Interaction Between Stock Area, Stock Abundance, and Catchability Coefficient

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The relationship between commercial catch-rates and population density upon which many stock assessment models depend assumes that stock area (A) is constant and independent of population abundance. Starting from a theoretical demonstration that the catchability coefficient (q) is inversely proportional to A, we establish the empirical basis of this relationship through comparisons of q and A of various Northwest Atlantic herring (*Clupea harengus harengus*) stocks and, in more detail, for Fortune Bay herring. For these stocks the relationship was of the form $q = cA^{-b}$. For Atlantic herring stocks, levels of b were in excess of 0.80. In Fortune Bay herring, reductions in abundance were accompanied by proportional reductions in A, which in turn was inversely correlated with changes in q. School size, measured as catch per set, also declined as population levels declined but the change was not proportional. Published findings indicate that pelagic stocks in particular, and fish stocks in general, exhibit a common response of reductions in A with interactive increases in the q during periods of rapid population decline. We conclude that the conventional assumption of a constant stock area is usually violated due to the systematic interaction between A and population abundance which is reflected in an inverse relationship between stock abundance and q. Calibration of sequential population models should therefore be restricted to research vessel data collected in a standard manner and covering the distributional area of the stock.

Pour la relation entre les taux de capture commerciale et la densité des populations dont dépendent de nombreux modèles d'évaluation des stocks, on suppose que la zone du stock (A) est constante et indépendante de l'importance numérique d'une population. La preuve théorique que le coefficient de capturabilité (q) est inversement proportionnel à A sert à établir la base empirique de cette relation à l'aide de comparaisons de q et de A chez divers stocks de hareng (*Clupea harengus harengus*) de l'Atlantique nord-ouest et, en plus grand détail, chez le hareng de la baie Fortune. Pour ces stocks, la relation prenait la forme $q = cA^{-b}$ et chez les stocks de hareng de l'Atlantique, b était supérieur à 0,80. Pour le hareng de la baie Fortune, une baisse du nombre s'accompagnait de réductions proportionnelles de A qui était en corrélation inverse avec les variations de q. La taille des bancs, quantifiée par les prises / mouillage, a aussi baissé en fonction d'un déclin de la population mais cette variation n'était pas proportionnelle. Les données publiées révèlent que les stocks pélagiques, en particulier, et les stocks de poissons, en général, montrent une réaction commune aux baisses de A et des accroissements interactifs de q pendant les périodes de baisse démographique rapide. Les auteurs formulent la conclusion que l'hypothèse classique d'une zone du stock constante est habituellement faussée à cause d'une interaction systématique entre A et l'importance numérique d'une population, interaction généralement traduite par une relation inverse entre l'importance numérique d'un stock et q. L'étalonnage des modèles démographiques séquentiels devrait donc être restreint aux données recueillies de façon normalisée par des navires de recherche dans la zone de répartition du stock.

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The relationship between indices of fishing effort, catch-rate, and fish abundance is of critical importance to the effective management of commercial fisheries, particularly with the increasing use of catch quotas as a means of optimizing yield. Such quotas place high demands on the timeliness and accuracy of scientific advice, which in turn requires detail and precision in the assessments of stock status and the impact of fishing on the resource. A perusal of the scientific reports of such fisheries commissions as NAFO and ICES indicates a continued heavy dependence of stock assessments on commercial catch and effort data, mainly as a source of calibration of sequential population models. This persistent reliance on commercial catch-rate data is surprising given the extensive literature (e.g. Paloheimo and Dickie 1964; MacCall 1976; Clark and Mangel 1979; Pope 1980; Ulltang 1980) on the failure of the underlying assumption of a constant catchability coefficient (q) (Beverton and Holt 1957) which underpins the classic catch equation of Baranov (1918). Garrod (1964) and Gulland (1964) have pointed out that variations in q may result from any number of factors including changes in fishing power, vulnerability to the gear, seasonal and spatial patterns of distribution, and changes in stock abundance. Some of these factors can be readily measured and taken into account to provide standardized catch-rates such as those derived by the multiplicative model of Gavaris (1980). However, other factors such as those inherently related to changes in abundance are more difficult to assess, since they require a long time-series of independent estimates of abundance. In this paper we demonstrate that there is an additional property of the catchability coefficient relating to stock area which is fundamental to the proper interpretation of commercial catch-rate data. The theoretical basis of this property is presented and an instructive example is described. The degree of adherence of empirical results to theory allows us to evaluate the acceptability of commercial catch data as unbiassed estimates of population density.

Theoretical Basis

The catch of a particular gear per unit of its operation (c/f) is a product of the number of fish (n) present in the area swept by the gear times the elemental efficiency (Paloheimo and Dickie 1964) of that gear (p), i.e.

$$(1) \quad c/f = pn.$$

In the context of this single unit of effort, p is the proportion of fish in the swept area that will be caught. Extension of relationship (1) to the entire populaton (N) for combined catches from a number of localities and over a period of time (C/F) requires an estimate of the fishing power of the gear, i.e. the proportion of the total area (A) occupied by the stock that is covered by a single sweep of the gear (a). Thus, we have

$$(2) \quad C/F = \frac{paN}{A}$$

whence,

$$(3) \quad \frac{C/F}{N} = \frac{pa}{A}$$

from which we define

$$(4) \quad q = \frac{pa}{A}.$$

This proportionality constant, q, is equivalent to the catchability coefficient as defined by Holt et al. (1959) and is in effect the probability of capturing a fish in a single unit of effort. As noted by Paloheimo and Dickie (1964) the catchability coefficient is inversely proportional to the area, A, occupied by the stock. However, the corollary of the inverse relationship between q and A has received little attention in the published literature; it implies that a unit of effort will generate not only a higher fishing mortality rate but also a higher catch-rate in a small area as compared with a larger area for the same size of stock. Since stock area is difficult to measure, it is the common practice among fisheries biologists to assume that this parameter remains constant and independent of changes in population abundance. We now attempt to demonstrate that this assumption is often violated due to the systematic interaction between stock area and population abundance which tends to be reflected in an inverse relationship between stock abundance and q.

An Empirical Test

Expressions (3) and (4) demonstrated that q is inversely proportional to both stock area, A, and population size, N. If the systematic interaction between N and A is linear then the relationship between q and A will be adequately described by expression (4). However, the rate of population expansion and retreat within the general stock range is unlikely to be uniform, since habitat conditions will be less favourable at the extremes of the range than at its centre. Blaxter and Holliday (1963) have concluded, for example, that stock movements will occur more rapidly in areas of unfavourable habitat. In this case the interaction between N and A will be nonlinear. We posit, therefore, that the relationship between q (defined as the ratio of catch-rate to biomass) and A will take the form

$$(5) \quad q = cA^{-b}$$

where $c = pa$ is a constant and b is a coefficient that describes the rate at which q will systematically vary with stock area; i.e. q will only be constant in the special case when $b = 0$. A value of $b = 1$ will indicate that changes in stock area have occurred in direct proportion to changes in stock abundance. In general, the larger the value of b the greater the distortion it will introduce into the catch-rate index. We have chosen as our standard vessel class the large purse-seine fleet which exploited nearly all of the herring populations in Atlantic Canada during the late 1960's and 1970's. The effort standard refers to operating time (which includes both searching and fishing time), and stock areas have been defined according to boundaries established by their respective NAFO or Canadian Statistical Areas and are consistent with stock assessment definitions of stock areas. For the special case of Bay of Fundy (4VWX) herring which belong to the "oceanic" complex of herring (Anthony and Waring 1980), the seaward stock boundaries have been defined by the 200-fathom (300-m) depth contour. The period chosen for comparison reflects the need for insensitivity of sequential population estimates of biomass to input parameters and a common time period to account for any technological changes within the constraints of data availability. The stock areas are shown in Fig. 1 and relevant data are summarized in Table 1. From Fig. 2, we can confirm that the catchability coefficient of the large purse-seine fleet is inversely proportional, in nonlinear fashion, to stock area and is of the form described by relationship (5).

It may be argued that the inverse relationship between catchability coefficient and stock area is peculiar to such active encircling gears as purse seines whose catchability coefficient is affected by a wide variety of factors (Powles 1981). To demonstrate that the relationship is not gear-specific, we examined the stock-specific catchability coefficients of herring gill nets, a passive gear for which there is a series of catch-rates based on a common effort standard (catch per net-landing). The relevant data are summarized in Table 2. Consistency with expression (5) is also demonstrated by the gillnet data (Fig. 3), and the inverse relationship between q and stock area is best expressed by a power curve whose exponent coefficient is almost identical to that derived for the purse-seine catch-rate data. We now proceed to examine the existence of this inverse relationship and its interaction with stock abundance within a particular stock.

An Instructive Example

We have chosen the population of spring-spawning herring in Fortune Bay (Fig. 1) as a basis for demonstrating the interdependence between q, stock area, and stock abundance. This choice is based not only on the extensive data base relating to the biological characteristics of this stock (Parsons and Hodder 1973; Parsons 1973; Moores and Winters 1979) but also on the fact that the population dynamics of this stock have been described during a period of substantial population change due,

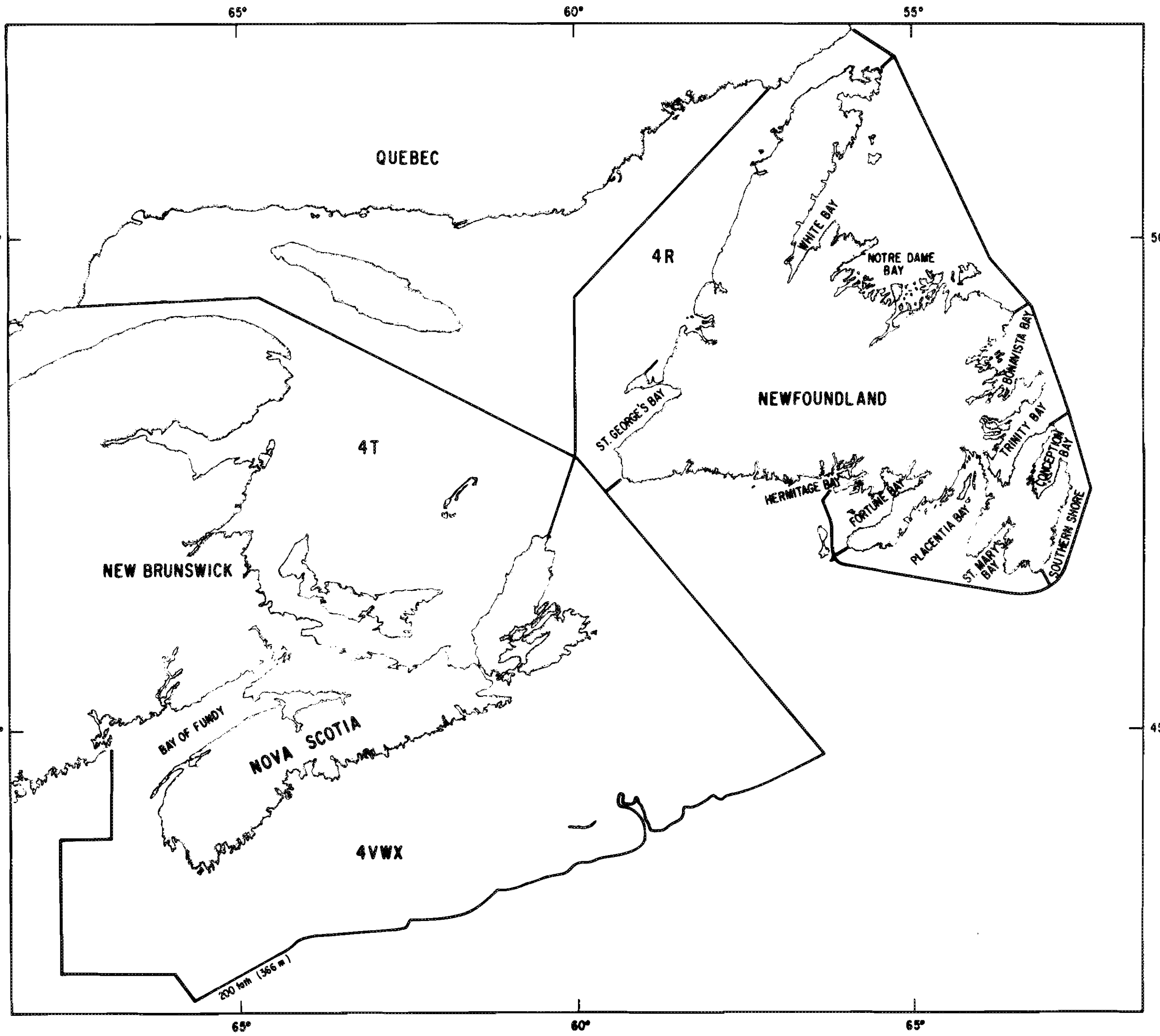

FIG. 1. Location of stock areas mentioned in the text.

TABLE 1. Comparison of abundance and catch-rate (purse seines) characteristics of various herring populations in the Canadian Atlantic area. Exploitable biomass is defined as the sum of the fully recruited biomass plus that portion of the age-specific biomass of recruiting age groups defined by the ratio of their fishing mortality rates to the fully recruited fishing mortality rate.

Stock	Period	Area of stock (km^2)	Mean exploitable biomass (kt)	Mean catch rate (t/d)	Catchability coefficient (q)	Data source
White Bay – Notre Dame Bay	1975–76	21 900	110	91	0.00083	Winters and Moores 1977 Wheeler and Winters 1981
Bonavista Bay	1975–76	3 950	60	114	0.00190	Winters and Moores 1977
Trinity Bay	1975–76	3 750	25	87	0.00348	Winters and Moores 1977
Fortune Bay	1967–74	3 600	20	54	0.00270	Winters et al. 1985
Western Newfoundland	1970–76	30 900	210	57	0.00027	Tremblay et al. 1983
Southern Gulf	1971–76	79 250	180	42	0.00023	Winters and Moores 1980
Bay of Fundy	1970–76	122 000	400	46[a]	0.00012	Sinclair et al. 1982

[a]Catch per night.

TABLE 2. Comparison of abundance and catch-rate (gill nets) characteristics of various herring populations in the Canadian Atlantic area.

Stock	Period	Area of stock (km^2)	Mean exploitable biomass (kt)	Mean catch rate (kg/d)	Catchability coefficient (q)	Data source
White Bay – Notre Dame Bay	1979–80	21 900	32.5	48.0[a]	0.00148	Wheeler and Winters 1981
Bonavista Bay	1979–80	3 950	19.5	83.0[a]	0.00426	Wheeler and Winters 1981
Trinity Bay	1979–80	3 750	7.5	85.9[a]	0.01145	Wheeler and Winters 1981
Conception Bay	1979–80	5 400	2.5	31.3[a]	0.01252	Wheeler and Winters 1981
St. Mary's Bay – Placentia Bay	1979–80	9 820	10.0	34.6[a]	0.00346	Moores et al. 1981
Fortune Bay	1979–80	3 600	2.8	20.9[a]	0.00745	Winters et al. 1985
Western Newfoundland	1979–80	30 900	90.0	92.0[a]	0.00102	Trembley et al. 1983
Southern Gulf	1973–80	79 250	105.0	82.4[b]	0.00078	Cleary 1982

[a]Spring fishery.
[b]Spring and fall fishery.

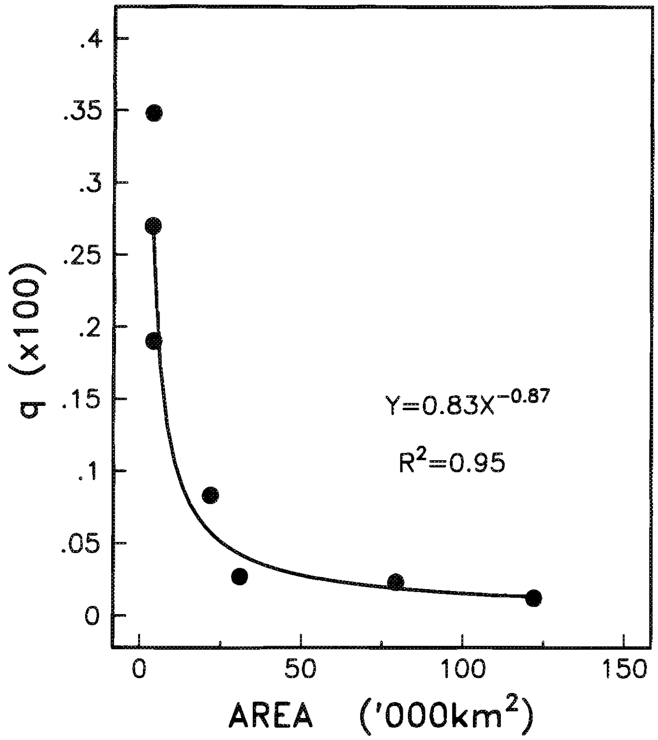

FIG. 2. Catchability coefficient (q) of the large purse-seine fleet and stock area for various Northwest Atlantic herring stocks (see Table 1 for source details).

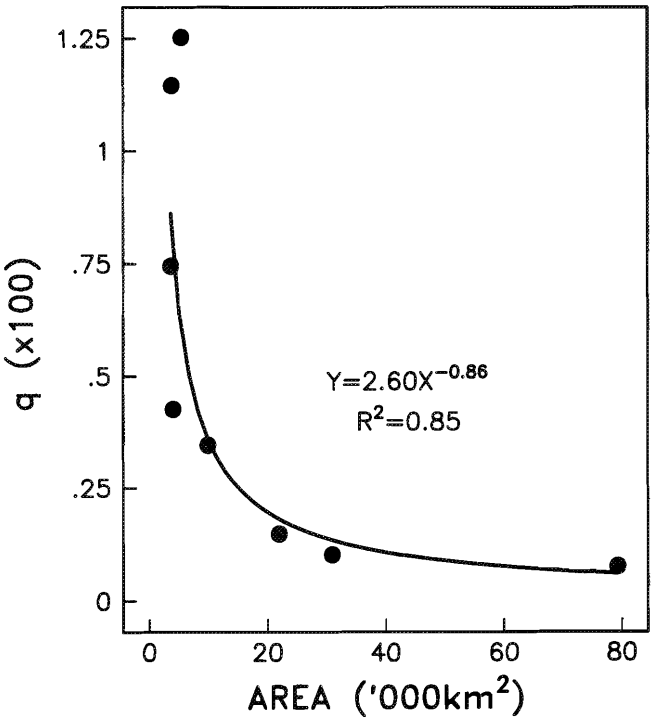

FIG. 3. Catchability coefficient (q) of herring gill nets and stock area for various Northwest Atlantic herring stocks (see Table 2 for source details).

in large part, to the fishing activities of a purse-seine fleet that exploited this stock during a consistent period of the year (Winters et al. 1985).

Annual Fishing Patterns 1967–74

The large Atlantic purse-seine fleet began a winter (January–April) fishery in Fortune Bay in 1967 (Winters et al. 1985) and maintained significant catches in that area until 1974. Logbook records and interview reports are available for this period and contain sufficient detail to identify the location of most reported fishing sets whereas information on the area searched and time searched is much more limited and usually in insufficient detail. We subdivided Fortune Bay into a grid of 3.3 × 3.3 km squares and, from logbook records, plotted for each year the distribution and intensity of purse-seine fishing effort in terms of fishing sets. The results (Fig. 4 and 5) indicate that when the fishery began in 1967, effort was concentrated mainly at the head of Fortune Bay in the Bay L'Argent – Terrenceville area. Considerable expansion of the purse-seine fishery occurred in 1968 although fishing effort was again mostly concentrated at the head of the bay. The range of the fishery decreased in 1969, particularly at the western extremes, and a shift in fishing effort to Long Harbour and Belleoram occurred. This westward shift in fishing effort continued in 1970 although the range of the area fished remained extensive. By 1971 there was a substantial

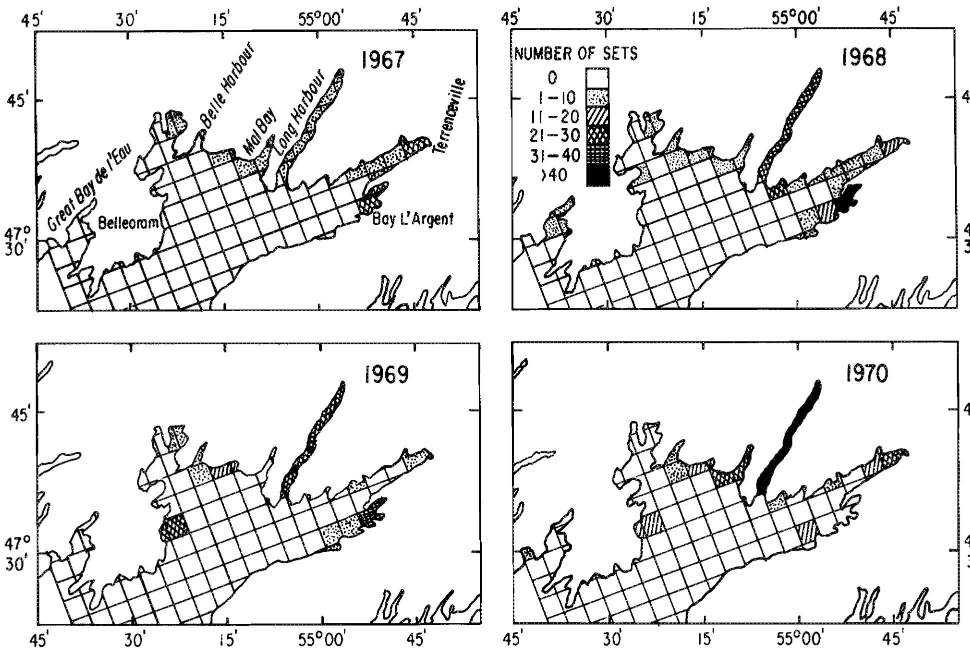

FIG. 4. Distribution of fishing effort (in terms of fishing sets) of the large purse-seine fleet in Fortune Bay, 1967–70.

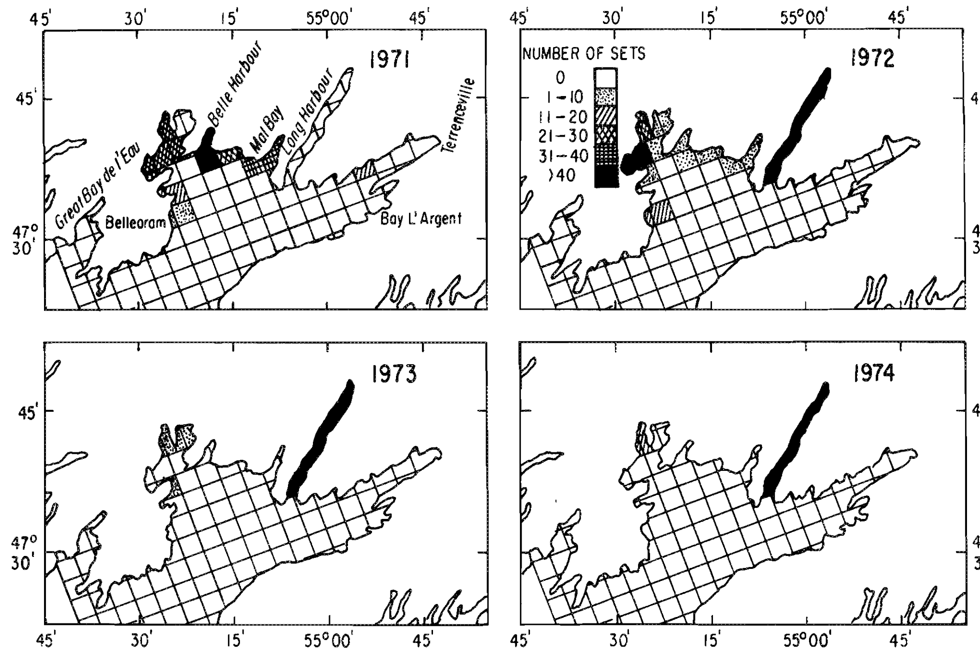

FIG. 5. Distribution of fishing effort (in terms of fishing sets) of the large purse-seine fleet in Fortune Bay, 1971–74.

reduction in both the eastward and westward limits of the applied fishing effort, and a further attrition in the eastward limits of fishing effort occurred in 1972 when most of the fishing effort was concentrated in the Long Harbour and Cinq Island Bay area. In 1973 an additional reduction in the westward limit of the fishery was evident, and this continued into 1974 when nearly all of the fishing effort was concentrated in the Long Harbour area. In summary, these data indicate that there was a substantial reduction in the area fished by the purse-seine fleet in Fortune Bay during the 1970's.

Catch-Rate Characteristics

Catch-rate data of the purse-seine fleet are available from interview reports and log records for the period 1967–74. These data have been analyzed by Winters et al. (1985) for the period 1967–73 in terms of fishing effort defined as the standard operating day (i.e. time between departure from and return to landing port, excluding down time). Such analyses have been extended in this paper to include additional data from 1974 and an alternative, more precise expression of fishing effort in

TABLE 3. Regression coefficients of purse-seine monthly catch-rates as calculated by the multiplicative model of Gavaris (1980).

Month	Catch per set[a]	Catch per standard operating day[b]
January	0.000	0.000
February	−0.165	−0.067
March	−0.258	−0.141
April	−0.479	−0.462

[a]F value = 37.8 (3 df); $p < 0.05$.
[b]F value = 66.3 (3 df); $p < 0.1$.

terms of fishing sets. For both expressions of fishing effort the multiplicative model of Gavaris (1980) indicates significant seasonality factors (Table 3) which have been taken into account through the Gavaris (1980) standardization procedure. These standardized catch-rates (Tables 4 and 5) indicate similar trends in abundance and suggest a cycling downwards of abundance since 1967. A similar trajectory of population change is indicated by cohort analysis (Winters et al. 1985) with the exception that population decline continues after 1973 rather than increases, as indicated by catch-rate data. Searching success, measured as the ratio of searching time (operating days (Table 5)) to fishing time (number of sets (Table 4)), was not correlated with stock abundance (Fig. 6) as estimated by cohort analysis. This may reflect a systematic bias in the catchability coefficient of the purse-seine fleet in Fortune Bay and/or that the measure of searching time (operating days) was so crude that it overshadowed any real changes in that parameter. To avoid this ambiguity in fishing effort we confine our estimates of fishing effort to the number of fishing sets which are more precisely known.

Interrelationship Between Catch-Rates and Population Change

Although logbook records contained insufficient detail on the area searched, general comments by the fishing captains indicated that in all years the area searched extended well beyond the areas in which herring concentrations were found and fished. In addition, Fortune Bay is such a small area that a single vessel could easily search the entire bay in a single day. We have therefore assumed that the spatial distribution of fishing effort shown in Fig. 4 and 5 is representative of the changes in the area occupied by herring in Fortune Bay during their overwintering phase in the period 1967–74. We have defined the area within the limits of this spatial distribution as the "stock range" and these data are summarized in Table 6 along with estimates of stock biomass (from Winters et al. 1985) and values for annual catchability coefficients defined as the ratio of catch-rate (tons per set) to exploitable biomass. From such data we can now examine the interdependence between catch-rate, stock abundance, and stock area.

There is a positive nonlinear relationship between the stock range and stock abundance of Fortune Bay herring (Fig. 7). This nonlinearity is consistent with our expectations and with the observations of Blaxter and Holliday (1963). The 1967 value for stock range appears anomalous and was excluded from further analysis. This exclusion is considered justifiable on the basis that 1967 was the first year of the purse-seine fishery in Fortune Bay and therefore it is likely that a learning factor was involved

TABLE 4. Catch-rate data of the purse-seine fleet operating in Fortune Bay during the period 1967–74. Numbers in parentheses refer to the effort (number of sets).

Year	Catch per set (t)				Standard catch rate (Jan.–Apr.)	Estimated total effort (sets)
	Jan.	Feb.	Mar.	Apr.		
1967	—	—	—	45.0 (56)	70.5	80
1968	54.6 (1)	53.0 (72)	51.2 (65)	50.1 (35)	69.5	212
1969	58.2 (26)	16.4 (5)	—	—	50.2	138
1970	94.2 (8)	32.8 (12)	30.6 (19)	0.0 (1)	47.5	198
1971	50.3 (19)	67.0 (30)	29.6 (4)	27.3 (3)	64.7	232
1972	55.6 (14)	18.2 (2)	44.7 (25)	13.8 (9)	47.5	222
1973	14.9 (15)	69.0 (16)	41.0 (1)	54.6 (1)	26.6	122
1974	—	—	—	34.4 (22)	51.3	44

TABLE 5. Catch-rate data of the purse-seine fleet operating in Fortune Bay during the period 1967–74. Numbers in parentheses refer to the effort (in operating days).

Year	Catch per day (t)				Standard catch rate (Jan.–Apr.)	Estimated total effort (days)
	Jan.	Feb.	Mar.	Apr.		
1967	—	—	—	41.5 (35)	64.4	88
1968	—	64.6 (67)	55.2 (70)	33.8 (51)	63.4	232
1969	62.3 (45)	34.8 (31)	47.6 (3)	—	51.1	134
1970	67.0 (57)	49.7 (25)	60.4 (40)	79.6 (67)	67.7	139
1971	48.3 (103)	59.4 (58)	50.4 (96)	32.6 (31)	55.8	269
1972	44.9 (75)	49.0 (11)	31.7 (128)	22.5 (68)	39.7	266
1973	22.1 (24)	22.1 (21)	18.7 (2)	38.3 (3)	25.3	129
1974	—	—	—	38.5 (43)	60.2	38

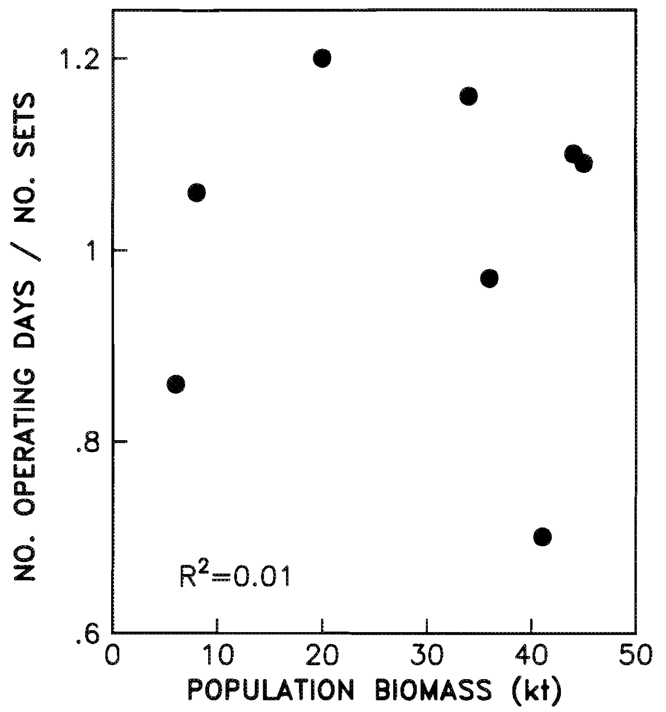

FIG. 6. Searching success (i.e. searching time per set) and population abundance of Fortune Bay herring, 1967–74.

TABLE 6. Biomass, catchability coefficient (q), and stock range of Fortune Bay herring, 1967–74.

Year	Mid-year 2+ biomass (kt)	q	Stock range (km^2)
1967	39.9	0.00246	297
1968	39.4	0.00275	743
1969	33.5	0.00207	545
1970	37.8	0.00192	726
1971	26.7	0.00392	396
1972	13.7	0.00593	330
1973	6.7	0.00578	297
1974	4.8	0.01655	182

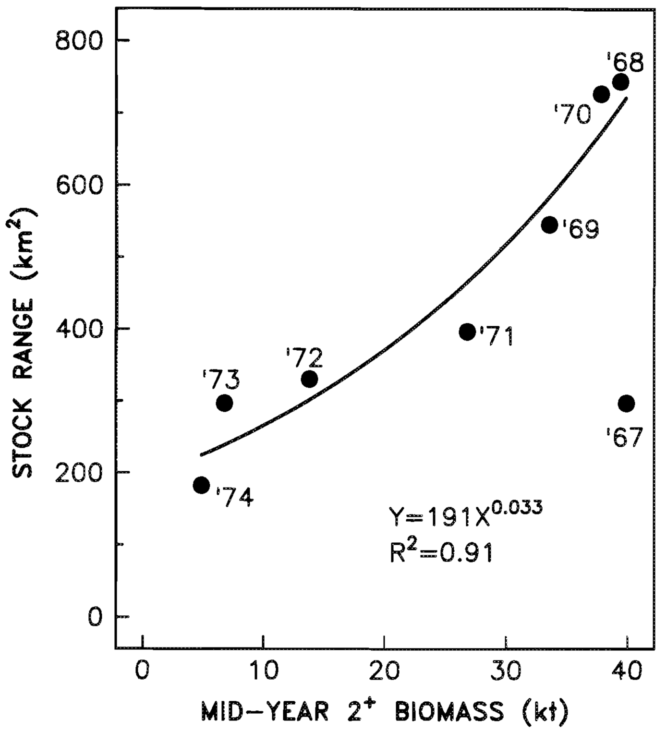

FIG. 7. Stock range and population biomass of Fortune Bay herring.

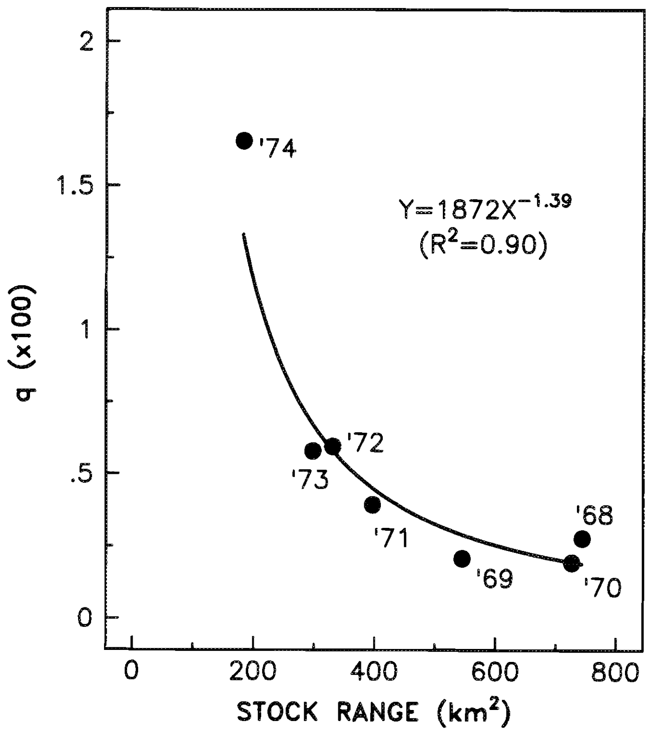

FIG. 8. Catchability coefficient (q) and stock range of Fortune Bay herring (the 1967 data point is excluded).

in similar fashion as was documented for the same fleet fishing along southwest Newfoundland (Winters and Hodder 1975) in 1967. Analysis of temporal variations in the catchability coefficient of the purse-seine fleet indicates that q is negatively correlated with "stock range" (Fig. 8), which is in accordance with the theoretical expectations as described in expression (4). Furthermore, the exponent of the relationship is significantly different than unity ($p < 0.01$) and supports the evidence from Fig. 7 and our hypothesis that the relationship between q and A will be as described in expression (5). This nonlinearity in the relationship of the catchability coefficient to stock area is an important property of q, since it implies that larger changes in q will occur at the lower stock levels when the need for unbiassed stock indices is most critical. The bias that this relationship imparts to commercial catch-rate data will likely cause such indices to substantially underestimate both the rate of decline and the rate of recovery of a depleted fish stock.

We conclude that the catchability coefficient of the purse-seine fleet in Fortune Bay during the period 1968–74 was a direct function of the area occupied by the herring stock, which was itself a density-dependent function of population abundance. This implies, of course, that q is an indirect density-dependent function of stock abundance and will probably be of the form $q = kN^{-g}$ (Ulltang 1976); unfortunately we cannot test this proposition due to the absence of an independent stock abundance index of Fortune Bay herring.

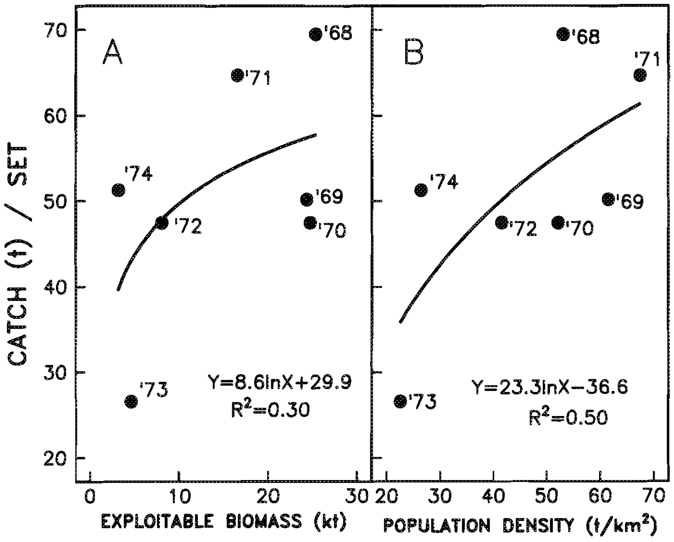

FIG. 9. (A) Catch-rate (catch per set) and exploitable biomass and (B) catch rate (catch per set) and population density of Fortune Bay herring.

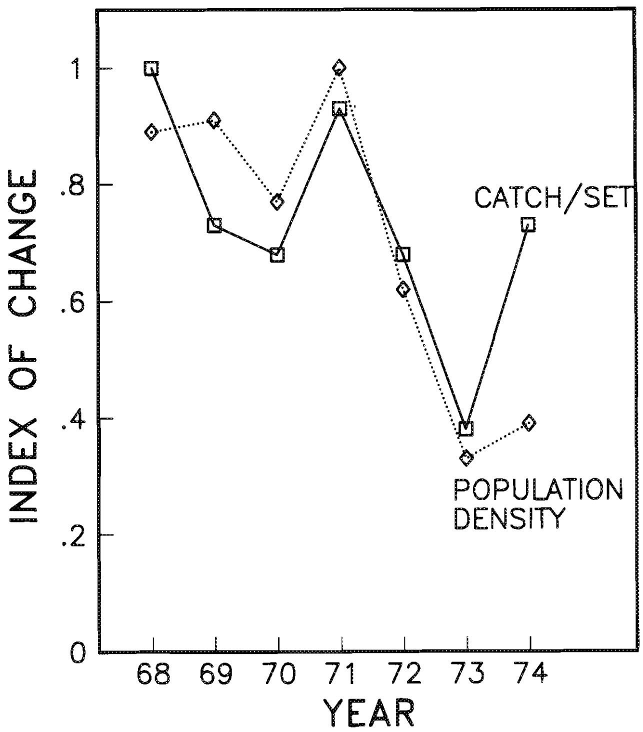

FIG. 10. Time-series trends in school size (catch per set), population density (biomass/km), and population biomass of Fortune Bay herring.

Catch-Rates, Population Abundance, and School Size

The inverse relationship between the catchability coefficient and stock area (Fig. 8) of Fortune Bay herring implies that the purse-seine catch-rate index will be significantly correlated with population density (biomass per area) but not with population biomass. Regression analyses confirm this observation (Fig. 9) although the relationship between catch-rate and population density is barely significant ($p = 0.05$) and best expressed as a logarithmic curve. This weak relationship probably reflects an additional property of the purse-seine catch-rate index relating to school size. Interviews with purse-seine skippers, supported by observations of senior technicians on selected cruises of the large purse-seine fleet during the 1960's and 1970's, suggest that in most cases successful sets capture the entire target of the set. Therefore, catch per set may be used as an index of school size (Ulltang 1980), and we have replotted this catch-rate index in a temporal series along with density (biomass per square kilometre) in Fig. 10. The close correspondence between the track of school size and population density for the years 1968–73 demonstrates that Fortune Bay herring compensated for changes in biomass through a combination of changes in stock area and school size. However, school size increased at a much greater rate between 1973 and 1974 than was evident in the population density. This may reflect the possibility that at very low stock sizes the reduced distributional area occupied by the stock resulted in an overlap of the area searched by individual vessels and/or an overlap of school radii such that school amalgamation occurs (Paloheimo and Dickie 1964). In either case there is a further confounding of the catch-rate index.

Discussion and Conclusions

We have shown that the theoretical expectation of catchability coefficient (q) being inversely proportional to stock area has an empirical basis which is borne out not only through comparisons of q between Atlantic herring stocks but also in the example of Fortune Bay. Fortune Bay herring reacted to depletions in abundance by reducing their distributional range rather than by counterbalancing such abundance changes through commensurate adjustments in density in a constant stock area as is commonly assumed in interpretation of commercial catch-rate data. Furthermore, school size (i.e. catch per set) of Fortune Bay herring also decreased as population biomass declined, which in conjunction with the independence between catch-rates and fishable biomass implies that school numbers probably remained constant. At very low stock levels, however, there may have been a reversal of this response such that school aggregation occurred.

The analyses of Fortune Bay data support our hypothesis that density-dependent changes in stock area will occur in nonlinear fashion and therefore the relationship between q and stock area will be of the form $q = cA^{-b}$. This finding is consistent with observations by Ulltang (1976) and MacCall (1976) that the interaction between q and population abundance of pelagic fish species can be adequately described by the relationship $q = kN^{-g}$. For values of $g > 0$, catch-rates may vary with population abundance but the change will not be proportional; as g approaches 1, catch-rates will become constant and a constant effort will then generate a steadily higher fishing mortality as stock size increases.

The changes in the stock range of Fortune Bay herring in response to population abundance are not unique. The southern Gulf of St. Lawrence herring stock supported a large winter fishery along southwestern Newfoundland and extensive spring, summer, and fall fisheries in the southern Gulf during the 1960's and early 1970's when population levels were high (Winters and Hodder 1975). Since then, biomass levels have decreased substantially and this has been accompanied by the collapse of the southwest Newfoundland winter fishery (Winters and Beckett 1978) and the spring and fall fisheries at the Cabot Strait entrance to the southern Gulf (L. Cleary, pers. comm.). Wheeler and Winters (1984) have shown that tagged herring along eastern Newfoundland exhibited much less dispersion in the early 1980's when population levels were lower than in the

1970's when population levels were higher. Similarly, Dragesund et al. (1980) have shown that the area occupied by the Atlanto-Scandian herring stock shrunk in proportion to changes in stock size. North Sea herring also decreased its distributional area after the mid-1960's when population abundance began to decline (Saville and Bailey 1980). This general response of herring stocks to changes in abundance will result in q being inversely related to stock abundance, and there is ample evidence in the published literature (Pope 1980; Ulltang 1980; Jakobsson 1980; Anthony and Waring 1980) to support this property of q. Furthermore, a variety of other pelagic fish stocks have shown similar interactive changes in area and catchability during periods of rapid population declines. These include the Atlantic menhaden (*Brevoortia tyrannus*) (Shaaf 1980), Pacific sardine (*Sardinops sagax caerula*) (MacCall 1976; Radovich 1979), northern anchovy (*Engraulis mordax*) (Radovich 1976), and Peruvian anchovy (*Engraulis ringens*) (Csirke 1980). These examples, taken together with our analysis of Fortune Bay herring, lead us to conclude that commercial catch-rate data of pelagic fish stocks will usually provide a biassed index of population abundance and this will be particularly so for such active encircling gears as purse seines which superimpose their own varying biasses (Clark and Mangel 1979; Powles 1981) on those dictated independently by stock dynamics. Among dermersel fish stocks, published literature on their distributional responses to changes in abundance is scanty. However, Lear (1984) has noted that the dispersion of tagged cod of the 2J3KL stock was much greater during the 1950's and 1960's (see Templeman 1974) when biomass levels were relatively higher than in the late 1970's when abundance levels of cod were much lower. Gavaris et al. (1984) have shown that the catchability coefficients of 2J3KL cod increased substantially during the 1970's as stock sizes declined. Pope and Garrod (1975) showed that for both Arctic-Norwegian and West Greenland cod there was also an increase in q as stock size became smaller, and ascribed their findings to real changes in stock availability. These observations lead us to conclude that the inverse relationship between q and stock abundance may be a general feature of marine fish populations and that this relationship is probably mediated through systematic changes in stock area. This conclusion strongly supports the findings of Paloheimo and Dickie (1964) who demonstrated, from a theoretical viewpoint, that fishing success depended not only on the abundance of fish but more importantly on their distribution. Thus, commercial catch-rates, even when measured with the utmost precision, are likely to be biassed and should be used with caution particularly as a means of calibrating sequential population models; instead, emphasis should be placed on research vessel survey data collected in a standard manner and covering the distributional area of the stock.

The mechanism responsible for fish populations expanding or contracting their distributional range as abundance varies is poorly understood, although a variety of models have been developed that assume that such a response is related to a behavioural tendency towards maintaining an optimum density per unit area (Pope and Garrod 1975). It has been argued, for example, that such behaviour has evolved in response to specific selection pressures such as predator avoidance (Radovich 1979). There is, however, another feature of stock range variations that may be related to the demographic compositions of the population. Large, unexploited populations have a predominance of older, larger fish, and since swimming speed is a power function of fish length (Yates 1983), these fish will tend to migrate farther than smaller fish which are usually characteristic of depleted populations. This type of distributional response was exhibited by southern Gulf of St. Lawrence herring whose overwintering migration rates were a direct positive function of age (Winters and Hodder 1975). Similar findings have been reported for Atlanto-Scandian herring (Dragesund et al. 1980), southern Gulf of St. Lawrence cod (Jean 1964), and Arctic-Norwegian cod (Trout 1957). In the example of Fortune Bay herring there was an order of magnitude decrease in the number of large (age 7 and older) herring from 1968 to 1974. We suggest that this reduction in the numbers of larger herring was responsible, at least in part, for the observed reductions in the range of Fortune Bay herring during the period 1968–74.

Finally, we reemphasize the significance of the inverse relationship between catchability and stock area; i.e. a unit of fishing effort will generate a higher fishing mortality and a higher catch-per-unit-effort in a small area compared with these same parameters in a larger area. The general occurrence of this observation is not only evident in marine fish populations (as we have demonstrated) but it also applies to freshwater populations where it has been generally shown that small lakes are more efficiently exploited per unit surface area than large lakes when both are subjected to proportionally similar fishing effort (Ryder et al. 1974).

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