Variation in the Competitive Abilities of Fishermen and its Influence on the Spatial Distribution of the British Columbia Salmon Troll Fleet

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Abrahams, M. V., and M. C. Healey. 1990. Variation in the competitive abilities of fishermen and its influence on the spatial distribution of the British Columbia salmon troll fleet. Can. J. Fish. Aquat. Sci. 47: 1116–1121.

We estimated the catch rates of individual fishing vessels within the British Columbia salmon troll fleet from the data of a 7-yr log book program. Catch rates varied considerably among vessels. A portion of the variation could be attributed to environmental variation. However, there were also significant differences in competitive ability among vessels. The top ranked vessels had a catch rate 3.6 times that of the lowest ranked vessels. Top ranked vessels distributed their fishing effort among more fishing areas than bottom ranked vessels, but were also more successful at catching fish when fishing in the same areas as bottom ranked vessels. This information, through an application of the ideal free distribution theory, can be used to develop a model that will describe the expected relationship between vessel distribution, vessel catch rate, and fish distribution, potentially allowing vessel distributions to be used as a tool for assessing fish stocks.

Nous avons évalué les taux de capture de chaque navire de la flotte de pêche à la ligne traînante au saumon en Colombie-Britannique à partir des données recueillies dans le cadre d'un programme de levé de sept ans. Les taux de capture variaient considérablement entre les divers navires. Une partie de ces variations pourrait être attribuée aux variations du milieu. Toutefois, on a également noté d'importantes différences dans la capacité concurrentielle des navires. Le taux de capture des meilleurs navires était 3.6 fois plus élevé que celui des navires en bas de liste. L'effort de pêche des premiers était réparti sur une plus vaste superficie que les seconds et leurs captures étaient également plus importantes lorsqu'ils pêchaient dans les mêmes secteurs. En appliquant la théorie de la distribution libre idéale, ces renseignements peuvent servir à mettre au point un modèle pour décrire le rapport prévu entre la distribution des navires, leurs taux de capture, et la distribution des poissons, et permettre éventuellement d'évaluer les stocks de poissons à partir de la distribution des navires.

Received July 13, 1989
Accepted January 2, 1990
(JA226)

Reçu le 13 juillet 1989
Accepté le 2 janvier 1990

Studies on the fleet dynamics of commercial fishing vessels have traditionally viewed the problem from a population perspective. Typically, questions of interest include factors which affect the size of (or investment in) the fleet, such as changes in the abundance of prey species and their economic value (Botsford et al. 1983; Gatto et al. 1975; Charles 1983). Recently, there has been growing interest in examining strategies adopted by fleets for exploiting their resource. These include strategies used for finding fish (Mangel 1982; Mangel and Clark 1983), and movement patterns of fishing vessels (Hilborn and Ledbetter 1979). Few studies have considered the consequences of variation in catch rate on the spatial distribution of the fleet (but see Hilborn and Ledbetter 1979). This study is a detailed examination of the catch rates of a group of trollers and the consequences of catch rates on the spatial distribution of the west coast troll fleet through an application of the ideal free distribution theory (IFD).

Fretwell and Lucas (1970) and Fretwell (1972) introduced the IFD as a theoretical model to explain the distribution of animals with respect to their resources. For animals to distribute themselves in accordance with an IFD, they must satisfy two assumptions. First, all animals must have perfect information about the distribution of resources in their environment (i.e. they are ideal). Second, all individuals should be equal in their competitive abilities such that they have 'free' access to resources anywhere in their environment. When animals conform to these assumptions, they will distribute themselves so that they all receive equal amounts of the resource, regardless of where they occur.

Fretwell (1972) recognized that these assumptions were unlikely to be true. However, deviations from this model can identify factors important in determining the spatial distribution of animals. Recently, a number of studies have examined the spatial distribution of predators with respect to their prey (see Abrahams 1986 for a review). In the majority of these studies, predators tended to overuse poor patches (areas with a below-average proportion of resources) and underuse good patches (areas with an above-average proportion of resources). In many cases, the authors of these papers argued that their animals were not all of equal competitive ability and that this was the most likely reason their results did not comform exactly to an IFD.

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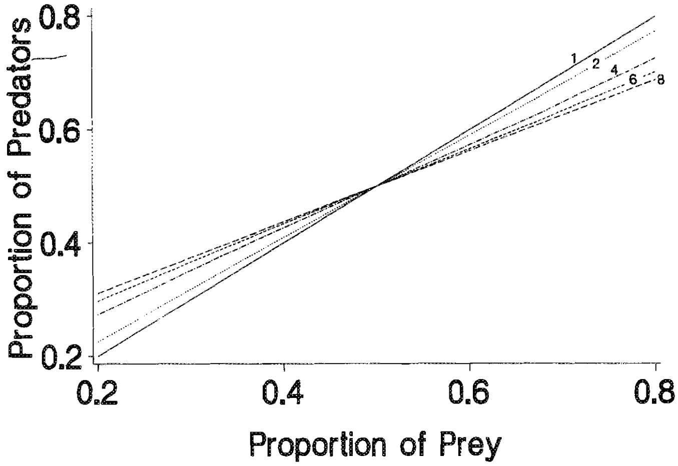

FIG. 1. Expected distribution of predators with respect to their prey as the range of competitive abilities changes (ratio of the best competitor to the worst competitor). Numbers on each line represent the ratio of competitive abilities. (From Houston and McNamara 1988).

Parker and Sutherland (1986) and Sutherland and Parker (1985) suggested that when animals differ in competitive ability, the sum of competitive abilities rather than the animals themselves will be distributed in accordance with an IFD. There are a number of numerical distributions of animals relative to their resources that will satisfy Parker and Sutherland's model, but Houston and McNamara (1988) have demonstrated that overuse of poor patches is statistically the most likely distribution. Furthermore, increasing the difference in competitive abilities, or the number of competitors, or both will increase the magnitude of this effect (Houston and McNamara 1988, Fig. 1).

Fishermen are faced with a patch choice problem in their search for fish. Although the ocean appears to be a homogenous environment (at least at the surface), fish are known to aggregate in particular areas. For salmon trollers, aggregations of salmon are typically found in upwelling areas associated with steep slopes on the continental shelf and, thus, are identifiable from navigational charts (Healey et al. 1990).

That trollers recognize and focus on patches of salmon is evident from the spatial distribution of the troll fleet off the west coast of Vancouver Island (Fig. 2). In this paper we examine characteristics of trollers to determine the extent to which they deviate from the assumption of equal competitive ability. This information can then be used to describe the extent to which the troll fleet should deviate from an IFD and thus the predicted distribution of the troll fleet relative to the distribution of fish.

Characteristics of Troll Vessels in the Salmon Fishery

Troll vessels off the coast of British Columbia fish for salmon (*Oncorhynchus* sp.) by hook and line, using six lines baited with lures and flashers placed at different depths. Within the fleet there are three classes of vessels: day boats, ice boats, and freezer boats. The majority of the vessels in the fleet (and in this study) are ice boats, which preserve their catch with ice, and undertake fishing trips no longer than 2 wk in duration. Day boats also preserve their fish with ice, but return to port daily to sell their catch. Freezer boats freeze their catch, "glazing" them in ice for preservation. They are the largest and most sophisticated in the fleet and need only return to port when they have a full load of fish or require supplies, allowing them to fish continuously for periods in excess of 60 d. Typically trollers own and operate their own vessel with the assistance of a hired deck hand.

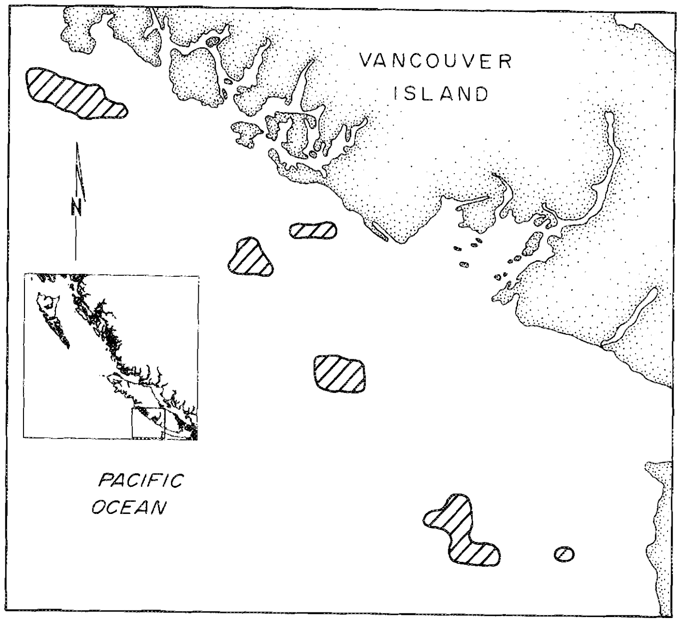

FIG. 2. Observed aggregations of trollers off southwest Vancouver Island July 28, 1982. Observation from Tofino traffic control radar. Minimum vessel density within aggregations $= 0.105 \cdot \text{boats} \cdot \text{km}^{-2}$. Inset shows British Columbia coast.

Methods

The Canadian Department of Fisheries and Oceans has maintained data for the British Columbia coast (except for the Strait of Georgia) on daily catch of salmon by species from individual troll boats during the years 1981 to 1987. Twenty-eight, 20, 26, 70, 82, 79, and 86 vessels provided data in 1981 to 1987, respectively (Healey 1986, Jordan and Carter 1987).

The vessels participating in this program caught six different species of Pacific salmon: chinook (*Oncorhynchus tshawytscha*), chum (*O. keta*), coho (*O. kisutch*), pink (*O. gorbuscha*), sockeye (*O. nerka*), and steelhead (*O. mykiss*). As these fish vary considerably in both size and value, catch composition differed among vessels, and we converted the catch data for each boat to a dollar value. To do this, the weight of the fish was assumed equal to the average weight of each species landed in each statistical area each week (Canada Department of Fisheries and Oceans, unpubl. data). Dollar value of the catch was then: $V = \Sigma W_i N_i P_i$ where W_i = average weight of species i, N_i = number of species i caught, P_i = price of species i.

We assumed that the goal of each skipper was to maximize the rate at which he made money while fishing. If this is true, then competitive ability can be represented by the short-term rate of accumulating income. We calculated a daily estimate of each vessel's competitive ability by dividing the total cash value of a daily catch by the number of hours spent fishing. This estimate of competitive ability is independent of the total amount of money each vessel earned.

Results

Variation in Catch Rates Among Years

Over the 7 yr of this study, the price of each salmon species changed in both absolute and relative terms (Fig. 3). From 1981

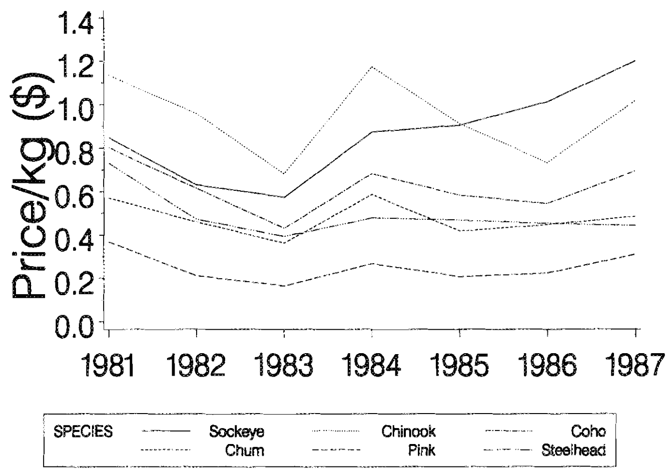

FIG. 3. Average annual price (in 1981 dollars) for six species of pacific salmon from 1981 to 1987.

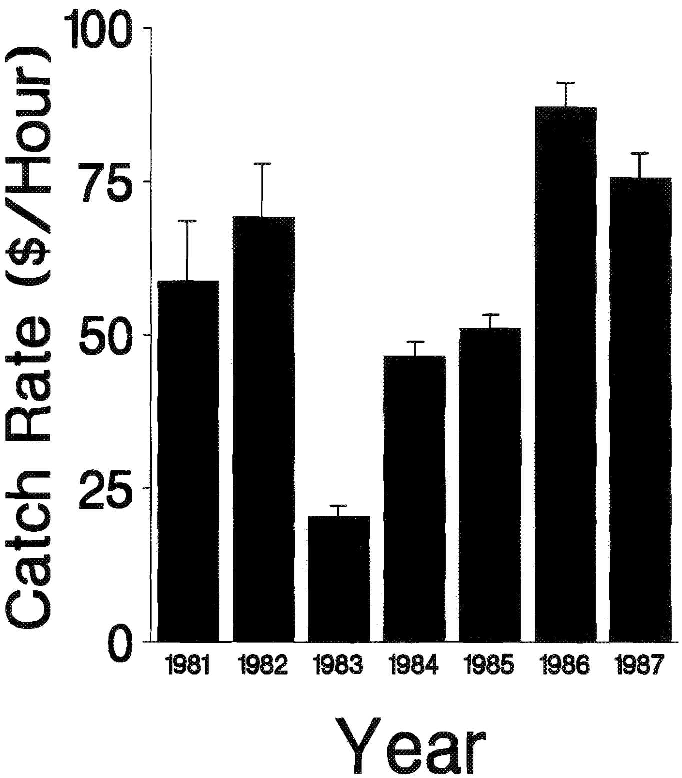

FIG. 4. Average catch rates (in 1981 dollars) for July and August of each year. Error bars represent one standard error.

to 1984, chinook salmon commanded the highest price/kilogram, and their price/kilogram increased with their size. During 1986 and 1987, however, sockeye salmon commanded the highest price/kilogram and their value relative to the other species increased from 1983 to 1987.

Between 1981 and 1987, regulations changed to restrict the fishing season. Details of these regulatory changes, which were implemented to conserve declining stocks of chinook salmon and to meet terms of the Canada/United States salmon interception agreement are given in Healey (1986); Argue et al. (1987); and Shardlow et al. (1986, 1988). In relation to the analyses we planned to perform, the most significant changes in regulations were a gradual elimination of the spring fishing season for chinook salmon and earlier closure of the troll fishery in September. The fishery was gradually restricted to the months of July and August. Although these regulation changes cut the annual fishing time by more than half, most of the catch was historically taken during July and August. In addition, in 1985 and thereafter, catch ceilings were imposed on all species on the west coast of Vancouver Island. We therefore restricted our analysis to log book records from July and August each year.

Catch rates (1981 dollars/hour) during these summer months varied considerably between years (multifactor ANOVA, $F_{6,2683} = 58.6, P = 0.0001$); the catch rate of 1986 being almost four times that recorded in 1983 (Fig. 4). The range of variation exceeded that which could be accounted for by changes in the value of salmon and are likely due to changes in the abundance of fish (Healey 1986).

Within Year Variation

When catch data were grouped by week, there was a significant effect of week on catch rates (multifactor ANOVA, $F_{9,2683} = 54.7, P = 0.0001$). Catch rates were highest in the mid and late summer and were due to pink and sockeye salmon becoming available to the trollers at this time of the year whereas earlier only chinook and coho were available (Healey 1986).

Variation in Catch Rates Among Areas

There was also a significant effect of fishing area on the reported catch rates for all years (multifactor ANOVA, $F_{19,2683} = 30.9, P = 0.0001$). Unlike the within year variation, this effect was less consistent (and less predictable) among years. Fishing areas that had catch rates significantly higher than all others ranged from southern to northern British Columbia in different years.

Variation in Catch Rates Among Vessels

There was high variation in catch rate among vessels within a year (multifactor ANOVA, $F_{128,\ 2683} = 10.15$, $p < 0.0001$). This variation should reflect competitive ability, but it was also influenced by the temporal and spatial variability in the availability of fish noted above. There may be no real difference in competitive ability among fishing vessels, and therefore the variation in catch rates may simply be due to some boats being in the right place at the right time. To determine whether variation in catch rates among vessels was at least partly due to differences in competitive ability we compared the observed frequency distribution of catch rates to a null distribution in which all variation was environmentally determined.

We transformed catch rates for each vessel for each year to the number of standard deviates from the mean for all vessels. This number represented each vessel's relative competitive ability, independent of the absolute catch rate for that year. From these data we calculated an average catch rate for each vessel that provided three or more years of data (73 of the 141 different vessels in this program). The frequency distribution of these average catch rates was assumed to represent the range of competitive abilities within the fleet.

We constructed the null distribution using all the observed data. Our fundamental assumption was that no differences existed in competitive ability so that the range of catch rates observed each year was generated solely by environmental variation. To create this distribution new catch rate values were assigned to each of the 73 vessels by randomly drawing (with replacement) one observation from the observed data for all

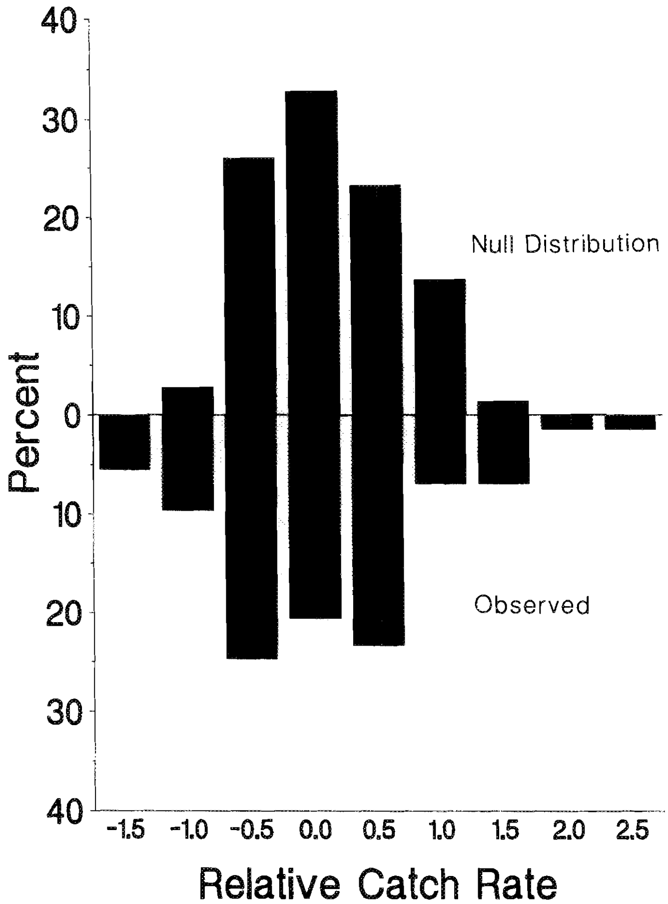

FIG. 5. Observed and predicted distribution of average relative catch rates (catch rates as unit normal deviates). Predicted model (null distribution) assumes there are no differences in the competitive abilities of fishing vessels.

vessels for each year this vessel contributed data. For example, if vessel 1 contributed data in 1981, 1983, and 1986 then a new catch for 1981 was assigned to this vessel from the set of catch rates for all vessels in 1981, and similarly for 1983 and 1986. The average catch rates calculated from these assigned numbers were taken to represent a catch rate distribution due to chance encounters with environmental factors (temporal and spatial) alone. The frequency distribution of these new average values was the null distribution.

If there are real differences in competitive ability among trollers the observed distribution of catch rates should be significantly broader than the null distribution. The two distributions are illustrated in Fig. 5, and are significantly different (χ^2 = 50.67, P<0.001). The null distribution shows much less variation in catch rates than the observed data, indicating that environmental variation alone cannot account for the observed range of catch rates in the troll fleet, and real differences in competitive abilities must exist.

We selected the top five and bottom five ranked vessels from the observed distribution as representative of the range of competitive abilities of the vessels sampled and examined their absolute rates of catch and distribution of fishing effort. All of the vessels in this sample reported catch rates for 1985 through 1987. During this time period, the average catch rate of the top five vessels was 3.6 times that of the bottom vessels. Furthermore, this ratio was 3.5 for those instances in which top and bottom ranked vessels were fishing in the same area at the same time, suggesting that the ratio of catch rates represents a difference in the ability to catch fish, not a difference in the ability to find fish.

The top and bottom ranked vessels differed in the proportion of their time spent fishing in different statistical areas (Fig. 6a, b). All the top vessels fished in a number of different areas. This was in striking contrast to the bottom vessels (Fig. 6b) which spend more than 75% of their time in a single or two adjacent areas, only occasionally fishing in other locations.

To determine whether the fishing patterns of different vessels were a major determinant of fishing success, we described the diversity of where the boats fished by the Shannon-Wiener diversity index. The Shannon-Wiener diversity index is derived from information theory and is calculated as Σp_i (log p_i) where p_i is the proportion of time spent fishing in area i. The minimum value occurs if a vessel fishes only in one area. The index increases as vessels distribute their time equally between a large number of areas. We calculated a diversity index for each vessel for each year and averaged these values. As with the previous analysis, we used only vessels that provided three or more years of data. A significant positive correlation existed between the average diversity index and catch rate expressed as a unit normal deviate (Fig. 7, multifactor ANOVA, $F_{1,71}$ = 17.3, P<0.0001, r^2 = 0.196). The diversity index was also positively correlated with the proportion of sockeye in the catch (proportions arcsin square-root transformed, $F_{1,71}$ = 11.69, P = 0.001, r^2 = 0.141), suggesting that a broad distribution of fishing effort may be a strategy to promote the capture of sockeye. A significant, but weak negative correlation existed between the diversity index and the proportion of chinook in the catch (proportions arcsin square-root transformed, $F_{1,71}$ = 7.75, r^2 = −0.098, P = 0.007). No other significant correlations existed for other species, or the diversity of species caught.

Another factor which may contribute to differences in competitive ability is vessel size. Vessel length was significantly positively correlated with catch rate (Fig. 8, $F_{1,71}$ = 22.1, r^2 = 0.237, P<0.0001). Whether larger vessel size is a cause or an effect of higher competitive ability is unclear. However, if mobility is a significant factor contributing to fishing success and competitive ability then possession of a larger vessel probably enhances any competitive advantage that a successful fisherman already has. Vessel class (i.e. ice boat or freezer boat) had no significant influence on relative catch rate (multifactor ANOVA, $F_{1,71}$ = 1.72, P = 0.19). Presumably, the advantage of operating a freezer boat may be to increase the time available for fishing since they require fewer trips to port.

Discussion

Analysis of catch rates among individuals in the British Columbia salmon troll fleet indicates that boats differ substantially in competitive ability. These differences are in addition to considerable temporal and spatial variation in catch rates. The source of the differences in competitive ability is less clear. Striking differences were observed in the allocation of fishing effort between the top and bottom ranked vessels. Top ranked vessels fished in a large number of areas whereas the bottom ranked vessels tended to concentrate their effort in one or two areas. The relationship between catch rate and dispersion of fishing effort was consistent over all vessels.

Vessel length also was positively correlated with catch rate. However, the mechanism responsible for this correlation is not clear. Some fishermen argue that larger vessels fish better

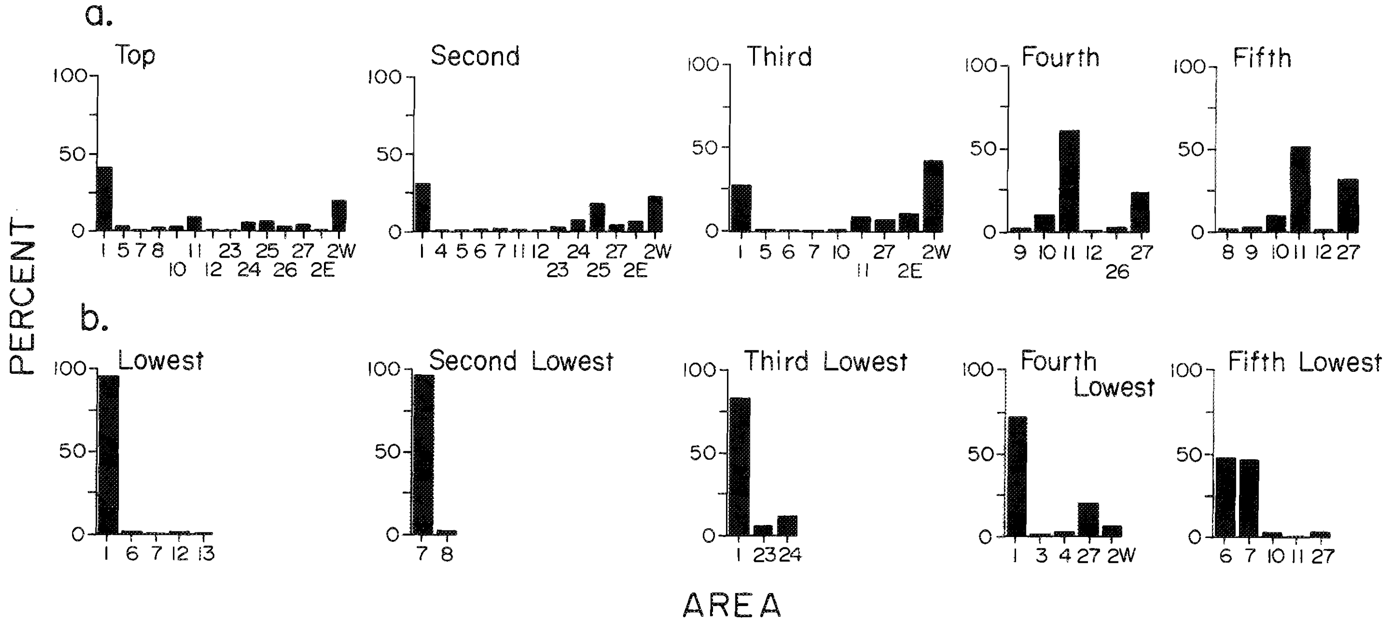

FIG. 6. Percent of time spent fishing in different statistical areas by (a) the top five ranked vessels and, (b) the bottom five ranked vessels.

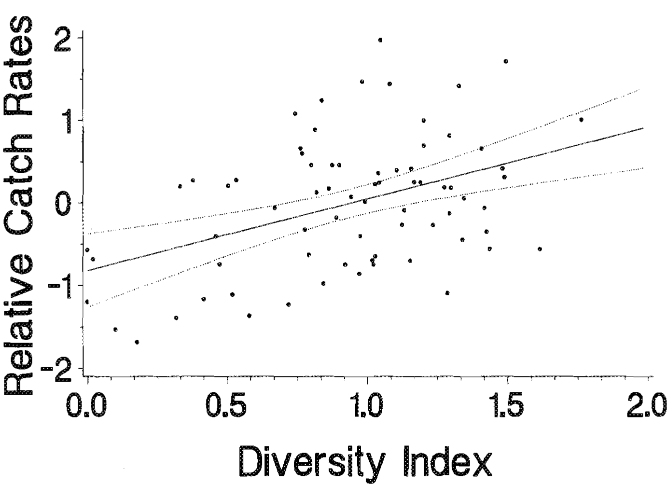

FIG. 7. Relative catch rates as a function of diversity index. Line fitted by least squares (dotted lines are 95% confidence intervals). See text for details.

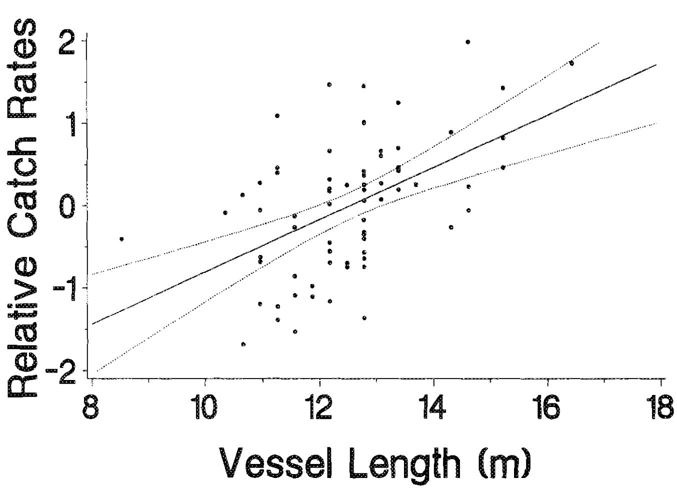

FIG. 8. Relative catch rates as a function of vessel length. Line fitted by least squares (dotted lines are 95% confidence intervals).

because of their greater momentum, allowing them to fish at a constant speed in rough water. A small vessel fishing in the same conditions has its speed slowed by each wave, possibly rendering the gear less effective. Alternatively, only successful fishermen could afford to own large fishing vessels. Therefore, the higher catch rates of the larger vessels may be due to differences in the skills of the skippers, not the vessels per se.

Other factors that may affect competitive ability include characteristics of the vessels such as electrical grounding of the hull, and the type and condition of the equipment on board, as well as the experience and competence of the skipper which would determine the efficiency with which a vessel's equipment was used (e.g. structure and type of lures deployed). Finally, fishing strategies of the skippers may differ in ways other than the way they allocate effort among fishing areas. Evidence that factors such as these are related to competitive ability is provided by a comparison of catch rates among vessels fishing in the same area at the same time. In such a situation, top vessels still did much better than bottom vessels.

Data provided in this study indicate only the gross financial benefits from fishing, not the costs. Vessels with higher catch rates may incur greater financial costs due to movement or hardship due to isolation (see R. Hilborn and R. B. Kennedy, unpubl. data for a discussion of this latter point). Net benefits may be more similar among vessels than indicated by these data but are unlikely to be of a magnitude sufficient to offset our observations (see Figs. 7 and 8).

Hilborn (1985) has suggested that, within the commercial purse seine fishery, two strategies could exist for maximizing the number of fish caught. One strategy is to specialize in a particular area and, by learning everything possible about catching fish in that area, maximize the rate of capture within that area (area specialist). The other strategy is to develop skills appropriate to any area and then to fish opportunistically in a large number of different areas in order to maximize the number of fish captured (movement specialist). In this study, vessels with the highest catch rates were movement specialists and vessels with the lowest catch rates were area specialists. However, area specialists were not more skilled at fishing in their chosen area than were movement specialists, rather the reverse was true. Nor is there evidence that area and movement specialization exist as discrete strategies within the troll fleet. Rather, these strategies appear to be ends of a continuum. An alternative explanation may be that vessel movement patterns are tied to a skipper's decision about which salmon species to fish for. Increased movement may be necessary if the troller wishes to follow schools of sockeye salmon as they migrate along the British Columbia coast. Area-restricted fishing may reflect a decision to target on chinook salmon. Intermediate movement patterns represent less species specificity in harvesting.

Whatever their underlying causes, absolute differences in competitive ability among vessels will have a profound influence on the distribution of fishing vessels relative to the distribution of fish. As the variation in competitive abilities increases, so does the deviation from an IFD (Houston and McNamara 1988). Therefore, knowledge of the relative competitive abilities of troll fishermen can be used to describe the spatial distribution of the fleet relative to the distribution of available fish. In the case of the troll fishermen, the fleet distribution should be skewed toward regions of lower profitability.

A further benefit of this type of model is that the distribution of fishing vessels may be used to assess the distribution of fish. The distribution of fishing vessels can be mapped from aircraft overflights or from coastal radar installations much more easily than the distribution of fish (Borstad et al. 1982; Healey et al. 1990).

However, if Houston and McNamara's (1988) model is to be used as a stock assessment tool, three problems must be addressed. First, their model assumes that interference (the slope of the relationship between catch rate and vessel density) is -1. Currently, data on this relationship are not available so that this assumption can not be evaluated.

Second, their model assumes that a predator chooses between only two locations. No solution is provided for situations in which the predator has a number of choices. Other studies indicate that the inflection point (i.e. the point at which patches contain fewer predators than prey) should shift towards the origin, tracking the inverse of the number of locations among which the predator is choosing (Abrahams 1986). However, an analytical solution to this question is required before the model could be used in stock assessment.

Finally, a method must be found to convert the relative measures of fish distribution generated by the model to an absolute measure. If the relation between catch rate and vessel density is known, then the catch rate for a single vessel in any patch can be calculated. However, an independent estimate of the relation between fish number and catch rate will be required.

Acknowledgements

We are grateful to the skippers of the troll vessels that participated in the log book program. Ted Carter and Brent Hargreaves graciously provided information on the log book program from 1984 to 1987. We thank D. Gillis, R. Hilborn, P. Symons, and one anonymous referee for critical comments on earlier drafts of this manuscript. Funding for this research was provided by the Canadian Department of Fisheries and Oceans.

References

ABRAHAMS, M. V. 1986. Patch choice under perceptual constraints: a cause for departures from an ideal free distribution. Behav. Ecol. Sociobiol. 19: 409–415.

ARGUE, A. W., M. P. SHEPARD, T. F. SHARDLOW, AND A. D. ANDERSON. 1987. Review of salmon troll fisheries in southern British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1502: 150 p.

BORSTAD, G. A., R. M. BROWN, D. TRAUX, T. R. MULLIGAN, AND J. F. R. GOWER. 1982. Remote sensing techniques for fisheries oceanography: examples from British Columbia. Northwest Atlantic Fisheries Organization, Sci. Council Studies 4: 69–75.

BOTSFORD, L. W., R. D. METHOT, JR., AND W. E. JOHNSTON. 1983. Effort dynamics of the northern California dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 40: 337–340.

CHARLES, A. T. 1983. Optimal fisheries investment: comparative dynamics for deterministic seasonal fishery. Can. J. Fish. Aquat. Sci. 40: 2069–2079.

FRETWELL, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, N.J. 217 p.

FRETWELL, S. D., AND H. L. LUCAS. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheor. 19: 16–36.

GATTO, M., S. RINALD, AND C. WALTERS. 1975. A predatory–prey model for discrete-time commercial fisheries. International Institute for Applied Systems Analysis, Laxenburg, Austria, Res. Rep. 75–5.

HEALEY, M. C. 1986. Regional and seasonal attributes of catch in the British Columbia troll fishery. Can. Tech. Rep. Fish. Aquat. Sci. 1494: 65 p.

HEALEY, M. C., R. E. THOMSON, AND J. F. T. MORRIS. 1990. The distribution of commercial troll fishing vessels off southwest Vancouver Island in relation to fishing success and oceanic water properties and circulation. Can. J. Fish. Aquat. Sci. (In press)

HILBORN, R. 1985. Fleet dynamics and individual variation: why some people catch more fish than others. Can. J. Fish. Aquat. Sci. 42: 2–13.

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.

HOUSTON, A. I., AND J. N. MCNAMARA. 1988. The ideal free distribution when competitive abilities differ: an approach based on statistical mechanics. Anim. Behav. 36: 166–174.

JORDAN, F. P., AND E. W. CARTER. 1987. 1986 west coast troll log program and summaries of 1984–86 data. Can. Tech. Rep. Fish. Aquat. Sci. 653: 69 p.

MANGEL, M. 1982. Search, effort, and catch rate in fisheries. Eur. J. Oper. Res. 11: 361–366.

MANGEL, M., AND C. W. CLARK. 1983. Uncertainty, search, and information in fisheries. J. Cons. Int. Explor. Mer 41: 93–103.

PARKER, G. A., AND W. J. SUTHERLAND. 1986. Ideal free distribution when individuals differ in competitive ability: phenotype limited ideal free models. Anim. Behav. 34: 1222–1242.

SHARDLOW, T. F., A. D. ANDERSON, AND A. W. ARGUE. 1986. Review of 1985 south coast salmon troll fisheries. Can. MS Rep. Fish. Aquat. Sci. 1895: 68 p.

SHARDLOW, T. F., T. G. HOYT, AND A. D. ANDERSON. 1988. Review of 1986 south coast salmon troll fisheries. Can. Tech. Rep. Fish. Aquat. Sci. 1560: 99 p.

SUTHERLAND, W. J., AND G. A. PARKER. 1985. Distribution of unequal competitors, p. 255–273. *In* R. M. Sibly and R. H. Smith [ed.] Behavioural ecology: ecological consequences of adaptive behaviour. Blackwell Scientific Publications, Oxford, UK.