MESOSCALE FISHING PATTERNS OF FACTORY TRAWLERS IN THE PACIFIC HAKE (MERLUCCIUS PRODUCTUS) FISHERY

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ABSTRACT

During 1991-95, up to 60% of the annual catch of Pacific hake (Merluccius productus) in the U.S. management zone was harvested by a U.S.-based fleet of factory trawlers. Optimal foraging theory was used to motivate a statistical analysis of movement patterns of these vessels. This study focused on the mesoscale characteristics of the environment (5-50 km), and vessel movement at these spatial scales. Geostatistical analyses of hake densities derived from the 1992 and 1995 National Marine Fisheries Service assessment surveys with quantitative echo-sounding techniques showed that strong spatial correlations of hake density do not extend beyond ~25-35 km. The range of Pacific hake spatial correlation suggests an association with mesoscale oceanographic features whose characteristic scale in the California Current system is determined by the Rossby radius of deformation (~25 km in mid-latitudes off the West Coast). The foraging patterns of factory trawlers can be described as a series of moves between trawling locations. The distance between successive hauls depends on whether the vessel continues fishing within a local area of high fish density, or moves to a different area. Generalized additive models (GAM) were used to examine influence of the catch rates of prior hauls on the distance between successive hauls. The GAM models suggested that deviations from the expected catch rate influence the decision to move from a local foraging area, as expected from optimization models of animal foraging. These decisions appeared to be based on relatively short time frames, such that information from only the most recent one or two hauls in the area is used. In addition, results indicated that the presence of other fishing vessels operating nearby reduces the probability that a vessel will leave an area.

INTRODUCTION

Factory trawlers—fishing vessels that both catch and process fish—are important in many fisheries worldwide (Garcia and Newton 1995). The advanced technology of these vessels (including hydraulic winches to set and retrieve extremely large nets, automated filleting machines, flash freezers, freezer holds, fish meal plants, electronic echo sounders, and GPS navigation and plotting equipment) enables them to efficiently catch and process large quantities of fish (up to 500 metric tons per day). The ability of these vessels to operate independently of port services for extended periods is a significant advantage in harvesting migratory species like Pacific hake (*Merluccius productus*), whose spatial distribution can vary greatly from one year to the next. Since fish can be processed immediately after they are caught, these vessels produce a high-quality product from fish species whose flesh undergoes rapid proteolysis when held at ambient temperatures.

In this paper, I discuss the fishing patterns of factory trawlers as an example of the foraging behavior of animal predators. Although a factory trawler is, of course, a complex machine operated by a crew, from the perspective of its role in the ecosystem, it is reasonable to view it as a single agent—a midwater filter feeder that detects prey by using echolocation. A similar approach was used by Gillis et al. (1995a, b) to study discarding behavior in a trawl fishery subject to trip limits.

The foraging choices available to these vessels depend on the spatial and temporal scale of their assessment of the environment (Holling 1992). This paper focuses on the mesoscale characteristics of the environment (5–50 km) and vessel movement at these spatial scales. Since factory trawlers do not return to port regularly to deliver fish to a processing plant, their movement patterns at this scale are assumed to be a pure foraging process. Foraging behavior at this scale can be described as a series of movements between successive trawling locations. The focus of this paper is to develop statistical models for investigating the factors that influence these movements, particularly the movements which indicate that the vessel has left the area where it had been fishing previously.

The analyses of vessel movement presented in this paper are motivated by Arditi and Dacorogna's (1985, 1988) contribution to optimal patch foraging theory. Their work generalizes the marginal value theorem (Charnov 1976) to habitats with arbitrary prey distributions. Although they limit their consideration to onedimensional habitats, this is not as restrictive an assumption as it seems. Many fisheries occur within relatively narrow depth limits parallel to the shelf break or the coastline. Arditi and Dacorogna (1988) show that when presented with an arbitrary prey distribution in a habitat, the optimal



Habitat dimension

Figure 1. Schematic of the Arditi and Dacorogna (1988) optimal foraging model. The threshold density partitions the habitat into areas of two types: those in which it is optimal to forage, and those where the optimal strategy is to transit as quickly as possible.

forager should partition the habitat into contiguous areas of two types: areas in which it is optimal to forage, and areas in which the optimal strategy is to traverse as quickly as possible without foraging.

In the areas where it is optimal to forage, the forager should move on when the density of prey declines below the critical density that partitioned the habitat into foraging and nonforaging regions (figure 1). The critical density is determined by the mean density of prey in the habitat as a whole (similar to the marginal value theorem) and by the forager's functional response curve. For a factory trawler, the functional response is the relation between fish density and surimi production, and is a nonlinear function of the capture efficiency of the net, the time required to set and retrieve the net, and the production capacity of the factory (Dorn, in press).

The Arditi and Dacorogna foraging model implies that the forager perceives its habitat as a "behavioral landscape" in which different activities are performed in different regions. This emphasis on the forager's perception is different from the marginal value theorem, where the pattern of the environment is assumed. The model suggests that the "patches" of classic optimal foraging theory may not be intrinsic to the environment, but a result of the forager's imposing a particular cognitive structure on the environment.

The critical threshold transforms an undifferentiated environment into a mosaic of two types of regions—foraging and nonforaging. The characteristic dimensions of those regions will depend on the spatial continuity of the prey population. A prey population with short-range spatial continuity would present the forager with many small patches to exploit. If the spatial correlation of the population extends to wider scales, the patches will be larger and fewer. Since the forager alternates between two patterns of movement (small-scale movements within a foraging area, and larger-scale movements of transit between foraging areas) the spatial continuity of the prey population has important implications for how the forager moves.

The transition from the theoretical models of Arditi and Dacorogna (1988) to a statistical analysis of how catch rates affect vessel movement must confront the real complexity of the environment—that is, those important environmental characteristics not included in the theoretical model. Although the model allows the catch rate to decline in a foraging area only because of fishing activity, in fact, local changes in prey abundance may result from a variety of factors, many of them unrelated to fishing activity. Moreover, although the model assumes perfect knowledge of the environment, fishing vessels typically will not know in advance where prey density is high.

Catch rates for Pacific hake also follow a diel pattern, with the daytime rates about twice as high as nighttime rates when hake are dispersed through the water column. Catch rates vary between vessels because of differences in the nets used, horsepower, and other technological characteristics of the vessel. To standardize the catch rates by accounting for the diel trend and for differences in fishing power, a preliminary model was fit to the haulby-haul catch rate data, with vessel and time of day as predictor variables. The residuals from this model were used in the analysis of vessel movement patterns. This approach follows Vignaux (1996a, b), who used a similar strategy to assess the spatial structure of fish distribution and to analyze fishing behavior in a trawl fishery off New Zealand.

The statistical analyses presented in this paper examine how catch rates and other information affect the decision to leave an area where a vessel is fishing. One might expect the catch rate of the target species to be the major factor in this decision, but other factors, such as the presence of other vessels nearby, may also be important. The first objective of the statistical analysis will be to evaluate how the catch rate of the most recent haul affects the decision to leave. Next, the effect of prior catch rates will be evaluated. Previous catches differ from the most recent catch by being farther away in space and time from the most recent catch. Since areas of higher than usual hake density are transient, fishermen may use a weighting function that assigns more emphasis to recent catches. An exponential weighting model has been used in theoretical work on other foraging situations (McNamara and Houston 1985) and will be evaluated here. In addition, how the presence of other vessels fishing nearby affects the decision to move will be evaluated. The presence of other vessels could induce the vessel to remain in the area longer than it would if the decision were based strictly on its own catch rate.

The subsequent sections of the paper are organized as follows. After a brief presentation of background information on the factory trawlers participating in Pacific hake fishery, results are presented from a geostatistical analysis of acoustic survey data to assess the spatial continuity of Pacific hake distribution. These results are used to select the appropriate spatial scale at which to assess vessel movement patterns. Then, from fishery data collected by at-sea observers, models are fit to the haulby-haul catch rates of the factory trawler fleet during 1991-95, with time of day and a categorical term for individual vessels as predictor variables. The residuals from this model are then used in a generalized additive model (GAM) to predict the probability of movement from a foraging area. Other variables are also assessed in the model. Finally, the results are compared with those from other studies of spatial correlation and fishing behavior, and recommendations are offered about further research into fishing behavior.

FACTORY TRAWLERS AND PACIFIC HAKE

During 1991-95, an average of 14 factory trawlers and 5 mother ships participated in the Pacific hake atsea fishery each year, with an average aggregate catch of 150,000 metric tons (t) per year. The factory trawlers in the Pacific hake fishery are large vessels (275-375 ft long), carry a crew of 70-100, and can remain at sea for several months. Between 50% and 70% of the crew is engaged in surimi production. Several work shifts operate the processing factory 24 h per day. Midwater trawls (mean trawl opening 90×55 m) are used exclusively for Pacific hake. The at-sea fishery operates as a "derby" fishery in which all vessels compete for the fleetwide quota. With the entry of U.S. factory trawlers and mother ships in 1991, the character of the at-sea fishery changed dramatically. Before 1991, the fishery had lasted for as long as 6 months; now it closes 3-4 weeks after the annual opening date of April 15.

As is usual with targeted midwater trawling, catches in the hake fishery are extremely pure, with bycatch typically amounting to less than 3% of the total catch by weight. The most common bycatch species are pelagic rockfishes and mackerels: yellowtail rockfish (Sebastes flavidus), widow rockfish (Sebastes entomelas), Pacific ocean perch (Sebastes alutus), jack mackerel (Trachurus symmetricus), and Pacific mackerel (Scomber japonicus). The bycatch is either discarded at sea or diverted to the fish meal plant. Although the bycatch of chinook salmon (Oncorhynchus tshawytscha) is low (4,000-6,000 fish per year), it is an important concern because of the extremely low abundance of many West Coast chinook salmon populations. Several West Coast chinook salmon runs are listed as endangered under terms of the U.S. Endangered Species Act (Waples et al. 1991; Fisher 1994).

METHODS

Analysis of Pacific Hake Spatial Pattern

Geostatistical techniques were used to assess the spatial continuity of Pacific hake by means of data from acoustic resource assessment surveys conducted by the NOAA research vessel *Miller Freeman* during July– September of 1992 and 1995 (Dorn et al. 1994; Wilson and Guttormsen 1997). Acoustic data were collected with a Simrad EK500 scientific echo-sounding system (Bodholt et al. 1989) that used a 38-kHz transducer mounted on the vessel's centerboard 9 m below the waterline. Acoustic data were processed on a SUN workstation with Simrad BI500 echo-integration and analysis software (Foote et al. 1991) to exclude non-hake sound-scatterers from the echo integration.

The survey design consisted of equally spaced east-west transects extending from 30 m to approximately 1,500 m bottom depth. Transects were spaced 10 nautical miles (nmi) apart for most of the survey, with higher-density spacing (5 nmi) in the Juan de Fuca Canyon–La Perouse region (48°-49°N lat.). Survey transects were run only during daylight hours because hake disperse at night. The acoustic backscatter attributed to Pacific hake by 0.5-nmi transect section was converted to fish density by means of a length-target strength relationship of $TS = 20 \log(length)$ - 68 (Traynor 1996). Since 40-60 days are required to conduct a coastwide acoustic survey of Pacific hake, some redistribution of fish would be expected during the survey operations. But adjacent transects were almost always surveyed within one day, and usually within several hours, so the effect of fish redistribution should be relatively minor at scales less than the transect spacing. To analyze spatial correlation with acoustic survey data, it is necessary to assume that the data provide an instantaneous "snapshot" of Pacific hake distribution patterns.

Directional correlograms (Rossi et al. 1992) were estimated for mean hake density by 0.5-nmi transect section, $z(x_i)$, where x_i is location of the transect section. Separate correlograms were estimated for E-W (eastwest) and (N-S) north-south directions, with a directional tolerance of $\pm 45^{\circ}$. In the E-W direction, binning intervals of 2.5 km were used to a maximum distance of 50 km; in the N-S direction, binning intervals of 10 km were used to a maximum distance of 80 km. Different binning intervals were used because the survey design of parallel E-W transects yields fine-scale information on spatial correlation along the transect in the E-W direction, but relatively coarser information in the N-S direction (Pelletier and Parma 1994). Since the orientation of the shelf break is north-south in the area where the fishery operates, the N-S correlogram measures alongshelf spatial correlation, while the E-W correlogram measures the cross-shelf correlation.

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In addition, I estimated an omnidirectional correlogram, using the same binning strategy as for the E-W correlogram. The estimation was restricted to acoustic data collected north of 41° and east of 127°W, an area roughly corresponding to the area where the fishery operates. The correlogram is a plot of the lag correlation, $\hat{\rho}(\boldsymbol{h})$, such that

$$\hat{\rho}(h) = \frac{\frac{1}{N(h)} \sum_{i=1}^{N(h)} [z(x_i) - m_{-h}][z(x_i+h) - m_{+h}]}{\sum_{i=1}^{s} [z(x_i+h) - m_{+h}]}$$

where $z(x_i)$ and $z(x_i + h)$ are pairs of hake densities separated by vector distance h; m_{-h} and m_{+h} are the means of the initial and terminal points of the vectors used to estimate the lag correlation; and s_{-h} and s_{+h} are the standard deviations of the initial and terminal points. Rossi et al. (1992) call this the non-ergodic correlogram to distinguish it from the more usual spatial correlogram where the global mean is subtracted out, and the global variance is used to scale the covariance. Rossi et al. (1992) recommend this form of the correlogram for ecological applications where nonstationarity in local means and variances is frequently encountered.

To demonstrate how the spatial structure in hake distribution might be perceived by fishing vessels, I used hake density by 0.5-nmi transect section to estimate structure functions. The structure function describes the spatial pattern of resources from the perspective of the forager (Mangel and Adler 1994). I applied an indicator transform to hake densities of the form

$$i(x;z) = \begin{cases} 1 & \text{if } z(x) \ge k \\ 0 & \text{if } z(x) < k \end{cases},$$

where the threshold density ($k = 635 \text{ kg } ha^{-1}$) is the value of hake density such that the median of all acoustic densities greater than the threshold is equal to the median density implied by the catch rates for factory trawlers during the fishery.

To obtain an expected density from the fishery catch rates, I determined the area swept by the net from the haul duration, towing speed, and the horizontal opening of the net (= 90 m, the mean net width recorded by several observers). Daylight hauls (between 0600 and 2000 Pacific Standard Time) made by factory trawlers during the 1991–95 seasons were used. Since a strong avoidance response has been reported for Pacific hake when encountering midwater trawl nets (Nunnallee 1991), the assumption of 100% capture efficiency is unjustifiable. To estimate the threshold density, I assumed that a commercial midwater trawl would capture 50% of the fish in the water column, and evaluated the sensitivity of the results to this assumption. It should be emphasized that the purpose here was to obtain a rough approximation of the spatial pattern and geographic extent of the regions where fishing would be successful.

The structure function is defined as

- p(i(x + h) = 1 | i(x) = 1)) = Prop {resource at vector distance h away, given that there is resource at the current point}
- $p(i(x + h) = 1 | i(x) = 0)) = Prop \{resource at vector distance h away, given that there is no resource at the current point \}.$

In this definition, the structure function has been generalized from Mangel and Adler (1994) to allow the structure function to vary depending on the direction away from the current point. This broader definition of the structure function makes it possible to consider directional structure functions similar to directional correlograms. To estimate the structure function, I followed the algorithm of Mangel and Adler (1994):

$$\hat{\rho}(i(x+h) = 1 | (i(x) = 1)) = \frac{\sum_{k=1}^{N(h)} i(x_k + h) i(x_k)}{\sum_{k=1}^{N(h)} i(x_k)}.$$

In estimating the structure function, I used the same binning strategies that were used to estimate the directional correlograms.

Catch Rate Model

NMFS-certified observers are placed on all factory trawlers and mother ships in the at-sea fishery. While on board, observers maintain a complete record of the catch weight, duration, set and retrieval times, and retrieval location for each haul made by the vessel. Set location, however, is not recorded, which limits the spatial resolution of estimated distances between trawling locations. A tow that retraces the path of the previous tow in reverse direction could have a retrieval location farther than 10 km away. Alternatively, two tows that end at the same location could have trawled toward that location from opposite directions. Since all vessels carry observers, there is a complete record of all hauls during the fishery. This record is kept in the NORPAC database, an ORACLE relational database maintained by the North Pacific Observer Program at the Alaska Fisheries Science Center (7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115-0070). The number of hauls in each fishing season by factory trawlers ranged between about 1,000 and 2,000 (table 1).

A generalized additive model (GAM) with Poisson error (Hastie and Tibshirani 1990) was used to standardize the catch rates. This form of GAM has been used in marine ecology applications to analyze trawl survey

TABLE 1
Number of Factory Trawlers and Mean Catch Rates
in the 1991–95 Pacific Hake Fishery

Year	Number of factory trawlers	Number of hauls	Average catch rate (t/hr)	
1991	9	1,940	41.8	
1992	14	1,743	43.4	
1993	13	1,227	44.2	
1994	7	1,192	60.5	
1995	9	954	39.6	

data (Smith 1990; Swartzman et al. 1992). Poisson regression is a pragmatic choice for "count-like" data where the variance is proportional to the mean (McCullagh and Nelder 1983),

$$E[cr_i] = \mu(\mathbf{x}_i)$$

Var[cr_i] = $\phi \ \mu(\mathbf{x}_i)$.

where cr_i is the catch rate in t hr⁻¹ for the ith haul; $\mu(\mathbf{x}_i)$ is the expected catch rate of the ith haul as a function of a vector of covariates \mathbf{x}_i ; and $\boldsymbol{\phi}$ is an overdispersion parameter that models the additional variability in the data relative to the Poisson distribution, where the variance is equal to the mean (Lawless 1987).

The structural part of the model consisted of two additive terms: a categorical term for vessel, and a "smooth" function of time of day (average of set and retrieval times) estimated with the loess scatterplot smoother (Chambers and Hastie 1992). Because of the short duration of the at-sea hake fishery (3-4 wk), a seasonal effect was not considered necessary in the model. The additive part of this model is log-linear; that is, $\mu(\mathbf{x}_i) = \exp[\eta]$, where η is the additive predictor. Separate models were fit for the 1991-95 seasons. A span width (fraction of the data used by loess to estimate local linear regressions) was fixed at 0.3 on the basis of a series of trial models in which the span width was varied systematically. A span width of 0.3 provided enough flexibility to capture the diel trend while at the same time excluding higher-frequency variation from the smooth term.

Statistical Models of Vessel Movement

Although the focus of this analysis is to determine the factors leading to a decision to leave a mesoscale aggregation of fish, without an extensive acoustic survey conducted at the same time as the fishery, it is difficult to know with certainty when this decision is made. Consequently, it was necessary to use some easily measurable proxy for this decision. If a critical distance between successive trawling locations is chosen appropriately, it should be possible to partition the intertrawl movements into those within an area and those representing a transit between areas. For this research, a distance of greater than 30 km between haul retrieval locations was selected as the criterion for moving to a new area. This criterion was based on the examination of Pacific hake spatial patterns during the 1992 and 1995 acoustic surveys reported in the results, which suggests that strong spatial correlations do not extend beyond ~25–35 km. Consequently, the dependent variable in the statistical model is the geometric distance between successive haul retrieval locations recoded as 0–1 variable, where 0 denotes a distance of less than 30 km, and 1 denotes movement of greater than 30 km. Mean trawling distance, assuming the vessel travels in a straight line for the duration of the haul, was 16.2 km during 1991–95, which is roughly one-half the range of spatial correlation of 30 km.

Logistic regression is the primary statistical model for analyzing binary response data. Logistic regression predicts the probability of an event (movement greater than 30 km) based on a set of covariates. Since the Arditi and Dacorogna (1988) model suggests that a threshold catch rate triggers the decision to move, a flexible regression technique (the GAM described above) was used for the statistical analyses. The expectation and variance for logistic regression are

$$E[\gamma_i] = \pi(\mathbf{x}_i)$$
$$Var[\gamma_i] = \pi(\mathbf{x}_i)[1 - \pi(\mathbf{x}_i)]$$

where y_i is the 0-1 response variable, and $\pi(x_i)$ is the probability of moving to a new area following the ith haul as a function of a vector of covariates x_i . In a GAM, the linear predictor of logistic regression is replaced by an additive predictor with the general form $\eta = f_1(x_1)$ $+ f_2(x_2) + \ldots + f_p(x_p)$, where $f_i(x_i)$ is a smooth function of x_i . As with the Poisson model, this "smooth" function is estimated with local linear regressions. The probability of the event is linked to the additive predictor by the logistic function $\pi(x_i) = \exp(\eta)/[1 + [\exp(\eta)]]$. Potential covariates examined with this modeling framework were the catch rate residual for the ith haul, an exponentially weighted average of the catch residuals for previous hauls within 30 km, and the number of other vessels fishing nearby, where nearby is defined as the number of vessels within 15 km over the previous 6 hrs. Separate models were fit for the 1991-95 seasons. This model and the Poisson regression model for catch rates were fit by means of the statistical modeling language S-Plus (StatSci 1993).

RESULTS

Spatial Analysis

In 1992 and 1995 NMFS acoustic surveys, areas of high Pacific hake density were found mostly in a narrow



Figure 2. Pacific hake density in 0.5-nmi transect segments for the 1992 and 1995 NMFS acoustic surveys. To show both surveys, data for the 1992 survey is offset to the west by 2° iongitude. Transect segments in which the Pacific hake density was greater than 635 kg ha⁻¹ (the nominal density required to support fishing activity) are marked with *vertical bars.* The 300-m isobath and survey transects are also shown.

N-S band close to the continental shelf break (figure 2). Consequently, the E-W dimensions of the area where the fishery can operate are much narrower than its N-S dimensions. Interspersed regions of high and low density extend along the entire coast. Certain features along the shelf break tend to support higher densities of Pacific hake (e.g., Heceta Bank off central Oregon and Juan de Fuca Canyon off Cape Flattery), but high densities are not confined to these areas.

In 1992, densities in excess of 635 kg ha⁻¹ represented 8.9% of the surveyed area north of 41°N and east of 127°W, but 18.2% of the area within the 150–600-m bottom-depth range, where most fishing occurs. In 1995, the percentages were 4.8% for the surveyed area and 11.4% for the area within the 150–600-m bottom-depth range. The decrease in the area of high fish density from 1992 to 1995 may be due to an estimated 23% decline in the total biomass within these depth and geographic boundaries. A relation between overall abundance and the proportion of potential habitat that is occupied has been observed for many fish populations (MacCall 1990).



Figure 3. Directional correlograms for the 1992 and 1995 NMFS acoustic surveys of Pacific hake.

The spatial correlograms support the depiction of hake spatial pattern in figure 2. The E-W directional correlogram for the 1992 survey declines from 0.56 at a distance of 0-2.5 km to near zero at ~25 km (figure 3). The N-S directional correlogram is similar to the E-W correlogram at larger distances (>8 km) where comparison is possible. Despite differences in overall abundance and the location of the higher-density areas in the 1995 survey, the directional correlograms for the 1995 survey show a similar pattern to the 1992 correlograms (figure 3). As with the 1992 correlograms, the E-W and N-S directional correlograms for the 1995 acoustic survey are similar at lag distances where comparison is possible. There is a slight positive correlation (~ 0.025) extending from 30 to 60 km in the 1995 survey that does not appear in the 1992 correlograms, but this correlation is only about 5% the correlation at a range of 0-2.5 km.

The data used to estimate the N-S correlation for the smallest lag distance (0-10 km) were collected along transects in the Juan de Fuca Canyon-La Perouse region, the only area where the transect spacing was 5 nmi in both the 1992 and 1995 surveys. Since this a bathymetrically complex region-with a narrow, steep-walled canyon and a large offshore bank-the correlation structure in this region may differ from other locations along the West Coast where the bathymetry is less complex. Additional acoustic data collected along transects oriented at angles to the usual survey grid are needed to adequately assess anisotropy. Although figure 2 suggests the presence of larger-scale N-S structure (that is, higher densities in the Heceta Bank and Juan de Fuca canyon area and lower densities elsewhere) the spatial statistics interpret these patterns as N-S trends rather than as a spatial correlation (Swartzman et al. 1992). From the perspective of the fishing vessel, the key spatial characteristics of the hake population would appear to be (1) a narrow, elongated region of potential occurrence, and (2) transient fishable aggregations of 20-30 km in size that can be fished on multiple times.



Figure 4. Directional structure functions for the 1992 and 1995 NMFS acoustic surveys of Pacific hake. Only the first part of the structure function is shown; that is, the conditional probability of finding hake densities higher than the threshold density at vector distance h away, given that the density is higher than the threshold at the current location.



Figure 5. Poisson catch rate regression predictions for noon catch rate by vessel in 1993 and by time of haul for 1991–95 for a single vessel that fished in all years.

The directional structure functions for the 1992 and 1995 NMFS acoustic surveys are shown in figure 4. The E-W and N-S structure functions are similar for both surveys. The structure functions for 1992 and 1995 show similar patterns, with a conditional probability of 0.5–0.4 of finding high fish densities at short distances (<2.5 km) and a rapid decline to baseline levels at 25–35 km. This decline is slightly steeper than the decline in the correlograms. As distance increases, the conditional probability for finding high fish density approaches the unconditional probability (~0.10 in 1992 and ~0.05 in 1995).

The estimated structure functions are fairly robust to the choice of a threshold density in the range of plus or minus 25% of 635 kg ha⁻¹. At higher threshold densities, there is a tendency for the conditional probability of high fish density to decline more rapidly than at lower thresholds, so that baseline levels are reached at ~20 km rather than 30 km. Consequently, inaccuracies of this magnitude in the length-TS relationship for hake or in the assumed 50% capture efficiency of midwater trawls would not cause a severe bias. These results suggest that if a vessel moves more than ~30 km away from its current fishing location, its probability of encountering high densities of hake is similar to the probability at a location chosen at random within potential hake habitat. Consequently, these results provide the rationale for the statistical analysis of vessel movement, where a movement of greater than 30 km between trawling locations is assumed to represent a decision by the fishing vessel to leave a local area of high density.

Catch Rate Model

Since the objective of fitting the Poisson regression model to the catch rates was to obtain a set of catch rate residuals for additional analysis, I present only general features of the model. For each year 1991–95, both terms in the model, vessel and time of day, are highly significant (p < 0.001). The high significance level indicates that vessel and time of day are important influences on the catch rate, but this result is at least partly due to the large amount of observational data available for fitting the model (table 1). The GAM analogue to the coefficient of determination-1.0 minus the ratio of the model deviance to the deviance for a null (mean) model (Swartzman et al. 1992)-ranged from 25.5% in 1991 to 43.9% in 1993. The relatively low r^2 values suggest that there is considerable variation in catch rates not explained by the model.

Model results are best interpreted by looking at model predictions rather than by directly examining the model coefficients. Most vessels tended to have similar predicted noon catch rates, although in each year, several vessels had predicted catch rates that were more than twice those of the rest of the fleet (figure 5). Figure 5 shows the predicted catch rates only for 1993, but the pattern for the other years was similar. In particular, vessels with higher catch rates in 1993 consistently experienced higher catch rates than the rest of the fleet throughout 1991–95. These variations may be explained by differences in vessel or net characteristics, variation in fishing skill, or differences in fishing strategy. For example, some vessels may spend more time searching, but target only the highest densities they encounter while searching.

The GAM smooth term for time of day (mean of set and retrieval times) generally shows an increase in catch rate at ~0600, and a decline at ~1800 (all times are Pacific Daylight Time, UTC+7; figure 5). Sunrise and



Figure 6. Mean catch rate residual versus intertrawl distance (distance between successive haul retrieval locations) for factory trawlers during 1991–95.

sunset on 1 May at 45°N, 125°W (the approximate location of Heceta Bank off central Oregon) occur at 0611 and 2024, suggesting that the diel variation in catch rates is closely coupled to ambient light levels. In 1992, fishing was prohibited during nighttime (from midnight to one hour after official sunrise) to reduce the bycatch of chinook salmon. In contrast to other years, the GAM smooth term for 1992 does not show an increase in the predicted catch rate at sunrise. In 1991, 1992, 1994, and 1995, catch rates peaked in midmorning (~1000), but in 1993, for reasons that are unclear, they peaked in the afternoon instead. Figure 5 shows the predicted diel pattern in catch rate for only a representative vessel in all years. Since the additive predictor for Poisson regression is log-linear, the pattern for other vessels would simply be scaled upwards or downwards by a multiplicative factor. The mean catch rates for the entire factory trawler fleet were similar in 1991–93 and 1995, whereas in 1994 the catch rate was 43% higher than the average for the other years (table 1).

The catch rate residuals $(cr_i - \hat{c}r_i)$ have a nearly symmetric distribution, with a mean of zero (as expected) and a median of -7.16 t hr⁻¹. There are a few extremely large positive residuals (maximum 1,628.0 t hr^{-1}), suggesting that some skewness is present. However, only 1% of the residuals are larger than 218.5 t hr^{-1} . A plot of the mean catch rate residual versus intertrawl distance provides additional support for the use of a 30-km intertrawl distance to indicate the decision to move to a new area (figure 6). For intertrawl distances less than ~ 30 km, the mean catch rate residual decreases with increased intertrawl distance, whereas at distances greater than ~30 km, the mean catch rate residuals are strongly negative, and show no consistent relationship with intertrawl distance. This suggests that the pattern of spatial correlation detected in the acoustic survey data is perceived in a similar way by fishing vessels.

GAM Models of Vessel Movement

The sequence of terms assessed in the models consisted of (1) the catch rate residual for the most recent haul; (2) a weighted average of previous hauls within 30 km, including an assessment of the appropriate exponential weighting coefficient to use; and (3) the number of other vessels operating nearby. This order was established so that the most recent information on the target species would be assessed first, while information on the activity of other vessels) would be addressed subsequently. Trial models with a term for the number of vessels added first showed smaller declines in deviance



Longitude W

Figure 7. Path of a single factory trawler during a 28-day opening in 1994, constructed by connecting the haul retrieval positions with straight lines. *Solid lines* connect consecutive haul retrieval locations less than 30 km apart; *dashed lines* connect those farther than 30 km apart. The E-W scale on this figure has been expanded to better depict the fine-scale structure of the path. The *box* is 30 km square.

than models with a term for the catch rate residuals added first. This suggests that the order in which terms were evaluated was a reasonable approach.

Before fitting models, I conducted several exploratory data analyses. Figure 7 shows the path of a single vessel during a 28-day opening in 1994, constructed by connecting the haul retrieval positions with straight lines. Searching behavior between hauls would, of course, not appear on this figure. The distribution of between-trawl move distances during 1991–95 has a mean of 14.2 km, a median of 8.0 km, and is skewed significantly to the right (figure 8). Out of a total of 6,914 valid observations for 1991–95, 530 (7.7%) consisted of move distances greater than 30 km, the criterion assumed to indicate a decision to move to a new area.

A comparison of models with linear and smooth terms for the catch rate residual of the immediately preceding haul evaluated whether there was significant nonlinearity between the catch rate residual and the probability of movement. I selected a span width of 0.5 for the smooth term by fitting a series of trial models with varying span widths for the 1994 data, and choosing a width that provided enough flexibility to capture the nonlinearity in the data, but did not result in an excessive amount



Figure 8. Frequency distribution of the distances between successive haul retrieval positions for factory trawlers in the Pacific hake fishery, 1991–95. The final bar of the histogram includes all distances greater than 100 km.

of roughness in the smooth term. The addition of a smooth term for the catch rate residual for the immediately preceding haul was significant at $\alpha = 0.05$ in the GAM models for four out of the five years (table 2). *P*-values based on likelihood ratio tests (Hastie and Tibshirani 1990) for adding the nonlinear smooth term ranged from <0.001 in 1991 to 0.128 in 1993.

Year	Model ^a	Residual df	Residual dev.	Δdf^b	Δ dev.	<i>P</i> -value ^c
1991	Null	1908.0	1046.1		_	
	+ linear CR	1907.0	1013.3	1.0	32.8	0.000
	\pm smooth CR	1902.2	991.1	4.8	22.2	0.000
	\pm AVGCR	1902.3	983.9	-0.2	7.2	No test
	± NVESS	1898.1	933.8	4.2	50.1	0.000
1992	Null	1680.0	1052.4		_	_
	+ linear CR	1679.0	1037.9	1.0	14.4	0.000
	± smooth CR	1673.6	1025.6	5.4	12.3	0.039
	\pm AVGCR	1673.7	1012.5	-0.1	13.2	No test
	+ NVESS	1670.4	970.7	3.3	41.8	0.000
1993	Null	1201.0	533.9		—	_
	+ linear CR	1200.0	527.8	1.0	6.1	0.014
	± smooth CR	1194.9	519.1	5.1	8.7	0.128
	± AVGCR	1195.0	516.1	-0.1	3.1	No test
	+ NVESS	1191.3	497.7	3.7	18.4	0.001
1994	Null	1176.0	468.2	_		
	+ linear CR	1175.0	464.8	1.0	3.4	0.065
	± smooth CR	1170.0	446.1	5.0	18.7	0.002
	± AVGCR	1170.2	442.0	-0.2	4.1	No test
	+ NVESS	1166.8	435.2	3.4	6.7	0.107
1995	Null	943.0	603.1	_	_	_
	+ linear CR	942.0	582.1	1.0	21.1	0.000
	± smooth CR	937.5	570.5	4.5	11.6	0.030
	\pm AVGCR	937.4	556.1	0.1	14.4	No test
	+ NVESS	932.9	537.6	4.5	18.5	0.002

	TABLE 2				
Analysis of Deviance for Logistic Regression	GAMs for the	Probability	of Vessel	Movement in	n 1991–95

^aTerms in additive predictor: null—intercept term only; linear CR—linear term for catch rate residual of the most recent haul; smooth CR—smooth term for catch rate residuals within 30 km using an exponential coefficient of 3.5; NVESS—smooth term for the number of vessels operating within 15 km over the previous 6 h. Terms were added to the models in the order they occur in the table. The "+" symbol indicates that the term has been added to the model; the "±" symbol indicates that the term replaces the previous term. ^bThe degrees of freedom for smooth terms quantify the degree of "smoothness" of the term (Hastie and Tibshirani 1990). ^cP-values (from a χ^2_{Adf} distribution) are for a likelihood ratio test of the change in deviance between models.



Figure 9. Generalized additive model (GAM) predictions of the probability of movement as a function of the catch rate residual for the most recent haul. The upper and lower limits of the x-axis are the 0.05 and 0.95 quantiles of the catch rate residual.

The smooth term for the catch rate residual for each year consistently shows an increased probability of movement with declining catch rates (figure 9). Although there are some differences between years, in general the predicted probability of movement is low when the catch rate residual is positive, increases relatively rapidly when the catch rate residual becomes negative, then remains stable at higher levels with further decreases in the catch rate residual. To address whether these results were being driven by the behavior of only a few vessels, models with individual terms for vessel were fit for 1993 and 1994 by means of regular logistic regression. Patterns of increasing probability of movement with declining catch rates were consistent for all vessels, although there was considerable variation in the slope and the inflection point of the logistic curves.

To model the role of earlier information in the decision to leave an area, it was necessary to consider which hauls would be used and how much influence they should have. Certainly, recent nearby hauls should receive the most weight, but during the course of a fishing season a vessel moves several times, and often returns to a location that was fished earlier in the season. The particular summary of previous experience used for this analysis was an exponentially weighted average, m_j , of previous hauls, such that the catch rate residual for the most recent haul received a weight of 1.0, and previous hauls within 30 km of that haul received progressively less weight the further back in time that they occurred:

$$m_{j} = \frac{\sum_{k=1}^{j} (cr_{k} - \hat{c}r_{k}) i_{j}(k) e^{-rr_{j}(k)}}{\sum_{k=1}^{j} i_{j}(k) e^{-rr_{j}(k)}}$$



Figure 10. Deviance profiles for 1991–95 of the exponential coefficient (r) in the exponential average summarizing previous fishing experience. The farthest right point of the profile is the deviance for a model with only the most recent haul. The *bold line* is the mean for all years.

where $i_j(k)$ is an indicator function that takes the value 1.0 if the kth haul is within 30 km of the jth haul and zero otherwise; $t_j(k)$ is the time in days from the kth haul to the jth haul; and r is an exponential coefficient that governs the rate that the catch rate residuals from earlier hauls are down-weighted relative to the most recent haul. This summary of previous fishing experience was calculated on a vessel-by-vessel basis, not for the fleet as a whole.

The key parameter in this approach to modeling past information is the exponential coefficient, r. To gain some insight into the appropriate choice for r, I obtained deviance profiles across r for each year by varying r incrementally from 0.5 to 10 in steps of 0.5. Although the shape of the r profile differed between years, in each year there was a value of r that resulted in a lower deviance than the model which used only the most recent catch rate residual (figure 10). The minimum deviance r values were generally in the range of 2.0-6.5 (which imply half weights of 2.5-8 hrs). The value of r with minimum deviance for all years was 3.5, which results in a half weight of 4.8 hrs; that is, a haul retrieved 4.8 hrs before the current haul receives half the weight in the weighted average. The average time between haul retrievals on a factory trawler is usually about 5 hrs (mean haul duration 2.5 hrs, mean time between hauls 2.5 hrs). This suggests that the decision to leave an area is based on information from only the most recent 1-2 hauls. The change in deviance for r = 3.5 ranged between 3.1 in 1993 and 14.1 in 1995 (table 2), but no attempt was made to associate *p*-values with these changes in deviance. Determining the appropriate degrees of freedom for the likelihood ratio test is difficult because of correlation in the catch rates of successive hauls, and the choice of the exponential coefficient r used in the weighted average.



Vessels within 15 km over previous 6 hrs

Figure 11. Frequency distribution of local fishing activity during 1991–95 (the number of vessels fishing within 15 km over the previous 6 hrs).



Number of vessels within 15 km during previous 6 hrs

Figure 12. Generalized additive model (GAM) predictions of the probability of movement as a function of local fishing activity for 1991–95. Predictions are for a model with two terms: an exponential average of the catch rate residuals for previous hauls, and local fishing activity. The catch rate residual term was fixed at zero to produce the model predictions.

The influence of local fishing activity on the decision to leave an area was examined next. Similar issues about the choice of an appropriate spatial and temporal frame to summarize information on local fishing activity must be addressed. The summary of local fishing activity used for this analysis was a simple count of the number of unique vessels (both catcher processors and catcher boats delivering to mother ships) within 15 km that had conducted trawling operations within the previous 6 hrs. Fifteen kilometers is an approximation of the range of sight from a vessel at sea. This summary of local fishing activity ranged from 0 to 12 vessels, with a mean of 2.6 vessels (figure 11). Nineteen percent of the time there were no other vessels within 15 km. The GAM smooth terms for local fishing activity show a decrease in the probability of movement with increasing local fishing activity (figure 12). The smooth terms are fairly linear throughout their range. The smooth terms are significant at $\alpha = 0.05$ in all years except 1994 (table 2).

DISCUSSION AND CONCLUSIONS

The analysis of acoustic survey data indicated that the spatial correlation extended to 25–35 km. These results are generally comparable with other research on similar species. Sullivan (1991) found that spatial correlations of spawning pollock in Shelikof Strait, Alaska, extended to about 30 km. Other analyses of survey or fishery data have reported spatial-correlation ranges. For haddock on Georges Bank the range is 9 nmi (Polacheck and Vølstad 1993); for hoki off New Zealand, the range is 11 nmi (Vignaux 1996a).

The factors that produce spatial correlation in fish populations are poorly understood. Ultimately, the physical oceanography of the summer feeding habitat of Pacific hake probably determines its correlation structure. Instability in the California Current mean flow produces mesoscale meanders and eddies that are sites of enhanced primary production (Abbott and Zion 1987) and that create fronts which concentrate zooplankton, including euphausiids, the primary food of Pacific hake (Rexstad and Pikitch 1986; Mackas et al. 1991). The spatial scale of these mesoscale oceanographic features is determined by the baroclinic Rossby radius of deformation, which is ~25 km in midlatitudes off the West Coast (Thomson et al. 1992). If Pacific hake concentrate in areas of high zooplankton density, aggregations may occur in association with these mesoscale oceanographic features. However, this is an area of active research, and additional work is needed to elucidate the biophysical linkages between the physical environment and regions of high fish abundance.

The geostatistical analyses of Pacific hake spatial structure demonstrate the importance of considering the spatial characteristics of fish populations when interpreting vessel movement patterns. Other research on fishing behavior has usually imposed ad hoc models of decision making by looking at movement between arbitrary geographic blocks or statistical reporting areas, which may be unrelated to how fishermen perceive their environment (Hilborn and Ledbetter 1979; Gillis et al. 1993; Vignaux 1996b). Eales and Wilen (1986), however, examined fishing location choice in a shrimp fishery where the potential fishing area was divided into smaller regions based on fishing patterns. The structure function illustrates how the foraging landscape would be perceived by a fishing vessel that requires a threshold fish density in order to operate profitably. To estimate the structure function, however, it was necessary to link fishery catch rates with acoustically measured fish densities by making some fairly crude assumptions about the capture efficiency of commercial fishing gear. Independent information is needed about the level of fish density that can support fishing activity, such as might be obtained by placing a calibrated echo sounder on a commercial fishing vessel.

The results of the GAM models of vessel movement showed that there is a low probability that a vessel will leave a foraging area when its catch rate is higher than its expected catch rate. The probability of moving increases sharply when catch rate residuals become negative. This result generally agrees with the Arditi and Dacorogna (1988) prediction of a threshold prey density that triggers movement by the forager. But the results also suggest that there may be additional factors involved in the decision to move. Although the probability of moving is clearly a nonlinear function of the catch rate residual on a logistic scale, there is no evidence of a discontinuity. This may in part be due to the GAM approach to modeling, which estimates smooth terms in an additive predictor. Also, the probability of movement for negative catch rate residuals is between 0.05 and 0.15, which indicates that fishing vessels still have a fairly low probability of leaving an area when their catch rates are below average. Since factory trawlers usually target their midwater nets on acoustically detected aggregations of fish, the ability to locate a suitably dense aggregation may play an important role in the decision to move.

The GAM models of vessel movement showed that an exponentially weighted average of previous hauls with a half-weight of approximately 4.8 hours was more successful at predicting movement than only the catch rate residual of the most recent haul. This result suggests that vessels base their decisions on relatively short time frames. Evaluating different frame lengths is a new approach to interpreting fishing behavior, but similar approaches have been used with bumblebees in artificial foraging environments (Real 1991). Previous research on fishing behavior has assumed an arbitrary time window over which experience is averaged, typically one day (Eales and Wilen 1986; Vignaux 1996b) or one week (Hilborn and Ledbetter 1979; Gillis et al. 1993). The time frame that the vessels use to evaluate fishing success may be related to the temporal persistence of hake aggregations and also to the inherent stochastic variation in the catch rates. If hake aggregations are extremely transient, earlier information would rapidly become useless as a predictor of current conditions. A fishing vessel that used an inappropriate weighting scheme would remain too long in an area where the fishing is no longer good or, conversely, would leave too soon and spend an excessive amount of time in transit between areas.

The tendency for vessels to be less likely to leave an area if there are other vessels nearby is an advantageous strategy from two perspectives. First, the presence of other vessels in an area suggests high fish densities. Information on the local density of fishing vessels can be collected easily and quickly in comparison to surveying an area acoustically or by test fishing. Second, each vessel fishing in the same area can be certain that no other vessel has a higher average catch rate than it does. This is particularly important in a fishery that is managed with a fleetwide quota. If only a few days remain to the close of season, a risk-averse strategy such as fishing near other vessels will guarantee that the remaining quota will be shared equally among vessels. Searching for a new area with higher catch rates runs the risk that the season will close before higher catch rates can compensate for the time spent searching or in transit. Since the north-south variance in trawling locations in the at-sea fishery typically decreases toward the close of the season, there is some evidence that the spatial distribution of fishing activity is affected by these considerations.

Vignaux (1996b) conducted a similar analysis of fishing behavior in a trawl fishery for hoki off New Zealand. Instead of using a GAM model to predict vessel movement as a function of catch rates, Vignaux (1996b) tested for differences in the probability of movement when the catch rates were below and above average. Vignaux's results regarding the effect of low catch rates were similar to those in this paper, suggesting that this may be a common characteristic of fishing behavior.

The GAM models for vessel movement developed in this paper offer advantages over the more ad hoc approaches that have been used up to now to study fishing behavior. The GAM models allow a more detailed examination of vessel response. For example, my evaluation of nonlinearity in the response to declines in catch rates would have been difficult with conventional approaches. Also, GAM models provide a unified framework for evaluating different sources of information and other attributes of the catch in addition to the catch rate.

One of the initial objectives of this research was to investigate vessel responses to salmon and rockfish bycatch. In addition to the catch rate of the target species, decision making may depend on the amount of bycatch and other attributes of the catch, such as the mean size or sex ratio of the target species. But it became evident that observer sampling procedures and record keeping do not provide enough information for such analysis. Since bycatch estimates are often derived from a small sample of the catch, sampling variability may occasionally result in unrealistic bycatch estimates for individual hauls. This sampling variability is not a problem when the objective is to estimate the bycatch for the entire fleet, but it does present difficulties for the statistical models developed in this paper, where accurate information is needed for each haul. In addition, observers sample only a subset of hauls for species composition, ranging from 35% to 70%. Consequently, it is difficult to assess decision making based on more than one haul. The cumulative bycatch over a number of hauls may be a

more important predictor of vessel response than bycatch from a single haul.

The spatial structure of salmon and rockfish distribution is also likely to differ in scale from that of Pacific hake. An analysis of the spatial correlation of bycatch species is a prerequisite for developing models of vessel response to bycatch. Methods developed by Vignaux (1996a) using fishery data to analyze spatial structure in the distribution of the target species may also be applicable to bycatch species. Since observers record only the retrieval locations of hauls, the spatial resolution of the observer database is not adequate to examine spatial correlation and vessel movement at smaller scales than those examined in this paper. Once the spatial scale of the bycatch species has been identified, vessel responses at this scale could be explored with the techniques developed in this paper. Since bycatch is an important concern in managing the Pacific hake fishery, expanded data collection procedures in the fishery should be considered.

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LITERATURE CITED

- Abbott, M. R., and P. M. Zion. 1987. Spatial and temporal variability of phytoplankton pigment off northern California during Coastal Ocean Dynamics Experiment 1. J. Geophys. Res. 92:1745–1756.
- Arditi, R., and B. Dacorogna. 1985. Optimal foraging in nonpatchy habitats. I. Bounded one-dimensional resource. Math. Biosci. 76:127–145.
- -------. 1988. Optimal foraging on arbitrary food patches and the definition of habitat patches. Am. Nat. 131:837–846.
- Bodolt, H., H. Nes, and H. Solli. 1989. A new echo sounder system. Proceedings of the Institute of Acoustics 11:123–130.
- Chambers, J. M., and T. J. Hastie. 1992. Statistical models in S. Pacific Grove, Calif.: Wadsworth and Brooks, 608 pp.
- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. Theor. Pop. Biol. 9:129–136.
- Dorn, M. W. In press. Fine-scale fishing strategies of factory trawlers in a midwater trawl fishery for Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci.
- Dorn, M. W., E. P. Nunnallee, C. D. Wilson, and M. E. Wilkins. 1994. Status of the coastal Pacific whiting resource in 1993. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-47, 101 pp.
- Eales, J., and J. E. Wilen. 1986. An examination of fishing location choice in the pink shrimp fishery. Mar. Res. Econ. 2:331-351.
- Fisher, F. W. 1994. Past and present status of Central Valley chinook salmon. Conserv. Biol. 8:870–873.
- Foote, K. G., H. P. Knudsen, R. J. Korneliussen, P. E. Nordbo, and K. Roang. 1991. Postprocessing system for echo sounder data. J. Acoust. Soc. Am. 90:37–47.
- Garcia, S. M., and C. Newton. 1995. Current situation, trends and prospects in world capture fisheries. Conf. on Fisheries Management. Global Trends, Seattle (USA), 14–16 Jun. 1994. FAO, Rome (Italy), 63 pp.
- Gillis, D. M., R. M. Peterman, and A. V. Tyler. 1995. Movement dynamics in a fishery: application of the ideal free distribution to spatial allocation of effort. Can. J. Fish. Aquat. Sci. 50:323–333.

- Gillis, D. M., R. M. Peterman, and E. K. Pikitch. 1995a. Implications of trip regulations for high-grading: a model of the behavior of fisherman, Can. J. Fish. Aquat. Sci. 52:402–415.
- . 1995b. Dynamic discarding decisions: foraging theory for highgrading in a trawl fishery. Behav. Ecol. 6:146–154.
- Hastie, T., and R. Tibshirani. 1990. Generalized additive models. London: Chapman and Hall, 289 pp.
- Hilborn, R., and M. Ledbetter. 1979. Analysis of the British Columbia salmon purse-seine fleet: dynamics of movement. J. Fish. Res. Board Can. 36:384–391.
- Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecol. Monog. 62:447–502.
- Lawless, J. F. 1987. Negative binomial and mixed Poisson regression. Can. J. Stat. 15:209–225.
- MacCall, A. 1990. Dynamic geography of marine fish populations. Seattle: Univ. Wash. Press, 153 pp.
- Mackas, D. L., L. Washburn, and S. L. Smith. 1991. Zooplankton community pattern associated with a California Current cold filament. J. Geophys. Res. 96:14781–14797.
- Mangel, M., and F. R. Adler. 1994. Construction of multidimensional clustered patterns. Ecology 75:1289–1298.
- McCullagh, P., and J. A. Nelder. 1983. Generalized linear models. London: Chapman and Hall, 261 pp.
- McNamara, J. M., and A. I. Houston. 1985. Optimal foraging and learning. J. Theor. Biol. 117:231–249.
- Nunnallee, E. P. 1991. An investigation of the avoidance of Pacific whiting (*Merluccius productus*) to demersal and midwater trawl gear. Int. Coun. Explor. Sea., Paper/B:5, sess. U., Fish Capture Meeting 26 Sep-4 Oct 1991, La Rochelle, France.
- Pelletier, D., and A. M. Parma. 1994. Spatial distribution of Pacific halibut (*Hippoglossus stenolepis*): an application of geostatistics to longline survey data. Can. J. Fish. Aquat. Sci. 51:1506–1518.
- Polacheck, T., and J. H. Vølstad. 1993. Analysis of spatial variability of Georges Bank haddock (*Melanogrammus aeglefinus*) from trawl survey data using a linear regression model with spatial interaction. ICES J. Mar. Sci. 50:1–8.
- Real, L. 1991. Animal choice behavior and the evolution of cognitive architecture. Science 253:980–986.
- Rexstad, E. A., and E. K. Pikitch. 1986. Stomach contents and food consumption estimates of Pacific hake, *Merluccius productus*. Fish. Bull., U.S. 84:947–956.
- Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecol. Monog. 62:277–314.
- Smith, S. J. 1990. Use of statistical models for the estimation of abundance from groundfish trawl survey data. Can. J. Fish. Aquat. Sci. 47:894–903.
- StatSci. 1993. S-Plus for DOS reference manual. Seattle, Wash.: Statistical Sciences Inc.
- Sullivan, P. J. 1991. Stock abundance estimation using depth-dependent trends and spatially correlated variation. Can. J. Fish. Aquat. Sci. 48:1691–1703.
- Swartzman, G., C. Huang, and S. Kaluzny. 1992. Spatial analysis of Bering Sea groundfish survey data using generalized additive models. Can. J. Fish. Aquat. Sci. 49:1366–1378.
- Thomson R. E., M. C. Healey, J. F. T. Morris, and G. A. Borland. 1992. Commercial troll fishing vessel distribution of Vancouver Island during July 1988: relation to observed physical oceanography. Can. J. Fish. Aquat. Sci. 49:820–832.
- Traynor, J. J. 1996. Target-strength measurements of walleye pollock (*Theragra chalcogramma*) and Pacific whiting (*Merluccius productus*). ICES J. Mar. Sci. 53:253–258.
- Vignaux, M. 1996a. Analysis of spatial structure in fish distribution using commercial catch and effort data from the New Zealand hoki fishery. Can. J. Fish. Aquat. Sci. 53:963–973.
- . 1996b. Analysis of vessel movements and strategies using commercial catch and effort data from the New Zealand hoki fishery. Can. J. Fish. Aquat. Sci. 53:2126–2136.
- Waples, R. S., R. P. Jones, B. R. Beckman, and G. A. Swan. 1991. Status review for Snake River fall chinook salmon. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-194, 81 pp.
- Wilson, C. D., and M. A. Guttormsen. 1997. Echo integration-trawl survey of Pacific whiting, *Merlucius productus*, off the west coasts of the United States and Canada during July–September 1995. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-74, 70 pp.