 ± 0.57 if encountered as a group. If a species is not included in the latter model, then maximum age and diet provide a proxy for species and an estimate can be made from the greater generality of Model 1 of Table 1 (Figs. 2, 3). For instance, if 3 single individuals of a species that is a benthic predator of mobile prey and has a

maximum lifespan of 80 years are observed during summer at a 50-m depth, then the corrected count is 2.53 individuals with upper and lower 95% confidence interval bounds of 2.82 and 2.20.

More generally, our study illustrates how predation risk and life history theories can guide efforts to understand behavioural differences between species that might bias survey results. That theoretical framework not only generated predictions, but also guided interpretation of results and generated a next iteration of predictions, streamlining the search for improved understanding of marine ecosystems and their conservation status.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.01.011>.

References

- Abrahams, M.V., Dill, L., 1989. A determination of the energetic equivalence of the risk of predation. *Ecology* 70, 999–1007.
- Anholt, B., Werner, E., 1995. Interaction between food availability and predation mortality mediated by adaptive behavior. *Ecology* 76, 2230–2234.
- Bates, D., Maechler, M., Bolker, B.M., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48.
- Burnham, K., Anderson, D., 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*, 2nd edn. Springer, New York.
- Clark, C.W., 1994. Antipredator behavior and the asset-protection principle. *Behav. Ecol.* 5, 159–170.
- Dill, L.M., 2017. Behavioural ecology and marine conservation: a bridge over troubled water? *ICES J. Mar. Sci.* 74, 1514–1521.
- Elgar, M., 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.* 64, 13–33.
- Fraser, H.M., Greenstreet, S.P.R., Piet, G.J., 2007. Taking account of catchability in groundfish survey trawls: implications for estimating demersal fish biomass. *ICES J. Mar. Sci.* 64, 1800–1819.
- Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. *Ecol. Soc.* 6.
- Frid, A., Marliave, J., Heithaus, M.R., 2012. Interspecific variation in life history relates to antipredator decisions by marine mesopredators on temperate reefs. *PLoS One* 7.
- Frid, A., McGreer, M., Gale, K., Rubidge, E., Blaine, T., Reid, M., et al., 2018. The area-heterogeneity tradeoff applied to spatial protection of rockfish (*Sebastes* spp.) species richness. *Conserv. Lett.* 0, e12589.
- Haggarty, D.R., Shurin, J.B., Yamanaka, K.L., 2016. Assessing population recovery inside British Columbia's rockfish conservation areas with a remotely operated vehicle. *Fish. Res.* 183, 165–179.
- Hamilton, W.D., 1971. Geometry for the selfish herd. *J. Theor. Biol.* 31, 295–311.
- Heithaus, M.R., Frid, A., Wirsing, A.J., Dill, L.M., Fourqurean, J.W., Burkholder, D., et al., 2007. State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *J. Anim. Ecol.* 76.
- Jagiello, T., Hoffmann, A., Tagart, J., Zimmermann, M., 2003. Demersal groundfish densities in trawlable and untrawlable habitats off Washington: implications for the estimation of habitat bias in trawl surveys. *Fish. Bull.* 101, 545–565.
- Laidig, T., Krigsman, L., Yoklavich, M., 2013. Reactions of fishes to two underwater survey tools, a manned submersible and a remotely operated vehicle. *Fish. Bull.* 111, 54–57.
- Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68, 619–640.
- McCullagh, P., Nelder, J.A., 1989. *Generalized Linear Models*. Chapman and Hall, London.
- Nilsson, A., Brönmark, C., 2003. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos* 88, 539–546.
- Rizzari, J., Frisch, A., Hoey, A., McCormick, M., 2014. Not worth the risk: apex predators suppress herbivory on coral reefs. *Oikos* 123, 829–836.
- Rooper, C.N., Williams, K., De Robertis, A., Tuttle, V., 2015. Effect of underwater lighting on observations of density and behavior of rockfish during camera surveys. *Fish. Res.* 172, 157–167.
- Ryer, C.H., Barnett, L.A.K., 2006. Influence of illumination and temperature upon flatfish reactivity and herding behavior: potential implications for trawl capture efficiency. *Fish. Res.* 81, 242–250.
- Ryer, C., Stoner, A., Iseri, P., Spencer, M., 2009. Effects of simulated underwater vehicle lighting on fish behavior. *Mar. Ecol. Prog. Ser.* 391, 97–106.
- Stoner, A.W., Ryer, C.H., Parker, S.J., Auster, P.J., Wakefield, W.W., 2008. Evaluating the role of fish behavior in surveys conducted with underwater vehicles. *Can. J. Fish. Aquat. Sci.* 65, 1230–1243.