

Advancing the application of the ideal free distribution to spatial models of fishing effort: the isodar approach

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Abstract: The ideal free distribution (IFD) of behavioral ecology has been used in the study of the distribution of fishing effort since the 1990s. Concurrently, evolutionary perspectives on forager distributions have led to the development of theoretical curves of equal fitness, named isodars, to test IFD hypotheses. We develop isodars, based upon catch rates and unknown costs, to quantify regularity in the distribution of fishing effort among alternative areas. Our analyses indicate that these isodars provide significantly better predictions than a simple IFD without costs. Autocorrelation in the catch and effort data necessitates the use of generalized linear least squares when estimating model parameters. Differences in costs that are proportional to effort are more clearly identified in the model than nonlinear effects, which may arise from extreme interference competition. The isodar approach provides a new tool for examining the spatial dynamics of catch and effort data. It improves the accuracy of predictions and provides new parameters related to costs and vessel interactions that can be applied to rapidly identify situations where effort dynamics have changed.

Résumé : Le concept de la distribution libre idéale (IFD) du domaine de l'écologie comportementale a été utilisé pour étudier la distribution de l'effort de pêche depuis les années 1990. En parallèle, des perspectives évolutives sur la répartition des fourrageurs ont mené à l'élaboration de courbes théoriques de valeur sélective identique, appelées isodars, afin de vérifier des hypothèses relatives à l'IFD. Nous avons établi des isodars, basés sur les taux de prise et les coûts inconnus, dans le but de quantifier la régularité de la répartition de l'effort de pêche dans différentes régions. Nos analyses indiquent que ces isodars donnent des prévisions significativement meilleures que la simple IFD appliquée sans y intégrer de coûts. L'autocorrélation dans les données sur les prises et l'effort nécessite l'utilisation de moindres carrés généralisés linéaires pour estimer les paramètres du modèle. Les différences de coûts proportionnelles à l'effort sont plus clairement cernées dans le modèle que les effets non-linéaires, ce qui peut découler d'une extrême compétition par interférence. L'approche basée sur les isodars constitue un nouvel outil pour étudier la dynamique spatiale des données sur les prises et l'effort. Elle améliore l'exactitude des prévisions et fournit de nouveaux paramètres relatifs aux coûts et aux interactions de navires qui peuvent être utilisés pour cerner rapidement des situations où la dynamique de l'effort a changé.

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Introduction

Since its inception, the ideal free distribution (IFD; Fretwell and Lucas 1969; Fretwell 1972) has seen broad application in the study of spatial distributions across taxa (Kennedy and Gray 1993; Houston 2008) and within fisheries (Gillis et al. 1993; Rijnsdorp et al. 2000b; Poos et al. 2010). Briefly, it predicts that when interference competition exists, effort allocation is unrestricted, and information flows freely among foragers, the productivity (catch value divided by costs) will tend to be equalized among all locations. This is an example of an n -person, frequency-dependent game (Maynard Smith 1982; Křivan et al. 2008). The dynamics of the IFD follow

from the same logic as Gordon's classical paper on the common property nature of fisheries, specifically that the reallocation of fishing effort between two simultaneously exploited fishing grounds should continue "... until the average productivity of both grounds [is] equal" (Gordon 1954, p. 131). The IFD continues to be topical in ecology today (Griffen 2009; Matsumura et al. 2010) and remains part of the theory used to examine the behaviour of fish harvesters (Branch et al. 2006; van Putten et al. 2012).

In spatially structured fisheries, the IFD suggests that the proportion of effort in an area will tend to equal the proportion of catch taken from that area (Gillis et al. 1993; Gillis 2003). This provides a starting point for the investigation

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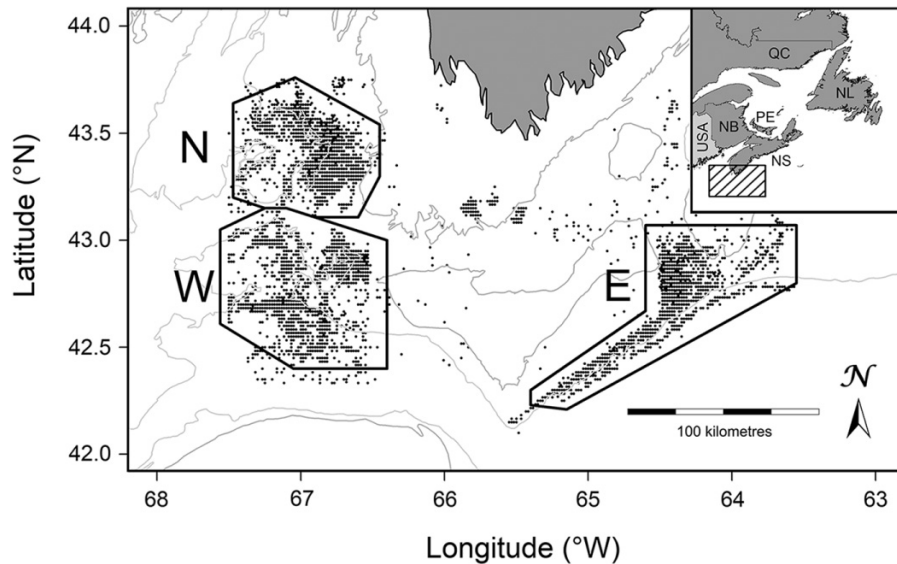
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Fig. 1. Fishing activity around the Browns Bank regulatory closure. Fishing areas were defined based upon the observed distribution of fishing effort, illustrated as points in this figure, into three principle areas: east of the Browns Bank (E), west of Browns Bank (W), and north of Browns Bank (N). The position of the study area relative to eastern Canada is indicated on the inset map (NB – New Brunswick, QC – Quebec, PE – Prince Edward Island, NS – Nova Scotia, NL – Newfoundland). Only fishing activity between 1 February and 15 June for each year studied (2005–2008) was used for model comparisons.



(Abrahams and Healey 1993; Swain and Sinclair 1994) and modeling (Gillis and Peterman 1998; Cox et al. 2003) of fisheries systems, which have proven useful in past studies. For example, applications of the IFD have shown that fishing effort tracked changes in distribution of Atlantic cod (*Gadus morhua*) abundance on the Scotian Shelf (Gillis and Frank 2001) and snow crab (*Chionoecetes opilio*) in the Gulf of St. Lawrence (Swain and Wade 2003). The IFD in fisheries research has been criticised as being too simplistic (Holland and Sutinen 1999) and has been found to fail to predict effort distributions in specific fisheries (Pet-Soede et al. 2001; Abernethy et al. 2007), especially when one or more of its underlying assumptions are strongly violated. However, its simplicity is an asset as a conceptual model and when data are limited to the spatial record of catch and effort. Furthermore, its assumptions can provide a framework to investigate the underlying mechanisms and constraints when the IFD is found not to apply.

Though IFD predictions can be based upon measured foraging or catch rates, Morris (1988, 2003) developed a methodology, the “isodar”, which predicts numbers in one area based upon the numbers in an alternative area and explicit expressions of local, density-dependent per capita fitness. The resulting curve defines the combinations of numbers in each area that result in equal fitness among all individuals at all locations. This is termed an “isodar” as a contraction of “iso-Darwin”. The method was originally demonstrated with rodents (Morris 1988), but has been extended to fish in lake basins (Haugen et al. 2006) and even human settlement patterns between urban and rural areas (Morris and Kingston 2002). The definition of an isodar requires (i) the identification of a density-dependent fitness function for the foraging areas, (ii) the statement of the equation that defines equal per capita fitness among areas, and (iii) the rearrangement of the equation so that the numbers in one area are predicted by the numbers in the other. Morris and Kingston (2002) used

the population growth rates of the theta-logistic as the basis of per capita fitness; Haugen et al. (2006) used movement, survival, and fecundity data. We will base our initial estimates of per capita “fitness” on the average catch rates (calculated from aggregated catch and effort statistics) experienced among the areas fished. This choice is based upon productivity, defined as catch value divided by costs, where costs are proportional to nominal effort. Then, alternative cost expressions will be considered, based upon previous behavioural studies.

Materials and methods

The fishery data

The performance of alternate isodar models was examined using data from the Nova Scotian haddock (*Melanogrammus aeglefinus*) fishery in Northwest Atlantic Fisheries Organization (NAFO) Division 4X. This was a subset of data from a larger study contrasting discrete choice and aggregate approaches to modelling vessel distribution (A. van der Lee and D.M. Gillis, unpublished data). In this paper, we focused on trawlers fishing around the Browns Bank regulatory closure and defined aggregations of effort to the east and west of the closure, as well as an area north of the closure and closer to shore. The delineation of the areas considered and the spatial scale of the study is illustrated (Fig. 1). Haddock is the common target species in this fishery, but other species are also regularly captured either deliberately or as bycatch. These species include redfish (*Sebastes* spp.), pollock (*Pollachius virens*), Atlantic cod, and flounders (Pleuronectiformes). To account for this, all catches were converted to their Canadian dollar value using weekly landed prices in Nova Scotian ports available from the Web site of the Prince Edward Island Department of Fisheries, Aquaculture and Rural Development (<http://www.gov.pe.ca/fard/index.php3?number=1024862>, accessed May 2011).

Thus, our “catch” is a price-corrected revenue that incorporates the multispecies nature of the fishery and the weekly variation in price by species and size class through the period examined. Quantified fishing effort (including both time and location) was obtained from mandatory logbook records maintained by the Marine Fish Division of Fisheries and Oceans Canada (Dartmouth, Nova Scotia). Data on catch (value landed) and effort (hours fished) was aggregated weekly for each area (Fig. 1) from 2005 to 2008. Though typical in many ways, these data are not intended to represent all trawl fisheries. In addition to reflecting the fleet dynamics of this fishery, these data also provided an opportunity to develop a methodology to examine alternate models that could be applied to other fisheries in the future.

The models compared

The definition of accurate isodars depends upon the selection of an appropriate model to represent the density-dependent “fitness” of each of the foraging areas being utilized. We developed four isodars, based upon conceptual models of increasing complexity, to select the most parsimonious relationship describing the resulting effort distribution under active area selection.

The ideal free distribution (IFD) without costs

Earlier applications of IFD have focused on the first approximation solution, disregarding potential costs, which we shall refer to as the simple IFD model. In this case, the estimate of production is the revenue from the catch. Productivity is provided by the catch rates, which should be equalized among all foraging areas at equilibrium. This would result in the proportion of catch taken from each area equalling the proportion of total effort expended in that area (Gillis 2003). Alternatively, this can be used to define an isodar that predicts the numbers in one area from the numbers in the other. When catch rate is equalized between two areas, then

$$(1) \quad \frac{C_2}{f_2} = \frac{C_1}{f_1}$$

where C_1 and C_2 are the catch taken from areas 1 and 2 in the time examined (1 week), and f_1 and f_2 are the total amount of nominal fishing effort (hours fished) in each area through the same time period. This relationship can be rearranged to define an isodar that predicts the effort in the second area based upon the catches and the effort in the first area:

$$(2) \quad \log(f_2) = -\log\left(\frac{C_1}{C_2}\right) + \log(f_1)$$

On a logarithmic scale, this represents a linear relationship with a slope of 1 and an intercept of $-\log(C_1/C_2)$. This is true for any logarithmic base, but we use natural logarithms in our models and analyses. No parameter estimates are required to apply this model; the prediction of f_2 is based entirely on the values of the other variables. Furthermore, if C_1/C_2 can be treated as a constant value, a single line will describe the relationship. However, catches taken from neighbouring areas will often differ among the times considered (weeks or months). In these cases, predictions will be made from a

number of parallel lines of slope 1 and intercepts reflecting the changing catches.

Constant catch rate ratio (CCR)

Hilborn and Ledbetter (1979) suggested that differences in the costs between areas could result in catch rates that differed among areas but maintained a constant ratio. This assumes that productivity remains equalized among areas, and the variation in costs is represented in the ratio of catch rates among areas. These costs were stated to represent differing “desirability” among fishing areas, which was related to their unique operating costs and risks. Furthermore, for the ratio to be constant these costs would have to scale with the effort expended. Their conceptual model can be represented mathematically as

$$(3) \quad \frac{C_2}{f_2} = e^\alpha \cdot \frac{C_1}{f_1}$$

where e^α is the proportionality constant expressed as a power of e , the base of natural logarithms. The resulting isodar predicting the effort in the second area is

$$(4) \quad \log(f_2) = \left[\alpha - \log\left(\frac{C_1}{C_2}\right) \right] + \log(f_1)$$

Constant productivity ratio with common nonlinear effort effects (CPRc)

Factors that do not scale proportionally with changing effort may not be adequately represented by the model of eq. 3. Interference competition among foragers (Hassel and Varley 1969) is a well-known ecological factor that could cause this effect. The impact of different levels of interference on IFD was introduced by Sutherland (1983), developed theoretically for IFDs in a fisheries context (Gillis and Peterman 1998), and related to isodar theory by Morris (1994). When interference is not proportional to forager density, the costs of additional foraging can increase in a nonlinear fashion. In a fishery, these costs could be realized immediately (i.e., course alterations in crowded grounds) or they could be more probabilistic in nature (i.e., risk of gear entanglement). Thus, a doubling of effort in an area would not double the costs, but would result in some greater value. A simple way to represent such costs in our model is by adding an exponent to effort, so that productivity is represented by C/f^β rather than simply the catch rate C/f . A β that is greater than 1 represents a negative impact on productivity that occurs in a disproportionate, nonlinear manner in relation to increasing effort. When this effect is common between areas, equalized productivity can be represented as

$$(5) \quad \frac{C_2}{f_2^\beta} = e^\alpha \cdot \frac{C_1}{f_1^\beta}$$

and the resulting isodar is

$$(6) \quad \log(f_2) = \frac{1}{\beta} \cdot \left[\alpha - \log\left(\frac{C_1}{C_2}\right) \right] + \log(f_1)$$

Constant productivity ratio with unique nonlinear effort effects in each area (CPRu)

The final productivity model considered is similar to eq. 5, but allows for unique nonlinear effort effects in each area:

$$(7) \quad \frac{C_2}{f_2^{\beta_2}} = e^\alpha \cdot \frac{C_1}{f_1^{\beta_1}}$$

This can be rearranged into the isodar predicting the effort in area 2 from the other measured variables:

$$(8) \quad \log(f_2) = \frac{1}{\beta_2} \cdot \left[\alpha - \log\left(\frac{C_1}{C_2}\right) \right] + \frac{\beta_1}{\beta_2} \cdot \log(f_1)$$

The progression through each these models follows a common productivity model based upon the ratio of catch to costs:

$$(9) \quad \text{Productivity} = \frac{C_i}{K_i \cdot f_i^{\beta_i}}$$

where C_i is the total value of the catch in area i , K_i is an area-specific cost coefficient, and β_i is an exponent that defines the relationship between effort and effort-related costs. When the β_i values are greater than 1, the costs increase disproportionately with effort, as discussed in the context of interference above. When all β_i values are equal to 1, the expected ratio of catch rates becomes the ratio of the cost coefficients (K_i), resulting in Hilborn and Ledbetter's (1979) model and the isodar in eq. 4. When the cost coefficients are identical, the isodar is developed from the original IFD (eq. 2). In this representation of costs, $K_i \cdot f_i^{\beta_i}$, the parameters K_i and β_i do not directly relate to specific influences. Instead, they define an empirical relationship that represents a variety of cost structures with minimum complexity.

Statistical methods

Parameter estimation (fitting the models)

None of the models that we examined could be represented by classical linear regression, so nonlinear methods were used to estimate the values of their parameters using the R statistical language (R Development Core Team 2011). It is likely that spatial distributions of vessels will be correlated among weeks, and the act of aggregating data itself can result in autocorrelated errors around model predictions (Granger and Morris 1976). Therefore, we employed generalized nonlinear least squares using the `gnls()` function from the `nlme` library (Pinheiro et al. 2010). Initial parameter estimates were set to 1 for all β values and 0 for α values. Autocorrelation was visually examined by inspection of the autocorrelation function out to a lag of 5 weeks. Autocorrelation was represented in the models as an autoregressive moving average (ARMA) process whose order (p autoregressive terms and q moving average terms) was determined by comparing the sample-size-corrected Akaike information criterion (AIC_c) values of different orders (Brockwell and Davis 1991). AIC_c is a refinement of AIC that controls for biases caused by small sample sizes in model selection (Anderson 2008). AIC_c was chosen over AIC to reduce the tendency to overparameterize ARMA models. AIC_c was chosen over the Bayesian or Schwarz information criterion because of the relatively small sample sizes (53–70) relative to the number of parameters (3–7) estimated. For parsimony, only cases where $p' + q' \leq p$ were considered, where p' and q' are the orders of the ARMA model, and p is the order of the simpler autoregressive (AR) model. Thus, the final model had a number of parameters (k) equal to

the number of parameters of the isodar model (one to three), plus one for the variance estimate, plus $(p + q)$ for the autocorrelation. The autocorrelation function, based upon residuals that were normalized by the correlation structure, was examined to ensure that the ARMA model had removed the effects of autocorrelation from the parameter estimates. In all cases, no lag had a significant autocorrelation ($p < 0.05$).

Model comparison and selection

Typically, isodars are examined by plotting the forager densities (or logarithm of the densities) observed on each other to reveal the underlying relationship. This is effective when habitat quality varies much more slowly than the foragers can redistribute themselves. However, in our case area quality varied within each season because of unobserved factors that influenced local availability of fish, such as fish movement among adjacent areas. Instead, we illustrated our models by plotting the observed logarithm of effort in the predicted area on the prediction based upon the other variables. The linear regression of these values provided an indication of model quality. This empirical regression was compared with the theoretical regression (intercept = 0, slope = 1) that would indicate a perfect fit. However, these figures and regressions were not used for model selection. The choice of the isodar model that best reflected the data was entirely based upon the lowest AIC_c value, as described above.

Results

Model comparison and selection

The simple IFD model's predictions were strongly correlated to the observed values, but these predictions were consistently biased in each of the cases examined (Fig. 2). The IFD tended to underestimate effort at low values, but the predictions and observations agreed more closely at higher effort values. The CCR model showed some improvement, but the addition of nonlinear effort effects in the CPRc and CPRu models finally brought predictions and observations into alignment. The closest agreement was seen with the most complex model (CPRu), which allowed for unique nonlinear effort effects within the areas. This pattern is reflected in the confidence intervals (CIs) for the slope of the observed on predicted lines (Table 1). The CIs of both the IFD and CCR models have slopes that do not encompass 1. However, a slope of 1 is within the CIs for both the CPRc and CPRu models. These results are consistent among all of the area comparisons examined. In the case of the CPRu, it is difficult to see the deviation between the predicted and observed lines (Fig. 2).

The effect of increasing model complexity can also be seen in the change in outliers on the plot of observed and predicted effort values. In particular, the deviation observed around the line when predicting northern effort from western effort using the CCR model (Fig. 2) shows an extreme outlier at the lower right. Examination of the original data revealed that this was a week with relatively low total effort (22 h, median for all weeks = 279) and a large variation in catch rates between areas (13.7 times greater CPUE in the west, median for all weeks = 3.5). The incorporation of the nonlinear effort parameter significantly improved the placement of this, and other outliers, as seen in the CPRc and CPRu model fits (Fig. 2). However, this point still remained one of the

Fig. 2. Predictive performance of each isodar formulation examined. The models used are indicated at the right of the graphs, and the areas examined are indicated along the top of the graphs. Each point represents the amount of effort predicted in the area of interest (North, East, and West) and the amount of effort observed in that area during the same week. The dashed line represents the 1:1 line that indicates perfect agreement between the model's predictions and the observations. The solid line is the least squares regression of observed on predicted effort.

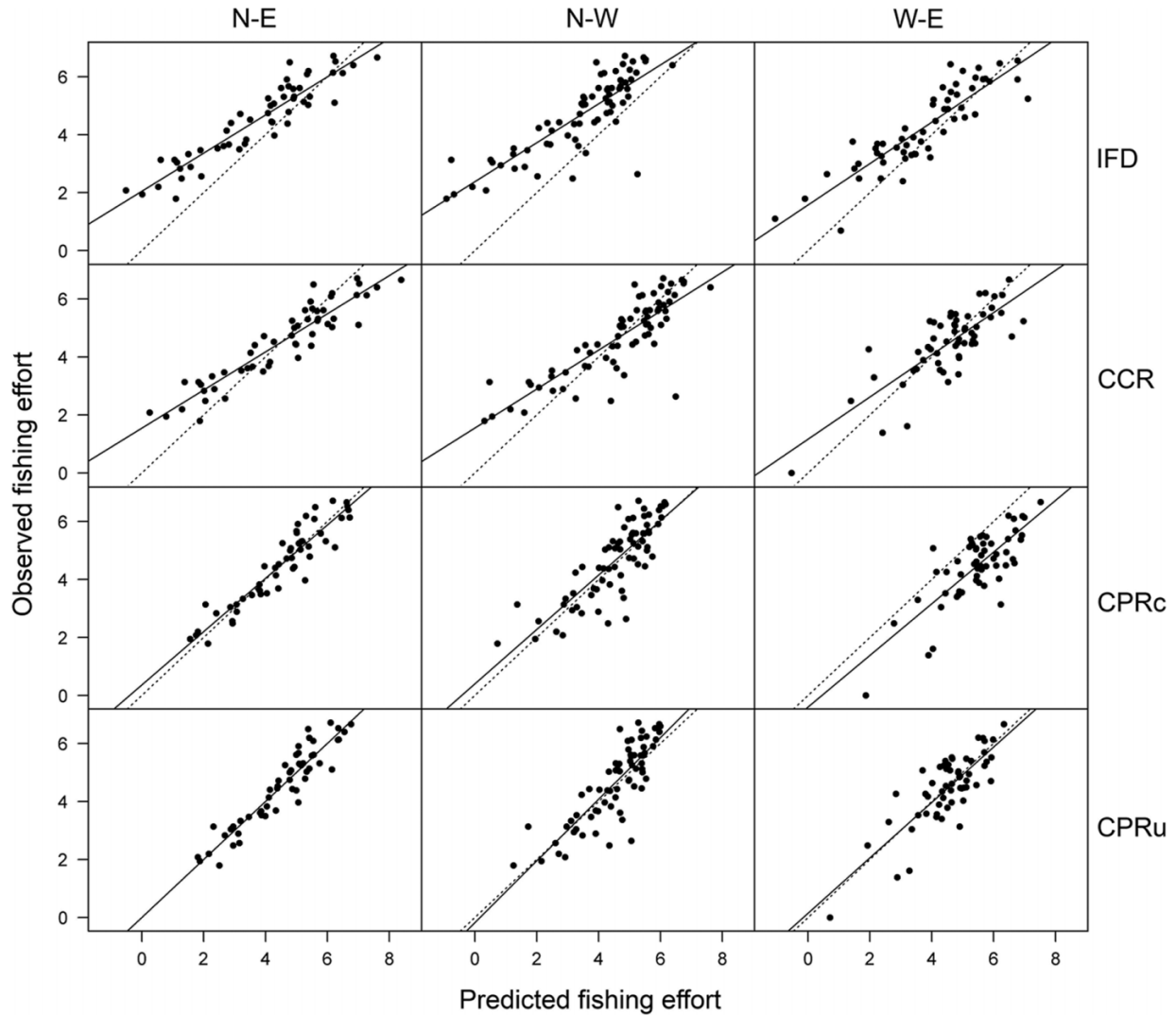


Table 1. Isodar model comparisons.

Area	Model	<i>n</i>	<i>K</i>	ARMA	CI _{lower}	CI _{upper}	AIC _c	ΔAIC _c
N-E	IFD	53	NA	NA	0.586	0.730	NA	NA
	CCR	53	3	AR(1)	0.586	0.730	124.77	47.80
	CPRc	53	4	AR(1)	0.821	1.020	81.32	4.34
	CPRu	53	4	NULL	0.897	1.103	76.97	0.00
N-W	IFD	70	NA	NA	0.567	0.775	NA	NA
	CCR	70	3	ARMA(0,1)	0.567	0.775	184.75	36.78
	CPRc	70	5	ARMA(1,1)	0.782	1.095	148.01	0.04
	CPRu	70	7	ARMA(3,0)	0.894	1.231	147.97	0.00
W-E	IFD	57	NA	NA	0.610	0.817	NA	NA
	CCR	57	4	ARMA(1,1)	0.578	0.878	137.21	22.80
	CPRc	57	6	ARMA(3,0)	0.697	1.085	114.48	0.07
	CPRu	57	7	ARMA(3,0)	0.768	1.143	114.41	0.00

Note: The quality of each model's predictions is presented for the three area relationships examined. The effort is predicted for the North (N) and East (E) areas from the effort in the East and West (W) areas. For each model, the number of weeks (*n*), the total number of parameters estimated (*K*), and the order of the autoregressive moving average (ARMA) model used to account for autocorrelation in residuals is provided. The quality of the models is indicated by the 95% confidence intervals of the observed–predicted regressions (CI_{lower}, CI_{upper}) corresponding to Fig. 2, the AIC_c, and the ΔAIC_c values of the fitted models.

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Table 2. Parameter estimates from the constant productivity model with unique nonlinearities in effort between the areas (CPRu).

Areas	Parameter	Estimate	CI _{lower}	CI _{upper}
North–East	α	2.083	1.094	3.072
	β_{East}	1.182	1.042	1.322
	β_{North}	1.462	1.312	1.612
North–West	α	2.338	0.828	3.848
	β_{West}	1.418	1.165	1.672
	β_{North}	1.675	1.394	1.955
West–East	α	0.259	–0.803	1.321
	β_{East}	1.248	1.091	1.405
	β_{West}	1.389	1.194	1.584

Note: This model predicts the effort in one area from the other; for example, the first model listed predicts effort in the North from effort in the East during the same week. Model parameter estimates are presented with their 95% confidence limits (CI_{lower}, CI_{upper}). See text for parameter definitions.

most distant from the predicted relationship. Overall, the improvement in the relationship between predicted and observed values among models is more noticeable than the influence on any specific data point.

Our formal model selection, using AIC_c, showed consistently increasing model quality with each refinement (Table 1). The simple IFD model does not directly enter into these comparisons, as no parameters were estimated. However, it can be dismissed because of the general pattern of decreasing AIC_c values as the models differ more from it. The lowest AIC_c value was obtained with the CPRu model in all of the models examined. However, in the cases of the North–West and West–East relationships, the difference in AIC_c between CPRu and CPRc was slight — less than 0.1 and much less than the typical threshold value of 2 (Burnham and Anderson 2002), which indicates models having similar levels of support in the data.

The form of autocorrelation in residuals varied among the models examined (Table 1). In the North–East CPRu model, there was no significant autocorrelation, but significant autoregressive patterns (lag 1) in the CPRc and CCR models. In the other areas, the autocorrelation varied among MA(1), ARMA(1,1) and AR(3) processes. This added to the number of parameters in the models, reaching a maximum of seven for the CPRu form of the North–West and West–East models, which both had autoregressive correlation structures suggesting influences out to 3 weeks.

Parameters of the best model

The α values of the CPRu models (Table 2), representing ratios between the areas measured at one unit of effort, show their greatest values in the prediction of log(effort) in the North area from either the East or West areas (2.08 and 2.34, respectively) in contrast with the small α value when predicting log(effort) in the West area from the East area (0.26), which are both located in open ocean adjacent to Browns Bank. Closer examination of the West area prediction revealed that the CI for α spanned 0. Furthermore, an alternate model that excluded α (CPRu – α) while retaining the β values had a lower AIC_c (112.05) than the CPRu model. These results indicated that there was no evidence for differences in the productivity ratios between the areas that could not be associated with nonlinear effort effects (β values).

The estimates and 95% CIs for all of the β values indicate that they are larger than 1. However, the width of the CIs results in substantial overlap between areas (Table 2), even though AIC_c selected the model with unique β values (Table 1). Though there is strong evidence to suggest nonlinearity, the evidence for area-specific effects is substantially weaker.

Discussion

The isodar approach that we develop has clear advantages over earlier applications of the IFD to commercial fisheries. First, the isodar makes predictions in terms of numerical effort, rather than percentages. This circumvents the statistical issues associated with proportions and allows direct comparisons to observed effort values. Second, it allows the estimation of additional parameters that empirically represent the possible effect of costs and risks on the distribution of fishing effort. This results in better agreement between the model and the data according to information-theoretic criteria and is illustrated by the improved relationship between observed and predicted effort in an area when this prediction is based upon a combination of observed catch in both areas and effort in the alternative area. Third, a single productivity model unites all of the empirical models examined, of which the IFD, based on catch rates, is a special case.

Previous tests of the IFD in fisheries contexts have examined the proportional distribution of effort in relation to the proportional distribution of catch (Gillis et al. 1993) or directly tested for the equalization of productivity among areas fished or the relationship between the resource and forager distributions (Abernethy et al. 2007). There can be difficulties with each of these approaches. Testing for equalization in catch or catch rates can easily miss relevant cost effects that may not be recognized or easily quantified a priori. Hilborn and Ledbetter (1979) suggested a constant ratio of catch rates could be a first approximation in accounting for these unknown factors (the basis of our CCR model). They suggested that alternate areas could differ in “desirability”, which could be related to the risk of damage or injury associated with more open waters. Abernethy et al. (2007) found that lifestyle choices apart from monetary costs were associated with consistent differences between alternative fishing strategies (i.e., catch rates were not equalized among alternatives). Differences like this, when found, are very informa-

tive, as sample size and variability (low to moderate statistical power; Peterman 1990) will tend to mask differences and favour acceptance of the IFD-based hypothesis of equal catch rates. Abernethy et al. (2007) also compared the distribution of fishing effort and independently surveyed resource abundances and found them to be unrelated. However, their survey estimates differed from the perspective of the fishers, suggesting imperfect knowledge within the fishery, a potentially important violation of the IFD assumptions (but see Gillis 2003; Griffen 2009).

The examination of proportional catch and proportional effort among alternative fishing areas allows a direct test of the IFD outcome (equalization of catch rates) across a range of effort and catch values (Gillis et al. 1993; Gillis 2003), which focuses on the identification of a relationship rather than the rejection of the null hypothesis of randomness. However, it does not readily allow for factors, such as cost or risk, unless they can be incorporated into the “catch” values before the analysis by subtracting their associated costs and examining the resulting “adjusted catch”. For costs that vary with effort, this is not a useful approach. Proportional data require transformation prior to regression to avoid biases caused by the restriction of values between 0 and 1. Finally, irregular deviations from the expected 1:1 line are often observed (Gillis 2003) but not easily interpreted. For example, a low proportion of effort in an area may occur when overall effort is high, and conversely a high proportion could be observed when very little fishing is occurring. Processes that vary with the amount of fishing activity, like interference, will not be well represented by statistical models based upon proportions. This mathematical representation of the IFD is useful as a first approximation for exploratory data analysis and a visual representation of the perspective that proportional effort should follow the proportion of catch from each area. Unfortunately, it is a poor choice for developing more refined empirical models of effort dynamics.

Isodar-based effort predictions are easier to treat statistically, even on a logarithmic scale. They lack the difficulties in interpreting patterns found with percentages. However, the construction of our isodars departs somewhat from previous work. Environmental quality is often examined on an annual basis (Morris and Kingston 2002; Haugen et al. 2006), where the quality of alternate habitats varies much more slowly than the rate at which foragers can disperse and redistribute themselves. In contrast, we are attempting to model effort responses to short-term (weekly) changes in habitat quality. These are common, in part because regulatory boundaries often divide natural fish habitat in an arbitrary manner. For example, the West area is close to the boundary with another area outside of our data set (NAFO Division 5Z), which shares ecologically contiguous habitat through which fish regularly move. To account for rapid variation in quality, we initially assume that the relative resource availability in each area is approximated by the relative catch value taken from that area (our simple IFD-based isodar). Though this method has some predictive value, there was also clear bias. Our more complex models attempt to address the departures of this model’s predictions using parameters that represent differences between the areas that are proportional and nonlinear effects of increasing effort.

The CCR model showed some improvement over the sim-

ple IFD isodar. The addition of a “proportionality parameter” (α) allowed us to represent consistent differences between the fishing areas. Differences such as these could result in costs that scale proportionally with effort, similar to the “qualitative” differences among areas in Morris’ (1988) development of isodar theory. However, biased predictions were still evident. These biases could be generated by fish availability or cost differences among areas that were not related to the effort expended, what Morris (1988) termed “quantitative” differences among areas. In isodar theory, this can result in a positive intercept in the curve that describes the relationship in forager numbers between two areas. In our formulation, quantitative differences would initially result in more effort being expended in the area with higher availability or lower cost. As effort increased, the impact of these fixed differences on productivity would become less important. Instead, additional effort would cause an increase in costs and reduced fishing success (i.e., the density-dependent aspect of productivity). The result would be increasing utilization of the “poorer” area with increases in total effort expended across both areas.

The CPRc and CPRu models, with their exponents (β) for nonlinear effort effects, reduced apparent biases in the predicted effort to more acceptable levels. The exponents allowed the productivity term (C/f^β) to be reduced disproportionately with increasing levels of effort. The more rapid reduction in productivity was indicated by the estimated β values that were all greater than 1. It is conceivable that enhanced efficiency with greater local vessel numbers could result in β values less than 1, but this was not observed. The reduction in the efficiency of effort that is indicated by these parameter estimates could result from different factors. The numerical effect of quantitative differences in an isodar framework was described above. Another possible cause is the presence of interference among fishing vessels (Gillis 1999; Rijnsdorp et al. 2000a, 2000b; Poos and Rijnsdorp 2007). Additional vessels may not simply “share” the resources equally, but may cause more effort to be marginalized into sites with lower fish abundance. Fish tend to be heterogeneously distributed, concentrating in locally favourable habitat within any larger areas defined for research or management purposes. Limitations to the total amount of gear that can be deployed on these concentrations can force additional effort into surrounding habitat where fish abundance and fishing success are lower. In this way, heterogeneity in bathymetry, habitat composition, and fish distributions within the defined areas could interact with vessel behaviour to generate nonlinear effort effects. Greater local vessel densities may also directly increase risks and costs through increasing gear entanglement or course adjustments to avoid such events. The resulting reversible decline in overall fleet efficiency will occur even if fish abundance is not appreciably altered (interference competition). Either effort displacement or increased local costs (or risks) could be realized as interference. This interference competition would generate “undermatching”, as reviewed by Kennedy and Gray (1993), where the proportion of foragers found in better habitats is below the IFD predictions. The impact of interference would be likely to scale nonlinearly with the number of vessels, as doubling the vessel density would more than double the encounter rate. This nonlinearity is similar to the repre-

sensation of encounter in classical ecological models. For example, in the logistic equation the potential population growth rate increases linearly with population size, but the magnitude of the negative effects of intraspecific interactions that limit this growth increases according to the square of population size.

Though model refinements tended to reduce the magnitude of extreme outliers, they were not eliminated. Various factors could contribute to specific weeks or groups of weeks fitting our model more poorly. For example, weeks with low total effort may leave an area poorly explored and violate the “ideal knowledge” assumption of the IFD to a greater extent than weeks with greater fleet activity. The effect of differences in travel costs among areas would also vary with the amount of effort expended in an area, being less important when effort in an area is high within a trip. The impact of such factors will vary among fisheries and through time within a fishery. However, costs related to effort (density-dependent factors) dominate, so we can expect patterns such as those that we have modeled to be evident in the aggregated catch and effort data.

The current parameterization does not allow us to distinguish among the mechanisms that could lead to nonlinear effort effects. Though unfortunate, it can be expected with simple models whose small set of predictor variables limit the number of estimable parameters. In such cases, a parameter may lump the influence of a variety of mechanistic factors into a single value. This is also true in more complex models of individual choice, such as the sorting model developed by Zhang and Smith (2011) in which a single choice-specific constant incorporated all aspects of an area that could influence its attractiveness. In two of our three area predictions, the differences between the CPRc and CPRu models were slight, suggesting that there is only weak evidence for unique nonlinear effects between the areas. This is not surprising, because vessels could be expected to interact similarly to crowding in many areas. However, the frequency and intensity of these crowding encounters could differ among areas with spatial differences in the size and arrangement of fishing opportunities (Branch et al. 2005; Rijnsdorp et al. 2011). Thus, we expect that the best model will vary among different fisheries and area definitions. It could be argued that at least for the North–West and West–East predictions, the CPRc, with common nonlinear effort effects between areas, should be selected for parsimony. Model averaging (Anderson 2008) could also be employed, using both the CPRc and CPRu to allow predictions to incorporate our uncertainty in the correct model. We chose to retain the simple minimum AIC_c criteria because our goal was model comparison, but other criteria should be considered when specific predictions are the objective.

The CPRu, with unique nonlinear effort effects and significant productivity ratio differences, was identified as the best model for most area predictions. Furthermore, it illustrated the effectiveness of our models in detecting differences in effort distribution patterns among areas. Unlike the North–East and North–West models, there was little evidence for regular differences in the underlying productivity ratio parameter in the West–East models. This is consistent with the location of each of these areas, which are both distant from shore and similarly exposed. These areas are more likely to be similar

to each other than with the North area that is closer to port. Unfortunately, as a consequence of the nonlinear terms (β values), the α values are not simply additive among areas. Such additivity would be expected if the CCR model was optimal.

The generalized nonlinear regression approach allows the explicit treatment of correlation structures generated by catch and effort time series. It is likely that current effort distributions influence future effort distributions because of information exchange within fishing fleets (Allen and McGlade 1986; Gillis 2003; Branch et al. 2006). In addition, the act of aggregating daily data into weekly time periods is likely to generate temporal correlation structures that can bias parameter estimates (Granger and Morris 1976). This bias was avoided by selecting AR or ARMA processes that eliminated significant autocorrelation from the residuals. Third-order AR processes often were found to be effective, suggesting that the “inertia” in the fishery due to exploration, discovery, and information exchange could be weeks in duration. The occasionally preferred ARMA model is likely the result of fitting aggregated time series data aggregation where AR processes may be more effectively modeled using ARMA (Granger and Morris 1976). Generally, the patterns in the residuals suggest that lags in information dynamics play a role in the effort distribution. However, some of the autocorrelation may be due to the aggregation of data in our analysis.

For simplicity, we present only three of the possible area combinations, focusing on the prediction of effort in the northern area and adding the prediction of western effort from eastern effort for completeness. Ideally, our method would prefer to simultaneously predict the effort distribution among all areas, but this would involve employing more complex model formulations and fitting methods that could account for spatially heterogeneous autocorrelation structures. Our present application of generalized nonlinear least squares is tractable and readily available. In practice, it will result in multiple predictive relationships for each area, which could easily be compared to check consistency and combined into a single value, possibly by a weighted average. At the exploratory stage, it would be simple to quickly estimate the CPRu models and examine the CIs of their parameters. However, final model selection should be based upon AIC_c values similar to the procedure followed here.

Generalized nonlinear regressions can be expected to share similar issues to more traditional Model I regression (Quinn and Keough 2002) when examining the estimated parameters. Maximum likelihood estimation in this method is performed by assigning all variability to the predicted values and assuming that the predictors are observed without error (“error in variables”; see Hilborn and Walters 1992 for discussion in a fisheries context). This is unlikely to be true in our commercial catch and effort data, especially when the choice of predictor and predicted effort is arbitrary. This treatment is appropriate when the goal is simply prediction, but caution must be exercised when interpreting the values of the parameter estimates of specific predictor variables.

Finally, it should be noted that costs are represented abstractly by isodar parameters. Costs that vary with the effort expended in an area are readily captured by our models. However, costs that are fixed for a trip, such as travel to and from a fishing ground, are not easily related to our isodar pa-

rameters. Such costs could be explicitly incorporated if they were known by adding them to the cost term prior to fitting the isodar, but this data is not readily available in most commercial fisheries data sets. These costs could also be estimated with additional model parameters, but this would also require additional predictor variables. Travel costs and other fixed costs are not directly related to nominal effort measured as hours fished, but to the number of trips aggregated in the analysis. There will be a difference in aggregated travel costs between a single 100 h trip and ten trips of 10 h each. To accurately represent these costs, our predictors would have to include both the number of vessels in an area as well as the fishing effort expended. This more complex model was beyond the scope of our current isodar approach, which attempts to improve the predictive relationships possible with the fishery data used in the typical calculations of CPUE. Furthermore, if the aggregated fixed costs scale closely with total fleet effort, they can be statistically absorbed into the existing parameters of our models. The CPRu model predicting effort between the most distant areas (North predicted from East) showed the closest relationship between predicted and observed values among the areas examined. This suggests that travel and similar costs did not consistently influence effort distributions or that they were effectively represented within the parameters already present. The success of our simple model, with parameters that aggregate the potential effects of different costs, is consistent with the principle that simpler models can often outperform more complex models, even when the more complex model more accurately reflects the underlying reality (Ludwig and Walters 1985; Adkison 2009).

Though independently derived, our final model bears some similarity to Houston's (2008) input matching model. Houston showed that the generalized matching law from psychology can be extended to the habitat distribution of natural foragers to generate an IFD. His equations predicted that the ratio of habitat use between two areas would be a power function of the ratio of resource input rates in the areas. If this is re-expressed in isodar form, predicting the number at one site as a function of the number at the other will cancel the power terms for each number, as they did in our CPRc model. Like the CPRc model, this results in a slope of 1 on a logarithmic scale. Thus, the relationship between numbers, under a static resource distribution, is expected to be linear when foraging effort follows the generalized matching law. Houston attributed the constant in this application of the matching law to differences in habitat desirability not captured directly by resource levels, similar to the ideas of Hilborn and Ledbetter (1979) and the role of the constant α in our models. However, our model is based upon an expected a posteriori distribution of catch between areas, while Houston's model is based upon underlying resource renewal rates. The similarities between the models are related to the similar game theoretic perspectives (equalizing rewards) and the prevalence of power relationships in natural phenomena (Newman 2005) rather than an exact equality of the models.

The success in applying isodars in this example invites the extension of their more general results to fisheries. For example, Morris (1994) developed an isodar model from a different "fitness" function that suggested a logarithmic relationship between abundance in two habitats whose slope

was related to the ratio of interference in each area, similar to our CPRu model. Also, through isodars Morris et al. (2001) suggest that "undermatching" deviations from a simple IFD may be caused by interactions among foragers that share benefits. Their work focused on the foraging distributions of related individuals through inclusive fitness. In the case of a fishery, analogues to relatedness could be found in fleet organization. Large fleets with central managers could favour fleet rather than vessel optimization and result in behaviour similar to that expected from related foragers. In our case, most vessels belonged to small companies with a few vessels each, so the effect is unlikely to be strong. However, the effects of group optimization on effort distributions would be stronger in large fleets controlled by a single company or in large socialist fleets such as those of Cuba and the former Soviet Union (Gillis and Showell 2002). Vessels that form informal groups to share information or improve safety at sea may result in similar "inclusive" benefits and distributional biases. Morris et al. (2001) also suggested that broader social and economic patterns may be influenced by the contrast between group and individual maximization goals. Specifically, their analysis suggested that the distribution of group optimizers will undermatch resource distributions and provide higher total benefits, but this distribution will be unstable when individuals outside of the group are free to exploit the better opportunities. In this context, the parameters of our models provide a simple means of quantitatively examining the impact of changes in fleet organization on the distributional patterns of fishing activities when only catch and effort data are available across the time period being examined.

The simplicity of our aggregate model stands in stark contrast with current economic models that predict specific decisions by individuals from a variety of covariates related to characteristics of the fishing grounds and fish harvesters (Haynie and Layton 2010; Zhang and Smith 2011; Hicks et al. 2012). These methods have developed from the analysis of discrete choices in a random utility model framework (Train 2009). They have quantified individual variation in fish harvester responses (Zhang and Smith 2011) and congestion effects homologous to interference effects in the ecological literature (Hicks et al. 2012). The insights provided by these models are obvious, but the tradeoff between model complexity and the quality of predictions remains. This was observed directly by Smith (2002) when he found that the forecast performance of an aggregate model of spatial effort allocation was often better than that of a discrete choice model. We feel that fisheries study and practice will benefit from the continued development of both complex models of individual choice and aggregate models that can be quickly and simply related to fisheries data.

The utility of our models to fisheries science and management is similar to that of the IFD from which it was developed. In the case of a simple catch rate equalizing IFD, the distribution of local abundances will be more closely related to effort distributions and poorly reflected by catch rates (Gillis and Peterman 1998). Our empirical models incorporate new parameters related to unknown costs, but effort movements in responses to area productivity will still make CPUE a poor indicator of local abundance. Though explicit costs are not estimated in our models, the resulting patterns are

simply quantified. The parameters of our models could be used as indicators to detect variation in fleet dynamics that may be associated with changes in management actions, environmental conditions, or exploitation. Once a change in effort dynamics is identified, more detailed and costly data collection can be more easily justified. Our model could also be used to represent effort dynamics within other simulation models examining aggregate patterns in catch and effort relationships, especially when detailed cost data is not available but historical series of catch and effort can be obtained. Our final model was the best fit to the data set that we have examined, but this may not be true for other data sets. However, our methodology of model comparisons is more general. Other fisheries may display common nonlinear effort effects between areas or fail to show significant deviations from a simple IFD. To distinguish such cases, a systematic series of model comparisons should reveal the most parsimonious model to summarize the observations. Alternatively, examining the coefficients of the full CPRu model could provide a rapid indication of optimal model complexity. This latter approach can be useful during initial explorations of the data, but we prefer formal model selection procedures to quantify the evidence for final model selection.

The observation that the proportional distribution of fishing effort among alternative fishing areas is often close to that expected with the IFD has provided useful insights into the spatial dynamics of fish exploitation. By recasting the catch and effort based IFD as an isodar model that explicitly predicts effort, we have been able to refine the model to incorporate parameters that can capture the effects of area-specific costs that vary with effort (including risk) and nonlinear effort effects (such as interference) among vessels. The use of generalized nonlinear least squares to estimate the parameters of the isodars has allowed us to develop more complex models and reduce biases in parameter estimates due to autocorrelation in the data. This novel approach to fisheries analysis provides a readily accessible tool for those who wish to examine the dynamics of aggregated fishing effort data from the perspective of frequency-dependent n -person games. The theoretical foundation is provided by the evolutionary principles underlying the IFD (Maynard Smith 1982, p. 90) and the development of isodar theory (Morris 1988).

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