Abstract—A bottom trawl catch of flatfish is composed of fish that were initially in the path of the trawl net and fish that were initially in the path of the bridles and were subsequently herded into the net path. Bridle efficiency (i.e. the proportion of fish in the bridle path that are herded into the net path) for seven species of flatfish was estimated by fitting a model of the herding process to data collected during a field experiment. The experiment consisted of repeatedly making trawl hauls with three different bridle lengths. The model was then fitted to the catch of each species, by length class, as a function of the widths of the net and door spreads at the three bridle lengths. Bridle efficiency was independent of body length for five species (yellowfin sole, Limanda aspera; flathead sole, Hippoglossoides elassodon; rock sole, Lepidopsetta bilineata; Dover sole, Microstomus pacificus; rex sole, Glyptocephalus zachirus) and ranged from 0.22 for rex sole to 0.40 for rock sole. Bridle efficiency declined with increasing body length for two species (English sole, Parophrys vetulus; Pacific sanddab, Citharichthys sordidus), ranging from about 0.35 to 0.10 over the lengths sampled.

Bridle efficiency of a survey trawl for flatfish

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Swept-area estimates of biomass produced by bottom trawl surveys are typically used as relative indices of stock size rather than absolute measures because the sampling efficiency of the trawls1 is rarely known. As a means to estimate trawl efficiency, Dickson (1993a) developed a model describing the trawling process and the associated fish behavior from an undisturbed state before arrival of a fishing vessel until passage of a trawl codend. For benthic species that remain closer to the sea bottom than the head-rope height, this model specifies that trawl efficiency is primarily determined by two processes: escapement of fish out of the net path by passing either under the footrope or through the mesh (net efficiency) and herding of fish into the net path by the doors, mudclouds, and bridles (bridle efficiency). In our study, we focused on fish herding, considering the problem of quantitatively estimating bridle efficiency or the proportion of fish encountering the bridles that are herded into the net path.

Underwater observations of trawls in operation have revealed that the process of herding differs between semipelagic species, such as Atlantic cod (Gadus morhua) and haddock (Melanogrammus aeglefinus) that tend to swim near the bottom, and benthic species, such as flatfish that often remain in direct contact with the bottom (Main and Sangster, 1981b). Atlantic cod are apparently stimulated to herd by the sight of the trawl doors and the mudclouds that form in the wake of the doors, whereas flatfish are stimulated to herd by the close proximity or actual touch of the doors and lower bridles as they sweep along the bottom (Hemmings, 1969; High, 1969; Martyshevskii and Korotkov, 1969; Main and

Sangster, 1981a, 1981b). Flatfish, once stimulated to move, tend to swim a relatively short distance in a direction perpendicular to the bridles where they slow down or settle on the bottom until the bridle again overtakes them. This pattern is usually repeated, producing what appears to an observer on the trawl headrope as a zigzag path toward the center of the trawl footrope (Main and Sangster, 1981b). While this is occurring, however, flatfish may either swim over the bridle or become exhausted and be overtaken by the bridle and thereby escape the herding process. Bridle efficiency is determined by the relative frequency of such events.

Perhaps because the mechanism of herding seems more obvious for flatfish than other types of fish, the earliest mathematical models of fish herding were based on the contact-swim-contact pattern of flatfish herding (Hemmings, 1969; Foster et al., 1981; Fuwa et al,. 1988; Fuwa, 1989). These models were focused on individual fish and typically considered both the physical aspects of the trawl, such as shape and speed, as well as the biological aspects of the fish, such as size and endurance. Although these models provided a more structured way of examining fish herding and allowed the quantitative evaluation of the relative importance of the various aspects of the process, they were of limited use in estimating bridle efficiency of specific trawls because some of the required parameters were unknown or difficult to estimate.

The approach to modeling fish herding changed markedly after Engas and Godø (1989a) conducted trawling ex-

¹ Throughout this paper, we will refer to the trawl as an entire fishing gear comprising the net, bridles, and doors.

periments to quantitatively examine the effects of variations in bridle length on catch for each area and fish size. Reasoning that the changes in catch that accompanied the changes in bridle length provided information on the efficiency of herding, Dickson (1993b) estimated the bridle efficiency coefficients for Atlantic cod and haddock by fitting a simple linear model of the trawl herding process to data from Engas Godø's (1989a) experiments. Ramm and Xiao (1995) conducted a similar trawl herding experiment and developed a new type of herding model appropriate for cases in which escapement at the center of the trawl is zero.

In our study, we extended Dickson's (1993a) herding model so that it is more specific to the peculiarities of flatfish herding and additionally extended Dickson's (1993b) approach to fitting the model to data by providing a more rigorous statistical foundation. The model was then applied to herding data for the 83-112 Eastern bottom trawl (Armistead and Nichol, 1993) used by the Alaska Fisheries Science Center (AFSC) to conduct its annual bottom trawl survey of the Eastern Bering Sea. These data were collected during two herding experiments, patterned after those of Engas and Godø (1989a), in which emphasis was placed on seven species of flatfish: yellowfin sole (*Li*manda aspera), flathead sole (Hippoglossoides elassodon), rock sole (Lepidopsetta bilineata), English sole (Parophrys vetulus), Dover sole (Microstomus pacificus), rex sole (Glyptocephalus zachirus), and Pacific sanddab (Citharichthys sordidus).

Materials and methods

Development of the herding model

Consider that the area of the bottom swept by a trawl consists of two components, the area between the wingtips of the net (net path), and the area between the wing tips and the doors (bridle path; Fig. 1). The catch (N) obtained in a trawl can be represented as some proportion, k_n , of the number of fish in the net path (N_n) plus some proportion, P, of the number of fish in the bridle path (N_b). If the probability of capture for a fish herded into the net path is identical to that of a fish initially in the net path, then P can be considered equal to $k_n k_b$, where k_b is the bridle efficiency² or the proportion of fish within the bridle path that is herded into the net path. Algebraically this is expressed as

$$N = k_n N_n + k_n k_b N_b. (1)$$

The numbers of fish within the net and bridle paths are equal to the fish density (*D*) multiplied by the path areas, that is.

$$N_n = DLW_n$$

$$N_b = DL (W_d - W_n),$$
(2)

where L = tow length;

 W_n = the width of the net path; and W_d = the width of the door path (Fig. 1).

Combining all terms, the total catch then can be expressed as

$$N = k_{p}DLW_{p} + k_{p}k_{b}DL (W_{d} - W_{p}).$$
 (3)

At this point the model is quite similar to the one proposed by Dickson (1993a) to describe the trawl catching process for Atlantic cod and haddock. We now modify the model to make it more specific to flatfish by considering that herding is restricted to the portion of the bridle path in which the lower bridle is in contact with the bottom. This can be expressed as

$$N = k_n DLW_n + k_n hDL (W_d - W_n - W_{off}),$$
 (4)

where W_{off} = the width of the path in which the bridle is not in contact with the bottom; and

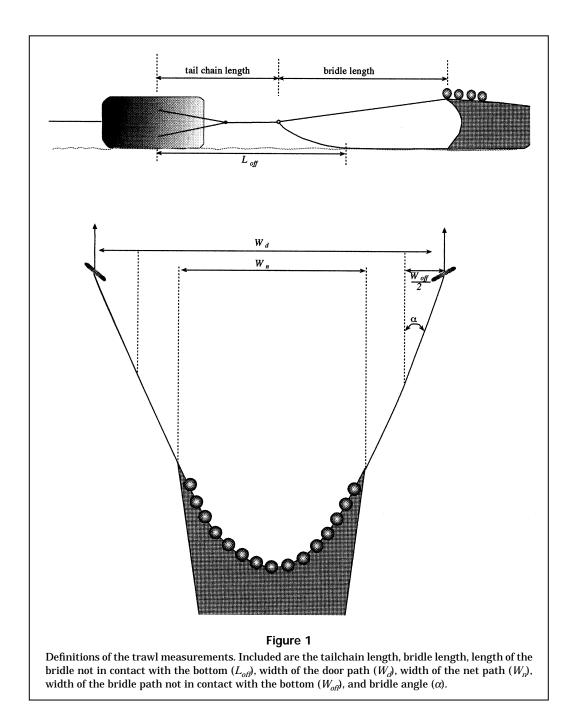
h = the herding coefficient or the proportion of fish in the bridle contact path that is herded into the net path.

Thus, k_b is the average efficiency over the entire bridle path and h is the average efficiency in the portion of the bridle path where herding actually occurs.

Description of the herding experiments

The strategy that we used in our herding experiments was to repeatedly trawl in such a way that the width of the net path was held approximately constant, whereas the width of the door path was varied among three distances by changing the length of the bridles. The first of two herding experiments was conducted 25 July-2 August 1994 aboard the FV Arcturus in the eastern Bering Sea and focused on yellowfin sole, flathead sole, and rock sole. The second experiment was conducted 14-25 September 1994 aboard the RV Alaska off the coast of Washington State and focused on English sole, Dover sole, rex sole, and Pacific sanddab. For both experiments, we used a blocked sampling design to minimize the effects on catch of the spatial variation in fish density. In each geographic block, three nearby, but nonoverlapping, 30-min trawl hauls at a speed of 1.5 m/s were made with each of three bridle lengths chosen in random order. Bridles measured 27 m, 55 m (the standard length used on AFSC surveys), and 82 m in length and were constructed of 16-mm diameter steel cable. Tailchains connecting the doors to the bridles (Fig. 1) were always constructed of 13-mm diameter long link chain but differed in length between vessels (Table 1). Trawl doors were always a "V" style measuring 1.8 m × 2.7 m and weighing 910 kg. On all hauls, spreads of the doors were measured at the tops of the wings simultane-

 $^{^2}$ In Dickson (1993a) this same quantity is referred to as sweep efficiency (k_s). We use the term "bridle efficiency" because the 83-112 Eastern trawl does not have sweeps connecting the bridles to the doors as does the trawl considered by Dickson.



ously and continuously with an acoustic trawl mensuration system. Tow length was measured as the straight line distance between the GPS positions of first and last footrope contact with the bottom determined with a time-depth recorder attached to the headrope. Bottom temperature was recorded at two second intervals with a bathythermograph and averaged 3.0°C during the eastern Bering sea experiment and 7.0°C in the West Coast experiment. Bottom depth averaged 76 m during the eastern Bering sea experiment and 67 m in the West Coast experiment. The catch from each haul was first sorted to species; then the catch of each species was weighed in the aggregate and fish

of each species were individually measured for total length in centimeters. Both experiments were conducted during daylight hours to best approximate the sampling protocol used on most AFSC bottom trawl surveys.

Estimating W_{off}

The herding experiments provided data on N, L, W_{c^h} and W_{n^*} but obtaining data to estimate W_{off} required a different type of experiment. We obtained the necessary data by directly observing the contact of the lower bridle with the bottom on an experimental cruise conducted 9–12 Septem-

Table 1

Trawl configuration parameters for each herding experiment. Included are the bridle and tail chain lengths that were used, the number of sampling blocks occupied, and the means and standard deviations (in parentheses) of the wing spread, door spread, and bridle angle. Also included are the mean values for the bridle off-bottom path width (W_{off}). WA = Washington State.

Experiment	Bridle length (m)	Tailchain length (m)	Number of blocks	Wing spread (m) (<i>W_n</i>)	$\begin{array}{c} \text{Door} \\ \text{spread} \\ \text{(m)} \\ \text{(W_d)} \end{array}$	Bridle angle (deg) (α)	Bridle off-bottom path width (m) (W_{off})
Bering Sea	27.3	13.9	15	18.0 (0.6)	44.6 (2.1)	18.9 (1.2)	23.3
	54.6	13.9	15	17.3 (0.6)	58.7 (2.9)	17.6 (1.0)	21.8
	81.6	13.9	15	17.1 (0.5)	71.6 (3.7)	16.6 (1.0)	20.5
West Coast (WA)	27.3	8.0	19	17.7 (0.3)	41.9 (0.7)	20.0 (0.5)	24.1
	54.6	8.0	19	17.1 (0.6)	57.5 (1.5)	18.8 (0.7)	23.1
	81.6	8.0	19	16.8 (0.3)	70.0 (1.5)	17.3 (0.5)	21.3

ber 1995 aboard the RV *Alaska* off the coast of Washington State using the 83-112 Eastern trawl equipped with standard 55-m bridles. The experiment consisted of recording views of the lower bridle with a silicon-intensified target (SIT) video camera while the trawl was in operation. The camera was mounted in a positively buoyant case attached to the upper bridle with a 1-m tether line and aligned so that the lower bridle directly below the attachment point could be viewed. The tether was positioned at 5-m intervals between 23 m and 43 m behind the doors. One 15-min tow at each of the five bridle positions was taken at both depths of 20 m and 35 m.

The video tapes were subsequently analyzed to determine the degree of bottom contact at each bridle position. This was done by viewing each tow at ten randomly chosen 10-sec sampling intervals. Bottom contact was recognized by the presence of sediment that is mixed into the water at the point of contact. Because the bottom is irregular, when the bridle has weak contact, just the tops of the irregularities are touched, whereas when the bridle has strong contact, the entire bottom in the field of view is touched. The average percentage of the bridle in the field of view that was in contact with the bottom was scored according to the following four-level scale: 1) no contact, 2) \leq 25% contact, 3) \geq 25% and \leq 75% contact, 4) \geq 75% contact. The degree of bottom contact at each bridle position and depth was then estimated as the mean of the ten evaluations.

The length of the bridle not in contact with the bottom $(L_{off}, Fig.~1)$ was defined as the distance between the attachment of the tailchain to the door and the point along the bridle where bottom contact was 50%. To estimate L_{off} a logistic function was fitted to the bottom-contact and bridle-position data with generalized linear modeling (Venables and Ripley, 1994), then the fitted logistic equation was evaluated at a bottom contact score of 3.0 (i.e. bottom contact >25% and <75%). Variance of L_{off} was estimated with bootstrapping (Efron and Tibshirani, 1993), where the bootstrap samples were obtained by randomly choosing, with replacement, from the haul mean scores at each bridle position.

In subsequent analysis, L_{off} was treated as a constant for all three bridle lengths and for both vessels. However the variable actually used in the herding model, W_{off} , was calculated as L_{off} multiplied by the sine of the bridle angle (Fig. 1) and therefore varied slightly between bridle lengths and experiments because the bridle angle varied.

In addition to the camera placements for measuring $L_{\it off}$, we also made placements at bridle positions both closer to the doors to examine for any evidence of herding in the area where the lower bridles were not in contact with the bottom and closer to the wing tips to determine if bottom contact was maintained continuously near the junction of the bridle and wing.

Fitting the model to the herding data

The herding model (Eq. 4) was modified in several ways to clarify the way it was fitted to the experimental data and to better define its underlying statistical structure. First, because of the block design of the experiment, fish density (D) was considered to be a constant within each block but to vary between blocks. Furthermore, net efficiency (k_n) was also considered to be a constant for all tows within a block because depth and other bottom conditions are nearly constant but vary between blocks. Because D and k_n are both block-specific constants and are confounded in the model, they were combined into a new constant k. Second, herding can vary with fish length (Engàs and Godø, 1989a; Dickson, 1993b), therefore Equation 4 was modified to allow length dependency. The modified equation is

$$N_{ijk} = k_i [LW_n]_{ij} + k_i h_k [L(W_d - W_n - W_{off})]_{ii} + \varepsilon$$
 (5)

where the subscript i = block number;

j = bridle length within a block;

k =fish length class and

 $\varepsilon = \sim N(0, \sigma).$

For each size class, fitting Equation 5 to the herding data required estimation of N+1 parameters, where N is the number of blocks sampled (i.e. a unique value of k for each block and a common value of h for all blocks). Because the model is nonlinear, because of the product of k and h, it was fitted to the catch and trawl measurement data by using nonlinear regression (Venables and Ripley, 1994). Fish length classes used in the calculations were chosen such that the number of length observations was approximately equal among classes. Ten length classes were usually chosen, but for species with narrow length ranges, as few as eight were used. After fitting the model, estimates of the variances of the parameters were obtained from the inverse of the information matrix (Seber and Wild, 1989).

Bridle efficiency (k_b) for each size class was calculated from the estimated value of the herding coefficient (h) by using the relationship

$$k_b = h \left(1 - \frac{W_{off}}{(W_d - W_n)} \right).$$
 (6)

Although up to this point h was treated as a constant for all bridle lengths, k_b is not a constant because the proportion of the bridle path in contact with the bottom will vary with bridle length. Therefore k_b was evaluated only for the standard bridle length. Variance of k_b was approximated as

$$Var(k_b) = \left(1 - \frac{W_{off}}{(W_d - W_p)}\right)^2 Var(h). \tag{7}$$

Although the model that we used allows for length-dependent herding, herding may not be a length-dependent process in all species. We performed a simple test of linear length-dependency by regressing the estimated values of k_b on the midpoints of the associated length intervals. For species in which the slope was not significantly different from zero, the herding model was refitted to the data with all length intervals combined. For species in which the slope differed significantly from zero, we calculated a functional relationship between k_b and fish length. Among the possible relationships examined, the best fit was obtained with the exponential model

$$k_b = a + b \exp(cL), \tag{8}$$

where a, b, c are parameters; and L = the midpoints of the length classes.

Model fitting was done by using nonlinear regression. Variance of the predicted value of k_b was estimated with bootstrapping (Efron and Tibshirani, 1993), where the bootstrap samples were obtained by sampling the residuals from the regression, with replacement, and adding them to the predicted values of k_b . The functional relationship between the standard deviation of k_b and fish length was approximated by using a parabolic model fitted by linear regression.

One implicit assumption of the herding model is that h is constant for all three bridle lengths. We tested the validity of this assumption by comparing the goodness of fit of a modified version of the herding model to that of the original. In the modified model, the herding coefficient was represented as

$$h_l = h + dL$$

where h_I = the herding coefficient at bridle length L;

h = the mean herding coefficient for all bridle lengths;

d = a free parameter; and

L = a coded value of bridle length equal to -1, 0, 1 for the short, medium, and long bridles (with this notation, negative values of d indicate that h_l declines with increasing bridle length).

Because this is a comparison of two nonlinear models with differing numbers of parameters, we used as a measure of fit the penalized sum of squares; that is, RSS/(n-2p), where RSS is the residual sum of squares, n is the number of data values, and p is the number of parameters (Hilborn and Mangel, 1997, page 115). A linear change in h_l is considered significant when the penalized sum of squares for the modified model is less than that for the original model.

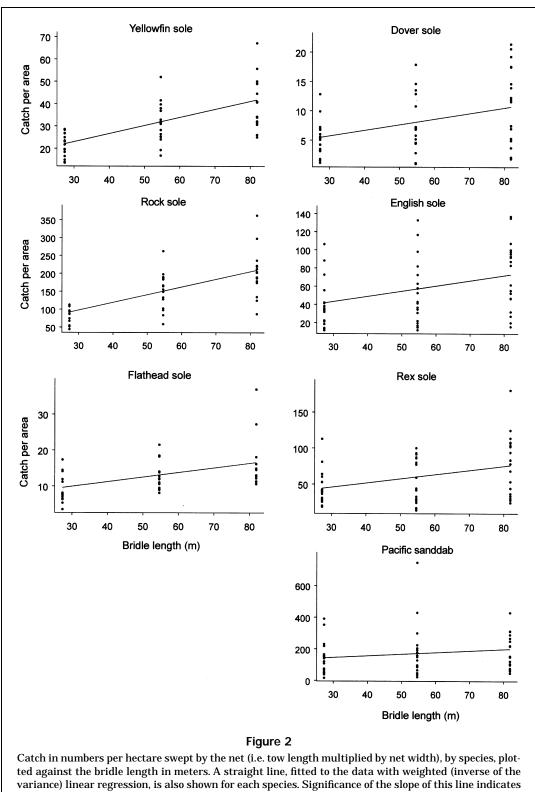
Results

Herding experiments

Fifteen blocks were completed in the Bering Sea herding experiment; 19 blocks were completed in the West Coast herding experiment. Although the intention of the experiments was to maintain a constant trawl geometry at all bridle lengths, in both experiments wing spread decreased 0.9 m and bridle angle decreased an average of 2.5% from the shortest to the longest bridles (Table 1). The experimental change in bridle length had a pronounced effect on the area swept by the bridles. In the Bering Sea experiment, for example, total bridle length (i.e. bridle plus tailchain length) was increased by 143% from the shortest to the longest bridle, which, in turn, produced a 64% increase in door path width (W_d) and a 113% increase in total bridle path width $(W_d - W_n)$. However, this increase in bridle length also produced a 930% increase in the bridle contact path width $(W_d - W_n - W_{off})$ Table 1) because only a small portion of the bridle remained in contact with the bottom at the shortest bridle length.

Catch per area swept by the net increased significantly with increasing bridle length for six of the seven species (rock sole, yellowfin sole, flathead sole, Dover sole, English sole, rex sole; weighted linear regression, P<0.010) indicating strong herding by the bridles (Fig. 2). For Pacific sanddab, however, the increase was not significant (P=0.096).

Fish length changed significantly (*P*<0.05) with increasing bridle length for only two species (English sole and Pacific sanddab; Table 2) and in both cases smaller fish were



that herding contributes to the catch.

caught at longer bridle lengths. Because four of the remaining five species also displayed declining, but nonsignificant, changes in fish length, a decrease in fish length with increasing bridle length seems to be a general flatfish pattern for this trawl. In all cases, however, the magnitude of the decrease was quite small (Fig. 3).

Table 2

Relationship of mean fish length to increasing bridle length. The total number of fish measured, the slope of the regression line fitted to mean length at each tow versus bridle length, and the probability that the slope equaled zero is shown for each species. Only English sole and Pacific sanddab are significant. Note that a negative slope indicates that smaller fish are caught with longer bridles.

Species	Number of fish measured	Slope	P(slope=0)
Rock sole	23,586	075	0.23
Yellowfin sole	7231	0.008	0.83
Flathead sole	2927	-0.311	0.31
Rex sole	22,774	-0.052	0.56
Dover sole	12,507	-0.036	0.75
English sole	21,968	-0.277	< 0.01
Pacific sanddab	34,209	-0.383	< 0.01

Estimating W_{off}

The degree of contact of the lower bridles with the bottom varied with increasing distance from the doors. Contact never occurred in the first 28 m (Fig. 4). At greater distances, contact became intermittent and was focused primarily at the tops of sand ripples. Contact reached 50% at 36 m and nearly 100% at 40 m (Fig. 4). The estimated value for $L_{\it off}$ was 36.0 m (95% confidence intervals; ± 1.4 m). This value was assumed to be constant for all three bridle lengths and both vessels.

Fit of the model

Of the seven species examined for length-dependent herding, only Pacific sanddab and English sole had significant slopes in the regressions of k_b on fish length (Table 3, Fig. 5). In both cases the slope was negative indicating that herding efficiency decreased with increasing fish length.

For the five species displaying no significant length-dependent herding, the estimated herding efficiency in the bridle contact path (h) varied from 0.50 for rex sole to 0.84 for rock sole, whereas the herding efficiency in the entire bridle path ($k_{\rm b}$) varied from 0.22 to 0.40 (Table 4). For the two species showing significant length-dependent herding, English sole and Pacific sanddab, $k_{\rm b}$ varied from about 0.35 at the shortest lengths to about 0.08–0.10 at the longest lengths (Fig. 5).

Test of model assumptions

For six of the seven species, the fit of a modified herding model, with h parameterized as a linear function of bridle length, produced a larger penalized sum of squares than the fit of the original model with a constant h. This finding indicates that the fit was not improved by the specification of a linear variation in h, and that the assumption

Table 3

Regression of k_b on the midpoints of fish-length classes. The number of length classes, the slope of the regression line, and the probability that the slope equals zero are shown for each species. Only English sole and Pacific sanddab have significant (P<0.05) slopes.

Species	Number of size classes	Slope	P(slope=0)		
Rock sole	10	-0.006	0.088		
Yellowfin sole	10	0.001	0.767		
Flathead sole	10	-0.004	0.249		
Rex sole	10	-0.004	0.354		
Dover sole	9	-0.003	0.564		
English sole	8	-0.027	0.006		
Pacific sanddab	10	-0.016	0.008		

of constancy of *h* at all bridle lengths is valid. However, for Pacific sanddab the fit was significantly improved by the modification. Because the sign of the slope parameter of the linear change was negative, it indicates that for this species herding was less effective at longer bridle lengths.

Discussion

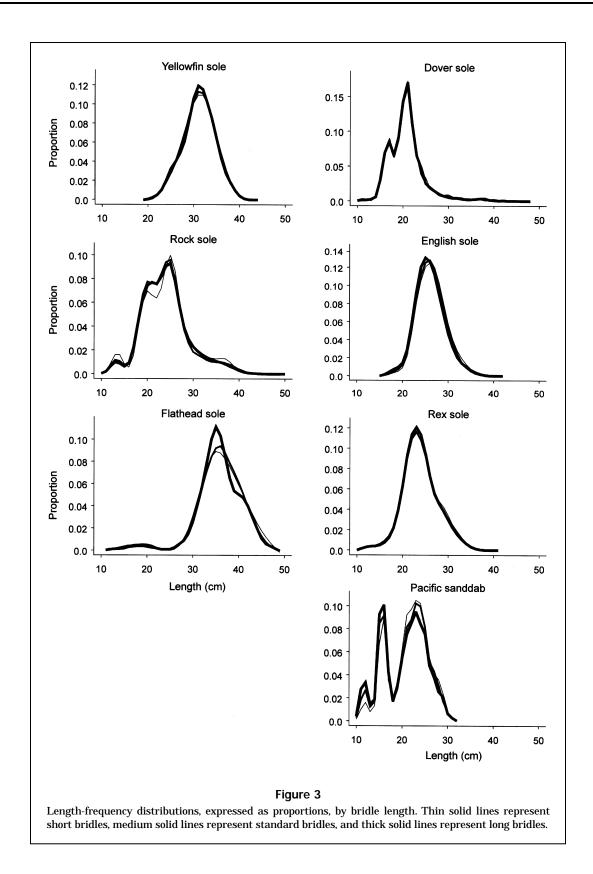
Bridle efficiency

Herding by the bridles of the 83-112 Eastern trawl substantially contributes to the catch of flatfish. For rock sole, as an example, approximately 49% of the catch comprised fish that were herded into the net path.³ This contribution is ignored when swept-area estimates of abundance are based on wing spread rather than door spread. Although such an assumption could lead to an overestimate of abundance, herding is only one component of the trawl catching process and the gains from herding could be offset by the losses due to net escapement.

Bridle efficiency did not vary with fish length for five of the seven species examined (Table 3); consequently, for these species, herding by the bridles is not length selective. A similar lack of length selection was observed by Bridger (1969) in a study examining the herding of lemon sole (*Pseudopleuronectes americanus*). For English sole and Pacific sanddab, however, bridle efficiency clearly declined with increasing fish length and therefore herding is length selective.

Such length selectivity should lead to a change in mean fish length when the average duration of herding experienced by an individual fish is increased by an increase in bridle length. Without exception, the changes in mean fish length that we observed with increasing bridle length are

³ From Equation 4, it can be shown that the herded proportion in the catch is equal to $hw_{or}/(w_n + hw_{op})$, where $w_{on} = w_d - w_n - w_{off}$.



consistent with the observed changes in bridle efficiency with fish length. All five species with length-independent herding efficiency displayed no change in mean length, whereas both species with herding efficiency that declined with fish length displayed a decline in mean length with increasing bridle length (Tables 2 and 3).

Table 4

Estimates of bridle efficiency, k_b , the standard deviation (SD) of k_b by species, and the r^2 for the model fitted without length dependency. For the two species where k_b varies with length, parameters for predicting k_b and $SD(k_b)$ as functions of fish length are provided. The two functions are $k_b = a + b \exp(cL)$ and $SD(k_b) = a + bL + cL^2$, where L = fish length in centimeters; and h = the average efficiency in the portion of the bridle where herding occurs.

Species	r^2			$\mathrm{SD}(k_b)$	Parameters of $k_b = f(\text{fish length})$			Parameters of $SD(k_b) = f(fish length)$		
		h	k_b		а	b	с	a	b	с
Rock sole	0.91	0.840	0.400	0.056						
Yellowfin sole	0.77	0.580	0.275	0.057						
Flathead sole	0.70	0.510	0.242	0.065						
Rex sole	0.71	0.502	0.216	0.061						
Dover sole	0.80	0.636	0.274	0.064						
English sole	0.81	0.384	0.165	0.041	0.033	42.667	-0.221	0.3338	-0.0232	0.00042
Pacific sanddab	0.83	0.161	0.070	0.030	0.046	36.783	-0.354	0.0774	-0.0059	0.00012

Form of the herding model

The herding model that we propose is essentially the same as Dickson's (1993a) model except that it includes an additional parameter (W_{off}) needed to correct a potential shortcoming of the original. This shortcoming can be seen in the following example, which for simplicity considers a herding experiment with only two bridle lengths. Starting with Dickson's model (similar to Eq. 3 in our study), an estimator for k_b can be derived from the quotient of the catches obtained with long bridles to the catches obtained with short bridles:

$$k_b = \frac{W_n - RW_n}{R(W_{d1} - W_n) - (W_{d2} - W_n)},$$

where $R = N_2 / N_1$;

 W_{d1} , W_{d2} = the door spreads with the shorter and longer bridles; and all other variables are the same as those in Equation 3.

Estimates of k_b , based on values of W_{d1} , W_{d2} , and W_n from the Bering sea experiment, increase with catch ratio (R) and reach a value of 1.0 when R equals the ratio of the door spreads (W_{d2}/W_{d1}) . This increase indicates that the bridles are completely efficient $(k_b=1.0)$ when the proportionate increase in the area subjected to herding equals the proportionate increase in catch. If R exceeds the ratio of the door spreads, then $k_b>1.0$, which is not feasible. In our herding experiments, however, R exceeded door spread ratios for all species except English sole and Pacific sanddab; therefore, in most cases the unmodified herding model failed to provide feasible estimates of k_b . By comparison, estimates of k_b from the modified model are feasible over the entire observed range of catch ratios.

In our initial attempts to fit the herding model to experimental data, we treated W_{off} as an additional parameter to

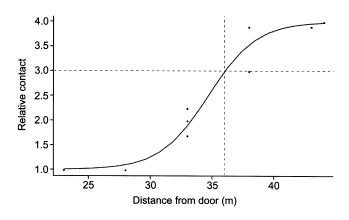
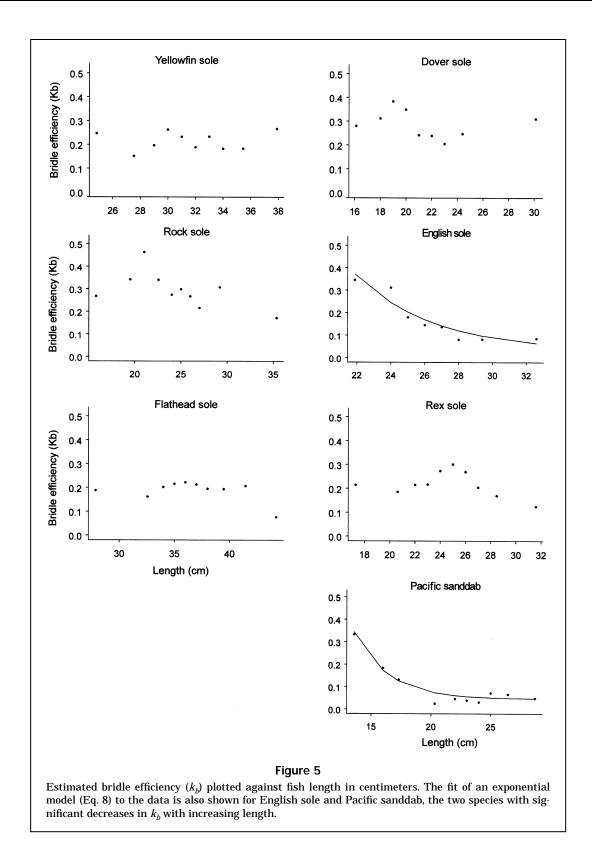


Figure 4

Relative bottom contact of the lower bridle plotted against the distance measured from the door for each camera position and depth. Also shown is the fit of a logistic equation. $L_{\rm off}$ is defined as the distance (vertical dotted line) corresponding to a relative bottom score of 3.0 (horizontal dotted line).

be estimated in the fitting process. However, it soon became clear that $W_{\it off}$ and h are confounded in the model and that convergent solutions required an independent estimate of $W_{\it off}$. We were able to obtain such an estimate and observe fish behavior near the bridle by using video methods, because in the standard configuration of the 83-112 Eastern trawl the bridles are not obscured by mudclouds over much of their lengths. However, in perhaps more typical cases where the bridles are obscured by the mudclouds, estimation of $W_{\it off}$ with video methods would be problematic. A further complication in such cases is that the mudclouds themselves might provide a herding stimulus and confuse the interpretation of $W_{\it off}$



Model assumptions

The adequacy of the herding model and the appropriateness of our herding efficiency estimates rest on a variety

of assumptions. First, we assumed herding efficiency was independent of bridle length. If, however, exhaustion was a primary determinant of bridle efficiency, then it is possible that individual endurance would be exceeded more frequently at longer bridle lengths and would thereby diminish herding efficiency. This assumption was tested by comparing the fit of a herding model with a bridle-length dependent h to that of an unmodified model. The modified model provided a better fit for only one species, Pacific sanddab. Because this species is the smallest of the seven (Fig. 3), it is likely that its swimming endurance might have been exceeded at the longest bridle length. However, for the remaining species the assumption is valid.

Second, we assumed that none of the fish in the area spanned by $W_{\rm off}$ are herded into the net path. Although we recognize that the doors and the mudclouds immediately behind the doors must herd some fish toward the net path, such fish would be herded into the section of the bridle unobscured by the mudcloud and likely escape beneath the lower bridle. We attempted to confirm this possibility by examining video observations from this area of the bridle to see if flatfish escaped or showed any herding behavior, but the results were equivocal because few fish, and probably only moving fish, were seen.

Third, we assumed that in changing the length of the bridles we did not alter trawl geometry in any way other than by increasing the area exposed to herding. As in the studies of Engas and Godø (1989a) and Ramm and Xiao (1995), increased bridle length in our study produced a small, but significant, reduction in wing spread (Table 1). If this change produced a change in footrope contact and net efficiency, then it would lead to a biased estimate of herding efficiency (net efficiency is explicitly assumed to be independent of bridle length in Eq. 4). Other possible changes in trawl geometry are that 1) at the longest length the upper bridle may sag sufficiently to touch the bottom within $L_{\it off}$ and 2) at the shortest length the bridle tension may be sufficient to lift the wingtip off the bottom. With such changes, and perhaps even without, $L_{\it off}$ may not be constant at all bridle lengths. Although we examined the performance of the trawl along the entire distance from the wing tips to the doors at the standard bridle length, we had insufficient ship-time to examine the performance at all bridle lengths to verify that the bridles performed as intended. We recommend that further studies of herding efficiency include additional research to verify that standard trawl performance is maintained for all experimental configurations. One approach for doing this is to simultaneously estimate escapement under the footrope, perhaps by using an auxiliary net attached beneath the trawl net as in Engas and Godø (1989b), so that the assumed independence of net efficiency and bridle length could be tested.

Fourth, we have conducted these experiments in relatively small areas that do not encompass all of the bottom conditions found over the areas covered by the bottom trawl surveys; therefore the results are potentially biased and certainly less variable than if they were conducted over such a range of conditions.

Bridle efficiency is only one component needed to determine trawl efficiency (i.e. the proportion of fish within the door path that are caught). The remaining component, for flatfish at least, is net efficiency (i.e. the proportion of fish within the net path that are caught). If estimates of net ef-

ficiency are also available, perhaps obtained with the use of an auxiliary net to capture escaping fish (Engas and Godø, 1989b), they can be included with estimates of bridle efficiency in Dickson's (1993a) model of the trawl fishing process to produce estimates of trawl efficiency. Such estimates could then be used to convert relative indices of fish abundance from trawl survey to absolute estimates of abundance.

Acknowledgments

We thank Asgeir Aglen, Martin Dorn, Olav Rune Godø, Jack Turnock, and Gary Stauffer for reviewing the manuscript and for making helpful suggestions.

Literature cited

Armistead, C. E., and D. G. Nichol.

1993. 1990 bottom trawl survey of the eastern Bering Sea continental shelf. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-7, 190 p.

Bridger, J. P.

1969. The behaviour of demersal fish in the path of a trawl. FAO Fish. Rep. 62(3):695–715.

Dickson, W.

1993a. Estimation of the capture efficiency of trawl gear.I: Development of a theoretical model. Fish. Res. 16: 239–253.

1993b. Estimation of the capture efficiency of trawl gear. II: Testing a theoretical model. Fish. Res. 16:255–272.

Efron, B., and R. Tibshirani.

1993. An introduction to the bootstrap. Chapman and Hall, New York, NY, 436 p.

Engas, A., and O. R. Godø.

1989a. The effect of different sweep lengths on the length composition of bottom-sampling trawl catches. J. Cons. Int. Explor. Mer 45:263–268.

1989b. Escape of fish under the fishing line of a Norwegian sampling trawl and its influence on survey results. J. Cons. Int. Explor. Mer 45:269–276.

Foster, J. J., C. M. Campbell, and G. C. W. Sabin.

1981. The fish catching process relevant to trawls. Can. Spec. Publ. Fish. Aquat. Sci. 58:229–246.

Fuwa, S.

1989. Fish herding model by ground ropes considering reaction of fish. Nippon Suisan Gakkaishi 55:1767–1771.

Fuwa, S., O. Sato, K. Nashimoto, and N. Higo.

1988. Fish herding model by ground rope. Nippon Suisan Gakkaishi 54:1155–1159.

Hemmings, C. C.

1969. Observations on the behaviour of fish during capture by the Danish seine net and their relation to herding by trawl bridles. FAO Fish. Rep. 62:645–655.

High, W. L.

1969. Scuba diving, a valuable tool for investigating the behavior of fish within the influence of fishing gear. FAO Fish. Rep. 62(3):323–331.

Hilborn, R., and M. Mangel.

1997. The ecological detective: confronting models with data. Princeton Univ. Press, Princeton, NJ, $315\,\mathrm{p.}$

Main, J., and G. I. Sangster.

1981a. A study of the sand clouds produced by trawl boards

and their possible effect on fish capture. Scott. Fish. Res. Rep. 20:1-20.

1981b. A study of the fish capture process in a bottom trawl by direct observations from a towed underwater vehicle. Scott. Fish. Res. Rep. 23:1–23.

Martyshevskii, V. N., and V. N. Korotkov.

1969. Fish behaviour in the area of the trawl as studied by bathyplane. FAO Fish. Rep. 62(3):781–791.

Ramm, D. C., and Y. Xiao.

1995. Herding in groundfish and effective pathwidth of trawls. Fish. Res. 24:243–259.

Seber, G. A. F., and C. J. Wild.

1989. Nonlinear regression. Wiley, New York, NY, 768 p. Venables, W. N., and B. D. Ripley.

1994. Modern applied statistics with S-plus. Springer-Verlag, New York, NY, 462 p.