

Trawl stress and escapee vulnerability to predation in juvenile walleye pollock: Is there an unobserved bycatch of behaviorally impaired escapees?

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ABSTRACT: Recent studies suggest that mortality of undersized fishes escaping through trawl codends may range from 0 to 100%, with mortalities of 10 to 30% being common. These values may be low, as they do not account for fishes which become behaviorally compromised by their passage through the trawl and ultimately succumb to predators. The goal of this study was to simulate in the laboratory the stressors associated with trawl passage and determine if they degrade the behavioral capabilities of juvenile walleye pollock *Theragra chalcogramma* to avoid predation. In the first of 2 experiments, groups of Age 1 yr+ walleye pollock were subjected to 3 treatments: (1) controls: no stressor; (2) swim/escape: forced swimming for 90 min at 0.33 m s⁻¹ in a towed net, followed by escape through 8 cm square mesh; (3) swim/crowd/escape: forced swimming followed by 3 min of crowding, followed by escape. To evaluate the effect of these treatments on pollock behavior, a sablefish *Anoplopoma fimbria* (48 to 53 cm) was placed in an observation arena with the group and pollock anti-predator behavior was quantified. Beginning immediately after simulated trawling and for up to 24 h afterwards, pollock exposed to both trawl-stressor treatments were less likely to avoid the predator than controls, allowing it to approach closer. They were also less able to form a cohesive shoal, and in the case of the swim/crowd/escape treatment, swam more slowly than control fish. To determine if trawl-stressed fish are more vulnerable to predation, in a second experiment I mixed control and swim/crowd/escape pollock together and then subjected them to predation by a 48 to 60 cm lingcod *Ophiodon elongatus*, observing the behavior and enumerating the number of pollock consumed in each treatment. Lingcod concentrated attacks upon solitary individuals or those straggling behind the shoal, were more likely to lunge at pollock that did not move away when approached, and were more successful the closer the pollock at lunge initiation. As a result, trawl-stressed pollock were consumed in greater numbers than controls. On the basis of these results, it is reasonable to expect that juvenile walleye pollock passing through trawls suffer behavioral deficits, subjecting them to elevated predation risk. If this is a generic effect, these results suggest that there may be a significant bycatch associated with many commercial trawl fisheries which is generally unrecognized, unmeasured, and unaccounted for in current stock-assessment models.

KEY WORDS: Bycatch · Predation · Stress · Trawl · Walleye Pollock · Behavior

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INTRODUCTION

The bycatch of undersized and nontarget fishes by trawl gear is increasingly perceived by fisheries man-

agers, ecologists, conservationists and society at large, as an undesirable consequence of commercial fishing (Alverson & Hughes 1996, Agardy 2000). In its broadest sense, the bycatch includes both an observed component (i.e. undersized fishes and nontarget species that arrive on deck and are either kept or discarded) and an unobserved component, i.e. fishes that never

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appear on deck, but die after encountering and escaping the fishing gear (Crowder & Murawski 1998). To reduce the observed bycatch, many trawl fisheries have adopted larger mesh sizes, allowing smaller fishes to escape from the codend. While larger meshes, square mesh, escape panels and bycatch-reduction-devices can effectively reduce the observed bycatch (Tumilty et al. 1998), if fishes escaping trawls do not survive, they simply become part of the unobserved bycatch.

Mortality of fishes that pass through trawls is problematic for scientists and managers because it is unmeasured and infrequently incorporated into stock-assessment calculations (Chopin & Arimoto 1995, Alverson & Hughes 1996, Crowder & Murawski 1998). However, recent studies utilizing cages to surround the trawl codend and retain escapees (Lehtonen et al. 1998) demonstrate that mortality can be extensive and vary greatly between species. For example, the Baltic cod *Gadus morhua* displayed a 10 to 14 d mortality of only 1% after passing through a bottom trawl equipped with 95 mm square-mesh escape panels (Suuronen et al. 1996a), while 2 other gadids, the haddock *Melanogrammus aeglefinus* and the whiting *Merlangius merlangus*, displayed 60 d mortalities of 11 to 52% and 14 to 48%, respectively, after escaping through various codend meshes ranging from 70 to 110 mm (Sangster et al. 1996). The herring *Clupea harengus* had 7 d mortalities ranging from 72% for small fish (<12 cm) to 30% for larger fish (12 to 17 cm) (26 and 36 mm stretch-mesh codends: Suuronen et al. 1996b), and the vendace *Coregonus albula* 50% mortality (24 mm square-mesh codend: Suuronen et al. 1995). However, these mortality estimates are probably low, as they ignore sublethal effects upon fish behavior that may influence survival. In these studies, the cage which retains escapees is detached from the trawl and either rests on the seafloor or is suspended in the water column, with fish survival monitored over time. While holding fishes captive for monitoring, the cage also has the unintended consequence of protecting them from some of the rigors of their environment, most notably predators.

Increased vulnerability to predation may be an important yet unobserved source of mortality for fishes escaping trawl gear. The stressors involved and their influence upon fishes probably varies with fish size and species, type of trawl gear, tow speed and duration, catch size, and oceanographic conditions such as temperature and illumination. Yet, diver and video observations suggest a common scenario. Fishes encountering trawls swim so as to maintain their position ahead of or within the gear (Wardle 1983, Suuronen et al. 1997b). As they tire, they gradually fall farther back towards the codend. Severe exhaustion may

result in decreased muscle and liver glycogen levels (Suuronen et al. 1996b, Turunen et al. 1996) as well as osmotic imbalance (Turunen et al. 1996). Also, the fishes may periodically strike other fishes, debris and the meshes, causing abrasions and scale loss (Sangster et al. 1996, Suuronen et al. 1996a,b, Broadhurst et al. 1997). As a fish approaches the catch ball at the rear of the codend, it may be further crowded by other fish and debris. Lastly, to escape, a fish must swim through an opening in the mesh, which may also result in abrasion and scale damage. These more obvious physical injuries and exhaustion may induce a subsequent cascade of biochemical and physiological changes that can directly modify innate and/or learned behavioral responses to environmental stimuli (reviewed by Schreck et al. 1997). While short-term modification of feeding and aggressive motivation may have little effect upon survival, even a brief hiatus in predator detection, avoidance, schooling and shelter seeking could have profound implications for survival.

I conducted experiments on the effect of simulated trawl passage upon the anti-predator behavior of juvenile walleye pollock *Theragra chalcogramma*. This species supports a large commercial fishery in Alaskan waters, with more than 10^6 t taken in 2000 (NOAA; see www.fakr.noaa.gov/2000/bsa00b.txt). This mid-water fishery targets predominantly 3 yr and older fish (>30 cm total length). Although younger fish tend to occur at shallower depths than the older fish (McKelvey 1996), their similar distribution suggests that substantial numbers may pass through codends unnoticed. Indeed, many fishers have switched to larger and/or square mesh codends to reduce their catch of undersized/unmarketable fish. Yet, mortality of undersized walleye pollock exiting codend intermediates through 93 mm square mesh escape panels may be 36 to 68% (Erickson et al. 1999). Therefore, a low retention of fish < 20 cm (Fritz 1996) affords little assurance that they are not being impacted. Similarly, various other Alaskan trawl fisheries for both flatfishes and roundfishes probably encounter juvenile walleye pollock.

I present the results of 2 experiments designed to address the possible effects of trawl passage upon juvenile walleye pollock. In the first, I sought to determine what aspects of behavior might be impaired. I exposed pollock to stressors designed to simulate passage through a trawl and then observed their behavior in the presence of a threatening, but non-lethal predator. In the second, I sought to determine whether trawl-induced stress might increase escapee vulnerability to predation. Fish having undergone a simulated trawl passage were combined with control fish and then exposed to a lethal predator, allowing comparison of their relative mortality.

MATERIALS AND METHODS

Fish collection and maintenance. Juvenile walleye pollock *Theragra chalcogramma* were collected from Puget Sound, Port Townsend, Washington, USA, during June 1999 and transported back to the laboratory in Newport, Oregon, USA. Two additional fish species were collected for use as predators: the sablefish *Anoplopoma fimbria* and the lingcod *Ophiodon elongatus*. Sablefish were captured as juveniles during April 1998, while lingcod were captured as adults during April and May 1999, both off Newport. Each species of fish progressed through a range of holding tank sizes as they grew, but during the last several months prior to experimentation walleye pollock were kept in 3700 l circular tanks (2.3 m diameter, 0.9 m depth), while sablefish and lingcod were kept in 25 400 l circular tanks (3 m diameter, 0.9 m depth). Holding tanks were provided with a continuous flow of seawater (salinity range 28 to 33‰, temperature range 9 to 11°C). Walleye pollock and sablefish were fed pelletized food daily for the first 6 mo, after which the walleye pollock continued on pellets thrice weekly and the sablefish received thawed squid *Loligo* sp. twice weekly. Rations for pollock and sablefish were periodically adjusted to promote growth. Lingcod were fed once weekly on a maintenance ration of assorted live or thawed baitfish.

Nonlethal predation experiment. The behavioral response of juvenile walleye pollock to a nonlethal but threatening sablefish predator was quantified after sequential exposure to stressors simulating those associated with entrainment and escape from a trawl. The experiment incorporated 3 treatments: swim/crowd/escape, swim/escape and control. Six replicates of each treatment were conducted in 6 replicate 25 400 l circular arenas (3 m diameter, 0.9 m depth) monitored by overhead video cameras. Arenas received a continuous flow of 9 to 11°C seawater and were illuminated by fluorescent lighting ($4 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ at the water surface). For controls, groups of 6 walleye pollock were placed into the arenas 18 h prior to experimental procedures, while for the 2 trawl-stress treatments, 7 pollock were placed in arenas, the extra fish was included to allow for occasional deaths. The swim/crowd/escape trials simulated sustained swimming, followed by crowding prior to escape through codend meshes. Walleye pollock were dipnetted from their arenas using a fine nylon-meshed net and transferred by bucket to a net-towing apparatus (see Olla et al. 1997 for complete description). Briefly, the apparatus consists of a 16 000 l circular tank (4.5 m diameter, 1.0 m depth) in which nets are towed in a circular path around the tank's perimeter. The tow net consisted of a rigid plastic cylinder (30 cm diameter, 35 cm length)

attached to a 60 cm sleeve of 3.2 cm mesh (diagonal stretch measured) knotted near its end (Fig. 1A). The other end of the cylinder was fitted with a removable cover made from a rigid plastic ring covered with 3.2 cm mesh. Pollock were gently poured from the bucket into the submerged tow net, the cover was secured, and the net was towed around the tank with the water entering through the cover at the front of the cylinder and exiting through the net sleeve to the rear. While towed, the fish typically maintained position in the rear of the cylinder and/or in the front of the mesh sleeve. In commercial trawls towed at 1.0 to 2.6 m s^{-1} (2 to 5 knots), fishes probably experience codend water velocities of 0.3 to 0.8 m s^{-1} , assuming water velocity in the codend is reduced to 30% of the tow speed (Thiele et al. 1997). In preliminary trials it became apparent that, while many fish would swim indefinitely at the higher of these speeds, other fish would not. This may have been related to the confined nature of the tow apparatus: in a larger tow net Olla et al. (1997) found that walleye pollock of comparable size were able to swim for over 3 h at 0.7 m s^{-1} . While fish that tire or fail to swim in a trawl can fall back and potentially pass through the mesh of the codend, in my apparatus these fish became pinned against the mesh and typically died if they remained there for more than 15 min, as judged by cessation of opercular movement. Therefore, I adopted a tow speed that forced fish to swim at 0.33 m s^{-1} , a pace at which most fish would swim. Nonetheless, even at this speed, in some groups 1 fish, or less frequently 2, still failed to swim, thus the addition of an extra fish in trawl-stress groups. How long individual fish swim in trawls is unknown, so I arbitrarily chose a swim duration of 90 min. At the end of this 90 min the cover of the tow net was detached and any

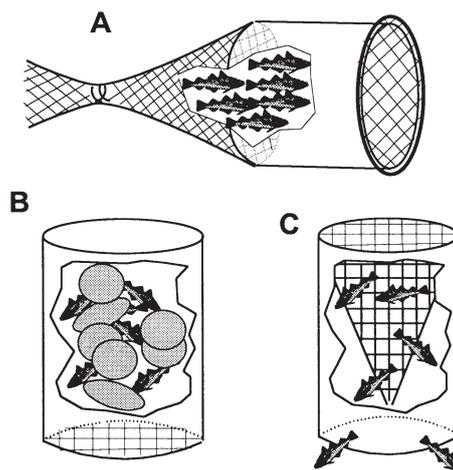


Fig. 1. (A) Forced-swimming apparatus; (B) crowding apparatus; (C) codend escape apparatus

fish that had failed to swim were removed: these were always dead. If there were no non-swimmers, a single fish was haphazardly removed. The remaining fish were gently poured into the crowding apparatus (Fig. 1B) where they were subjected to a 3 min period of 'crowding', while being transferred back to their arena. This apparatus consisted of a 19 l bucket with a soft nylon 3 mm-mesh bottom situated in a larger container filled with 10°C seawater. As soon as the fish were placed into the bucket, 24 balloons, filled with water to a diameter of 10 to 13 cm, were added by hand. Then, a second bucket with a mesh bottom was nested into the first and weighted down so that the fish, while still in water, were confined to the spaces between the spherical balloons. Again, it is unknown how long fish will endure crowding at the front of an accumulating catch ball before they effect their escape, so I arbitrarily chose to subject the fish to 3 min of crowding, after which the balloons were removed and the fish were gently poured from the bucket into the codend escape cone (Fig. 1c), which was suspended in the arena. The escape cone was made of knotless square mesh suspended in a rigid plastic cylinder (40 cm diameter by 54 cm; Fig. 1C). The mesh, made of 9 mm diameter poly-twine, was held in square configuration, with individual openings measuring 4.3 cm along the side (6.0 cm diagonal). This mesh is commonly utilized in the Alaskan mid-water trawl fishery as a means of reducing the landing of undersized fish. The cylinder and cone were gently agitated in the water until all fish had 'escaped' through the mesh into the arena. In all cases, it took less than 30 s for all the fish to make their escape.

The swim/escape trials simulated sustained swimming followed by immediate escape. These trials were conducted exactly like the swim/crowd/escape trials, except the walleye pollock were transferred in a bucket from the swimming apparatus to the codend escape cone, without the crowding sequence. For control trials the juveniles remained in the arena. Six replicate trials of each treatment were conducted. During each of 2 successive weeks, 3 swim/crowd/escape trials and 3 control trials were conducted concurrently. In the week that followed, all 6 swim/escape trials were conducted concurrently. In each of 2 swim/escape trials and 2 swim/crowd/escape trials, a single fish failed to swim, became pinned against the mesh and died. In 2 swim/escape trials and 1 swim/crowd/escape trial, 2 fish died in this manner. Therefore, while each of the controls utilized 6 fish, 2 of the swim/escape and 1 of the swim/crowd/escape trial groups contained only 5 fish during the subsequent observations of behavior.

Juvenile walleye pollock faced 4 predator challenges, the first as they escaped into the arena, the sec-

ond 2 h later, then 1 and 3 d later. For each challenge a single sablefish (48 to 53 cm total length) was dipnetted into the arena and then dipnetted back out 20 min later. In their holding tanks, the sablefish were kept at 6°C, approximately 4°C below the temperature in the arenas. As a result of the temperature change they experienced upon transfer into the arenas the sablefish made no overt attempts to consume the juvenile pollock, although they swam continuously around the perimeter of the arena until removed. In 1 instance, a sablefish settled to the arena bottom and remained motionless for 1 min before it commenced swimming.

One, 2, 3 and 6 d after simulated net stresses, each group of fish was given pelletized food over a 3 min period and the number of fish in each group which consumed at least 1 pellet was recorded. Several hours after the last feeding (day 6) the fish were removed from the arena, weighed, measured, and then transferred to 3700 l holding tanks (2.3 m diameter, 0.9 m depth), where they were segregated by experimental treatment and monitored daily for mortality over 4 wk. Fish total length ranged from 171 to 216 mm, with no differences in mean length or weight between treatments: mean length (SE) = control 192.6 (1.8), swim/escape 194.0 (1.8), swim/crowd/escape 193.7 (1.4), $F = 0.19$, $df = 2$, $p = 0.824$; mean weight (SE) = control 54.5 g (1.6), swim/escape 57.1 (1.9), swim/crowd/escape 56.4 (1.4), $F = 0.67$, $df = 2$, $p = 0.516$.

From videotapes, for each predator challenge (0, 2, 24 and 72 h), I digitized the swim path of each walleye pollock in each group, as well as the predator, for a 2 min period. This period began 1 min after the predator was introduced. I calculated the average swimming speed for both predator and prey over the 2 min period. This data set also provided a time series of 2-dimensional spatial coordinates describing the position of each fish, relative to the others, at 0.5 s intervals. I calculated the distance between each walleye pollock and its nearest neighbor (Clark & Evans 1954) and the distance between each walleye pollock and the predator for each interval. From the distance-to-predator data I determined the closest-approach distance, i.e. the smallest distance between each pollock and the predator during the 2 min period. Nearest-neighbor and distance-to-predator data were averaged over the 2 min period for each fish and then averaged by group. Swim speed and closest-approach distance were averaged for each group. Characterizing 3-dimensional spatial relationships using only 2-dimensional data has obvious shortcomings; however, both walleye pollock and sablefish tended to swim predominantly near the water surface, so it is my impression that the distance measurements I derived were not greatly affected. Furthermore, there were no obvious differences in fish vertical distribution between treatments. Therefore, I

assume any errors introduced through 2-dimensional measures were comparable across treatments. Data were homoscedastic, as indicated by Bartlett's test of equal variance (Sokal & Rohlf 1969), and were analyzed by repeated-measures ANOVA (Hicks 1982). Where statistical effects were significant ($p < 0.05$), *a posteriori* multiple comparisons were conducted utilizing Ryan's *Q*-test (Day & Quinn 1989).

Lethal predation experiment. Equal numbers of control and swim/crowd/escape walleye pollock were mixed together and then exposed to predation by a single lingcod to compare their relative vulnerability to predation. Four arenas were fitted with opaque plastic vertical partitions which divided each arena in half. The partitions could be raised completely out of the arenas using wires running through pulleys attached to the ceiling. In all respects, including color, position of inflows and drains, water temperature and lighting, these partitioned arenas were identical. Eighteen hours prior to initiation of experimental procedures, groups of 5 walleye pollock were measured for total length and then had either the upper or lower tip of their caudal fin clipped to allow for identification of control versus stress groups. Only a small amount of fin was removed, and this was unlikely to affect fish performance; in addition, both trawl-stress and control fish received clips, which were alternated for each trial, i.e. controls that received upper caudal clips in one trial received lower clips in the next trial, and vice versa. With the partitions down, control fish were placed into one half of an arena, while fish to be stressed were placed in one half of a second arena. In each case, a single lingcod (48 to 60 cm) was placed on the opposite side of the partition. The lingcod had not been fed for 10 to 14 d. Water entered the arena through an inflow pipe on the predator side of the arena and exited via an overflow fitting on the prey side. The partition had numerous 1.2 cm holes that allowed water movement from one side to the other.

The next morning, the stress group was dipnetted from their arena and put through the same swim/crowd/escape procedure described for the nonlethal experiment. Rather than being put back into their arena, the stress fish were instead allowed to 'escape' into the arena with the control fish. As a result, the arena now contained 5 stressed and 5 control fish on one side of the moveable partition, with the predator on the other side. Immediately after the stress fish were released, the lights in the room were turned off for approximately 30 s and the partition was raised allowing the predator to mingle with the control and stressed walleye pollock, then the lights were turned back on. The trials were continued for 30 min or until the lingcod had consumed 5 pollock, whichever came first. The walleye pollock were then dipnetted out of

the arena and enumerated by fin clip to determine the number of control and trawl-stressed fish consumed. Seven replicate trials were conducted. Total fish length did not differ between treatments within any of the paired control/stress trials, or in the experiment as a whole (student's *t*-tests, $p > 0.05$ for each). Mortality data were analyzed using a 1-tailed sign test (Sokal & Rohlf 1969).

Overhead video recordings were made of each trial, and observations of the behavior of both pollock and lingcod recorded. Lingcod initially rushed around the arena in pursuit of the pollock until they made their first capture: no behavioral data were recorded during this period. After taking their first pollock, the lingcod all adopted a stalking strategy, whereby the lingcod would slowly approach a pollock; some stalks were abandoned, while others culminated in a lunge at the pollock. For stalks that culminated in a lunge, the distance between predator and prey at lunge initiation was recorded, while for stalks that were abandoned the closest approach between predator and prey was recorded. To determine whether the distance between the lingcod and its prey influenced whether or not a lunge was initiated, mean lunge and closest-approach distances were calculated for each trial and the resultant data set analyzed by a paired *t*-test (Sokal & Rohlf 1969). Similar calculations were made to determine whether successful lunges (i.e. the pollock was at least temporarily captured) were launched from a shorter distance than unsuccessful lunges.

RESULTS

Nonlethal predation experiment

Simulated trawl passage compromised juvenile walleye pollock anti-predator behavior in several tangible ways, with the magnitude of degradation greatest for fish exposed to the swim/crowd/escape treatment. First, these fish were lethargic, that is they swam slower than control fish (Fig. 2, Table 1), with the effect most acute during the first 2 h post-trawl, but still significant 24 h afterwards. During the first 2 h post-trawl, swim/crowd/escape fish often appeared distressed, swimming at an upward angle relative to the horizontal and repeatedly poking their snouts out of the water, indicating disorientation and/or swim bladder dysfunction. While not obviously distressed, swim/escape fish also tended to swim slower than controls, although this was only statistically demonstrable 24 h post-trawl. Second, both swim/crowd/escape and swim/escape fish were less responsive than control fish to predator movements during the first 2 h post-trawl. As the predator swam about the arena, the trawl-

passage fish were closer to the predator than the control fish (Fig. 3, Table 1). Although the predator never made overt attempts to capture walleye pollock, the control fish tended to stay on the opposite side of the

tank, while trawl-passage fish often appeared unaware of the predator's approach, in many instances allowing the predator to pass within several centimeters. This was apparent from closest-approach dis-

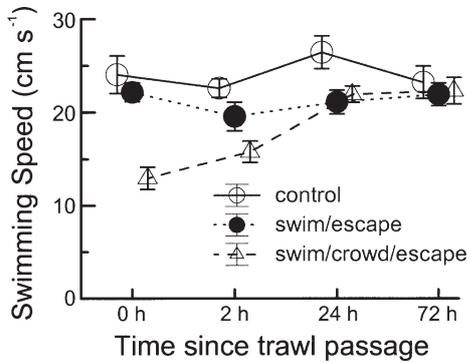


Fig. 2. *Theragra chalcogramma*. Mean swimming speed (\pm SE) of juvenile walleye pollock exposed to a sablefish predator (*Anoplopoma fimbria*) at times ranging from 0 to 72 h after simulated trawl passage

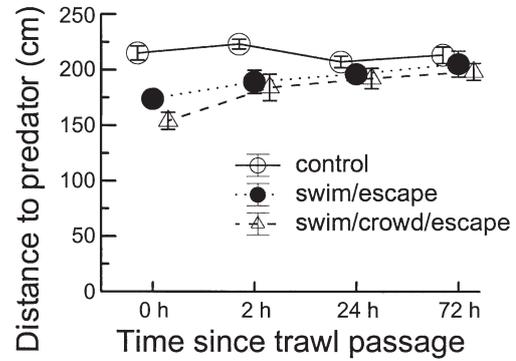


Fig. 3. *Theragra chalcogramma*. Mean distance (\pm SE) between juvenile walleye pollock and a sablefish predator at times ranging from 0 to 72 h after simulated trawl passage

Table 1. *Theragra chalcogramma*. Swim speed, distance from predator, closest approach distance and nearest-neighbor-distance analysis 0, 2, 24 and 72 h after simulated trawl passage. Min-dist-pred: minimum distance from predator; C: controls; S/E: swim/escape; S/C/E: swim/crowd/escape. Homogeneous subgroups of means are underlined

	df	SS	MS	F	p
Swim speed ANOVA					
Treatment	2	40672.9	20336.5	10.15	0.002
Treatment \times Replicate	5	30050.2	2003.35		
Time	3	20321.3	6773.76	7.73	0.000
Treatment \times Time	6	26013.9	4335.65	4.95	0.001
Treatment \times Time \times Replicate	45	39444.3	876.54		
0 h: <u>S/C/E</u> <u>S/E</u> C; 2 h: <u>S/C/E</u> <u>S/E</u> C; 24 h: <u>S/E</u> <u>S/C/E</u> C; 72 h: <u>S/E</u> <u>S/C/E/</u> C					
Distance-predator ANOVA					
Treatment	2	1372410	686205	11.16	0.001
Treatment \times Replicate	15	922712	61514.1		
Time	3	597172	199057	6.32	0.001
Treatment \times Time	6	496151	82691.9	2.63	0.029
Treatment \times Time \times Replicate	45	1416785	31484.1		
0 h: <u>S/C/E</u> <u>S/E</u> C; 2 h: <u>S/C/E</u> <u>S/E</u> C; 24 h: <u>S/E</u> <u>S/C/E</u> C; 72 h: <u>S/E/</u> <u>S/C/E</u> C					
Min-dist-pred ANOVA					
Treatment	2	1459191	729596	6.23	0.011
Treatment \times Replicate	15	1755917	117061		
Time	3	819447	273149	2.97	0.042
Treatment \times Time	6	448790	74798.3	0.81	0.566
Treat \times Time \times Replicate	45	4144213	92093.6		
Times combined: <u>S/C/E</u> <u>S/E</u> C					
Nearest-neighbor ANOVA					
Treatment	2	288109	144055	8.19	0.004
Treatment \times Replicate	15	263873	17591.6		
Time	3	105158	35052.8	4.01	0.013
Treatment \times Time	6	222962	37160.4	4.25	0.002
Treatment \times Time \times Replicate	45	39444.3	876.54		
0 h: C; <u>S/E</u> <u>S/C/E</u> ; 2 h: C; <u>S/E</u> <u>S/C/E</u> ; 24 h: C; <u>S/C/E</u> <u>S/E</u> ; 72 h: <u>S/E</u> C <u>S/C/E</u>					

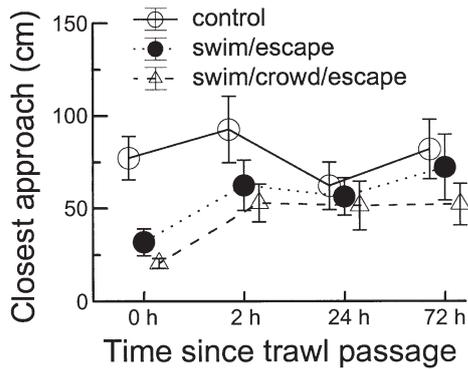


Fig. 4. *Theragra chalcogramma*. Mean closest approach (\pm SE) between juvenile walleye pollock and a sablefish predator at times ranging from 0 to 72 h after simulated trawl passage

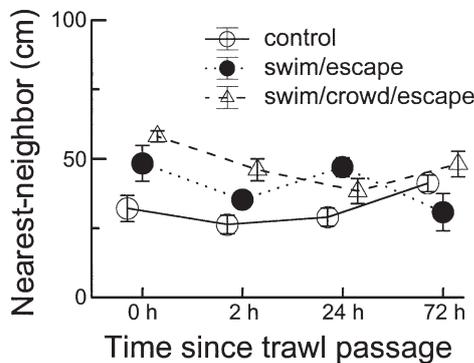


Fig. 5. *Theragra chalcogramma*. Mean nearest-neighbor distances (\pm SE) for juvenile walleye pollock exposed to a sablefish predator at times ranging from 0 to 72 h after simulated trawl passage

tances, which were approximately one third of those measured for control fish (Fig. 4). Although ANOVA indicated that closest-approach distances differed throughout the 72 h experiment (i.e. non-significant interaction in Table 1), from Fig. 4, I would infer that this effect was prominent for only the first post-trawl hour or so. Finally, just as trawl-passage fish were closer to the predator, so too were they less capable of shoaling. Statistical analysis (Table 1) and examination of Fig. 5 indicate that up to 24 h post-trawl, the trawl-passage fish maintained greater nearest-neighbor distances than control fish. Trawl-passage fish often splintered into smaller groups or swam solitarily, whereas control fish appeared more likely to maintain a single cohesive shoal.

Differences in juvenile walleye pollock behavior were not a result of variation in predator behavior. Predator swimming speed was relatively constant at approximately 30 cm s^{-1} and did not differ between treatments or over time (treatment: $F = 2.21$, $df = 2$, $p =$

0.116 ; time: $F = 1.63$, $df = 3$, $p = 0.190$; interaction: $F = 0.92$, $df = 6$, $p = 0.489$). In all trials, sablefish predators predominantly swam around the perimeter of the arenas, making only occasional forays across interiors.

Trawl-passage fish appeared to have recovered 72 h post-trawl, as I detected no differences between any of the treatment groups with respect to swim speed, distance from the predator or nearest-neighbor distances. Because fish remained in the arenas for 6 d after trawl-passage, I could not quantify scale loss or skin damage attributable to treatments. However, arena-side observations revealed a higher frequency of snout bruising among swim/crowd/escape fish (37%, $SE = 9$) compared to swim/escape (3%, $SE = 3$) and control (0%, Kruskal-Wallis $p < 0.001$) fish. On the first day after trawl passage, more of the control and swim/crowd/escape fish fed than did fish from the swim/escape treatment (control 94%, $SE = 4$; swim/crowd/escape 91%, $SE = 4$; swim/escape 65%, $SE = 4$; $F = 17.52$, $df = 2$, $p < 0.001$). On the 2nd, 3rd and 6th days there were no significant differences in feeding, with more than 83% (5 out of 6 fish) feeding in each treatment. There were no mortalities among juvenile walleye pollock, regardless of treatment, during the 6 d post-trawl in the arenas, or during the subsequent 4 wk in holding tanks.

Lethal predation experiment

As soon as the partition was raised and lights were turned on, lingcod charged the juvenile pollock, taking their first prey in an average of 18 s ($SD = 19$). Subsequently, the pollock were more wary and the lingcod adopted a stalking strategy entailing a slow approach towards an individual or group of pollock, sometimes culminating in a lunge. Lingcod appeared to stalk primarily those pollock which were not shoaling or were straggling behind a shoal. How close the lingcod was able to get to the pollock during the stalk determined whether a lunge was initiated. When the pollock moved away as the lingcod approached, the stalk was abandoned and the lingcod settled back to the bottom (38% of stalks). For these abandoned stalks, the mean closest approach between lingcod and pollock was 44.2 cm ($SE = 3.5$). However, when the stalk resulted in a lunge (62% of stalks), the mean distance between lingcod and pollock at lunge initiation was only 30.4 cm ($SE = 4.4$, paired $t = -2.55$, $df = 6$, $p = 0.043$). Fifty-one percent of lunges culminated in success (i.e. pollock were at least temporarily captured) and were initiated from a closer mean distance than were unsuccessful lunges (successful = 22.6 cm, $SE = 3.4$; unsuccessful = 38.5 cm, $SE = 6.6$; paired $t = 3.94$, $df = 6$, $p = 0.008$).

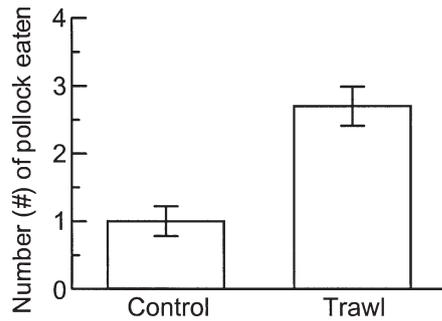


Fig. 6. *Theragra chalcogramma*. Mean number (\pm SE) of control and trawl-stressed walleye pollock consumed during 30 min encounters with a lingcod predator (*Ophiodon elongatus*). Trawl-stressed fish pollock were subjected to the swim/crowd/escape treatment

Trawl-stressed pollock were more vulnerable to predation than control fish (Fig. 6). In 6 of 7 trials, lingcod consumed more stressed than control pollock, while in 1 trial equal numbers of stressed and control fish were consumed (1-tailed sign test, $p = 0.016$).

DISCUSSION

In this study I subjected juvenile walleye pollock to 2 treatments simulating passage through a trawl. In both, the pollock resumed feeding several days afterwards and experienced no mortality over 5 wk. Therefore, I conclude that the stressors involved were, in and of themselves, nonlethal. However, both trawl-passage treatments produced measurable deficits in anti-predator behavior. Pollock from both treatments formed less cohesive shoals than controls, allowed the predator to make closer approaches, and in the case of the swim/crowd/escape treatment they were initially disoriented and more lethargic than control fish. Further, when pollock subjected to the higher of the 2 trawl-stress regimes were exposed to predation along with unstressed pollock, the trawl-stress fish experienced greater predation mortality. Taken together, these results indicate that juvenile walleye pollock passing through trawl codends may have their behavioral capabilities degraded and suffer elevated predation in the subsequent hours and/or days.

Were the stressors applied in this study reasonable and relevant compared to those experienced during actual trawling? Diver and video observations (Suuronen et al. 1996a,b, Olla et al. 2000) would suggest that the 'swim-crowd-escape' scenario captures the essence of what fish experience when passing through a codend. However, the magnitude of each stressor was, by design, scaled down to minimize mortality. Minimizing mortality was essential, since behavioral im-

pairment in fish already destined to die as a direct consequence of stress (as opposed to indirect behaviorally mediated predation) is of little consequence from either an ecological or population dynamics perspective. Rather, it is the behavior of individuals that would otherwise recover that is of interest. The stressors I utilized differed from real trawling in the following respects: (1) the 0.33 m s^{-1} swim speed was at the low end of the 0.3 to 0.8 m s^{-1} that walleye pollock probably experience in codends; (2) the walleye pollock were not exhausted, as they can swim at over twice this speed for over 3 h (Olla et al. 1997); (3) the crowding procedure did not subject the fish to the more extreme physical damage from collisions with debris, spines and calcified fin-rays, etc., that can accompany crowding in bottom trawls (Suuronen et al. 1997a,b); (4) during simulated codend escape, the pollock were not subjected to the turbulent shear forces experienced by fish escaping from actual codends (pers. obs.). Therefore, the entire stressor sequence utilized in this study probably simulated the minimum level of what walleye pollock and other fish experience in commercial gears (Suuronen et al. 1995, 1996b, Sangster et al. 1996). However, walleye pollock still experienced significant behavior impairment from these nonlethal stressors. Presumably actual trawl passage, which produces significant mortality in walleye pollock (Erickson et al. 1999), will also degrade behavior in the surviving escapees. Taken together, these factors suggest that the methodology utilized in this study constitutes a relatively conservative test of the hypothesis that trawl passage degrades walleye pollock behavior.

A variety of sublethal stressors, not unlike those experienced by trawl escapees, are known to compromise behavior and render fish more vulnerable to predation (see reviews by Mesa et al. 1994, Olla et al. 1997). Chinook salmon *Oncorhynchus tshawytscha* and coho salmon *O. kisutch* smolts stressed by handling (held out of water in a dipnet for 30 to 60 s) and then mixed with an equal number of control fish were consumed in greater numbers than controls by the lingcod *Ophiodon elongatus* (Olla & Davis 1989, 1992, Olla et al. 1995). Similarly, chinook salmon smolts stressed by either handling (simulating hatchery release) or agitation (simulating dam passage) were lethargic and more vulnerable than controls to predation by pike-minnows *Ptychocheilus oregonensis* (Mesa 1994). A host of other stressors including temperature shock (Coutant 1973, Webb & Zhang 1994), starvation (Herting & Witt 1967, Rice et al. 1987), disease (Mesa et al. 1998) and toxicants (Brown et al. 1985, Little et al. 1990) have similar effects upon prey vulnerability. Therefore, rather than being unique, trawl passage would appear to be 1 more addition to a growing list of stressors that may result in behavioral impairment and increased vulnerability to predation.

Whether trawl stress resulted in a degraded ability to detect predators, or a failure to respond appropriately, it is clear that juvenile walleye pollock demonstrated reduced avoidance capacity. In the nonlethal experiment trawl-stressed pollock allowed the predator to get closer than did controls, and in the swim/crowd/escape treatment the disorientation and lethargy of some individuals was so severe that they appeared oblivious to predator presence. This was probably partly responsible for the greater vulnerability of trawl-stressed pollock in the lethal predation experiment, where predators primarily lunged at those pollock they could get close to and were more successful the closer they got. Similarly, less cohesive shoaling may have also increased their vulnerability, as lingcod tended to stalk nonshoaling or straggling individuals. Concentration of predatory attacks upon lone fish or stragglers has been observed in both laboratory studies (Parrish 1989) and the field (Hobson 1968). Other more subtle aspects of juvenile walleye pollock behavior that were evident in trawl-stressed individuals, such as swimming at an upward angle or repeatedly poking their snouts out of the water, may have attracted the attention of lingcod, as predators often concentrate attacks upon individuals with disparate physical or behavioral characteristics (oddity effect: Hobson 1968, Landeau & Terborgh 1986, Theodorakis 1989).

The extent of predation upon behaviorally impaired fish will also depend upon the local abundance of predators. Predators often aggregate around schooling prey (Hobson 1968, Pitcher 1980, Parrish 1992), and those predators not caught by the trawl may immediately capitalize upon injured and/or disoriented escapees. Bottom trawling activities may further concentrate predators and scavengers, which aggregate to feed upon exposed and injured benthic invertebrates (Kaiser & Spencer 1994, 1996, Ramsay et al. 1996, 1998, Kaiser & Ramsay 1997, Prena et al. 1999). Caddy (1973) documented winter flounder *Pseudopleuronectes americanus* densities 30 times higher inside, as opposed to outside dredge tracks within 1 h of dredge passage. Predators with acute olfactory ability, such as the sablefish *Anoplopoma fimbria* (Løkkeborg et al. 1995), can detect baits kilometers away and may be attracted to the olfactory plume generated by trawls, thereby exposing lingering escapees to elevated predation risk. Some predators follow trawlers. Perhaps most conspicuous are seabirds, which feed upon discards as well as small fish escaping the gear during haul-back and de-watering. However, the bottlenose dolphin *Tursiops truncatus* commonly follow Gulf of Mexico shrimp trawls, feeding upon juvenile fishes as they escape through the trawl meshes and bycatch-reduction-devices (R. Overman, Georgia Sea Grant

Marine Extension Program, unpubl. video). Other cetaceans and pinnipeds are known to follow trawlers, but it is not known whether they predate escapees or simply feed upon discards and slippage (West 1983). Several species of predatory fish have been observed to follow Gulf of Mexico shrimp trawls, including the tuna *Euthynnus alletteratus*, the jack crevalle *Caranx hippos* and sharks, with the sharks occasionally biting the codend (Workman 1999). Clearly, whether as the result of learning, attraction to structure, or a simple optomotor response (Wardle 1983), any predator following a net would be well positioned to exploit behaviorally impaired escapees.

Numerous scientific studies have addressed the effect of mesh size, mesh geometry, and bycatch-reduction-devices upon the size and species selectivity of trawls (Rogers et al. 1997, Brewer et al. 1998, Farmer et al. 1998, Perez-Comas et al. 1998, Tumilty et al. 1998, Halliday & Cooper 1999). In many fisheries, such as the Bering Sea mid-water pollock fishery, larger mesh codends have been adopted by fishers, with the express goal of reducing the retention/bycatch of under-sized fish. This reflects a prevailing attitude among many fishers and managers that bycatch problems can be solved through mechanical separation in the trawl. However, reducing the numbers of under-sized fishes which are landed does not provide proof that such measures are successful in significantly reducing mortality of these fishes. Studies of other fisheries demonstrate that there is bycatch associated with fishing activities that is unobserved from the boat, that is, fish escaping trawls die as a direct result of injuries suffered through interaction with the gear (Sangster et al. 1996, Suuronen et al. 1996a,b). The present study supports the existence of an unobserved bycatch which results indirectly from gear interaction: those fishes which survive trawl passage but are behaviorally impaired and succumb to predators in the subsequent hours and/or days. The results of this study cannot predict the magnitude of this mortality or the species that may be susceptible; that must await additional field research, perhaps incorporating commercial gear fitted with cages to retain codend escapees, as well as the development of *in situ* behavioral and/or biochemical assays to assess behavioral impairment. However, this work clearly demonstrates the need for a more thorough understanding of the interaction between fishes and fishing gears, with the goal of better quantifying and reducing the unobserved bycatch.

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