Abstract—Survey selectivity can be viewed as a function of the availability of the stock to the sampling gear and the sampling efficiency of the gear. A dome-shaped survey selectivity function is one in which survey selectivity decreases with larger and older fish. Such a function is estimated for eastern Bering Sea (EBS) Pacific cod (Gadus macrocephalus) in the NOAA National Marine Fisheries Service stock assessment model, which would be appropriate if large (≥55 cm in fork length) Pacific cod avoid capture by the EBS survey bottom trawl. To test this assumption, a field study was conducted to determine whether large Pacific cod escape capture by either outswimming the survey trawl or by swimming above the trawl. Our results show that large Pacific cod do not outswim the trawl because catches did not increase when we increased towing speed. Additionally, large Pacific cod do not routinely swim above the trawl because analysis of acoustic backscatter collected concurrently with trawl hauls indicated that only 4% of the acoustic backscatter attributed to Pacific cod occurred at heights above the headrope. We found no evidence that survey-gear efficiency decreased with increasing fish length either because large fish outswam the trawl or because they tend to occur further from the bottom. Therefore the results of our experiment do not support the use of a dome-shaped survey selectivity function in the EBS Pacific cod assessment model.

Is the survey selectivity curve for Pacific cod (Gadus macrocephalus) dome-shaped? Direct evidence from trawl studies

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Fisheries stock assessment surveys are intended to produce an index of relative stock abundance that varies over time in constant proportion to the true stock abundance. In stock assessment models, the scaler that relates modeled abundance to a survey index is often considered a product of a constant catchability and of a fish age- or length-dependent survey selectivity function (which, hereafter, for reasons of simplicity, we refer to as length-dependent functions, but the same concept applies to age-dependent functions). Both catchability and selectivity are typically estimated when a stock assessment model is fitted to data (Maunder and Piner, 2015), although, in some cases, the catchability coefficient is fixed a priori (Thompson1,2,3). The selectivity of a survey can be viewed as a function of the availability of the various biological components of the fish stock to the sampling gear and of the sampling efficiency of the gear (i.e., the proportion of encountered animals that are captured; Maunder et al., 2014). However, the relative


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son1,2,3; Fig. 1). This dome-shaped functional form has
≥ function that, after being fitted to the data, decreases
configurations, includes a flexible survey selectivity
NOAA National Marine Fisheries Service for fishery
positions from 1994 onward (Lauth and Nichol, 2013).
length compositions dating back to 1982 and age com-
the survey provides estimates of relative abundance and
in the EBS (hereafter referred to as
Gadus macrocephalus
in fork lengths.
Figure 1
Length-based survey selectivity curve derived from the
stock assessment of Pacific cod (Gadus macrocephalus)
for the Bering Sea region in 2013. Lengths are given
in fork lengths.
importance of availability (e.g., Do small fish occur at
depths shallower than those of surveys?) and sampling
efficiency (e.g., Do small fish pass through trawl mesh?)
in determining the shape of a selectivity function is
difficult to determine without additional information.
The shape of the survey selectivity function is at
issue for the model used for stock assessment of Pa-
ic cod (Gadus macrocephalus; Thompson1,2,3) in the
eastern Bering Sea (EBS). The assessment model, con-
ducted with the Stock Synthesis package, vers. 3.24q
(Methot and Wetzel, 2013), is fitted to commercial
catch data dating back to 1977, as well as to fisheries-
independent data from the National Marine Fisheries
Service annual bottom trawl survey of demersal fishes
in the EBS (hereafter referred to as the survey). The
survey provides estimates of relative abundance and
length compositions dating back to 1982 and age com-
positions from 1994 onward (Lauth and Nichol, 2013).
The current assessment model accepted by the
NOAA National Marine Fisheries Service for fishery
management, in addition to several historical model
configurations, includes a flexible survey selectivity
function that, after being fitted to the data, decreases
at larger (≥55 cm in fork length [FL]) fish sizes (Thomp-
sen1,2,3; Fig. 1). This dome-shaped functional form has
rising and descending limbs to either side of the top.
The descending limb on the right side suggests that
larger fishes are less vulnerable to the survey in some
way, perhaps because they are better able to escape the
trawl or are separated spatially from smaller fishes.
In contrast, the more traditional asymptotic, survey
selectivity function implies that the survey is sampling
a greater proportion of the large fishes in the popula-
ion. If an assessment model is not well informed by
the data, there will be uncertainty about whether the
shape of the estimated function accurately reflects the
survey sampling processes or whether it reflects pa-
parameter confounding in the model (Maunder and Punt,
2013). The difference between interpretations of the
shape of the estimated function with regard to these
2 types of uncertainty may have a pronounced effect
on the determination of stock size and recommended
harvest rates.
Field studies designed to describe survey-gear effi-
ciency and stock availability provide a source of “di-
rect” evidence and can be useful in the fitting of the
selectivity function (Cadrin et al., 1999; Weinberg et
al., 2004; Clark and Kaimmer, 2006; Nichol et al., 2007;
Somerton et al., 2007; Somerton et al., 2013). We pre-
sent the results from a new study and review results
from previous works to determine whether direct evi-
dence from field studies corroborates the dome-shaped
survey selectivity function estimated by the current as-
essment model used for Pacific cod. Although we focus
on Pacific cod, the concept that field experiments can
better inform assessment models is applicable world-
wide for multiple species.
If it is assumed that the survey covers the entire
geographic range of Pacific cod in the EBS, a dome-
shaped selectivity function could result from a progres-
sive decrease in trawl sampling efficiency for larger fish
sizes. Sampling efficiency is dictated by 3 processes:
vertical herding, horizontal herding, and escapement,
all of which are dependent on trawl design, fishing pro-
duences, fish behavior, and swimming endurance. To-
gether, these processes play an important role in esti-
mates of abundance and size composition of groundfish
resources (Godø and Walsh, 1992).
Although studies on the behavior of Pacific cod are
scarce, evidence has been collected from various field
and laboratory experiments on other cold-water gadids
and various demersal species, clearly showing that fish
swimming stamina and reactions to trawling are spe-
cies specific (He and Wardle, 1988; Winger et al., 1999),
size dependent (Main and Sangster, 1981; He and War-
dle, 1988; Winger et al., 1999), temperature affected
(He, 1991; Winger et al., 1999), light responsive (Glass
and Wardle, 1989; Walsh, 1991), and often density de-
pendent (Godø et al., 1999; Kotwicki et al., 2014). Not
all studies have come to the same conclusions for all
species, or even within the same species in all cases,
but the most universal observation is the inverse re-
lationship between swimming speed and endurance.
The faster a fish swims, the more energy required and
the less time it is capable of sustaining such speed. If,
however, a fish is able to swim fast enough and long
enough to outpace a survey trawl, sampling efficiency
will be reduced. Likewise, if large Pacific cod, more so
than smaller Pacific cod, have the strength and stami-
na to outswim the survey trawl, survey selectivity will
be reduced for the larger animals.
In addition to the possibility that larger Pacific cod
avoid capture by outswimming the trawl, it is also pos-
sible that larger Pacific cod occur higher in the water
column and are more likely to swim over the headrope
of the survey trawl. The presence of fish in the wa-
ter column can be documented by using acoustic data
collected at the time of trawling. Analysis of acoustic
data to estimate abundance has not been attempted for Pacific cod because of concerns stemming from the confounding of backscatter signals close to the seabed (i.e., separating the weaker fish signal from the stronger seabed signal), in the area known as the acoustic dead zone (Ona and Mitson, 1996), and from the difficulty of separating species-specific backscatter when multiple species with swim bladders, such as Pacific cod and walleye pollock (Gadus chalcogrammus), co-occur.

Our objective was to report the results of an experiment aimed at examining whether survey trawl efficiency decreases for large-size Pacific cod because they outswim the trawl or because they pass over its headrope. If such size-specific trawl efficiency can be demonstrated, it would support the application of a dome-shaped function in the stock assessment model for Pacific cod.

Materials and methods

Experimental design

Our experiment was designed to test the hypothesis that a substantial proportion of large Pacific cod avoid capture by outswimming the survey trawl under standard survey protocols (Stauffer, 2004). Secondarily, we were also able to provide a test of the hypothesis that a substantial proportion of Pacific cod are unavaiable to the trawl because they are in the water column above the headrope of the survey trawl. A Pacific cod was considered large if its FL was ≥55 cm, a definition based on lengths at the right tail of the selectivity schedule estimated in the 2013 stock assessment of EBS Pacific cod (Thompson1), for which estimated survey selectivity was less than 100.0 percent (Table 1, Fig. 1).

The experiment took the form of paired parallel tows: one vessel trawled at the survey standard speed of 1.5 m/s (3 kn, slow), while the other vessel towed at a faster speed of 2.1 m/s (4.0 kn, fast). Various Bering Sea fishermen of Pacific cod have reported tow speeds that range from 1.25 to 2.25 m/s (2.5–4.5 kn), depending on vessel power, mesh size, and other trawl design features (senior author, personal commun.). We felt the upper limit for towing the survey trawl should be no more than 2.1 m/s in order to maintain proper fishing configuration (Weinberg, 2003). At such a speed, we were 0.15 m/s short of the fastest speeds for commercial towing. If the number of large Pacific cod captured in the standard slow tows is no different from the number caught in the faster tows, we would conclude that Pacific cod did not outswim the survey trawl.

Field operations

The experiment was conducted during 3–5 August immediately following the 2013 NOAA EBS bottom trawl survey aboard the 2 trawlers used for the survey. An 83-112 eastern trawl (standard for the EBS survey) was used in this experiment. The 83-112 eastern trawl is a 2-seam flatfish trawl with a 25.3 m (83 ft) long headrope and a 34.1 m (112 ft) long footrope (more details are provided in Weinberg, 2003; Lauth and Nichol, 2013). The simple 5.2 cm diameter footrope is weighted with 75 kg of chain hung in equal loops along its length from which the nylon netting is attached. Mesh size varies from a maximum of 10.2 cm in the wings and throat to a minimum of 3.2 cm for the liner in the codend. Each side of the net is attached to a steel V-door (1.8×2.7 m) that weighs approximately 816 kg by a pair of 54.9-m-long, 1.6-cm-diameter bare wire bridles. Because faster trawling has been shown to exacerbate inconsistencies in seabed contact of this trawl (Weinberg, 2003), an additional 34 kg of weight was secured to the footrope, then monitored with a bottom contact sensor for all tows in this experiment.

The major difference between tows of our experiment and standard survey tows was towing speed. All other trawling procedures followed those used during the survey (e.g., straight-line towing, locked winches with equal lengths of warp, standard warp length to depth ratios, and setting and retrieval methods designed to lower the net down on the seabed in fishing configuration quickly at the start of a tow and to raise it off the seabed quickly at the end of a tow). Our balanced-pair design called for repetitive parallel towing and vessels safely separated by no more than 463 m (0.25 nmi). On odd-numbered pairs, one vessel was randomly selected to tow at the standard survey speed of 1.5 m/s, while the other vessel towed at the faster speed of 2.1 m/s. On even-numbered pairs, the vessels switched towing speeds. To reduce potential bias from sea conditions, the faster boat was randomly appointed to fish either the port or starboard side of the slower boat.

When fishing with 2 boats at different speeds, we had a choice of enforcing either consistent tow duration (time) or consistent tow length (distance). Because it has been shown that variation in tow durations (15.0

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<th>Length group (cm FL)</th>
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<td>0.9</td>
<td>55–60</td>
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<tr>
<td>0.8</td>
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<td>66–69</td>
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<tr>
<td>0.5</td>
<td>75–79</td>
</tr>
<tr>
<td>0.4</td>
<td>80–88</td>
</tr>
<tr>
<td>0.3</td>
<td>89–105</td>
</tr>
</tbody>
</table>

Table 1
Survey selectivity (rounded to one decimal place) by length group based on the length-based schedule of the 2013 assessment model used for Pacific cod (Gadus macrocephalus) in the eastern Bering Sea. Ranges for length groups are provided in fork lengths (FLs).
and 30.0 min) did not affect the size distribution of catches for some Atlantic species, including Atlantic cod (Gadus morhua; Gode et al., 1990; Walsh4), we elected to reduce the duration of the faster tows so that the distance fished and swept area of tows were similar between the 2 speeds (Wileman et al., 1996). Hence, the duration of the slow (1.5 m/s) and fast (2.1 m/s) tows were set at 30.0 and 22.5 min, respectively, measured from the time the nets were on bottom and the winches were locked to the time when trawl retrieval was initiated.

Towing occurred at 2 independent sites, one at a depth of 136 m and the other at a depth of 86 m. Ten successful pairs of fast and slow tows were made at the deep site, and 14 pairs were completed successfully at the shallow site. All captured Pacific cod (sex not determined) were measured to the nearest centimeter (FL).

Data analysis

Swept area Swept area for each haul was estimated as the average net width from data collected with a Marport5 acoustic net mensuration system (Marport Stout Inc., Snohomish, WA), multiplied by the length of the tow path, derived from GPS data of vessel locations at first and last contact of the footrope with the seabed; seabed contact was determined with a bottom contact sensor (Somerton and Weinberg, 2001). Outlier measurements of net width were removed by using a sequential outlier rejection algorithm, and the remaining data were fitted with a smoothed spline from which the average net width was calculated for each tow (Kotwicki et al., 2011).

Measuring the swept area of each tow was complicated by instrument failure during some tows. Therefore, only a subset of all tows produced valid net width data. Paired t-tests were used to test for a difference in the swept area between the fast and the slow tows of each pair where net widths were available for both tows. If the difference was found not to be significant (P>0.05) in this subset of tows after the data from our bottom contact sensors were examined thoroughly for anomalies that would indicate the likelihood of high variability in net width during a tow, we assumed the swept area was not different for any paired tows and used the raw catch (counts) from all tows as the dependent variable in subsequent analyses.

Effect of towing speed on catch The null hypothesis that the catch of large Pacific cod at a fast towing speed (c_f) was no different than the catch of large Pacific cod at a slow towing speed (c_s) was tested by using paired-sample tests, against the one-sided alternative that c_f was greater than c_s. First, the probability of either towing speed being equally likely to obtain greater catch was calculated with a sign test: the binomial probability that c_f was greater than c_s in x pairs (successes) out of the total y pairs of tows (trials) observed if the null hypothesis of no effect of speed on catch was true. A paired t-test was then conducted to further confirm the result of the less-sensitive, but more robust, sign test. The null hypothesis of the t-test was that there was no mean difference (d) between ln(c_f) and ln(c_s) of the paired tows (H_0: d=0, i.e. the mean ratio c_f/c_s = 1), assuming that the differences between pairs were normally distributed. The power (1−β) of the t-test was calculated for a 1-sided (H_0: d>0) alternative hypothesis on the basis of the t-distribution, observed standard deviation (SD) of ln(c_f) − ln(c_s), sample size (n) of 24 pairs of tows, and significance level (α) of 0.05. The power was calculated for a range of d for H_0 from 0.1 to 1.0, where e^d χ^2 (d/c_s).

Finally, we estimated d on the basis of the length-derived, double normal, survey selectivity schedule from the stock assessment model for Pacific cod in the EBS (see appendix A in Methot and Wetzel, 2013; Thompson). For our study, we assumed that at the fast towing speed, no large Pacific cod can escape the net and all available fish are caught and that at the slow towing speed, the large Pacific cod available can escape the net in the proportion indicated by the survey selectivity function. To increase our sample size, we pooled the numbers of fish caught in this experiment into length groups with the same survey selectivity, rounded to the first decimal place (Table 1). The total expected catch in a tow based on the curve (c_e) was calculated as the sum of the catch in each length group in the slow tow (c_e) divided by the survey selectivity for that length group (s_l): c_e = Σ c_l s_l. On the basis of the assumptions, c_e would be the expected catch in a fast tow. Therefore, the mean ratio of expected catch to the catch of the slow tow for the n pairs of tows, Σ c_l c_e/c_e, would be the expected mean ratio of catch in the fast tow over the slow tow.

Vertical distribution Simrad ES60 echosounders were used in both survey vessels (Kongsberg Maritime AS, Kongsberg, Norway) and operated at frequencies of 38 and 120 kHz with a sampling rate of 1–2 pings/s to collect acoustic backscatter data. The sampling resolution of these data was approximately 0.2 m vertically and 0.8–2.1 m horizontally at ship speeds of 1.5 and 2.1 m/s (at 3 and 4 kn). Given nominal beam widths of 7° at both frequencies, depth of the hull-mounted transducers (4 m), and depth of the seafloor at the deep study site (136 m), the extent sampled by each ping was a circle with a diameter of approximately 16 m (close to the 18-m average net width for this depth) and an area of 205 m². These data were analyzed with Echoview, vers. 5.4.90 (Echoview Software Pty. Ltd., Hobart, Australia), which afforded us the opportunity to detect whether Pacific cod occurred above our net opening at

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5 Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.
the moment they were sampled by the echosounder on the vessel.

The difference between frequencies (120 and 38 kHz) in mean volume backscattering strength ($S_v$, dB re 1/m; cf. MacLennan et al., 2002) was used to identify backscatter consistent with that of fishes with swim bladders. For analysis, backscatter data were grouped in bins, each of which had a resolution of 20 pings (horizontal) by 5 m (vertical). Bins for which the difference between $S_v$ at 120 kHz and $S_v$ at 38 kHz was between $-10$ and $8$ dB were classified as backscatter that indicated fish (De Robertis et al., 2010). Only bins for which the backscatter had a signal-to-noise ratio of at least 10 dB (De Robertis and Higginbottom, 2007) were included in the analysis.

Fish backscatter per unit of area ($s_A$, m$^2$/nmi$^2$) was then integrated by using an $S_v$ integration threshold of $-70$ dB in several depth layers referenced to a 0.25-m backstep above the seabed echo (0.25–2.0, 2.0–2.5, 2.5–3.0, 3.0–7.0, and 7.0–16.0 m). The upper bound of the first depth interval matched the mean headrope height of this experiment. Similarly, a height of 2.5 m corresponds to a survey-wide average headrope height for the 83-112 eastern trawl used to assess Pacific cod in the EBS (Nichol et al., 2007), a height of 7.0 m corresponds to a survey-wide average headrope height for the poly-Noreastern trawl used by the NOAA Alaska Fisheries Science Center to assess Pacific cod in the Gulf of Alaska region (Nichol et al., 2007), and a height of 16.0 m corresponds to an estimated effective fishing height for the 83-112 eastern trawl that is used to assess walleye pollock in the EBS (Kotwicki et al., 2013) and that perhaps may apply to Pacific cod as well.

The results of this analysis of backscatter data were examined for evidence of fish above the headrope height (mean: 2.0 m) during the time the demersal trawl was in contact with the seabed, after accounting for horizontal setback of the trawl behind the vessel (approximately 3–4 min depending on vessel speed). The acoustic assessment was restricted to the deep study site because catches there consisted almost exclusively of Pacific cod and flatfishes and, therefore, it was reasonable to assume that any backscatter that indicated fish with swim bladders was a result of the presence of Pacific cod. It was not possible to make such an assumption for data collected at the shallow study site because the catches there were dominated by walleye pollock, which cannot be acoustically distinguished from Pacific cod.

**Results**

**Summary of catches**

During the 48 experimental tows, 1462 Pacific cod, ranging in size from 34 to 105 cm FL, were caught, but only 2 fish were larger than 90 cm FL (Fig. 2). Of the captured fish, 701 individuals were large ($\geq 55$ cm FL) and included in further analyses. The bottom temperatures during the experiment ranged between 2.6°C and 2.7°C.

**Swept area**

Of the 24 paired tows, 16 pairs had reliable net mensuration data with which we could test differences in swept area by pair. The mean difference in swept area between paired tows (fast and slow) was $-0.072$ ha, a variance that was not significant ($t=-0.492$, df=15, $P=0.63$). The fast tows swept a greater area than that swept by the slow tows during half of the pairs (8 of 16 tows). Conversely, the slow tows swept a greater area than that swept by the fast tows during the other half of pairs. Bottom contact sensors provided reliable data...
on all tows, indicating that trawl footropes were firmly in contact with the substrate and providing evidence for our decision to use all 24 pairs of data in subsequent analyses.

**Effect of towing speed on catches**

Fast tows had larger catches of large Pacific cod in only 10 of 24 paired tows. In those 10 pairs, the catches from fast tows were 1.1 to 2.7 times (mean: 1.6 times) greater than the catches from slow tows (Table 2). A sign test indicated that larger catches were not significantly more frequent in fast tows (successes=10, trials=24, \( P = 0.924 \)); larger catches in at least 18 of the 24 pairs would be required for significance (\( P \leq 0.05 \)).

The mean difference \( \bar{d} \) between \( \ln(c_f) \) and \( \ln(c_s) \) of −0.08 (SD 0.55) was approximately normally distributed according to a \( \chi^2 \) goodness-of-fit test (\( \chi^2_{5,21}=1.226, P=0.54; \) Fig. 3). The mean of \( c_f/c_s \) was 1.1 (SD 0.58) (range: 0.3–2.7; Table 2). A paired \( t \)-test indicated that the difference in \( \ln(\text{catch}) \) between fast and slow tows was not statistically significant (\( t_{23}=-0.69, P=0.50 \)). The expected mean ratio of the catch of large Pacific cod in fast tows over slow tows (\( c_f/c_s \)) was 1.5 (range: 1.3–1.9). If the expected ratio of 1.5 were true, then the power of a 1-sided \( t \)-test (\( H_0: \bar{d}>0 \)) would be 97% in rejecting \( H_0 \) (Table 3).

**Vertical distribution**

Demersal fish backscatter was fairly low, as would be expected given the low numbers of Pacific cod captured. The strongest demersal fish backscatter (\( S_v \sim -45 \text{ dB} \)) appeared very close to the acoustically detected seabed; fish backscatter farther off the seabed was generally weaker in comparison (\( S_v \sim -65 \text{ dB} \)). The demersal fish backscatter observed below the average headrope height of 2.0 m during this study was a very large fraction of fish backscatter integrated over all depth layers examined (median proportion: 0.96; Fig. 4). In an absolute sense, the highest demersal fish backscatter values were found within the depth layer of 0.25–2.0 m (Fig. 5); the median fish \( s_A \) in this layer was more than 14 times that in any other depth layer.

**Discussion**

We failed to detect a difference between slow (1.5 m/s) and fast (2.1 m/s) towing speeds in the rates at which

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<td>1.4</td>
</tr>
<tr>
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<td>15</td>
<td>8</td>
<td>1.9</td>
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<tr>
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<td>7</td>
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<td>9</td>
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<tr>
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<td>16</td>
<td>9</td>
<td>1.8</td>
<td>13</td>
<td>1.4</td>
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</table>
Figure 3
Normal distribution curve fitted to a histogram of the differences in ln(catch) of large Pacific cod (Gadus macrocephalus) between fast and slow towing speeds (goodness-of-fit: $\chi^2_{5,2} = 1.226, P=0.54$) from this study conducted in 2013 in the eastern Bering Sea. ln(c$_{f}$) = catch at the fast towing speed of 2.1 m/s; ln(c$_{s}$) = catch at the slow towing speed of 1.5 m/s.

Table 3
Power of t-test (probability of rejecting H$_{0}$ when it is false) for the mean difference $d$ between ln(c$_{f}$) (c$_{f}$ = catch of fast tows) and ln(c$_{s}$) (c$_{s}$ = catch of slow tows), where H$_{0}$: $d = 0$, against one-sided H$_{a}$: $d > 0$ alternative hypothesis. The t-distribution was used with a degree of freedom of 23 and a significance level ($\alpha$) of 0.05.

<table>
<thead>
<tr>
<th>$d$</th>
<th>$e^{d} = c_{f}/c_{s}$</th>
<th>Power</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.1</td>
<td>1.1</td>
<td>0.21</td>
</tr>
<tr>
<td>0.2</td>
<td>1.2</td>
<td>0.53</td>
</tr>
<tr>
<td>0.3</td>
<td>1.3</td>
<td>0.83</td>
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<td>0.99</td>
</tr>
<tr>
<td>1.0</td>
<td>2.7</td>
<td>1.00</td>
</tr>
</tbody>
</table>

Figure 4
Boxplot indicating the proportion of demersal fish backscatter below headrope, in all depth layers examined (0.25–16.0 m above the sounder-detected bottom echo), found below the average headrope height but above the 0.25-m dead zone (0.25–2.0 m; n=20 tows), for this study conducted in August 2013 in the eastern Bering Sea. The line within the shaded box indicates the median value, the shaded box indicates the first and third quartiles, the horizontal lines outside the shaded box indicate a distance of 1.5 times the interquartile range above the third quartile and below the first quartile, and the plus marks indicate outliers outside these lines.

large Pacific cod (≥55 cm FL) were caught with the 83-112 eastern trawl. Therefore, we surmise that if the dome-shaped selectivity estimated in recent stock assessments (Thompson\textsuperscript{1,2,3}) is due to a decrease in trawl efficiency for large Pacific cod, that decrease is not attributable to fish outswimming the net. We are unaware of other direct studies on the swimming behavior of Pacific cod in relation to trawling activity. Consequently, to make inferences, we must draw upon the conclusions from research conducted on other, similar species.

Of the many species studied for their swimming capabilities, the Atlantic cod is most closely related to Pacific cod. Winger et al. (2000) performed a comprehensive tank study on the swimming stamina of At-
Atlantic cod and deduced that changes in towing speed would affect the catching efficiency of this species. In their study, Atlantic cod were subjected to water velocities that were slower than our towing speeds, but water temperatures were close to those in our study (2.6°C). At the towing speeds used by fishermen in the northeast Atlantic (1.0 m/s), Atlantic cod were able to maintain sustained swimming speeds for 10 min, but at a speed of 1.5 m/s (the slow towing speed in our study), they could maintain swimming speed for only 1 min. If Pacific cod swimming abilities are indeed similar to those of Atlantic cod, then, given the towing speeds of 1.5 m/s or greater used in our experiment, we expect that Pacific cod maximum sustained swimming speeds would not be enough to elude capture even during a haul lasting 22.5 min, the shorter tow duration used in our experiment.

Large Pacific cod do not escape capture by outswimming the survey trawl, as indicated by our study results: catches when towing at the fast speed were no different than catches when towing at the slow speed. This result indicates that, once Pacific cod reach the trawl mouth, they lack the means to swim fast enough or long enough to escape forward around the wing ends. In situ video evidence shows that this species tends to hold station in front of the footrope for only brief periods before slipping back into the net (Rose6). Large Pacific cod are unlikely to swim over the net because acoustic backscatter indicates that most Pacific cod, when in the presence of a trawler, occur very close to the bottom within the vertical fishing dimensions of the trawl. In addition, findings from previous studies on gadid behavior indicate that trawl gear elicits a diving response in fish, not a rising response. The remaining avenues for escapement that could explain lowered trawl efficiency are 1) large Pacific cod could swim through the small mesh of the survey net, an option that is physically impossible and 2) they could escape beneath the footrope, the frequency of which has been previously shown to be negligible (Weinberg et al., 2002).

If large Pacific cod are not outswimming the trawl, perhaps they are swimming over the headrope—a notion that would also explain a drop in selectivity for large fish related to both trawl sampling efficiency and availability. Here, we used fish backscatter to within 0.25 m of the seabed to assess the vertical distribution of Pacific cod near the seafloor during our experiment. This process discards potential backscatter from fish in the acoustic dead zone (Ona and Mitson, 1996), which is located very close to the seabed and could be an area of concern for an absolute estimate of all fish $s_A$. However, the distribution of fishes within the dead zone is less important for our main interest of detecting Pacific cod occurrence in relation to the headrope height of the trawl; indeed, if most Pacific cod are in the acoustic dead zone, they clearly are not above the headrope height during vessel passage.

Analysis of acoustic backscatter collected during towing indicated that only 4% of the total backscatter attributed to Pacific cod occurred above the height of the survey headrope, although the backscatter was measured at the vessel rather than at the net itself, meaning that any upward movement of fish after vessel passage would be undetected. Again, there are no previous studies on the vertical swimming behavior of Pacific cod in relation to trawls from which we can draw inferences. Studies of walleye pollock (Kotwicki et al., 2013) and Atlantic cod show that these 2 commercially important gadids were stimulated to dive, rather than rise; their response to trawl warps may be both acoustically, as well as visually, driven according to Handegard and Tjøstheim (2005). This behavior is also acknowledged by commercial fishermen who tend to drag their nets below semipelagic schools. There is, therefore, little reason to believe that Pacific cod swim over the headrope during this experiment.

Nichol et al. (2007) did, however, on the basis of 11 archival tags, provide evidence of an off-bottom portion of the Pacific cod vertical distribution during daylight hours (the time during which the EBS survey is conducted) when the fish were in an undisturbed state.
(i.e., tags were deployed in the absence of vessel noise or oncoming trawl gear). They postulated that large Pacific cod swim above the survey-wide average height of the headrope (2.5 m) approximately 53% of the time and within 10 m of the seabed 95% of the time. Although their study was based on an interpretation of estimated tidal activity, their work has had a pronounced impact on the current stock assessment model, such that the catchability coefficient was fixed so that the average product of catchability and selectivity size range (60–81 cm FL) equaled 47% (Thompson 1,2,3).

We agree with Nichol et al. (2007), in that it seems unlikely for the survey trawl to catch 100% of the Pacific cod in its path 100% of the time; however, we cast doubt on the conclusion that more than 50% of large fish swim above the trawl in the presence of trawling activity. Nichol et al.’s study was based on a very small sample, and one could argue that our study similarly lacked broad geographical range, over areas with varying habitat complexity, light intensity, and temperatures that (although never shown) may all have an effect on Pacific cod vertical distributions or perhaps even swimming speeds (Ferno et al., 2011). Additional experiments focusing on these factors would shed additional light on the matter.

Survey selectivity functions in stock assessment models are designed to be a parsimonious representation of the relative size dependency of the survey sampling process. However, stock assessment models can be quite complex, often including hundreds of parameters that must be estimated when the models are fitted to data (Maunder and Punt, 2013; Methot and Wetzel, 2013), and such complexity can lead to parameter correlation and confounding during model fitting. One example of this confounding is the correlation between survey selectivity parameters and the natural mortality rate (Thompson, 1994), a relationship that can lead to ambiguity in ascribing unexpectedly low catches at a particular fish length to either reduced survey selectivity or to an underestimated natural mortality rate.

We are, therefore, unable to corroborate the dome shape for the selectivity function of the survey of Pacific cod in the EBS by using direct evidence from this and other field studies in which trawl sampling efficiency has been examined. If the estimated survey selectivity function determined from the model is indeed correct, then the mechanisms that explain the steep descent of the right-hand tail must consist of something other than sampling efficiency. Four possible explanations for this steep descent of the right-hand tail are that 1) large fish migrate out of the survey grid, hence becoming unavailable to the survey; 2) sampling effort in preferred habitat of large fish embedded within the EBS survey area is not sufficient; 3) large fish prefer the small areas of rough, untrawlable bottom embedded within the EBS survey area; and 4) the relationships between availability and efficiency, on the one hand, and between catchability and selectivity, on the other, are complicated enough that studies of availability or efficiency alone are insufficient to explain catchability or selectivity (see Suppl. Text). If something is misspecified in the assessment model (e.g., perhaps the natural mortality rate is too low or varies with fish size), the selectivity of the survey for large Pacific cod would be closer to unity and could lead to a change in the harvest quotas. Therefore, further research on these subjects is needed to clarify the mechanisms responsible for the selectivity of the survey.

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