

Packed to the gills



Brett Favaro



Stefanie Duff



Isabelle Côté

Favaro, Duff, and Côté explain how crowded traps catch fewer prawns

Who should read this paper?

This paper is for anyone fascinated by what happens underwater when we deploy fishing gear to catch marine life. If there is seafood in your diet, this one is for you. Specifically, its findings will be relevant to fishers, fishery managers, scientists, and anyone interested in the processes that determine what ends up in our nets when we go fishing.

Why is it important?

To understand the environmental impact of a given fishing gear, we must study the gear underwater to understand the relationship between what we catch and what is present in the ecosystem. Advances in camera technology have made such research cheaper and easier than ever before, but as video proliferates, our understanding of how to use this technology to better manage our fisheries has lagged behind.

This study used underwater cameras to watch traps designed to catch spot prawns (a large shrimp that occurs on the Pacific coast of North America) deployed at sea. By recording the numbers of prawns that approached, tried to enter, and ultimately did enter the traps, the team was able to calculate the ‘catchability’ of prawns in relation to how many prawns were in and around the traps. Underwater video showed that when prawn density was low, catchability was at its highest, but it became harder to catch prawns as more prawns accumulated in and around traps. That meant that when there are few prawns outside the traps, a greater proportion of the population is caught than when more prawns are present in the environment. This matters because of the way the prawn trap fishery is managed. There are no quotas – instead, the fishery is closed when catch rates drop to a certain number of prawns per trap. The implication of these findings is that the traps could be having a larger relative impact on the remainder of the prawn population at the end than at the start of the fishery. The authors conclude that many fisheries could benefit from directly investigating the performance of fishing gear deployed underwater. This paper provides an example of why video data is important, and how it can be used to improve our understanding of fisheries and the impacts of fishing gear.

About the authors

Brett Favaro is a research scientist at the Centre for Sustainable Aquatic Resources in the Fisheries and Marine Institute of Memorial University of Newfoundland, and is a cross-appointed faculty member at Memorial’s Department of Ocean Sciences. Stefanie Duff is a professor of invertebrate ecology at Vancouver Island University, and Isabelle Côté is a professor of marine ecology at Simon Fraser University. The three authors are all conservation biologists interested in how best to translate quality science into workable conservation practice that improves the way we manage marine resources around the world.

DENSITY-DEPENDENT CATCHABILITY OF SPOT PRAWNS (*PANDALUS PLATYCEROS*) OBSERVED USING UNDERWATER VIDEO

Brett Favaro^{1,2,3,4}, Stefanie D. Duff³, Isabelle M. Côté⁴

¹Centre for Sustainable Aquatic Resources, Fisheries and Marine Institute of Memorial University of Newfoundland, St. John's, NL, Canada

²Department of Ocean Sciences, Memorial University of Newfoundland, St. John's, NL, Canada

³Department of Fisheries and Aquaculture, Vancouver Island University, Nanaimo, BC, Canada

⁴Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada

ABSTRACT

Understanding how fishing gear catches target species is an important part of understanding the impacts of commercial fishing. Here, we use underwater video to investigate the catch dynamics of spot prawn (*Pandalus platyceros*) traps, a fishing gear used in a large commercial fishery in British Columbia, Canada. We report, for the first time, interactions that occur as prawns accumulate in traps during the first eight hours of trap deployment at depths between 75 and 100 m, and test whether catchability of prawns depends on the density of prawns in and around traps. We found that prawn catchability decreased as the number of prawns in the trap increased. This process was driven by a diminishing proportion of approaching prawns that made entry attempts, as well as a reduced likelihood of entry attempts being successful as traps filled with prawns. Very few prawns exited traps during observations, but final catch rates demonstrated that exits must have occurred after the termination of our videos. Recording and examining the full 24 hours of a typical soak would clarify how trap saturation is achieved.

KEYWORDS

Crustacean; Behaviour; Deep water; Benthic ecology; Fishery management

INTRODUCTION

Catchability, the proportion of individuals in a given area that are removed by a unit of fishing effort, is a key factor in understanding the dynamics of a fishery [Arreguin-Sanchez, 1996]. Catchability is affected by a wide range of biological and environmental factors [Arreguin-Sanchez, 1996; Stoner, 2004], with one of the most well-studied determinants being the density of organisms in a fished area [see Wilberg et al., 2009].

Catchability and abundance of a given species generally vary inversely [Paloheimo and Dickie, 1964; Arreguin-Sanchez, 1996; Kotwicki et al., 2014]. That is, as stock abundance declines, a greater proportion of the available stock is removed per unit of fishing effort [Winters and Wheeler, 1985]. This phenomenon can contribute to hyperstability, where catch per unit effort (CPUE) remains stable despite declining abundance [Ward et al., 2013]. Catchability can be estimated by combining fishery-dependent data with fishery-independent data in a modelling framework [Crecco and Overholtz, 1990], or through simulations [Ihde et al., 2008]. However, catchability can also be directly measured using in-situ video [Godø et al., 1999]. Underwater video enables researchers to directly measure entry rates, exit rates, and determine saturation points of deployed fishing gear [Favaro et al., 2012; Bacheler et al., 2013]. In effect, this allows for direct measurement of catchability in deployed gear under a specific set of conditions.

In British Columbia, on the Pacific coast of Canada, a large-scale fishery targets spot

prawns (*Pandalus platyceros*) using trapping gear. Approximately 3.4 million traps are deployed annually at depths of approximately 100 m [Rutherford et al., 2010], resulting in an average landed value of \$23 to \$33 million, making this industry the third most valuable shellfish fishery in British Columbia [British Columbia Ministry of Agriculture, 2012]. The prawn fishery is managed based on an escapement model, which allows the fishery to remain open until populations are depleted to the point where the catch-per-trap meets a target level [Boutillier and Bond, 2000]. Whether this threshold is reached during the fishing season clearly depends on catchability.

Previous research on the catch dynamics of prawn traps focused exclusively on the composition and abundance of organisms caught in gear upon retrieval [e.g., Boutillier and Sloan, 1987; Boutillier and Bond, 2000; Rutherford et al., 2004]. More recently, the catchability of prawn traps has been estimated from depletion analyses derived from in-season catch data [Smith, 2013]. This approach provided a broad estimate of catchability across years, but did not directly measure the relationship between catchability and density.

Until recently, the depths and benthic conditions in which prawn traps are deployed made it difficult to observe prawn traps in-situ [Favaro et al., 2012]. Until recently, camera equipment was too large and heavy to effectively deploy on these lightweight traps. Alternative technologies such as remotely operated vehicles (ROVs) or surface-based systems are expensive, and would be difficult to keep stationary, focused on traps, for long periods of time. In this study, we perform

direct observations of deployed traps using a TrapCam apparatus designed specifically for this purpose [Favaro et al., 2012], and provide the first description of the catch process of prawn traps at depth. Lobster, crab, and fish traps have all been studied in this manner, revealing important processes related to territoriality, density dependence, and behavioural interactions that affect final catch [Jury et al., 2001; Barber and Cobb, 2009; Renchen et al., 2012].

More specifically, we describe the accumulation of prawns and other species in prawn traps across 13 TrapCam deployments. We examine how density affects catchability of prawns and model the relationship between the two factors. Our results should enable managers to better understand how the ecological impacts of traps could change as traps deplete the prawn population to the target escapement threshold across the fishing season.

METHODS

Trap Video Deployments

To observe the dynamics of spot prawn traps in-situ, we deployed an underwater camera apparatus attached to a spot prawn trap (“TrapCam”) [Favaro et al., 2012]. This camera apparatus provided a top-down view of the trap (Figure 1) and recorded high-definition video (1080p resolution) using a Sony HDR-XR550V camcorder. Illumination was provided by four Princeton Tec Torrent LED Scuba lights, each equipped with red Luxeon I LEDs that emitted red light (621 to 645 nm) to reduce visibility to fish and prawns [Phillips, 2007; Favaro et al., 2012]. We deployed all gear in Howe Sound, British Columbia (49°25’30”N, 123°20’00”W, Figure 2), using a 9.8 m research vessel. Each deployment consisted of one ‘string’ of gear, which had three traps attached (baited with commercial prawn bait made of fishmeal



Figure 1: Top-down view of a prawn trap deployed at a depth of 80 m, as observed by the TrapCam apparatus.

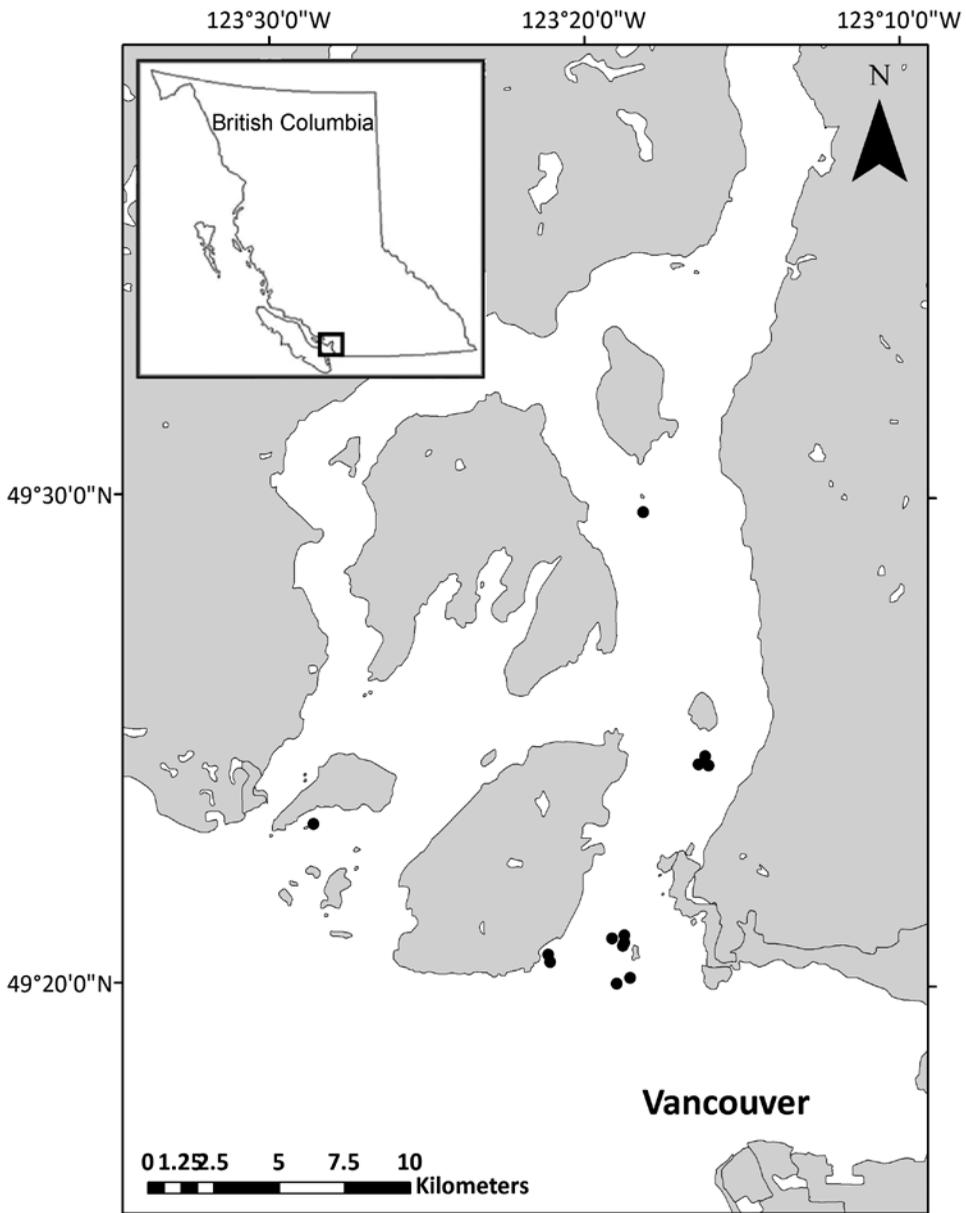


Figure 2: Map of TrapCam deployment sites within Howe Sound, British Columbia. Black dots represent the site of a single camera-trap deployment.

pellets [Rutherford et al., 2004]). The camera was attached to the middle trap, with standard traps on either side [see Favaro et al., 2012]. In a previous study, we found that the presence of a camera did not significantly alter final catch relative to traps without cameras [Favaro et al., 2012]. We selected deployment sites that we suspected to have relatively high densities of

prawns, based on personal experience and published locations of Fisheries and Oceans Canada (DFO) surveys [e.g., Favaro et al., 2010]. We analyzed 13 of 16 deployments (the apparatus tipped over in two, and silt obstructed the view in one), and eight hours of each 12 hour video (total = 105 hours), as light levels declined around the periphery of the

image in the final four hours, making it difficult to clearly view prawns and other species. We deployed the TrapCam during the day and recovered the gear an average of 26.2 hours after deployment (range 16.8 to 45.4 h), corresponding with the typical soak time of 24 hours used in the commercial fishery [DFO, 2011]. We recorded the final catch of the camera-bearing trap.

Coding Behaviours from Video

We recorded four variables from each video. First, we recorded the number of prawns that approached the trap (i.e., entering the video frame from any direction, see Video 1 in Appendix). Second, we noted whether approaching prawns attempted to enter the trap. A prawn was considered ‘attempting’ an entry if it moved from outside of the trap into the entry tunnel (Figure 3A, see Video 1 in Appendix). When a prawn proceeded all the way through the tunnel into the trap opening ring, the ‘attempt’ was scored as a ‘success’ (Figure 3B). Conversely, if a prawn turned back from the opening and failed to complete an entry, we scored the attempt as a ‘failure’ (Figure 3C, D). Third, we recorded the time it took prawns to successfully enter or fail to enter, defined as the time elapsed between the moment a prawn entered the tunnel to the time it (A) entered the opening ring or (B) turned back and left the tunnel. Finally, we recorded the number of ‘exits’ from the trap, i.e., when prawns which were fully in the trap escaped the trap through an opening.

Data Analysis

We used mixed-effects models for our analyses of density-dependent processes as they allowed us to account for the nested structure of our

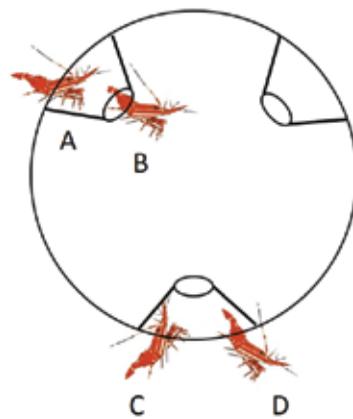


Figure 3: Diagram demonstrating the method used for scoring entry attempts. We recorded the length of time needed to complete a successful entry as defined by the time elapsed between the prawn first entering the tunnel opening (A) and entering the opening ring (B). We also recorded the duration of failed entry attempts as the time elapsed between the prawn first entering the tunnel opening (C) and subsequently backing out of the entry tunnel (D). (Video 1 listed in Appendix shows this process.)

data (i.e., observations nested within deployments [Zuur et al., 2009]). We examined the effect of prawn density on each of the two steps of the prawn catching process: first, attempted entry, and second, successful entry. First, we used a generalized linear mixed-effects model (GLMM) with a Gaussian distribution (functionally equivalent to a linear mixed-effects model [Bolker et al., 2009]) to test the relationship between the around-trap density, measured by the number of approaches in a given hour, and the number that attempted an entry in that same hour. All models used deployment number as a random effect. We conducted this test on binned data – that is, the number of prawn approaches and entry attempts in each one-hour period of video. We conducted our analysis on log-log transformed data to improve model fit, and excluded hours in which no prawns approached the trap ($N = 29$). Second, we used a binomial GLMM [Bolker et al., 2009] to test whether the number of prawns in the trap at the start of the hour predicted the likelihood of a successful entry attempt. GLMMs are an

effective tool to analyse proportional data as they allow the user to construct models that specify an appropriate distribution (binomial), a link function (logit), and random effects (deployment number) to assess the relationship between an explanatory variable and a variable of interest [Bolker et al., 2009]. We then used Gaussian GLMMs to test whether the time taken to successfully (or fail to) enter was related to the number of prawns in the trap at the start of the hour. Finally, we used a binomial GLMM to test whether the proportion of entries that were successful was associated with the density of prawns outside the trap (as measured by the number of approaches in a given hour).

We estimated the catchability, q , of spot prawns, defined as $C/(B*f)$ [Jul-Larsen et al., 2003], where C is the number of prawns that successfully entered a trap in an hour, B is the total number of prawns in the vicinity of the trap (i.e., number of approaches in an hour), and f is fishing effort, which in our case was always one trap-hour. Typically, B represents the true population size of the target species; however, our use of video limited us to measuring the abundance of prawns in the immediate vicinity of the trap. Therefore, our definition of catchability here refers to the likelihood that a prawn that has approached the trap will successfully enter the trap in an hour of trap deployment. We used a binomial GLMM to test the relationship between catchability in a given hour and the number of prawns in the trap at that time, weighted by the number of entry attempts within that hour. Here, we also excluded hours in which no approaches took place to avoid division by zero. All analyses were done in R, and we used the

MASS package to construct GLMMs [Venables and Ripley, 2002; R Core Team, 2013].

RESULTS

We observed a total of 1,930 approaches by spot prawns across all videos (Table 1, Figure 4). It took 92.4 min, on average, for the first prawn to approach a trap ($N = 13$, S.D. = 122 min, range: 4 - 317 min; Figure 4A), and a further 81.2 min, on average (excluding three deployments with no successful prawn entries; S.D. = 120 min, range = 8.5 - 160 min), before the first prawn entered a trap (Figure 4). We observed a total of 14 prawns exit traps, all through trap openings. Prawns did not enter traps en masse. Instead, there was a relatively slow but constant increase in the number of prawns in traps over the course of the eight-hour videos.

We observed significant density-dependent behaviours for spot prawns. As the rate of prawn approaches increased, the rate of entry attempts also increased, but at a diminishing pace (log-log Gaussian GLMM, $\beta_1 = 0.682$, $p < 0.001$, $df = 61$; Figure 5). As traps accumulated prawns, the proportion of prawns that successfully entered the trap declined significantly (Figure 6). For each additional prawn present in the trap, the probability of a prawn successfully entering decreased by 1% (binomial GLMM, $\beta_1 = -0.017$, $p < 0.001$, $df = 703$), from 53.3% in empty traps to 16.3% when 102 prawns (the maximum observed) were present in the trap. As a result, catchability of prawns around traps declined significantly as the number of prawns inside the trap increased (binomial GLMM, $\beta_1 = -0.020$, $p < 0.001$, $df = 61$; Figure 7).

Deployment #	Date (MM-DD-YY)	Start of deployment (hh:mm)	# prawn approaches	# entry attempts by prawns	# successful entries by prawns	# exits by prawns	# approaches by other species	# entry attempts by other species	# successful entries by other species	Final # of prawns caught
1	7/21/2010	08:05	243	32	19	1	22	1	0	44
2	7/23/2010	08:20	169	102	38	3	2	0	0	63
3	7/27/2010	11:45	55	33	21	0	1	0	0	39
4	7/29/2010	14:00	302	158	70	4	477	17	5	44
5	7/31/2010	14:30	9	9	5	1	3	1	0	18
6	8/3/2010	09:35	64	31	14	0	5	4	0	34
7	8/4/2010	16:00	10	2	0	0	64	4	1	4
8	8/13/2010	14:00	6	0	0	0	47	3	0	0
9	8/14/2010	12:20	7	0	0	0	73	1	0	1
10	8/16/2010	12:55	212	77	33	1	25	0	0	2
11	8/17/2010	12:45	2	0	0	0	36	1	0	0
12	8/18/2010	11:20	840	264	106	4	28	6	1	91
13	8/20/2010	11:55	11	11	7	0	157	15	7	0

Table 1: Summary data from each deployment of the TrapCam video apparatus. All deployments occurred in Howe Sound at depths between 75 and 100 m, and each video yielded eight analyzable hours.

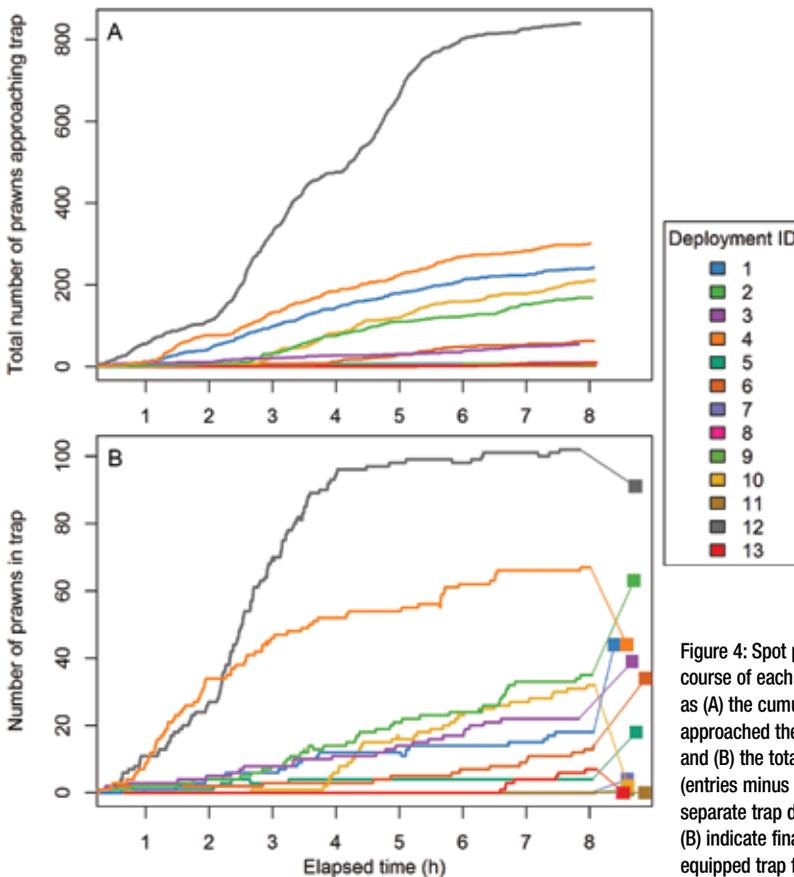


Figure 4: Spot prawn accumulation over the course of each trap deployment (N=13) described as (A) the cumulative number of prawns that approached the trap throughout a recording period and (B) the total number of prawns in the trap (entries minus exits). Each line represents a separate trap deployment. The coloured squares in (B) indicate final prawn catch in the camera-equipped trap for the corresponding deployment.

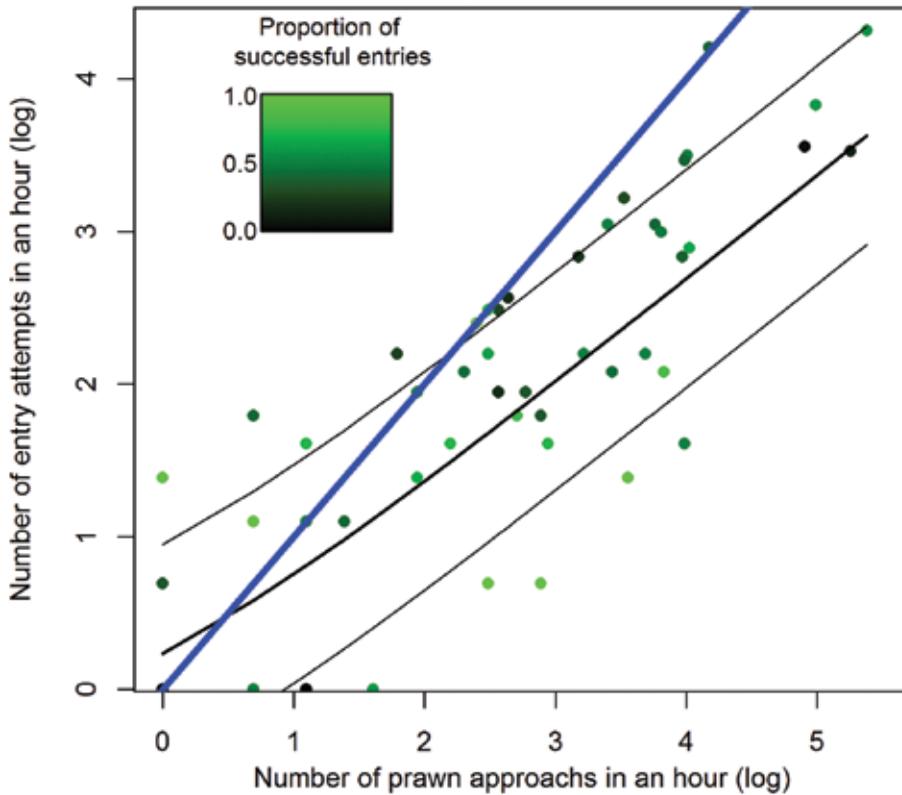


Figure 5: Relationship between the number of entry attempts occurring per hour and the number of prawns that approached traps in that hour, a proxy for prawn density around traps. Point colour reflects the proportion of entries that were successful in a given hour, with lighter colours representing higher success rate. Hours with no prawn approaches are excluded from this figure (N = 29). The thick blue line shows the 1:1 relationship. The predicted best-fit line is represented by the black line and the thin lines indicate 95% confidence intervals.

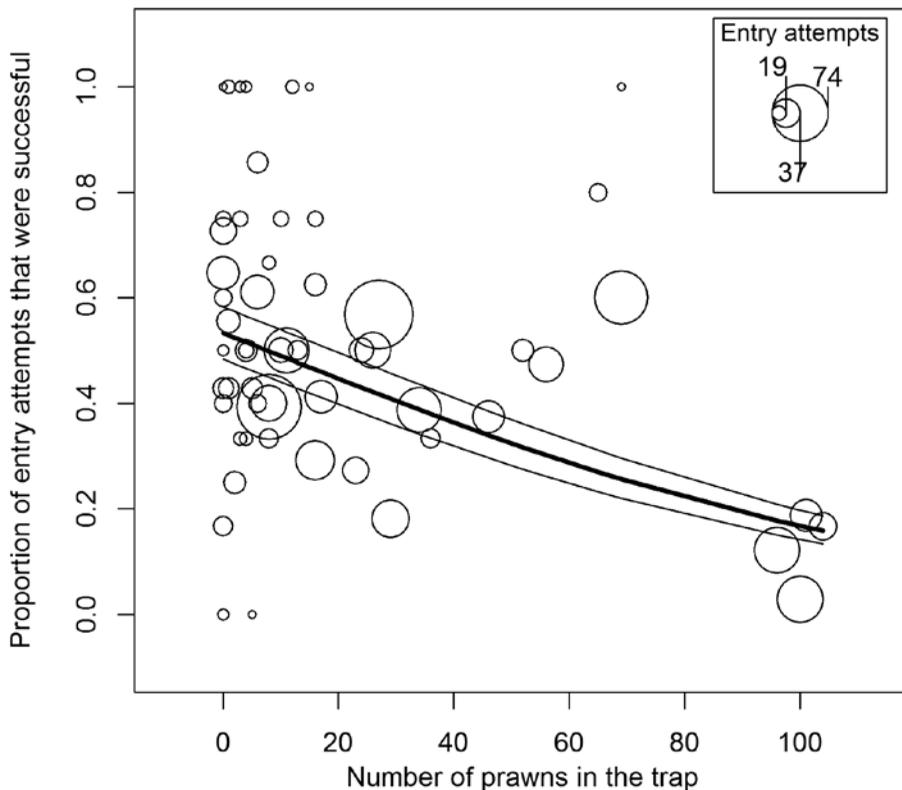


Figure 6: Proportion of entry attempts that were successful in a given hour and the number of prawns inside the trap at the start of each hour. Circle size indicates the number of entry attempts occurring in a given hour. The thick black line indicates predicted best-fit line with thin lines representing 95% confidence intervals.

The change in catchability was not attributable to prawns taking longer to either successfully enter traps (Gaussian GLMM, $\beta_1 = -0.001$, $p = 0.75$, $df = 303$) or abort their entry attempts (Gaussian GLMM, $\beta_1 = 0.004$, $p = 0.08$, $df = 393$) as neither measure was significantly related to the number of prawns present in the trap. In addition, it was not driven by crowding around the trap openings; there was no clear relationship between the proportion of entry attempts that were successful and the total number of entry attempts in a given hour (binomial GLMM, $\beta_1 = 0.001$, $p = 0.978$, $df = 703$).

DISCUSSION

This study represents the first description of the interactions that occur between spot prawns and traps deployed at depths similar to those of the commercial prawn fishery. We discovered that in-trap and around-trap prawn densities (as measured by the number of prawns approaching traps in a given hour) affect trap performance in two main ways. First, as the density of prawns around the trap increases, the rate at which prawns attempt to enter increases, but at a diminishing pace (Figure 5). Second, as the number of prawns in the trap increases, those attempts are less likely to be successful (Figure 6). Two caveats should be kept in mind. There was high variability of catch rates across deployments, possibly driven by environmental and habitat factors that went undetected by our camera apparatus. In addition, our outside-trap densities did not represent ‘true’ density, in part because individual prawns were not marked and could have been counted multiple times as they exited and re-entered the video

frame. Nevertheless, using the best available data, we have shown that the catchability of spot prawns declines with increasing prawn density in the trap (Figure 7).

The assumption that CPUE is proportional to population size is only true if catchability is constant or predictable [Erisman et al., 2011]. Our study demonstrates that the catchability of prawns with traps depends on ambient (near-trap) abundance as well as the number of prawns the trap has accumulated. Both traps and trawls can produce lower CPUE with longer soaks, and researchers have assumed that this effect is, in part, due to saturation [Fatih Can and Demirci, 2004; Boutillier and Sloan, 1987]. The shape of the relationship between catchability and density is rarely described [Bacheler et al., 2013]. Our results could provide the first step towards estimating how many prawns remain outside the trap given the catch produced by a trap – an important factor in understanding the ecological impact of prawn trapping.

The relatively small number of observed exits by prawns in traps was noteworthy as trap exits play an important role in determining saturation points in other fisheries. For example, in traps designed to catch black sea bass (*Centropristis striata*), the entry and exit rates of fish became equal, causing the traps to saturate, within 100 min of camera-equipped traps being deployed [Bacheler et al., 2013]. We did not observe saturation in prawn traps, presumably because ambient densities were too low to reach this point in the amount of time we were able to record. Our traps were deployed after the conclusion of the commercial prawn fishery, when stocks

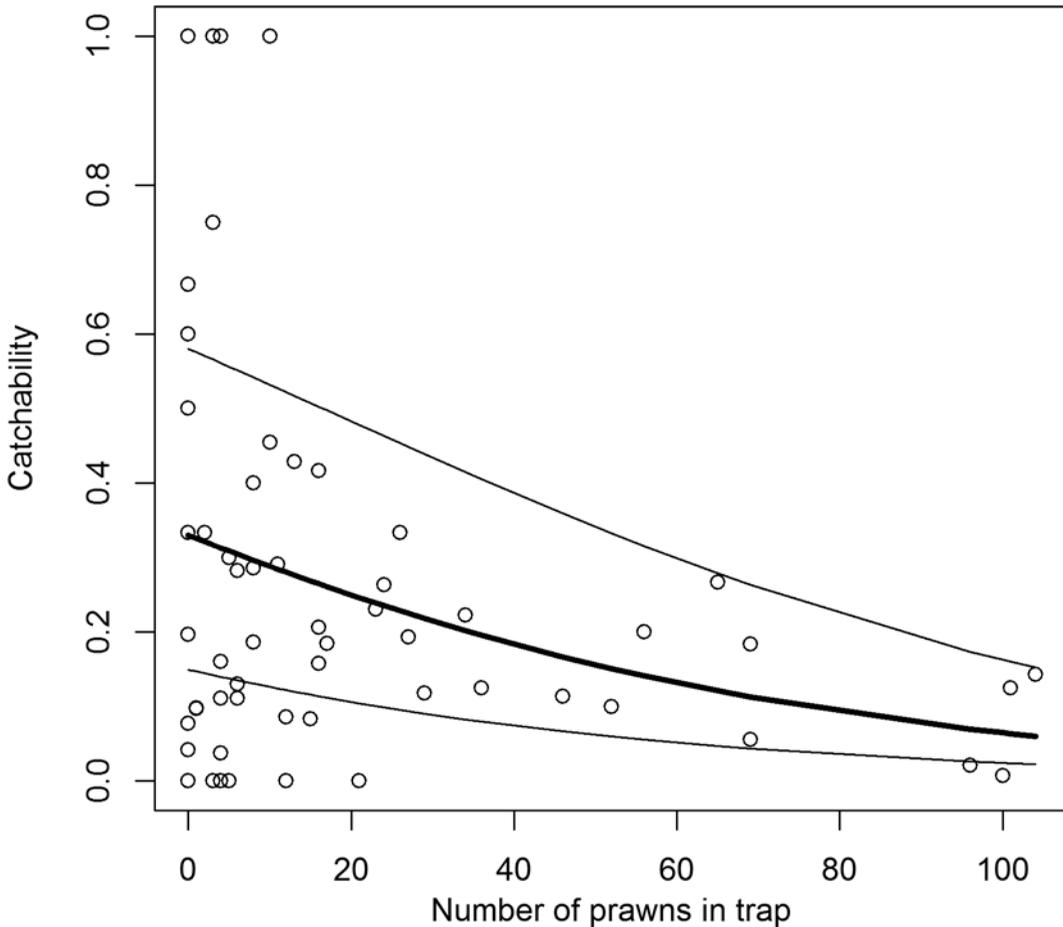


Figure 7: Catchability of spot prawns in a given hour in relation to the number of prawns in a trap at the start of that hour. Catchability is the likelihood that a prawn that has approached a trap will successfully enter the trap in an hour of trap deployment. The thick black line represents the predicted line of best fit and the thin lines are 95% confidence intervals.

were already depleted, and our final catch rates were lower than what would be typical of a commercial trap deployment (Favaro, personal observation). The final numbers of prawns retained when the gear was retrieved were often different from the number of prawns observed at the end of the video (Figure 4B), and the magnitude and direction of these differences were not consistent. In four of the 13 deployments, the final catch was less than the number of prawns observed in the trap, suggesting that exits occur in the latter part of the soak or when the gear is

being retrieved. It is likely that a decline in final catch would occur as a result of small (sublegal-sized) prawns falling through mesh during gear hauling, but our apparatus would not have recorded these events. An additional possibility is that predators entered the trap and consumed prawns. On four occasions across our videos, we observed quillback rockfish (*Sebastes maliger*) attempt to consume prawns, and in one of these occasions the fish did so inside the trap. While these prawns escaped predation, fish retrieved in the traps commonly showed evidence of

having consumed a prawn (Favaro, personal observation). Further investigation into whether final catch rates are shaped by exits, predation, or both is therefore warranted.

Some of the behaviours we observed in prawn traps differed from those reported for lobsters and crabs, which have also been studied in-situ using video techniques [Jury et al., 2001; Barber and Cobb, 2009; Watson and Jury, 2013]. American lobster (*Homarus americanus*) and Dungeness crab (*Metacarcinus magister*) have both been observed physically guarding trap entrances, using their bodies to prevent other individuals from entering [Jury et al., 2001; Barber and Cobb, 2009]. The outcome of agonistic behaviour in crabs and lobsters is often determined by the physical superiority of individuals [Kravitz and Huber, 2003]. By contrast, we did not observe prawns blocking entrances nor did we observe discrete clusters of prawns inside the traps (as has been noted with Dungeness crab [Barber and Cobb, 2009]). Instead, prawns positioned themselves somewhat uniformly throughout the trap, with constant sweeping motion of their first and second antennae (see Video 2 in Appendix).

The density-dependent catchability of prawns could have management implications. The British Columbia spot prawn fishery is managed using an escapement-based “spawner index,” where fishery areas are closed when the average catch-per-trap reaches a target determined by managers [Boutillier and Bond, 2000]. This threshold is calculated using catch data and does not explicitly consider the dynamics of prawn traps in-situ [Smith, 2013]. The current management model appears

appropriate at the scale of the fishery as catch has been relatively stable over time [DFO, 2011]. However, at the scale of each trap, our results suggest that prawn traps may have the potential to produce local depletions of prawns. When few prawns approached the trap in a given hour, a greater proportion of these prawns attempted to enter than when approach rates were higher. In addition, when traps were empty, the majority of entry attempts were successful, and as traps filled, the proportion of attempts that were successful diminished. Therefore, when traps are deployed in a depleted area (as would be likely to occur near the closure of the fishery), they are likely taking a greater proportion of the prawns available in the vicinity of the trap. Importantly, our conclusions are tempered by three factors that require further investigation. First, our observations cover only the first eight hours of each deployment, so the dynamics may change substantially (e.g., exits become more common) later in the deployment. Second, the effective area of prawn traps – i.e., the area around traps where prawns are influenced by the presence of fishing gear [Walter et al., 2007] – is not known. Third, the length of the videos precluded us from effectively investigate circadian processes, which may be important in understanding final catch. Further research into the range, intensity, and attractive properties of prawn trap bait plumes would be helpful in understanding the ecological impact of traps at depth.

Our study represents the first contribution to understanding the catch dynamics that occur in and around prawn traps in-situ. Our measure of catchability focused strictly on prawns

observed in the immediate vicinity of deployed traps, which may or may not approximate larger-scale density. Future research should examine the entire 24 hour deployment to determine saturation points of these traps and the mechanism by which saturation is achieved.

ACKNOWLEDGMENT

Thank you to Corinna Favaro and Vin Fogarty for assistance with fieldwork. Joyce Chan, Rachel Charish, Megan Cornall, Tina Dancau, Corinna Favaro, Angela Fortune, Chloe Hemsworth, Leslie Hurteau, Amy Lam, Benny Li, Evelyn Lo, Laura McArthur, Colin McCune, Kelsey Pailis, Karandeep Randhawa, Meghan Ray, Azim Shariff, Andrew Thomas, Byron Vallis, and Ryan Van Der Merwe contributed to video analysis. Ocean Quest Dive Centre provided dive lights used for video work and Sewell's Marina provided moorage for Simon Fraser University's research vessel *C.J. Walters*. We thank Michael P. Beakes for valuable feedback on the manuscript. This project was funded by a Natural Science and Engineering Council of Canada (NSERC) scholarship to Brett Favaro, NSERC operating grants to Isabelle M. Côté and Stefanie D. Duff, and grants provided by the Pacific Prawn Fishers Association, the Ocean and Marine Fisheries Branch of the British Columbia Government, and the Mitacs Accelerate program.

REFERENCES

- Arreguin-Sanchez, F. [1996]. *Catchability: a key parameter for stock assessment*. Reviews in Fish Biology and Fisheries, Vol. 6, pp. 221-242.
- Bacheler, N.M.; Schobernd, Z.H.; Berrane, D.J.; Schobernd, C.M.; Mitchell, W.A.; and Geraldi, N.R. [2013]. *When a trap is not a trap: converging entry and exit rates and their effect on trap saturation of black sea bass (*Centropristis striata*)*. ICES Journal of Marine Science, Vol. 70, No. 4, pp. 873-882.
- Barber, J.S. and Cobb, J.S. [2009]. *Qualitative observations of Dungeness crabs, Cancer magister, in and around traps: evidence of resource guarding and clustering*. Marine and Freshwater Behaviour and Physiology, Vol. 42, pp. 135-146.
- Bolker, B.M.; Brooks, M.E.; Clark, C.J.; et al. [2009]. *Generalized linear mixed models: a practical guide for ecology and evolution*. Trends in Ecology and Evolution, Vol. 24, pp. 127-135.
- Boutillier, J.A. and Bond, J.A. [2000]. *Using a fixed escapement strategy to control recruitment overfishing in the shrimp trap fishery in British Columbia*. Journal of Northwest Atlantic Fishery Science, Vol. 27, pp. 261-271.
- Boutillier, J.A. and Sloan, N.A. [1987]. *Effect of trap design and soak time on catches of the British Columbia prawn (*Pandalus platyceros*)*. Fisheries Research, Vol. 6, pp. 69-79.
- British Columbia Ministry of Agriculture [2012]. *British Columbia seafood industry year in review (2011)*. Retrieved from www.env.gov.bc.ca/omfd/reports/Seafood-YIR-2011.pdf.
- Crecco, V. and Overholtz, W.J. [1990]. *Causes of density-dependent catchability for Georges Haddock *Melanogrammus aeglefinus**. Canadian Journal of Fisheries and Aquatic Sciences, Vol. 47, pp. 385-394.
- DFO [2011]. *Integrated fisheries management*

- plan – prawn and shrimp by trap, May 1, 2011, to April 30, 2012.* Fisheries and Oceans Canada.
- Erisman, B.E.; Allen, L.G.; Claisse, J.T.; Pondella, D.J.; Miller, E.F.; and Murray, J.H. [2011]. *The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations.* Canadian Journal of Fisheries and Aquatic Sciences, Vol. 68, pp. 1705-1716.
- Fatih Can, M. and Demirci, A. [2004]. *Effect of towing duration on the catch per unit of swept area (CPUE) for lizardfish, Saurida undosquamis (Richardson, 1848), from the bottom trawl surveys in the Iskenderun Bay.* Turkish Journal of Fisheries and Aquatic Sciences, Vol. 4, pp. 99-103.
- Favaro, B.; Lichota, C.; Côté, I.M.; and Duff, S.D. [2012]. *TrapCam: an inexpensive camera system for studying deep-water animals.* Methods in Ecology and Evolution, Vol. 3, pp. 39-46.
- Favaro, B.; Rutherford, D.T.; Duff, S.D.; and Côté, I.M. [2010]. *Bycatch of rockfish and other species in British Columbia spot prawn traps: preliminary assessment using research traps.* Fisheries Research, Vol. 102, No. 1-2, pp. 199-206.
- Godø, O.R.; Walsh, S.J.; and Engås, A. [1999]. *Investigating density-dependent catchability in bottom-trawl surveys.* ICES Journal of Marine Science, Vol. 56, pp. 292-298.
- Ilhde, T.F.; Hoenig, J.M.; and Frusher, S.D. [2008]. *An index-removal abundance estimator that allows for seasonal change in catchability, with application to southern rock lobster Jasus edwardsii.* Transactions of the American Fisheries Society, Vol. 137, No. 3, pp. 720-735.
- Jul-Larsen, E.; Kolding, J.; Overå, R.; Nielsen, J.R.; and van Zwieten, P.A.M. [2003]. *Management, co-management, or no management? Major dilemmas in southern African freshwater fisheries.* FAO Fisheries Technical Paper 426/2.
- Jury, S.H.; Howell, H.; O'Grady, D.F.; and Watson, W.H. [2001]. *Lobster trap video: in-situ video surveillance of the behaviour of Homarus americanus in and around traps.* Marine and Freshwater Research, Vol. 52, pp. 1125-1132.
- Kotwicki, S.; Iannelli, J.N.; and Punt, A.E. [2014]. *Correcting density-dependent effects in abundance estimates from bottom-trawl surveys.* ICES Journal of Marine Science, Vol. 71, No. 5, pp. 1107-1116.
- Kravitz, E.A. and Huber, R. [2003]. *Aggression in invertebrates.* Current Opinion in Neurobiology, Vol. 13, pp. 736-743.
- Paloheimo, J.E. and Dickie, L. [1964]. *Abundance and fishing success.* Rapports et Proces Verbaux, Vol. 155, pp. 152-163.
- Phillips [2007]. Technical datasheet DS25, power light source Luxeon Emitter.
- R Core Team [2013]. *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. Version 3.0.2.
- Renchen, G.F.; Pittman, S.J.; and Brandt, M.E. [2012]. *Investigating the behavioural responses of trapped fishes using underwater video surveillance.* Journal of Fish Biology, Vol. 81, pp. 1161-1625.
- Rutherford, D.T.; Fong, K.; and Nguyen, H. [2010]. *Rockfish bycatch in the British Columbia commercial prawn trap fishery.* DFO Canadian Science Advisory Secretariat Research Document 2009/109:25.
- Rutherford, D.T.; Nguyen, H.; and Boutillier,

- J.A. [2004]. *Assessment and management of spot prawn Pandalus platyceros along the British Columbia coast*. Journal of Shellfish Research, Vol. 23, pp. 658-659.
- Smith, M. [2013]. *Trapped by uncertainty? A decision framework for evaluating escapement-based management procedures for the spot prawn (Pandalus platyceros) fishery in Howe Sound, BC*. M.RM thesis, Simon Fraser University, Burnaby, British Columbia.
- Stoner, A.W. [2004]. *Effects of environmental variables on fish feeding ecology: implications for the performance of baited fishing gear and stock assessment*. Journal of Fish Biology, Vol. 65, pp. 1445-1471.
- Venables, W.N. and Ripley, B.D. [2002]. *Modern applied statistics with S*. Fourth Edition, Springer, New York, ISBN: 0-387-95457-0.
- Walter, J.F.; Hoenig, J.M.; and Gedamke, T. [2007]. *Correcting for effective area fished in fishery-dependent depletion estimates of abundance and capture efficiency*. ICES Journal of Marine Science, Vol. 64, No. 9, pp. 1760-1771.
- Ward, H.G.M.; Askey, P.J.; and Post, J.R. [2013]. *A mechanistic understanding of hyperstability in catch per unit effort and density-dependent catchability in a multistock recreational fishery*. Canadian Journal of Fisheries and Aquatic Sciences, Vol. 70, pp. 1542-1550.
- Watson, W. and Jury, S.H. [2013]. *The relationship between American lobster catch, entry rate into traps and density*. Marine Biology Research, Vol. 9, pp. 59-68.
- Wilberg, M.J.; Thorson, J.T.; Linton, B.C.; and Berkson, J. [2009]. *Incorporating time-varying catchability into population dynamic stock assessment models*. Reviews in Fisheries Science, Vol. 18, No. 1, pp. 7-24.
- Winters, G.H. and Wheeler, J.P. [1985]. *Interaction between stock area, stock abundance, and catchability coefficient*. Canadian Journal of Fisheries and Aquatic Sciences, Vol. 42, pp. 989-998.
- Zuur, A.F.; Ieno, E.N.; Walker, N.; Saveliev, A.A.; and Smith, G.M. [2009]. *Mixed effects models and extensions in ecology with R*. Springer, New York, ISBN: 978-0-387-87458-6.

APPENDIX

- Video 1 [2014]. *Demonstration of data collection methodology*. Available online at http://figshare.com/articles/Video_S1_Demonstration_of_data_collection_methodology_/1018706.
- Video 2 [2014]. *Antenna sweeping behaviour of spot prawns*. Available online at http://figshare.com/articles/Video_S2_Antenna_sweeping_behaviour_of_spot_prawns_/1018707.