

**Abstract**—Commercial bottom trawls often have sweeps to herd fish into the net. Elevation of the sweeps off the seafloor may reduce seafloor disturbance, but also reduce herding effectiveness. In both field and laboratory experiments, we examined the behavior of flatfish in response to sweeps. We tested the hypotheses that 1) sweeps are more effective at herding flatfish during the day than at night, when fish are unable to see approaching gear, and that 2) elevation of sweeps off the seafloor reduces herding during the day, but not at night. In sea trials, day catches were greater than night catches for four out of six flatfish species examined. The elevation of sweeps 10 cm significantly decreased catches during the day, but not at night. Laboratory experiments revealed northern rock sole (*Lepidopsetta polyxystra*) and Pacific halibut (*Hippoglossus stenolepis*) were more likely to be herded by the sweep in the light, whereas in the dark they tended to pass under or over the sweep. In the light, elevation of the sweep reduced herding, and more fish passed under the sweep. In contrast, in the dark, sweep elevation had little effect upon the number of fish that exhibited herding behavior. The results of both field and laboratory experiments were consistent with the premise that vision is the principle sensory input that controls fish behavior and orientation to trawl gear, and gear performance will differ between conditions where flatfish can see, in contrast to where they cannot see, the approaching gear.

Manuscript submitted 8 June 2009.  
Manuscript accepted 15 December 2009.  
Fish. Bull. 108:145–154 (2010).

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## Flatfish herding behavior in response to trawl sweeps: a comparison of diel responses to conventional sweeps and elevated sweeps

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Trawl catches for many fish species exhibit diel patterns (Casey and Myers, 1998). This is generally viewed as a product of two independent factors: availability and catchability of the fish species. Many gadids exhibit diel changes in availability associated with vertical migration (Beamish, 1965; Casey and Myers, 1998; Schabetsberger et al., 2000). Gadids aggregate close to the bottom during the day and are highly available to bottom trawls. At night, dispersal into the overlying water renders them less available. Interestingly, for many flatfish species the opposite pattern, higher catches at night, has been observed (Walsh, 1991; Walsh and Hickey, 1993; Casey and Myers, 1998). Seasonal migrations will occasionally take flatfish into the water column (Metcalf et al., 1990; Nichol and Sommerton, 2009), as will the occasional exploitation of pelagic prey. However, under normal circumstances many flatfish species appear to remain on the bottom and are consistently available to trawl gear, day or night. As a consequence, greater flatfish catches at night are thought to be associated with higher catchability, that is, with a decreased ability to evade capture (Ryer, 2008).

Video cameras mounted on trawls, as well as supplemental bag nets behind the main net, have documented

extensive flatfish escapement beneath the footrope during the day (Main and Sangster, 1981; Walsh, 1988). For obvious technical reasons, behavior in front of the footrope, or sweeps, at night has not been observed in field studies, except with flash photography (Walsh and Hickey, 1993). However, laboratory experiments indicate that northern rock sole (*Lepidopsetta polyxystra*), Pacific halibut (*Hippoglossus stenolepis*), and English sole (*Parophrys vetulus*) are more likely to rise or hop into the water column during darkness, than to herd (Ryer and Barnett, 2006). By moving off the bottom, these fish remove themselves from the “zone of influence” of the ground gear, and as they cease swimming they pass over the footrope and into the net. This behavior potentially explains why flatfish are captured in greater numbers at night.

This paradigm, i.e., higher flatfish catches at night, stems largely from a series of published studies (Main and Sangster, 1981; Walsh, 1988, 1991; Walsh and Hickey, 1993; Casey and Myers, 1998; and references therein), based on survey trawls. On survey trawls, the combined length of bridles and sweeps is typically minimized. In contrast, on commercial flatfish trawls lengthy sweeps are used to herd fish inward toward the net (Winger et

al., 1999, 2004). On some modern flatfish trawls these sweeps may be up to 400 m in length, and as much as 90% of the seafloor is subject to the action of gear which is designed to affect capture by manipulating flatfish swimming behavior. But for the very reason that footropes are more efficient in the dark, sweeps may be less efficient. If flatfish, unable to see the approaching sweep, rise or hop into the water column, rather than herding as happens during the day, they will pass over the sweep and be lost to the catch. This situation raises the possibility that flatfish trawls that rely upon sweep herding may capture more flatfish during the day than during the night—a pattern not seen with survey trawls, which have minimal sweeps.

In this study we investigated the performance of trawls equipped with sweeps under day and night conditions, using a combination of manipulative at-sea and laboratory procedures. For our at-sea experiment, we used a data set acquired during a series of cruises in the eastern Bering Sea, the goal of which was to evaluate sweeps designed to reduce damage to benthic habitat (Rose et al., 2010). In brief, trawling was conducted with sweeps that were elevated, to various degrees, off the seafloor to evaluate the trade-off between reductions in habitat disturbance and decreased flatfish herding efficiency. Here we test hypotheses related to our principle premise: flatfish behavior initiated by ground-gear is principally controlled by ambient light levels. More specifically, first we test the hypothesis that trawls configured with control (commercial type) sweeps in contact with the bottom, will catch more flatfish during the day than during the night. Following from this, we test a second related hypothesis: the elevation of sweeps off the bottom will have differential effects, day as opposed to night. During the day, elevation will reduce sweep efficiency, resulting in lower flatfish catch. During the night, because sweeps are already relatively ineffective, elevation of the sweeps will have no influence upon their efficiency, as reflected by flatfish catch. Lastly, we conducted comparable experiments under both light and dark conditions, using simulated ground-gear in the laboratory where behavior could be quantified, to ascertain whether the proposed effects of elevated sweeps on catch are directly attributable to ambient-light-mediated differences in flatfish behavior in relation to ground gear.

## Methods

### At-sea experiments

Tows of paired trawls (control and elevated sweeps) were conducted during September 2007 in the eastern Bering Sea onboard the FV *Cape Horn*. Details of gear and onboard procedures can be found in Rose et al. (2010). Briefly, the Cape Horn is a 47-m trawler processor, configured so as to allow twin trawling, i.e., fishing with two identical nets side-by-side. Each net had a set of independent 180-m sweeps, being spread by one

otter board on each side of the vessel, and connected in the middle by a towed weight (clump). The sweeps were composed of 5-cm diameter combination rope, constructed of steel cable and covered by polyethylene fiber. Modifying the sweeps on one net, while keeping all other trawl characteristics consistent, allowed the difference between the two catches to reflect the effect of the modification. In this field study, disk clusters were attached to the experimental sweeps at 9-m intervals. The disks were either 15, 20, or 25 cm in diameter. This created a nominal spacing between the sweeps and the seafloor of 5, 7.5, and 10 cm, respectively. Test tows were made with modified sweeps on one net and unmodified sweeps on the other. Halfway through each experiment, the modified sweeps and unmodified sweeps were switched (left to right, right to left).

Catches from each trawl were kept separate until the entire catch had been sampled. As catches entered the sampling area, they were passed across a motion-compensated flow scale to determine total catch weight. The five or six most abundant species were then completely sorted into holding bins. Fish from each bin were then run across a second flow scale to measure the weight of each of those species. To estimate the weight of other species, samples of the unsorted catch were taken at intervals, sorted, and weighed by species. The composition of these samples was then expanded to the weight of the entire catch by calculating the fraction of the sample weight to the total catch weight. For the species cited in this paper, Pacific halibut and Alaska plaice catches were estimated from the samples and all other species were fully weighed on the second flow scale. During the sorting phase, samples of 50–150 fish of each species were drawn and measured to determine their length composition. Length samples were taken from throughout the catch as it passed through the sorting area and the length of each individual in the sample was measured.

Sixty-one paired hauls were made over depths ranging from 70 to 117 m. Ambient light on the bottom is greatly influenced by water depth. To minimize potential depth effects upon ambient light, we limited our analysis to hauls where depth was between 79 and 94 m: a 15-m range. In addition, we eliminated hauls where large debris (crab pots, etc.) were encountered, or where gear components became entangled, assuming that such conditions would influence gear performance and catch. After examining *in situ* light measurements (Wildlife Computers, MK9 light meter, Redmond, WA) we further eliminated daytime hauls where light levels fell below  $1.0 \times 10^{-4}$   $\mu\text{mol photons/m}^2/\text{s}$ , and nighttime hauls exceeding  $1.0 \times 10^{-5}$   $\mu\text{mol photons/m}^2/\text{s}$ . This step eliminated hauls made around dusk or dawn and set a clear differentiation between daytime and nighttime light. In the resulting data set (36 hauls), mean tow depth did not differ between nighttime and daytime tows (day:  $n=7$ , mean  $[\bar{x}]=82$  m, standard error [SE]=1; night:  $n=19$ ,  $\bar{x}=84$  m, SE=1;  $t_{[34]}=1.54$ ,  $P=0.133$ ). Tow durations ranged from 33 to 150 min, being somewhat longer at night ( $\bar{x}=115.8$ , SE=5.9) than during the day

( $\bar{x}$  = 87.5, SE = 6.3,  $t_{[34]} = 3.28$ ,  $P = 0.003$ ). During long tows, accumulating catch can distort meshes and back up into the intermediate portion of the net, altering gear selectivity (Herrmann, 2005). However, catches in this study were small compared to net capacity, never filling the codend. Hence, we assume that differences in duration between day and night did not influence net performance or fish catchability in a manner that would bias our results. Similarly, during long tows proportionately more fish will tire and fall back into the net, particularly so for many roundfish species, which can swim for prolonged periods in front of the net (Main and Sangster, 1981). However, flatfish typically swim for less than 1 minute in front of nets (Ryer, 2008), and thus this source of bias was also unlikely in our study.

For our first analysis, we compared daytime and nighttime catches from the control nets only; where sweeps were in contact with the bottom along their entire length. Catch per unit of effort (CPUE: kg/min) was calculated for total catch (all species) as well as for six flatfish species: yellowfish sole (*Limanda aspera*); flathead sole (*Hippoglossoides elassodon*); arrowtooth flounder (*Atheresthes stomias*); rock sole (*Lepidopsetta* spp.); Alaska plaice (*Pleuronectes quadrituberculatus*); and Pacific halibut. CPUE values were natural log (ln) transformed and tested for day and night differences with  $t$ -tests (Sokal and Rohlf, 1969). Where variances were heteroscedastic, Satterthwaite's adjusted degrees of freedom were used (Snedecor and Cochran, 1980). Because CPUE was based upon weight, we also compared mean total length between daytime and nighttime hauls for each flatfish species.

For our second analysis, we used the subset of samples from trawls where 25.4-cm disks were attached to elevate sweeps of the experimental net to an approximate height of 10 cm (the distance between sediment surface and bottom of the sweep material). For this analysis, catch of the experimental net was compared to that of the paired control net (with bottom contact sweeps) by using a paired  $t$ -test (Sokal and Rohlf, 1969). Separate analyses were conducted for daytime ( $n=10$  pairs) and nighttime ( $n=5$  pairs) hauls. Similar analysis was conducted for flatfish lengths.

### Laboratory experiments

Northern rock sole and Pacific halibut were collected as age-0 juveniles by using a 2-m plumb-staff beam trawl from Chiniak Bay, Kodiak, Alaska. Fish were transported to the Hatfield Marine Science Center in Oregon and reared in 2.2-m (diameter) circular tanks with flow-through seawater (28–35‰, 9°C [ $\pm$  1°]) on a diet of krill and gelatinized food. After reaching age 1, fish were transferred to 3-m diameter pools for continued growth.

Simulated sweep exposure took place in an elongated tank (10.7×1.5×1.2 m) filled to a depth of 0.9 m. This tank was provided with flow-through seawater (28–35‰) and located in a light-proof room, allowing for control of

illumination by an overhead bank of fluorescent lamps. The tank bottom was covered to a depth of 4 cm with sand, allowing flatfish to completely bury themselves. Details of this apparatus are presented elsewhere (Ryer and Barnett, 2006) and will only be described briefly here. By means of a moveable carriage a simulated sweep was propelled down the length of the tank. This sweep consisted of a piece of 5-cm diameter PVC pipe, painted green to resemble the actual sweep used in the field study. It could be positioned so that it ran down the tank in contact with the bottom, or elevated so that it was approximately 10 cm off the bottom.

Fish were maintained on a 12/12 h photo period during all experiments, with lights turned on at 0700 and off at 1900. At 1600 on the day before the trials, the length of the tank was subdivided into three equal 3-m sections, by means of four removable partitions, of which two of these partitions prevented fish from moving to the extreme ends of the tank. Next, fish were introduced to each of the three main sections of the tank. This sectioning assured that fish would not aggregate in a single area of the tank. At 0800 on the day of trials, the footrope carriage was lowered into the tank, behind one of the end partitions and secured to its tracks. Then the lighting was either turned off (dark trials) or kept on (light trials), and fish were allowed 2 h acclimation before a trial. Illumination at the sand surface was measured once at the beginning of the study. For light trials, illumination was approximately 1.5  $\mu\text{mol photons/m}^2/\text{s}$  (~125 lux), whereas, for dark trials illumination was  $<1 \times 10^{-8}$   $\mu\text{mol photons/m}^2/\text{s}$  (~ $10^{-6}$  lux). Both species used in this study have the same light thresholds ( $10^{-5}$   $\mu\text{mol photons/m}^2/\text{s}$ ) for visual discrimination of small motile prey (Hurst et al., 2007), and we assumed they would see approaching footrope in the light trials, but not in the dark trials. Illumination was measured with a research radiometer (International Light Inc., Model IL1700, Peabody, MA) equipped with a  $2\pi$  PAR (photosynthetically active radiation) sensor. Water supply to the tank was filtered through sand, making it unlikely that water clarity, and hence light levels, changed appreciably from day to day. At 1000 h, immediately before a trial, the partitions were removed; for dark trials red flashlights were used during this process, and care was taken to avoid shining the lights directly into the tank. Five minutes later the footrope carriage was pulled from one end of the tank to the other at a speed of 1.0 m/s ( $\pm$  0.1 m/s), a speed roughly equal 3.6 km/h or 2 knots; flatfish trawls are commonly towed at 2–5 knots. Afterwards, the lights in the room, if turned off, were turned back on and rakes were used to herd fish back into each of the three main sections of the tank, after which the partitions were put back in place and the footrope carriage was removed from the tank. This entire process was repeated in the afternoon, using the opposite lighting from that of the morning: at 1200 h, a footrope carriage was lowered into the tank and lighting was adjusted; at 1400 h, partitions were removed and the footrope carriage was pulled. We assume that this alternation

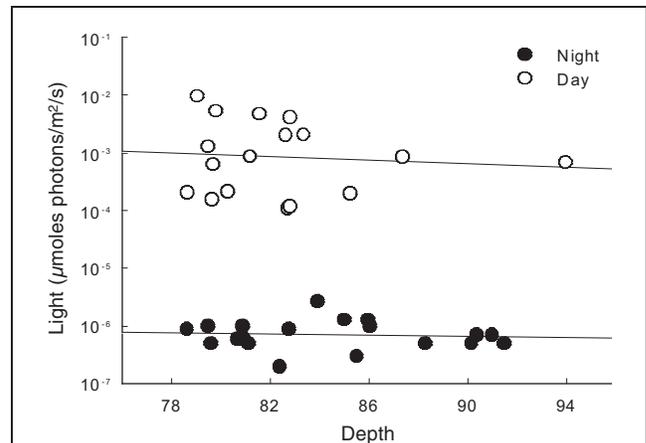
in treatment order precluded any bias attributable to flatfish habituation or learning.

Positioned behind and above the footrope were three (50W) infrared LED (light emitting diode) lamps, aimed forward and down, so that they illuminated the footrope and tank bottom immediately in front of the footrope. The wavelength of light emitted by these lamps peaked at 880 nm, and emissions dropped to 0 below 760 nm. Most fish are insensitive to light at those wavelengths (Douglas and Hawryshyn, 1990) and results from light-threshold feeding studies for all three flatfish species used in this study are consistent with this generalization (Hurst et al., 2007). Two underwater video cameras (Aqua-Vu, model ZT-120, Crosslake, MN) were mounted alongside the lamps, also directed at the area in front of the footrope. This arrangement allowed for visual monitoring out to 1.1 m in advance of the footrope. The video footage was captured from a remote location by digital mini-DV recorders.

Trials were conducted with three age classes of Pacific halibut: age-1, age-2, and age-3, as well as age-2 northern rock sole. For age-3 Pacific halibut, three groups of five fish each were examined. Trials took place over two consecutive days. On the first day sweep height was randomly set to either the “in contact” or “elevated” position. On the second day the alternative position was used. During each day, fish were exposed to the simulated sweep approach twice; once in the light and once in the dark. The order of application of light vs. dark trials was also randomly determined. After the second day fish were then removed from the tank, their total length was measured, and they were replaced by a new group. Age-3 Pacific halibut ranged from 37–52 cm in total length.

For age-2 Pacific halibut, age-1 Pacific halibut, and age-2 rock sole, groups consisting of 10 fish each were trialed differently. Each group was trialed for only a single day, at one sweep height. For age-2 Pacific halibut, six groups were trialed at each sweep height. For age-1 Pacific halibut and age-2 northern rock sole, five groups were trialed at each sweep height. As before, the order of light and dark trials was randomized. Age-2 Pacific halibut ranged from 19–31 cm, age-1 halibut from 8–14 cm, and age-2 northern rock sole from 9–17 cm.

Fish behavior was quantified by using the slow-motion playback of digital video. First, the number of fish encountered, i.e., observed, as the sweep made its transit from one end of the tank to the other, was recorded from each trial. Then the initial behavioral response of each observed fish was assigned to one of four categories: 1) pass under, 2) hop, 3) rise, and 4) herd. Fish characterized by “under” either did not react at all to the approaching sweep, or reacted when contacted by the sweep, but passed under the sweep as it progressed down the tank. “Hop” characterized fish that reacted to the sweep with one or two sinusoidal body undulations, typically after being struck by the sweep, which resulted in the fish “hopping” off the substrate. However, this initial startle reaction



**Figure 1**

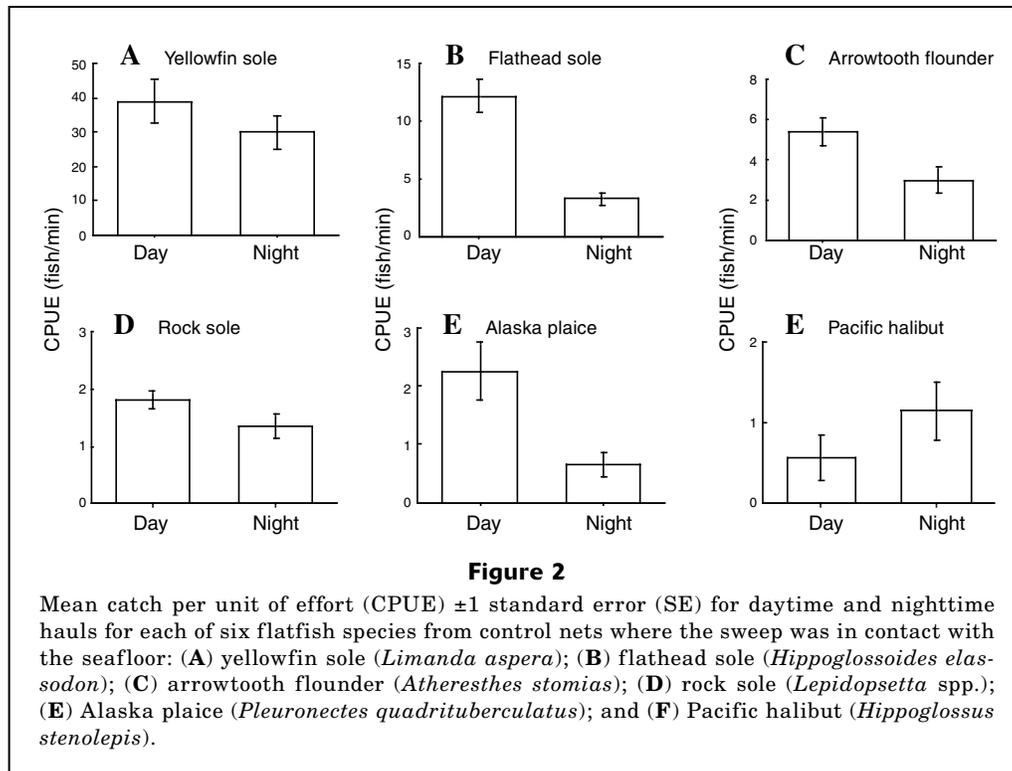
*In situ* natural log-transformed light data for trawl tows conducted during day and night, plotted by mean depth over the course of each tow. Regression analysis indicated no effect of depth upon ambient light over this relatively narrow range of depths and hence, regressions are plotted as zero-slope lines.

was not followed by any further swimming, such that the fish tended to hang stationary in the water, and passed over the sweep as it progressed down the tank. “Rise” characterized the motion of fish that departed the bottom with sustained swimming in an upward direction, such that the distance between fish and bottom continuously increased as the fish swam. This was in contrast to fish characterized by “herd” where fish maintained a distance of less than one body length between themselves and the bottom as they swam along in front of the sweep, i.e. herding behavior. Ryer and Barnett (2006) investigated whether initial orientation, i.e., the direction fish were facing, influenced behavioral response. No relationship was observed, and consequently, no data on fish orientation were recorded in this study. Categorical data on behavioral response were pooled across replicate groups and analyzed by contingency table analysis by using log-linear models (Fienberg, 1980).

## Results

### At-sea experiment

Mean ambient light on the seafloor (Fig. 1) was greater during daytime tows ( $2.0 \times 10^{-3}$   $\mu\text{mol photons/m}^2/\text{s}$ ) than during nighttime tows ( $8.4 \times 10^{-7}$   $\mu\text{mol photons/m}^2/\text{s}$ ,  $F_{[1,33]}=352.76$ ,  $P<0.001$ ). However, over the relatively narrow range of tow depths used in this analysis, depth had no influence upon bottom ambient light level ( $F_{[1,33]}=0.27$ ,  $P=0.607$ ). Mean total catch (CPUE) in terms of weight (kg/min) was greater during the day than at night (Table 1, day:  $\bar{x}=100.6$  kg,  $\text{SE}=9.61$ ; night:  $\bar{x}=53.07$  kg,  $\text{SE}=6.14$ ). This pattern of diurnally



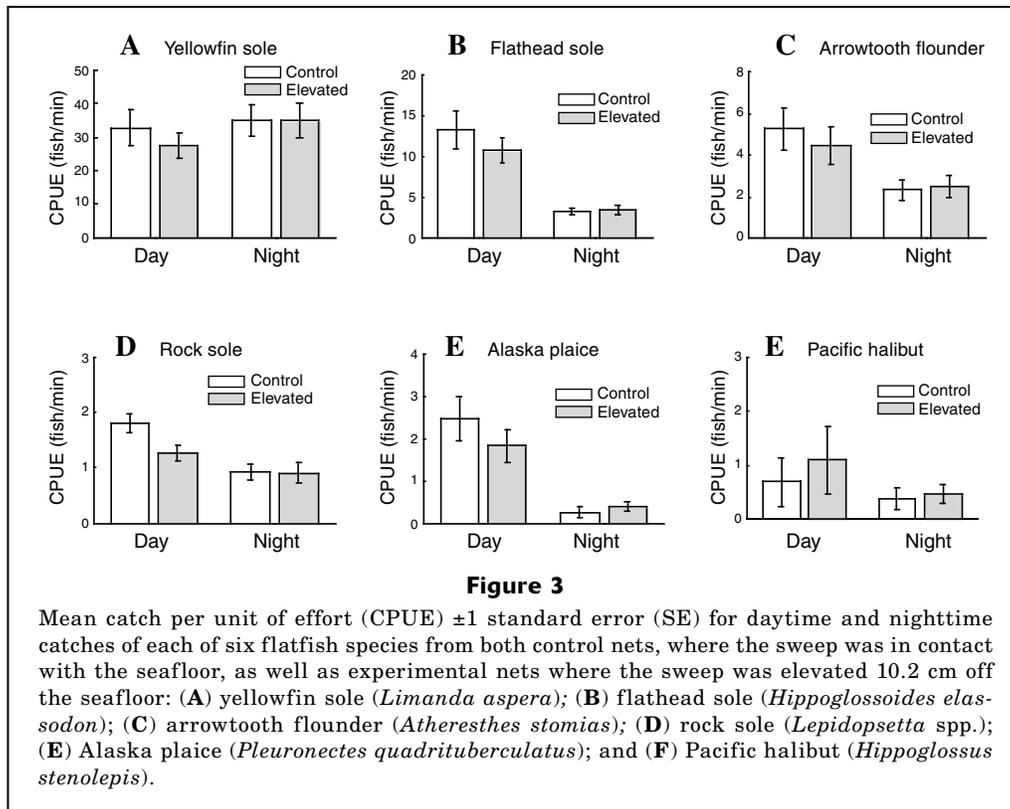
**Table 1**  
Statistics for a comparison of day and night trawl catches, by total catch, and catch of six individual species of flatfish. For both day and night tows, trawl nets were equipped with control sweeps (that had contact with the bottom). Where needed, Satterthwaite's adjusted degrees of freedom were used to mitigate for nonhomogeneity of variance.

Species	<i>t</i> -test statistic	df	<i>P</i> value
Total catch	4.85	31.3	<0.001
Yellowfin sole ( <i>Limanda aspera</i> )	1.71	30.6	0.097
Flathead sole ( <i>Hippoglossoides elassodon</i> )	-7.44	34	<0.001
Arrowtooth flounder ( <i>Atheresthes stomias</i> )	-3.26	34	0.003
Rock sole ( <i>Lepidopsetta</i> spp.)	-2.38	29.3	0.024
Alaska plaice ( <i>Pleuronectes quadrituberculatus</i> )	-3.74	26.4	0.001
Pacific halibut ( <i>Hippoglossus stenolepis</i> )	1.58	34	0.126

larger catches was also exhibited by four out of six flatfish species examined (Table 1, Fig. 2). Flathead sole, arrowtooth flounder, rock sole, and Alaska plaice were all characterized by higher CPUE during the day. Yellowfin sole and Pacific halibut exhibited no significant differences in catch between day and night. Of the four species for which fish total length was measured in catch subsamples (i.e., yellowfin sole, flathead sole, arrowtooth flounder, and rock sole), fish tended to be slightly larger at night. This was only statistically significant for yellowfin sole ( $t_{[24,4]}=3.93$ ,  $P=0.001$ ), where fish averaged 1 cm longer during the night ( $\bar{x}=32.8$  cm,  $SE=0.2$ ) than during the day ( $\bar{x}=31.8$  cm,  $SE=0.1$ ), and rock sole ( $t_{[32]}=2.91$ ,  $P=0.006$ ), where fish averaged 0.9

cm longer during the night ( $\bar{x}=33.3$  cm,  $SE=0.2$ ) than during the day ( $\bar{x}=32.4$  cm,  $SE=0.2$ ).

The effect of elevating sweeps 10 cm off the bottom differed, depending upon whether tows were made during the day or night (Fig. 3). During the day, total catch tended to decrease when sweeps were elevated (Table 2, elevated:  $\bar{x}=93.4$ ,  $SE=8.7$ ; control:  $\bar{x}=100.6$ ,  $SE=9.6$ ). However, during the night, elevation of sweeps had little influence upon catch (elevated:  $\bar{x}=55.1$ ,  $SE=6.8$ ; control:  $\bar{x}=53.1$ ,  $SE=6.1$ ). This same pattern was evident for four out of six flatfish species examined. Species for which daytime elevation of sweeps decreased catch included flathead sole, arrowtooth flounder, rock sole, and Alaska plaice. Sweep configuration had no significant effect on

**Table 2**

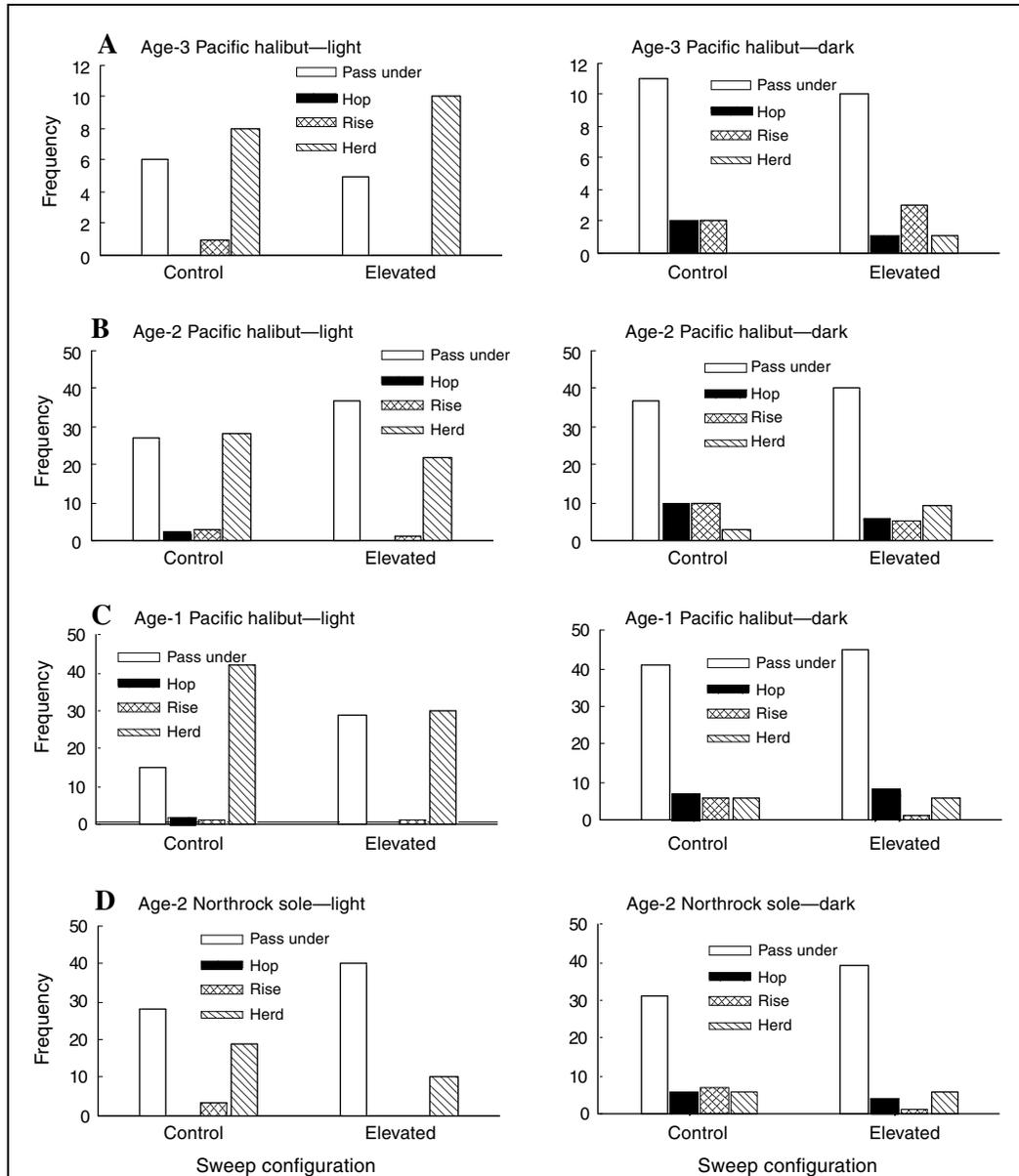
Statistics for comparison of total catch and catch of six individual species of flatfish between trawl nets equipped with control (bottom contact) and those equipped with elevated (10 cm off bottom) sweeps, from both day and night tows.

Species		Paired <i>t</i> -test statistic	df	<i>P</i> value
Total catch	Day	2.11	9	0.064
	Night	-0.22	4	0.834
Yellowfin sole ( <i>Limanda aspera</i> )	Day	1.84	9	0.099
	Night	0.09	4	0.935
Flathead sole ( <i>Hippoglossoides elassodon</i> )	Day	2.33	9	0.045
	Night	-0.78	4	0.481
Arrowtooth flounder ( <i>Atheresthes stomias</i> )	Day	4.35	9	0.002
	Night	-0.71	4	0.519
Rock sole ( <i>Lepidopsetta</i> spp.)	Day	5.42	9	<0.001
	Night	0.23	4	0.830
Alaska plaice ( <i>Pleuronectes quadrituberculatus</i> )	Day	2.39	9	0.041
	Night	-0.67	4	0.539
Pacific halibut ( <i>Hippoglossus stenolepis</i> )	Day	-0.59	9	0.753
	Night	0.29	4	0.785

daytime catches of yellowfin sole or Pacific halibut. In contrast to daytime results, elevated sweeps had no effect upon nighttime catches for any species. Of the four species that were measured, fish lengths did not differ between tows with elevated sweeps and control tows, regardless of time of day ( $P > 0.05$  for each species, day and night).

### Laboratory experiment

Overall, 28% of fish initiated herding behavior in response to simulated sweep disturbance. Herding was most prevalent in the light, and tended to be replaced by fish passing under the sweep, as well as hopping or rising off the bottom in the dark (Fig. 4). There was also



**Figure 4**

Behavioral response of flatfish, under light and dark conditions, with the simulated sweep both in contact (control) and elevated 10 cm off the bottom: (A) age-3 Pacific halibut (*Hippoglossus stenolepis*); (B) age-2 Pacific halibut; (C) age-1 Pacific halibut; and (D) age-2 northern rock sole (*Lepidopsetta polyxystra*). “Pass under” represents fish that either did not react to the sweep, or reacted late, such that they passed under the sweep as it progressed down the tank. “Hop” characterized fish that reacted to the sweep with one or two body undulations, but almost immediately pass over the sweep. “Rise” characterized fish in which the initial jump off the bottom was followed by sustained swimming in an upward direction, such that the distance between fish and bottom continuously increased as the fish swam. “Herd” characterized fish which, after reacting to the gear, swam along in front of the sweep, close to the bottom, typically maintaining a distance of less than one body length between themselves and the bottom.

a tendency for herding in the light to decrease when the sweep was elevated. These observations are supported by results of log-linear model analysis, in which ambient light (light, dark) mediated the influence of

sweep height upon behavioral response ( $G_{[3]}=9.96$ ,  $P=0.019$ ). All three age classes of Pacific halibut, and northern rock sole, behaved comparably; there were no significant effects of species or age on the type of

response displayed, or interactions with light level or sweep height ( $P > 0.05$  for all). Examination of Figure 4 could lead one to conclude that age-3 halibut behaved somewhat differently than the other species and age groups. However, the number of age-3 halibut tested ( $n=15$ ) was small compared to each of the other species and age groups ( $n > 50$  for each), and as a consequence, had little influence upon our statistical model. We pooled data across species and collapsed response categories down to those fish that herded in contrast to those that did not (pass under, hop, and rise combined), so as to render the data into a form most similar to our at-sea trawl-catch experiments. Again, ambient light (light or dark) mediated the influence of sweep height upon behavioral response ( $G_{[1]}=5.75$ ,  $P=0.017$ ). In Figure 5 we have simplified this relationship by graphing the percentage of fish herding under the two light and sweep height treatments. In addition to a conspicuous decrease in herding in the dark, elevation of the sweep decreased herding in the light but had little influence in the darkness—results consistent with those observed in the at-sea experiment.

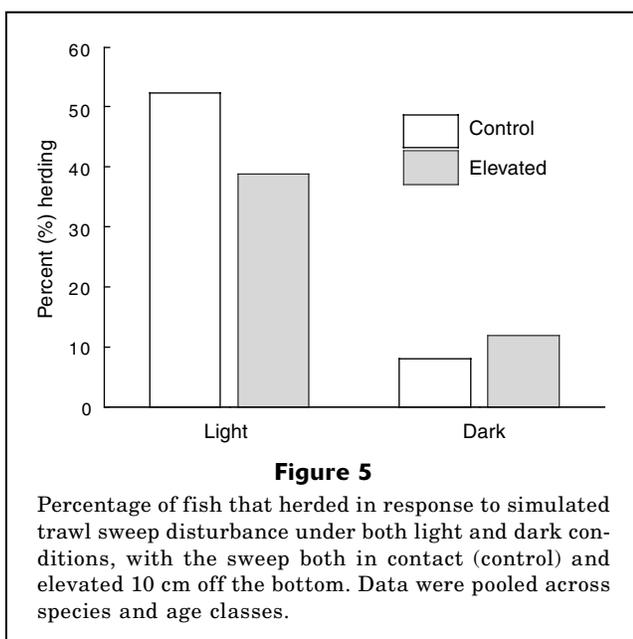
## Discussion

Ambient illumination controls many aspects of fish behavior, from feeding and habitat use (Janssen, 1978; Helfman and Schultz, 1984; Ryer and Olla, 1999; De Robertis et al., 2003; Petrie and Ryer, 2006) to social and antipredator behavior (Shaw, 1961; Ryer and Olla, 1998). Similarly, light has a pervasive influence upon interactions between fish and trawls. In this study, field data were largely consistent with our principal hypothesis; that trawls configured with sweeps that are in contact with the seafloor would catch more flatfish during the

day than during the night. This pattern was observed for four out of six flatfish species examined: flathead sole, arrowtooth flounder, rock sole, and Alaska plaice. Herding, as seen in both roundfish and flatfish, is an ordered behavioral response in which fish move away from an approaching threat, i.e., the doors, sweeps, bridles, and wings of the net. Through either continuous swimming, or sudden swimming bursts, interspersed with rests on the bottom (Winger et al., 1999, 2004), fish then funnel to the center of the gear, where they concentrate before tiring and falling back into net. Several studies have demonstrated that both roundfish (Olla et al., 2000; Ryer and Olla, 2000) and flatfish (Ryer and Barnett, 2006) lose the ability to orient themselves in relation to gear and initiate herding when ambient light falls below the threshold for visual perception of the gear (Kim and Wardle, 1998a, 1998b).

Given the brief evolutionary time during which fish have interacted with towed fishing gear, approximately 100 years, it is unlikely that specific gear avoidance behavior has evolved. Rather, we consider it most parsimonious to assume gear avoidance is rooted in antipredator behavior. Although flatfish may initially erupt from the seafloor upon being disturbed by trawl ground-gear, as when attacked by a predator, subsequent herding behavior is consistent with “distance keeping” behavior, during which the fish attempts to maintain a safe distance between itself and a slowly pursuing predator. Scuba and skin divers who have attempted to follow fish along the seafloor are certainly familiar with this behavior. For flatfish, movement in the vertical dimension also plays a critical role during herding. It has been observed that flatfish remain close to the bottom during herding, usually less than half a body length (Ryer, 2008). Staying close to the bottom reduces drag, lessening thrust requirements to achieve a given speed—the ground effect (Videler, 1993; Gibson, 2005). Rising off the bottom makes flatfish more conspicuous, and due to the location of a flatfish’s eyes, also interferes with visual tracking of a pursuing predator, in this case, the trawl ground-gear. Although they herd close to the bottom in the light, Pacific halibut and northern rock sole respond differently to ground-gear in the darkness, as demonstrated by laboratory experiments (Ryer and Barnett, 2006). Unable to see, the fish respond to contact with the ground-gear initially by hopping or swimming upward and away from the bottom. Similarly, in this study the percentage of fish moving off the bottom increased from 4% in the light to 21% in darkness, for all species and bar heights combined. Moving off the bottom in darkness probably functions as an antipredator tactic, making the flatfish more difficult to follow and may simply be the flatfish version of the Mauthner-cell triggered (lateral line) startle response (Eaton and Hackett, 1984).

Our second hypothesis, that elevation of sweeps off the bottom, 10 cm in this case, would decrease catch during daylight, but not at night, was also partially supported by our field experiment. Again, four of six flatfish species examined displayed the predicted



catch pattern. Arguably, our analysis is based upon a small set of paired tows, particularly at night ( $n=5$  pairs). Taken alone, these at-sea trials might not be convincing. However, these results were mirrored by our laboratory experiments, where the elevation of sweeps decreased herding to a greater extent in the light, compared to darkness. The elevation of sweeps had several consequences, all of which were likely to have influenced flatfish behavior. First, because most flatfish react to ground gear at a very short distance, often only after being struck, the likelihood that fish would simply not react and be passed over by sweeps was probably increased by sweep elevation. Further, part of the visual stimulus to herd that is associated with ground gear is the sand and mud cloud that is kicked up by the gear. This visual stimulus would be absent or greatly diminished by sweep elevation, further decreasing the likelihood of flatfish response. Our laboratory experiments with rock sole exhibited a pattern of response nearly identical to that seen in the field and indicated that passage under or over the gear was probably responsible for the decline in herding associated with sweep elevation during the day; in the light, fish passing beneath the sweep increased by 24% when the sweep was elevated. Lastly, even when herding is initiated, it must be maintained. Flatfish will sometimes dive under ground gear when they perceive a gap between the gear and the bottom—a trait that has been used to reduce flatfish bycatch (DeAlteris et al., 1997). Sweep elevation probably facilitated such escape. Unfortunately, our laboratory data were of little aid in evaluating this possibility. Because of the physical limitations of our apparatus, we characterized only the initial behavioral response of fish—not prolonged behavioral sequences that would characterize such deliberate escape tactics.

Our field data indicate that Pacific halibut could have a different pattern of availability or catchability, compared to that of the other flatfish species we examined. By virtue of size, Pacific halibut stand apart from most other flatfish. Beyond three or four years of age, their size likely renders them immune to most predators. This may make them more likely to venture from the bottom, as may their piscivorous diet. Consequently, they may be more likely than other species to rise off the bottom and swim back over sweeps. If so, it follows that most of the fish captured are those directly in the path of the net, excluding the area swept by the sweeps. Our trawling operations tended to produce larger, albeit not significant, Pacific halibut catches at night—a trend reported by commercial fishermen as well. It may be that with their greater speed and endurance, many halibut escape trawls during the day, but at night cannot see the gear to coordinate their escape. In contrast to the halibut results, the nonsignificant differences for yellowfin sole were similar in direction and magnitude to the significant differences detected for the other small flatfishes. This finding opens the possibility that these flatfishes had similar reactions, but our experiment just did not have the statistical power to detect them.

Diel patterns of catch in trawl fisheries and surveys reflect not only patterns in fish availability, but gear-specific behavioral influences upon catchability that are directly controlled by ambient illumination. Results of our laboratory experiments, along with earlier experiments (Ryer and Barnett, 2006), indicate that trawl footropes are likely to be more efficient at displacing flatfish from the bottom and rapidly transitioning them to the net under conditions of darkness (Ryer, 2008). In contrast, sweeps are probably more effective at herding flatfish inwards to the path of the net under daylight conditions. This disparity is probably responsible for the observed pattern of higher flatfish catches at night with survey nets, where bridles and sweeps are kept to minimal length, as compared to higher daytime catches with commercial flatfish nets and lengthy sweeps. These differences, as explained by the results of this work, highlight the importance of fish behavior for fish capture technology.

## Acknowledgments

We wish to thank C. Hammond and J. Gauvin for assistance with the at-sea portion of this project, as well as the captain and crew of the FV *Cape Horn*. M. Ottmar, and S. Haines assisted with animal husbandry and laboratory experiments. A. Stoner, M. Davis, B. Laurel, and T. Hurst provided helpful comments and discussion of ideas explored in this research, and R. Hannah and W. Wakefield provided helpful critiques of an early draft of this manuscript. C. Sweitzer assisted with manuscript preparation.

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