

## Dynamics of the Namibian hake fleet and management connotations: application of the ideal free distribution\*

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**SUMMARY:** In order to determine the factors governing the spatial distribution of effort, it is essential to better understand the relationship between CPUE and abundance. In this study the spatial distribution of effort of the Namibian hake trawl fleet is examined by looking at competitive abilities among vessels, spatial allocation of effort, competition between vessels and equalisation of catch per unit effort (CPUE). The Ideal Free Distribution (IFD) was used as the foundation for deriving the tests. The results show that interference competition does not occur among vessels. Nevertheless, the prediction of the IFD of the equalisation of CPUE was confirmed in this fishery and indicates that the number of vessels in a specific area reflects stock density. Since there is no interference competition among vessels, the catchability coefficient ( $q$ ) is not affected by this factor. Moreover, we infer that the CPUE from the whole area is not distorted as an index of abundance by the way effort is allocated in this fishery.

**Keywords:** Namibia, hake fishery, ideal free distribution, CPUE, vessels competition, management, effort distribution.

**RESUMEN:** DINÁMICA DE LA FLOTA DE MERLUZA DE NAMIBIA E IMPLICACIONES EN SU GESTIÓN: APLICACIÓN DE LA *IDEAL FREE DISTRIBUTION*. – Determinar los factores que gobiernan la distribución espacial del esfuerzo de pesca es esencial para conocer la relación existente entre la captura por unidad de esfuerzo (CPUE) y la abundancia del recurso pesquero. En este estudio se examina la distribución espacial del esfuerzo de la flota de arrastre de merluza de Namibia se examina por el análisis: la capacidad competitiva entre buques, la localización del esfuerzo, y la competición y equilibrio de la captura por unidad de esfuerzo (CPUE) entre buques. El procedimiento de los análisis realizados se fundamenta en las bases de la *Ideal Free Distribución* (IFD). Los resultados muestran que no hay diferencias en la capacidad competitiva de los buques y tampoco se observa competición entre ellos. Por otro lado, la predicción de equilibrio de la CPUE esperada por el IFD se cumple en esta pesquería, indicando que el número de barcos en un área es indicador de la densidad del stock. Consecuentemente, se deduce que la CPUE no está distorsionada como índice de abundancia por la distribución del esfuerzo de pesca.

**Palabras clave:** Namibia, pesquería de merluza, ideal free distribution, cpue, competición de barcos, gestión, distribución del esfuerzo.

### INTRODUCTION

The relationships between catch and fishing effort are known to be complex and not simply governed by fish abundance (Rothschild, 1977; Clark and Mangel, 1979). However, because of a lack of

better information, catch-per-unit-effort (CPUE) remains a common index of abundance in many fisheries. It is used either as a direct indicator of abundance (Cooke, 1985) or as a means of fine-tuning other stock assessment techniques (Deriso *et al.*, 1985). Both fish abundance and behaviour of fishers and their interaction will influence CPUE. In spite of the wide use of CPUE, until recently, little work

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has been directed towards understanding how the movement dynamics of fishing fleets affects fisheries statistics.

The ideal free distribution (IFD) theory explains the distribution of foraging animals in relation to the distribution of their resources (Fretwell and Lucas, 1970; Sutherland, 1983). Any fishery is a compound of two elements, the fleet and the resource, the former being the foraging population and the latter being resource. The components of the fleet within the theoretical framework of the ideal free distribution (IFD) must fit the following assumptions: (i) vessels have equal fishing power; (ii) skippers have perfect knowledge about the distribution of their target species; (iii) travel cost between fishing grounds is negligible; (iv) skippers select fishing grounds on the basis of maximising fishing efficiency. Although the assumptions will certainly be violated in the real world, Milinski and Parker (1991) showed that the IFD presented a reasonably robust starting point for such analyses. However, violations of these assumptions also generate typical spatial distributions (Fretwell, 1972; Abrahams, 1986; Houston and McNamara, 1988).

The IFD has been applied successfully to a wide variety of biological systems as well as to the problem of effort allocation within fishing fleets (Abrahams and Healey, 1990, 1993; Healey and Morris, 1992; Gillis *et al.*, 1993; Gillis and Peterman, 1998). Most models assume that some inverse relationship must exist between catch rate and vessel density. Abrahams and Healey (1990) suggested that the spatial distribution of the British Columbia salmon troll fleet could be described through a modified form of the ideal free distribution.

Although competitive interactions may be inferred from the distribution of fishing vessels (Hilborn and Ledbetter, 1979; Healey and Morris, 1992; Gillis *et al.*, 1993), direct evidence is scarce. Some work tends to model fishing effort in an aggregate manner from the effort or the space perspective (Mangel and Clark, 1983; Mangel and Beder, 1985; Allen and McGlade, 1986; Mangel and Clark, 1986; Hilborn and Walters, 1987; Anganuzzi, 1996). However, analysis on a fine scale of searching effort by individual vessels has seldom been done (Polacheck, 1988). In an experimental study, Abrahams and Healy (1993) manipulated vessel density of salmon trawlers and found that catch rates in the low-density area were higher for Chinook salmon and spiny dogfish, supporting the operation of competitive interactions, although no such effect was observed for Coho salmon. Competitive inter-

actions among beam trawlers in the southern North Sea are likely since beam trawlers exhibit a patchy distribution with more than 70% of effort concentrated in only 20% of the fished area (Rijnsdorp *et al.*, 1998). Strong support for interference interactions comes from a study of the Dutch beam trawl fleet which showed that individual catch rates of beam trawlers increased by 10% when vessel density was reduced to about 25% of the initial density (Rijnsdorp *et al.* 2000). It was also demonstrated that catch rate was positively related to engine power, while the increase in catch rate could only be partly explained by the larger area swept per unit of time by the more powerful vessels, suggesting that the competitive ability increased with engine power.

Applied to fisheries, the IFD theory predicts that vessels will distribute themselves over their resources in such a way that the density of vessels will be proportional to resource abundance and that vessels will have equal catch rates, irrespective of the vessel density. If vessels differ in competitive ability, better competitors will generally be over-represented in the better patches while poorer competitors will be over-represented in the poorer patches (Sutherland and Parker, 1985).

The most relevant assumptions of the IFD for our study are that: (i) vessels have equal competitive abilities; (ii) vessels can change areas without restrictions or travel costs; (iii) competition between foragers occurs in proportion to their local density. However, violations of these assumptions also generate typical spatial distributions (Fretwell, 1972; Abrahams, 1986; Houston and McNamara, 1988) that may be used to diagnose which assumptions have been violated.

Under these circumstances, the IFD predicts that the profit rate or catch rate for an individual in an area will be proportional to the availability of resources divided by the number of individuals foraging there. When each forager is free to move so as to maximise its own profitability, the result is an equilibrium distribution in which foragers in different spatial areas have the same catch rate, which is called equalisation of catch rate (Hilborn and Ledbetter, 1979). This theory thus predicts that the number of foragers in each area will reflect the abundance of resources better than catch rate. The objective of this study is to contribute to the knowledge of fleet dynamics specifically on the part of effort allocation. Effort allocation, within the theoretical framework of the ideal free distribution (IFD), will be investigated for the Namibian hake fishery.

TABLE 1. – Results of the stepwise regression. (from Voges, 2004). The partial F-test statistics for the proposed factors are given along with the eta-squared statistics to allow comparison of the relative contribution of each factor and interaction in the full model at each step.

Factor	SS	Regression df	MS	F	P	Eta-squared
Intercept		1			<0.000	0.741
GRT	18206.044	16	1147.878	1694	<0.000	0.272
Year	4608.945	7	658.421	1083	<0.000	0.095
Area	3040.930	12	253.411	447	<0.000	0.069
Month	1687.816	11	153.438	282	<0.000	0.041
Year * Month	3013.954	77	39.142	78	<0.000	0.077
Year * GRT	2200.369	98	22.453	47	<0.000	0.061
Area * Month	802.657	130	6.174	13	<0.000	0.024
Year * Area	472.236	83	5.690	12	<0.000	0.014

## MATERIALS AND METHODS

### Data

Catch and effort data from the bottom trawl fleet targeting both *Merluccius capensis* and *Merluccius paradoxus* off Namibia were used in the analysis for the period from 1994 to 1999. All vessels included were active in the hake fisheries for three years or longer. The basic data have a spatial resolution of grid squares (20 x 20 nautical miles) and a temporal resolution of one day. The data originated from the logbooks completed for each fishing vessel and handed to the authorities at the end of each fishing trip. The daily data comprise vessel code, engine power, gross registered tonnage, date, hours trawled, number of trawls, water depth, landings, target species and grid square number.

### Correction of effort

The generalised linear modelling (GLM) analysis from Voges (2004) shows that the gross registered tonnage (GRT) of the vessels explains most of the variability in CPUE (Table 1). Since the GLM analysis also showed that GRT-year interactions

have a significant influence on the CPUE, these effects need to be taken into account in this study of the movement and behaviour of the fleet.

In this analysis of fleet dynamics, the effect of the different GRT-classes on CPUE can be removed to a certain extent by applying the correction calculated by the GLM. From the GLM analysis, the factors for GRT and year, as well as the interaction between the two variables from the model, were used to standardise the effort for each GRT-class and year to be used in the analysis in this chapter (Fig. 1).

$$\text{The vessel factor (V)} = \exp(w_{\text{year}*\text{GRT}} + a_{\text{GRT}} + b_{\text{year}}) \quad (1)$$

The effort was standardised by:

$$\text{hours trawled} \times V \quad (2)$$

### Spatial dynamics of effort

In order to judge whether the movement assumption of the IFD that vessels can change areas without restrictions fits in this fishery, the distribution of effort over the fishing grounds was investigated. The number of trawling days was used as a measure

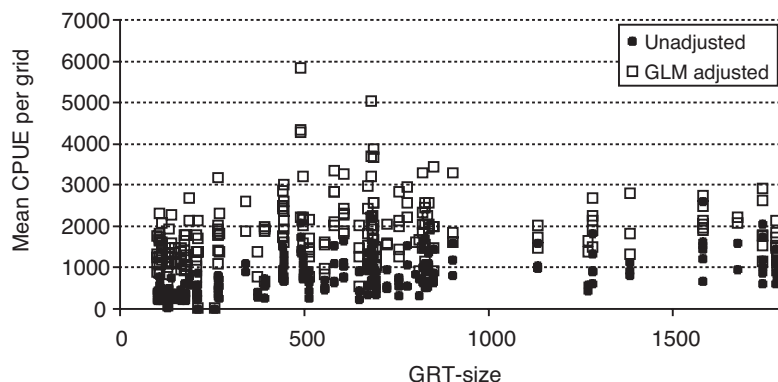


FIG. 1. – Mean CPUE per grid square and year for the unadjusted data and the GLM-adjusted for GRT and year effects for the period from 1994 to 1999.

of effort. To investigate to what extent the vessels move freely over the whole area, the number of trawling days for each latitude degree for vessels landing at the two ports, Walvis Bay and Lüderitz, was plotted separately for the period from 1994 to 1999. The total number of statistical grid squares in the fishing area (between 200 and 1000 m of depth) is 121 grid squares. The total number of grid squares covered during each fishing year is expressed as a percentage of the total fishing area.

To determine whether the spatial fishing strategies of different vessels were a major determinant of fishing success, the spatial diversity of each vessel for each year was described by the Shannon-Wiener diversity index (Margalef, 1956; Abrahams and Healey, 1990). The Shannon-Wiener diversity index ( $H'$ ) is calculated as:

$$H' = \sum_{i=1}^k p_i \log p_i \quad (3)$$

where  $p_i$  is the proportion of time spent fishing in grid square  $i$ , and  $k$  is the number of grid squares trawled (Zar, 1999).

The minimum value occurs if a vessel fishes only in one area. The index increases as vessels distribute their time equally among a large number of grid squares. The diversity index was calculated for each vessel for each year. The evenness index ( $E$ ) (Pielou, 1966) was calculated from the diversity index:

$$E = H' / \ln(S) \quad (4)$$

where  $S$  is the total number of grid squares covered by each vessel.

Evenness is a measurement of how well-dispersed the distribution of effort is. When effort is spread evenly over the whole area covered, evenness is one, but when the effort distribution is concentrated in certain areas the value decreases. A plot of  $E$  versus the CPUE of all vessels for the period from 1994 to 1999 year was made in order to determine whether there is any relationship between the evenness index and the relative catch rates of individual vessels, using a curve estimation method from the "SPSS" Base 9.0" statistical package (SPSS Inc. 1999).

### Competition among vessels

Competition is defined as an interaction between vessels that results in a decrease in CPUE associated with an increase in the number of vessels and is a

necessary condition for the operation of an IFD (Gillis *et al.*, 1993). Competition can be interference competition, exploitative competition, or a combination of the two. Interference competition usually results in a reversible reduction in CPUE due to interactions between foragers or between forager activities and prey behaviour. In this study the short-term effect of vessel activity on catch rates in a specific area is tested and thus interference competition is investigated.

For this analysis, data from the whole fleet were grouped into grid squares and weeks. Seven day standard weeks were used, beginning on January 1, 1994. The unit of effort used was hours trawled (corrected using the GLM). The comparison between the changes in CPUE values between weeks of increasing and decreasing effort was made using two different procedures, namely the Mann-Whitney U test, as applied by Gillis *et al.* (1993), as well as a 2 X 2 contingency table (Zar, 1999). The Mann-Whitney U test takes into account the magnitude of the changes in CPUE for increasing and decreasing effort. The second procedure was built up with the purpose of considering only the sign of the changes regardless of their magnitude. The numbers of increasing and decreasing events in CPUE were counted when effort decreased and increased for every year and for the whole study period. The null hypothesis was that frequencies of changes in CPUE are independent of the frequencies of changes in effort.

### Equalisation of CPUE

Previous authors (e.g. Hilborn and Ledbetter, 1979) focused their studies on the ratio of CPUE within an area to the average CPUE among all areas. They hypothesised that this ratio would remain constant over time and would reflect the relative costs of fishing in each area. Also, if CPUE and costs were equal in all areas, then this ratio would be one. Regressing the arcsine-transformed proportions of total catch and total effort in each grid square for each week in each year tested the equality of CPUE among areas. According to Gillis *et al.* (1993), if effort is allocated among areas so that CPUE is equalised among areas, then when  $C_i$  and  $f_i$  are the catch and effort in area  $i$  for a particular week:

$$C_i / f_i = \sum C_i / \sum f_i = R \quad (5)$$

where  $R$  is the ratio, or CPUE value, that is

equalised among all areas in the week being considered. By rearrangement, then:

$$C_i / \sum C_i = f_i / \sum f_i \quad (6)$$

This is the general form of a linear regression  $Y = bX + a$ , where  $b = 1$  and  $a = 0$ .

Thus, if the IFD applies, the regression of the proportion of catch in area  $i$  on the proportion of effort in area  $i$  will be a line with an intercept of 0 and a slope of 1. If the IFD holds, all points will fall on this line, regardless of the weekly values of.

## RESULTS

Both the adjusted and the unadjusted CPUE per grid square and each year for the period from 1994 to 1999 are shown in Figure 1. Clearly, the adjusted mean CPUE shows the higher efficiency of the mean size vessels in comparison with the bigger ones.

### Spatial dynamics of effort

The distribution of effort by latitude of the hake fleet, landing at the two different ports, is shown in Figure 2. It is clear from this that vessels from both ports cover the entire area, but that most effort is concentrated closer to the homeports. The area trawled by the fleet varied between years (Table 2) from a minimum percentage of total fishing ground in 1994 to a maximum in 1999.

The evenness index for all boats is below 0.5 (Fig. 3), indicating that effort is not evenly distrib-

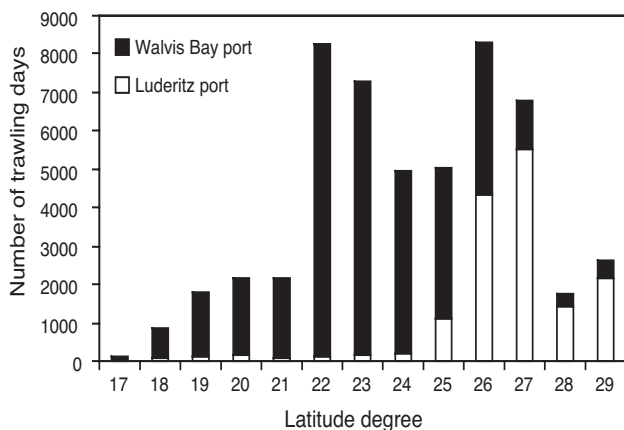


FIG. 2. – Number of trawling days per latitude spends by the hake fleet grouped by vessel's landing port, Walvis Bay and Lüderitz, over the period comprised between 1994 and 1999.

TABLE 2. – Percentage of the total number of grid squares covered by the hake fleet during each fishing year.

Year	% of grid squares
1994	68
1995	71
1996	81
1997	80
1998	88
1999	81

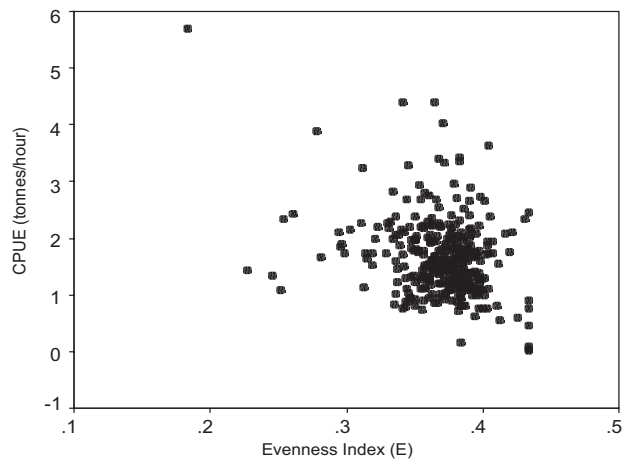


FIG. 3. – Relationship between Evenness index and CPUE (tonnes/hour) per vessel and year.

uted over the whole area, in which case the evenness index would have been close to 1. Therefore, the effort distribution can be considered as concentrated in certain areas to a certain extent. However, there was no significant relationship between the evenness index for each vessel for each year and the CPUE, in which the Pearson correlation coefficient was low and moreover negative (-0.29). This indicates that the strategy of effort distribution does not have an effect on catch rates.

### Competition among vessels

No significant inverse relationship was detected between changes in effort and the corresponding changes in CPUE within an area when the mean change in CPUE values was considered (Table 3), suggesting that there had been no interference competition between vessels. In 1994 and 1995 the distributions of changes in CPUE were not significantly different under the presence of increasing or decreasing effort. There was, however, a significant positive relationship from 1996 to 1999 (Fig. 4), with increasing CPUE when effort increased.

For the count of decreasing and increasing CPUE events with the increase in effort, as shown



TABLE 3. – Tests for competitive effects in catch-effort data. The values in parentheses are the number of cases in the category. U = Mann-Whitney U statistic, N = total sample size, and P-level. \* Significant difference between CPUE changes with decreasing and increasing effort.

Year	Decreased effort	Increased effort	U	N	P-level
1994	13.31 (456)	-151.42 (437)	98270	893	0.723
1995	69.57 (594)	-86.47 (563)	163595	1157	0.524
1996	-119.59 (702)	-54.70 (713)	218632	1415	<0.000 *
1997	-136.39 (814)	32.13 (775)	263542	1589	<0.000 *
1998	-56.68 (723)	-9.87 (677)	220726	1400	0.001 *
1999	-117.6 (830)	-35.53 (866)	323152	1696	<0.000 *

in the 2 x 2 tables (Table 4), basically the same results were obtained as when the two-tailed Mann-Whitney U test was used. For 1994 increasing or decreasing effort caused no significant change in CPUE. Thus, there was a significant difference between the change in CPUE during increasing and decreasing effort for all years except for 1994 using both tests. There was, however, a positive relationship, since overall CPUE decreased when effort decreased and increased when effort increased. Therefore, it can be concluded that there is little or

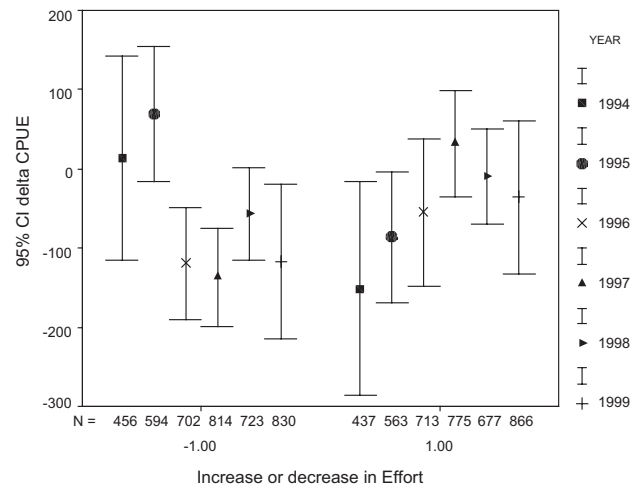


FIG. 4. – Relationship between Means of delta CPUE with increasing (1.00) and decreasing (-1.00) Effort per year (1994-1999). Means are illustrated with their 95% CI.

no evidence of either exploitation or interference competition between vessels.

### Equalisation of CPUE

The linear regression of the proportion of the weekly catch in an area on the proportion of weekly effort in that area provided a significant fit to the predicted data (Fig. 5). An examination of the transformed proportional effort values revealed a nearly bell-shaped distribution. Therefore, linear regression was used as the statistical model for the hypothesis tests about the equalisation of CPUE

TABLE 4. – Results of the Chi-square analysis (P<0.05) of the contingency table to test for competition between all vessels for each year and the whole study period combined. The Chi-square value and the P-level are reported.\* Significant difference between CPUE changes with decreasing and increasing effort.

Year	2X2 Table		Chi-square	P-level
	Effort decrease	Effort increase		
1994-1999	CPUE decrease	2436	80.40 Df = 1	0.000*
	CPUE increase	1683		
1994	CPUE decrease	253	0.34 Df = 1	0.516
	CPUE increase	203		
1995	CPUE decrease	343	5.07 Df = 1	0.025*
	CPUE increase	251		
1996	CPUE decrease	421	18.65 Df = 1	0.000*
	CPUE increase	281		
1997	CPUE decrease	495	28.42 Df = 1	0.000*
	CPUE increase	319		
1998	CPUE decrease	424	15.48 Df = 1	0.000*
	CPUE increase	299		
1999	CPUE decrease	500	20.00 Df = 1	0.000*
	CPUE increase	330		

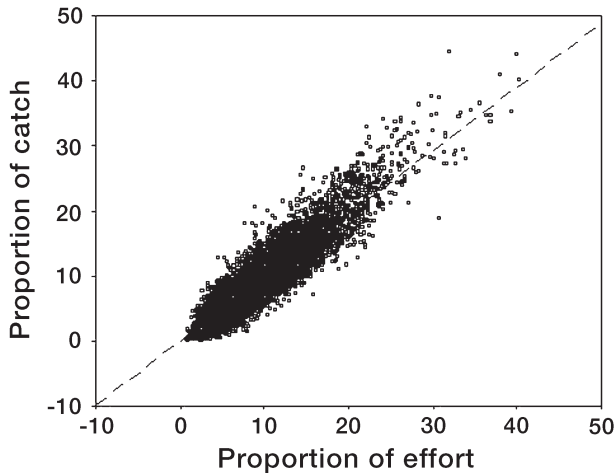


FIG. 5. – Test for equality of CPUE using proportions of effort and catch. The broken line is the least squares regression line for the data from 1994 to 1999 ( $r^2 = 0.955$ , slope = 0.975).

among areas. For each of the years and the years combined, there was no significant difference between the observed slope and the slope of 1 that was predicted by the IFD (Table 5). This suggests that CPUE was equalised among areas fished, as predicted by the IFD.

## DISCUSSION

The theory of IFD has proven to be a useful way to understand distribution of fishing effort and to predict its possible effect on CPUE as an index of abundance. In this analysis it was assumed that vessels have the same competitive abilities after the effort was adjusted using the results of the GLM analysis. Although the fleet does not distribute its effort evenly over the whole area, it does cover a considerable part of the total fishing area. It can be concluded that the fleet is generally able to move freely between fishing

TABLE 5. – Equalised CPUE is indicated by a slope (b) of 1 in the regression of proportional catch on proportional effort. The estimated slopes were compared to 1.0 using a two-tailed t-test ( $P < 0.05$ ). R-squared is the coefficient of determination and N is the sample size. \* b is not significantly different from 1.

	R-squared	b (SE)	N	P
All data	0.955	0.975 (0.002)	11183	<0.001 *
1994	0.957	0.963 (0.005)	1301	<0.001 *
1995	0.972	0.966 (0.005)	1577	<0.001 *
1996	0.960	0.980 (0.005)	1927	<0.001 *
1997	0.979	0.983 (0.004)	2149	<0.001 *
1998	0.975	0.978 (0.005)	1949	<0.001 *
1999	0.978	0.980 (0.004)	2280	<0.001 *

grounds. Moreover, the prediction of the IFD that was tested does hold for this fishery: vessels move between fishing areas in order to equalise catch rates between areas.

The GLM analysis, at present one of the most efficient procedures for analysing dependant factors, has shown that the different GRT-classes of the vessels, together with the year effect, play the most important role in influencing the CPUE. This effect changed over the years, with a resulting loss in the “fishing power” of the bigger vessels. The difference in catch rates between the small and big vessels can mainly be ascribed to differences in the fishing power of the vessels, while the decrease in efficiency of the big vessels over time can be ascribed to a change in fishing strategy. It is known, from the industry, that this loss in fishing power does not indicate changes in hake abundance but a change in the strategy of the big vessels. Quotas for the big freezer boats have been decreasing gradually since 1994, when an onshore processing policy was introduced in order to create more employment for Namibians. The result of this, as well as market preferences, forced owners of large vessels to increasingly produce value-added products. Therefore, smaller quantities of hake are caught in order to optimise the value of the catch. The search for bigger fish results in reduced catch rates.

The spatial distribution of effort is not completely even, but about 60% patchy. The fishing pattern of individual vessels (according to the evenness index) does not have a significant relationship with the catch rates of the vessel. Thus, whether a vessel distributes most of its effort only in a small area, or whether it covers a bigger area, has no significant influence on the catch rates of the vessel. The range of the evenness index is between 0.45 and 0.2. Coverage of the total fishing area is good in all years, with an average of about 80% of the number of grid squares covered. Although more effort is expanded in the area between 22 and 28°S, it can be assumed that the vessels are relatively free to move between areas, if needed. This is one of the assumptions of the IFD.

Another of the assumptions of the IFD is that competition between foragers occurs in proportion to their local density. In this study no evidence of interference competition was detected among vessels. Although this is surprising, it may be a positive sign for the Namibian hake fishery. This observation may indicate that the level of exploitation of the

resource was at a favourable level for both the fishers and the hake stock until the latest year analysed (1999). Increases in effort from one week to another in a specific grid square do not have a negative influence on CPUE, and this may be because the effort is not enough to have an interference effect or to disrupt the fish. Hilborn (1985) emphasised that the best starting point for the investigation of effort allocation is to assume that the vessels will move to equalise CPUE. In this study it was seen that this does indeed happen. If interference competition occurs between vessels, the slope would tend to be less than 1. Since CPUE is equalised over the whole area, the number of vessels in a specific area should be a better indication of stock abundance than the CPUE. This particular situation is valid for the period analysed in this study. This scenario may change in the future if effort increases to the level at which interference between vessels takes place. Annual analysis on vessel competition may be considered as an additional tool for examining the condition of many fisheries.

The main implication of the results from the proportional regression analysis is that the changes in CPUE values will reflect trends in abundance within the stocks. If equalisation of CPUE occurs, a local decline in abundance in the stock will be tracked by changes in the proportion of fleet effort expended on that stock rather than the CPUE value (Gillis *et al.*, 1993). CPUE for different areas may be pooled when used as an index of abundance.

Interference competition between vessels will contribute to variability in the catchability coefficient ( $q$ ), which is usually considered to remain constant in traditional stock assessment methods. In this study it has been shown that there is no evidence of interference competition between vessels, so  $q$  is not influenced by this factor for the period analysed (until 1999). The size of the Namibian hake fleet was reduced in 1994 and the effort expended by the fleet seems to be at a favourable level, so that there is very little to no interference competition between the vessels. If the fleet size changes in the future, the effect on competition between vessels should be monitored and the possible influence on  $q$  and the resulting breakdown of the relationship between CPUE and abundance should be kept in mind. A systematic monitoring of interference competition is recommended in future management strategies, as any change from present results will be indicative of a qualitative and quantitative change in the fishery scenario.

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## 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.
- 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.
- Abrahams, M.V. and M.C. Healey. – 1993. Some consequences of variation in vessel density: a manipulative field experiment. *Fish. Res.*, 15: 315-322.
- Allen, P.M. and J.M. McGlade. – 1986. Dynamics of discovery and exploitation: the case of the Scotian shelf groundfish fisheries. *Can. J. Fish. Aquat. Sci.*, 43: 1187-1200.
- Anganuzzi, A. – 1996. An aggregate model of effort distribution. In: Status of Interaction of Pacific Tuna Fisheries in 1995. *FAO Fish. Tech. Pap.*, 365, Rome, FAO, 1996, pp. 612.
- Clark, C.W. and M. Mangel. – 1979. Aggregation and fishery dynamics: a theoretical study of schooling and the purse seine tuna fisheries. *Fish. Bull. U.S.*, 77: 317-337.
- Cooke, J.G. – 1985. On the relationship between catch per unit effort and whale abundance. *Rep. Int. Whal. Comm.* 35: 511-519.
- Deriso, R.B., T.J. Quinn and P.R. Neal. – 1985. Catch-age analysis with auxiliary information. *Can. J. Fish. Aquat. Sci.*, 42: 815-824.
- Fretwell, S.D. – 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton.
- Fretwell, S.D. and H.L. Lucas. – 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.*, 19: 16-36.
- Gillis, D.M. and R.M. Peterman. – 1998. The implications of interference and the ideal free distribution to the interpretation of CPUE. *Can. J. Fish. Aquat. Sci.*, 55: 37-46.
- Gillis, D.M., R.M. Peterman and A.V. Tyler. – 1993. Movement dynamics in a fishery: application of the ideal free distribution to spatial allocation of effort. *Can. J. Fish. Aquat. Sci.*, 50: 323-333.
- Healey, M.C. and J.F.T. Morris. – 1992. The relationship between the dispersion of salmon fishing vessels and their catch. *Fish. Res.*, 15: 135-145.
- 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.
- Hilborn, R. and C.J. Walters. – 1987. A general model for simulation of stock and fleet dynamics in spatially heterogeneous fisheries. *Can. J. Fish. Aquat. Sci.*, 44: 1366-1369.
- 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.
- Mangel, M. and J.H. Beder. – 1985. Search and depletion: theory and applications. *Can. J. Fish. Aquat. Sci.*, 42: 150-163.
- Mangel, M. and C.W. Clark. – 1983. Uncertainty, search and information in fisheries. *J. Cons. Int. Explor. Mer.*, 41: 93-103.
- Mangel, M. and C.W. Clark. – 1986. Search theory in natural resource modelling. *Nat. Res. Mod.*, 1 (1), 3-54.
- Margalef, R. – 1956. Información y diversidad específica en las comunidades de organismos. *Invest. Pesq.*, 3: 99-106.
- Milinski, M. and G.A. Parker. – 1991. Competition for resources. In: J.R. Krebs and N.B. Davies (eds.), *Behavioral Ecology: an evolutionary approach*, pp 137-168. Blackwell Scientific Publications, Oxford.
- Pielou, E.C. – 1966. The measurement of diversity in different types of biological collections. *J. Theoret. Biol.* 13: 131-144.



- Polacheck, T. – 1988. Analyses of the relationship between the distribution of searching effort, tuna catches, and dolphin sightings within individual purse seine cruises. *Fish. Bull.*, 86(2), 351-366.
- Rijnsdorp, A.D., A.M. Buys, F. Storbeck and E. Visser. – 1998. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. *ICES J. Mar. Sci.*, 55: 403-419.
- Rijnsdorp, A.D., W. Dol, M. Hoyer and M.A. Pastoors. – 2000. Effects of fishing power and competitive interactions among vessels on effort allocation on the trip level of the Dutch beam trawl fleet. *ICES J. Mar. Sci.*, 57: 927-937.
- Rothschild, M.H. – 1977. Fishing effort. In: J.A. Gulland (ed.), *Fish population dynamics*, pp. 96-115. John Wiley and Sons Ltd., Toronto.
- Sutherland, W.J. – 1983. Aggregation and the “ideal free” distribution. *J. Anim. Ecol.*, 52: 821-828.
- Sutherland, W.J. and G.A. Parker. – 1985. Distribution of unequal competitors. In: R.M. Sibley and R.H. Smith (eds.), *Behavioral ecology. Ecological consequences of adaptive behavior*, pp. 255-273. Blackwell Scientific Publications, Oxford.
- Voges, E. – 2004. *Assessment and Patterns of the Namibian Hake Fishery Based on Commercial Data in Relation to Environmental Factors*. PhD thesis. University of Cape Town, Cape Town 2004, pp 126
- Zar, J.H. – 1999. *Biostatistical Analysis. Fourth Edition*. Prentice-Hall, Upper Saddle River.
- Scient. ed.: J. Lleonart

