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Density-dependent habitat selection and the ideal free distribution in marine fish spatial dynamics: considerations and cautions

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Abstract

Current methods and theory used in the study of the spatial dynamics of marine fish are problematic. Positive relationships between population abundance and occupied area are typically interpreted as evidence of density-dependent habitat selection. However, both abundance and area may co-vary with an un-parameterized variable, such as a density-independent effect. In addition, if density-dependent habitat selection is present, population growth rates in optimal habitats would be expected to be lower than in marginal habitats. This same pattern can also evolve from a large-scale, spatially autocorrelated change in a density-independent factor. The theory underlying density-dependent habitat selection, the ideal free distribution, can be tautological when no *a priori* information of how habitat suitability changes with density is known. In this case, an ideal free distribution can be defined for any pattern of habitat-specific population growth rates. However, these problems are not insurmountable and solutions may be found by considering spatial variation in proxies of fitness and explicitly allowing for the relative importance of habitat selection (density dependent) and environmental (density independent) effects to vary with spatial scale.

Keywords density-dependent habitat selection, ideal free distribution, marine fish, scale, spatial distribution, spatial dynamics

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Introduction

The concept that animal behaviour determines the spatial distribution of a group of conspecifics was developed through the theory of the 'ideal free distribution' (Fretwell and Lucas 1970). An ideal free distribution is one in which individuals are distributed among habitats such that their fitness is maximized (Morris 1987). An individual's choice of which habitat to settle into is based on the 'suitability' of each habitat. Suitability is assumed to be density dependent where higher densities of individuals will lower suitability within habitats. When a population is distributed according to an ideal free distribution, the realized suitability of each habitat is equal. This pattern of habitat exploitation, density-dependent habitat selection, has gained much favour in behavioural ecology (Morris *et al.* 2001).

Density-dependent habitat selection and the ideal free distribution were implemented by Myers and Stokes (1989) and MacCall (1990) in order to explain large-scale patterns of habitat usage by marine fish. These studies led to the adoption of density-dependent habitat selection as an important mechanism in marine fish spatial ecology. The acceptance of habitat selection theory by fishery scientists is, in part, the result of its prediction that the geographical area occupied by a population is positively related to abundance, something that has long been recognized in fishery science (Paloheimo and Dickie 1964).

Positive relationships between abundance and occupied area have been found in many marine fish populations (Winters and Wheeler 1985; Crecco and Overholtz 1990; Swain and Wade 1993; Marshall and Frank 1994; Swain and Sinclair 1994; Atkinson *et al.* 1997; Petitgas 1998; Anderson and Gregory 2000). While these appear to provide support for density-dependent habitat selection, occasionally no significant relationship is found (Swain and Morin 1996; Schneider *et al.* 1997; Petitgas 1998). The variety of spatial dynamics seen in marine fish populations can be explained by three key models: (i) the proportional density model, (ii) the constant density model and (iii) the basin model (reviewed by Petitgas 1998). Each model predicts a distinct pattern of distribution based on how localized density changes with respect to total population abundance.

While these models vary in their ecological appeal (Petitgas 1998), they all share a common, implicit assumption that spatial dynamics depend only on density-dependent processes. Density-independent effects play a role in these models only through differences in intrinsic suitability between habitats, i.e. some habitats are intrinsically more suitable than others. In addition, because intrinsic suitability is not dynamic in these models, it is implied to be static. Given the nature of the physical environment in which marine fish live, a more reasonable model may consider both density-dependent and density-independent effects as dynamic.

In this paper, we present a critique of various aspects and predictions of density-dependent habitat selection. We show that significant relationships between abundance and occupied area should not be taken as evidence of density-dependent habitat selection because they may conceivably arise from environmental mechanisms. Further, if movement between habitats is limited (not ideal and free) then environmental effects can lead to patterns predicted by density-dependent habitat selection. Finally, we examine the tautology of the theory underlying density-dependent habitat selection, the ideal free distribution. We show how an ideal free distribution can be defined for any spatial pattern and how all three key models may be considered ideal free distributions. This shows that *a priori* knowledge of how suitability changes with density must be incorporated into the analysis. This leads us to question of whether current methods of testing density-dependent habitat selection in marine fish can properly resolve how changes in the spatial distributions of marine fish populations relate to density, or whether observed patterns are the result of density-dependent or density-independent effects.

Abundance–area relationships

While habitat quality plays a role in habitat selection, it is implicitly assumed to be constant, within habitats, under ideal free distribution (Fretwell and Lucas 1970). Operating under this premise, it follows that a relationship between population abundance and the pattern of habitat usage is the result of changes in realized habitat suitabilities as a result of intraspecific competition. Thus, when abundance increases, some individuals settle in previously unoccupied, marginal habitats resulting in an increase in the area over which the population is distributed. The presence of this relationship in marine fish populations has been taken as evidence of density-dependent habitat selection (Marshall and Frank 1995). If one steps back from the ideal free ideology, a significant correlation between abundance and occupied area shows that the two are somehow related, but it does not demonstrate a causal relationship nor does it prove the presence of density-dependent habitat selection.

Taking an alternative approach, it would be reasonable to consider that both abundance and area of distribution may co-vary with other factors not parameterized by the ideal free distribution. It is well demonstrated that the abundance of marine fish is affected by both density-dependent and density-independent factors (Anderson and Gregory 2000; Fromentin *et al.* 2001; Julliard *et al.* 2001). By definition, the concept of density-dependent habitat selection addresses behaviourally mediated changes in habitat exploitation, and thus distribution, due to density-dependent effects. Density-independent effects are addressed in typical density-dependent habitat selection models through the existence of a mosaic or gradient of habitat types which vary in their intrinsic suitability (Fretwell and Lucas 1970; MacCall 1990). However, habitat-specific intrinsic suitability is not dynamic and is implicitly assumed to be constant. Density-independent factors, such as temperature, are certainly dynamic and may affect population status, e.g. recruitment (Anderson and Gregory 2000), growth (Michalsen *et al.* 1998; Swain *et al.* 2003) and indirect adult mortality (Dutil and Lambert 2000), on an entirely different spatial scale than any existing habitat mosaic or gradient.

This may be particularly important in populations where local dynamics are important, i.e. dispersion is small relative to the spatial scale over which the population is distributed. In this case, spatially autocorrelated, large-scale changes in a density-independent factor (e.g. water temperature) may affect birth and death rates on a scale much larger than the scale over which local population dynamics operate. For example, large-scale climatic changes caused by the North Atlantic Oscillation are believed to affect the population dynamics of many marine fish through a variety of direct and indirect mechanisms which operate, and are observed, on a much smaller scale (Hofmann and Powell 1998; Ottersen *et al.* 2001).

Consider a hypothetical population distributed in space where birth rate varies spatially. A simple example would be such that birth rate is highest at the centre of its distribution and decreases outward with distance (Fig. 1). The limits of the population's geographical range would then be where the sum of immigration and birth is less than, or equal to, the sum of emigration and death (Gaston 1990). Extending this example, consider that birth rate increased across all sites because of a large-scale environmental variation, such as a favourable change in temperature. Some areas at the limits of the spatial distribution which previously had an intrinsic rate of increase (r = birth rate − death rate) less than 0 would now have $r > 0$ because of an increase in birth rate and thus individuals would survive in those habitats. This increase in survival at the spatial limits would result in an increase in the area over which the population is distributed. Further, because r increases in all habitats, total population abundance increases. An emergent property of this effect is a positive abundance–range size relationship. This possibility was discussed to an extent by MacCall (1990) who noted that large-scale environmental changes may affect the area occupied by a population through an associated change in habitat suitabilities.

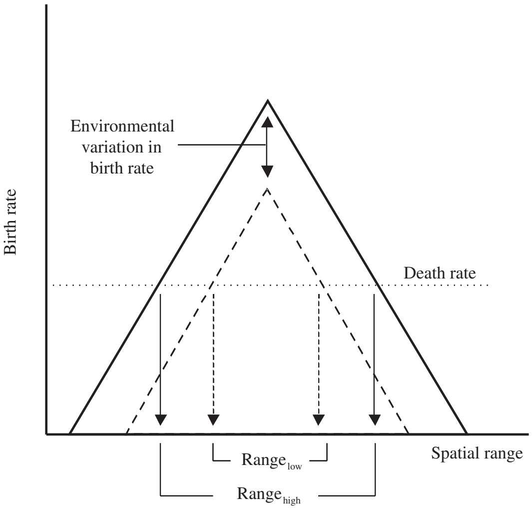

Figure 1 Result of a spatially invariant increase in birth rate on spatial range of occurrence in a hypothetical population. Limits of range are where birth rate is equal to death rate, where Range$_{low}$ = spatial range of occurrence at low abundance and Range$_{high}$ = spatial range of occurrence at high abundance.

This concept is similar to that on which Holt *et al.* (1997) developed 'vital rates' model in order to explain interspecific abundance–range relationships. If their model is cast in an intraspecific context, if a species shows a spatial gradient in intrinsic habitat suitabilities then any factor that

Table 1 Possible mechanisms which can give rise to positive intraspecific abundance–area relationships. Adapted from Gaston *et al.* (1997).

Hypothesis	Mechanism
Sampling artefact	Systematic underestimation of range size when it occurs at lower local densities
Range position	Temporal fluctuations in the proximity of the study area to the centre of the range of the species
Resource breadth	Temporal fluctuations in breadth of resource use
Resource availability	Synchronous temporal fluctuations in the local abundance and distribution or resource availability
Habitat selection	Temporal fluctuations in local density drive changes in habitat occupancy, and hence distribution
Metapopulation dynamics	Metapopulation structures of the form of the rescue effect hypothesis
Vital rates	Temporal fluctuations in birth and/or death rates

tends to change suitabilities across all habitats will naturally lead to a positive correlation between abundance and area occupied. The 'vital rates' model was only one of seven hypotheses identified by Gaston *et al.* (1997) as possible mechanisms that can lead to positive intraspecific abundance–area relationships (Table 1).

It is widely held in fisheries ecology that environmental factors can affect the distribution of marine fish populations (deYoung and Rose 1993; Hofmann and Powell 1998; Rose *et al.* 2000; Carscadden *et al.* 2001; Ottersen *et al.* 2001; Begg and Marteinsdottir 2002; Rodríguez-Sánchez *et al.* 2003). What we add here is a not so much support for or against environmental or density-dependent mechanisms but rather an alternative context in which hypotheses about the relationship between abundance and area occupied can be constructed. It is likely that both mechanisms interact in determining the distribution and abundance of a population.

Habitat specific – total population growth relationship

The presence and form of density-dependent habitat selection is often tested in fisheries ecology through examination of the relationship between habitat-specific and total population growth (Myers and Stokes 1989; Marshall and Frank 1995; Swain and Morin 1996). This is based on the argument that if some habitats are preferred over others, and habitat suitability is affected by density, then relative population growth rates between habitats should vary (Myers and Stokes 1989). When population density in habitat i in year t ($\bar{y}_{it}$) is modelled as a function of total population abundance in year t (N_t) as:

$$\bar{y}_{it} = a_i N_t^{b_i} \tag{1}$$

then if density-dependent habitat selection exists, values of b_i will be <1 for optimal habitats and >1 for marginal habitats (Marshall and Frank 1995). The ecological reason for this is that as population abundance increases, more individuals will choose to settle in marginal habitats where intraspecific competition is relatively low and thus suitability will be relatively high.

An alternate scenario could be imagined as a population composed of numerous, more or less discrete, local populations between which migration and dispersal is small but sufficient to allow persistence and colonization of available habitats. The first point to note is if density-dependence exists then when all local populations are at equilibrium, distribution of the total population will conform, at least superficially, to an ideal free distribution, i.e. the ratio of abundance to resources is equal between habitats (Rosenzweig 1991). In fact, it has been shown that an ideal free distribution can arise in two situations: when there is ideal habitat selection or when interhabitat exchange is zero (Palmqvist *et al.* 2000). If all populations are in equilibrium then we may question what effect a spatially invariant change in habitat suitability may have on distribution and local population growth.

If realized per capita growth rate (r'_{it}) of habitat i in year t is modelled following the most common logistic function used in habitat selection theory, the constant slope model (MacCall 1990) then:

$$r'_{it} = \frac{1}{N_{it}} \frac{dN_{it}}{dt} = (r_{oi} + \varepsilon_t) - bN_{it} \quad (2)$$

where r_{oi} is the intrinsic per capita growth rate of habitat i, b is a constant per capita decrease in realized per capita growth rate, N_{it} is abundance of habitat i in year t, and ε_t is a spatially invariant term representing environmental effects on habitat quality. An equivalent change in ε_t across all habitats will result in those habitats with lower intrinsic per capita growth rates (r_{oi}) having the greatest relative change in realized per capita growth rate (r'_{it}).

In our example, this means that if there is a favourable, spatially invariant change in habitat quality, those local populations exploiting poorer quality habitats will exhibit a higher per capita growth rate. This is because any change in ε_t will be larger relative to r_{oi} in poorer quality habitats than in better habitats. However, changes in habitat quality are not always favourable and are probably highly dynamic if not stochastic. When we modelled equation (2) as a difference equation over many years and considered ε_t as a stochastic variable, and then examined the relationship between habitat-specific and total population growth as given in Marshall and Frank (1995), we found poor quality habitats exhibited higher per capita growth rates than high quality habitats (Table 2).

This is equivalent to the prediction made by density-dependent habitat selection that under changing total abundance, poorer quality habitats should exhibit higher per capita growth rates when compared with high quality habitats (Morris 1987; Myers and Stokes 1989; Marshall and Frank 1995). This effect would only be most evident when the assumptions of the ideal free distribution are not met, i.e. if animals do not make ideal choices about habitats and if they cannot move between habitats without cost. Likewise, the more the assumptions are not met, the stronger will be the effect.

Table 2 Results of the model, $r'_{it} = \frac{1}{N_{it}} \frac{dN_{it}}{dt} = (r_{oi} + \varepsilon_t) - bN_{it}$, where r'_{it} is the habitat-specific realized per capita growth rate of habitat i in year t, r_{oi} is the habitat-specific intrinsic per capita growth rate of habitat i, b is a constant per capita decrease in realized per capita growth rate, N_{it} is abundance of habitat i in year t, and ε_t is a spatially invariant term representing environmental effects on habitat quality. The variable ε_t was considered as a stochastic variable (random uniform distribution from −0.50 to 0.50) and the difference equation was modelled over 25 years. This process was repeated 1000 times in order to develop estimates of variance.

Habitat quality[1]	Habitat-specific intrinsic rate of increase (r_{oi})	b	Mean rank of habitat-specific realized growth rate[2]
1	0.45	1×10^{-7}	4.41 (1.84)
2	0.40	1×10^{-7}	3.62 (0.66)
3	0.35	1×10^{-7}	2.87 (0.23)
4	0.30	1×10^{-7}	2.22 (0.66)
5	0.25	1×10^{-7}	1.88 (2.36)

[1] Ranked habitat quality, i.e. 1 is the highest quality habitat, 5 is the poorest quality habitat.

[2] Ranked habitat-specific growth rates, i.e. 1 represents the highest habitat-specific growth rate, 5 represents the slowest habitat-specific growth rate.

Estimates of variance are given in parentheses.

Commonality in spatial dynamic models

The nature of the relationship between local density, total abundance and the area over which a population is distributed can take a number of different forms. These differences help to define and distinguish three key conceptual models in marine fish spatial ecology (Hilborn and Walters 1992; Petitgas 1998). The 'proportional density model' is appropriate when localized population growth remains proportional between habitats, i.e. per capita growth rates are equal (Fig. 2; Hilborn and Walters 1992). In some situations, maximum density appears to be limited throughout the spatial range of the entire population, most population growth results in range expansion, and there is a positive abundance–occupied area relationship. This situation is referred to as the 'constant density model' (Fig. 2; Hilborn and Walters 1992). The most popular model, the 'basin model', is characterized by high per capita growth rates in marginal habitats and an expanding range size with increasing abundance (Fig. 2; MacCall 1990; Hilborn and Walters 1992). While these models are distinct in their appearance (Fig. 2) and predictions (Table 3), their range of behaviours can be described with a single model, the ideal free distribution, using different density-dependent suitability responses.

Density-dependent population growth models assume that realized per capita growth rate (r') declines with density, most often in a linear manner (Fig. 3). When an array of habitats is considered,

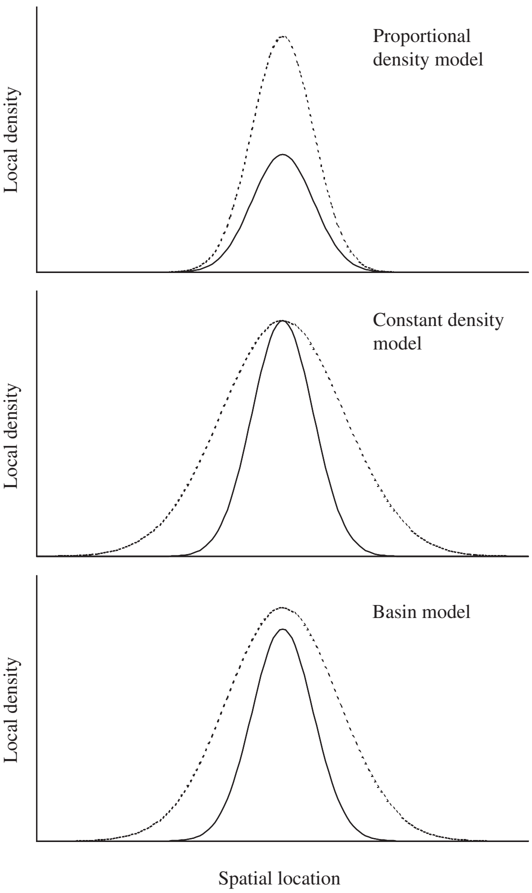

Figure 2 Simplified representation of three popular models describing spatial dynamics of marine fish. Solid lines and dotted lines represent spatial distribution of local densities under low and high population abundance respectively.

the density-dependent suitability response of each habitat represents a unique line, the habitat suitability curve, on a graph of r' vs. local density (Fig. 3). The y-intercept of the habitat suitability curve is the habitat-specific intrinsic rate of increase while the x-intercept is the habitat-specific carrying capacity. An ideal free distribution is defined by the points at which any horizontal line intersects the suitability curves. Habitat-specific densities for any ideal free distribution are determined by dropping a vertical line from each point (Fig. 3).

It is common to model the ideal free distribution using the 'variable r, variable K logistic model' (Fig. 4a; MacCall 1990). Under a density-dependent habitat selection scenario, an increase in total population abundance would lead each habitat to gain the same number of individuals. When habitat-specific growth rates are calculated, marginal habitats will show greater relative changes in abundance and thus higher per capita growth rates than optimal habitats (Morris 1987). This relationship between suitability and population growth rates appears to be closely related to the form of density-dependent habitat selection tested most often (Myers and Stokes 1989; Marshall and Frank 1995), and is a primary basis of the basin model (MacCall 1990). This pattern of local-total population growth has been found in Gulf of St Lawrence cod (*Gadus morhua*, Gadidae; Swain and Wade 1993) and Scotian Shelf haddock (*Melanogrammus aeglefinus*, Gadidae; Marshall and Frank 1995).

Under a 'constant r, variable K logistic model' (Fig. 4b), habitats share a common intrinsic rate of increase but different carrying capacities. If a population is distributed in an ideal free manner, an increase in total abundance will lead to equal population growth rates between habitats. This situation is analogous to the proportional density model and has been referred to as density-independent habitat selection (Marshall and Frank 1995), and perhaps more appropriately, the site-invariant response (Myers and Stokes 1989). Ecologically, this pattern could arise if two habitats are equal in resources, and thus have the same potential for population increase at low densities but predation is much higher in one habitat which limits carrying capacity. This pattern has been found in North Sea haddock (Myers and Stokes 1989), Gulf of St Lawrence American plaice (*Hippoglossoides platessoides*, Pleuronectidae; Swain and Morin 1996) and Bay of Biscay hake (*Merluccius merluccius*, Gadidae; Petitgas 1994).

Under a 'variable r, constant K logistic model' (Fig. 4c), habitats have different intrinsic rates of increase but common carrying capacities. When a population is distributed in an ideal free manner, the pattern of local population growth rates will be similar, but more extreme than the 'variable r, variable K logistic model'. This is equivalent to the constant density model and has been attributed to density-dependent habitat selection but traditionally classified as a model unique from the basin model. This could arise if resources were equal between habitats but recruitment rate was more favourable in one habitat because of a heterogeneous spatial pattern of larval dispersal. This pattern has been found in larval herring (*Clupea harengus*, Clupeidae; Iles and Sinclair 1982).

Table 3 Selected properties of three key conceptual models describing spatial dynamics of marine fish.

Relationship	Proportional density model	Constant density model	Basin model
Abundance–area	Independent	Positive	Positive
Habitat-specific per capita growth	Optimal = suboptimal	Optimal < suboptimal	Optimal < suboptimal
Abundance–maximum density	Positive	Independent	Positive
Abundance–average density	Positive	Independent	Positive
Population growth expressed	Local growth	Expansion	Local growth + expansion

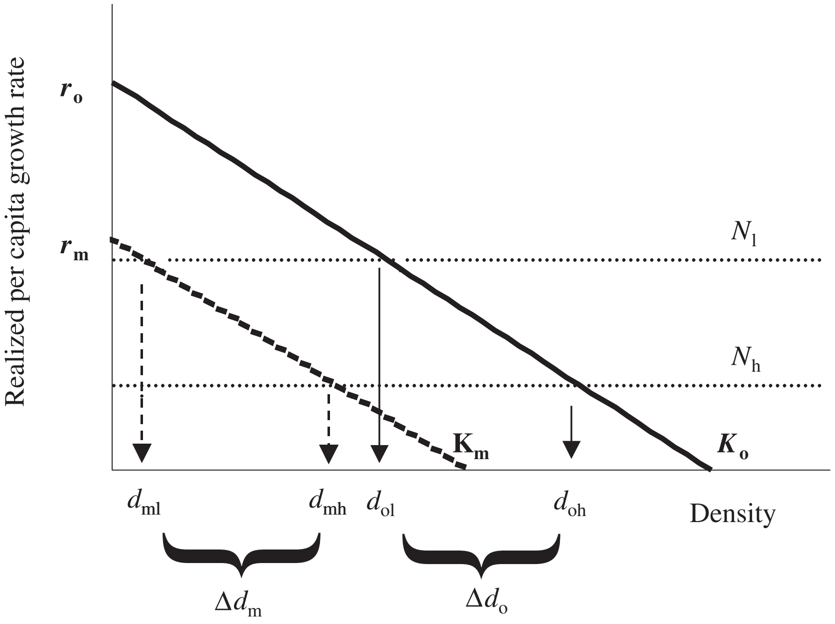

Figure 3 Example of an ideal free distribution and the graphical derivation of habitat-specific densities at two different total population abundances (N_l and N_h), where N is the total population abundance; r_o, intrinsic rate of increase of optimal habitat; r_m, intrinsic rate of increase of marginal habitat; K_o, carrying capacity of optimal habitat; K_m, carrying capacity of marginal habitat; d_{ml} and d_{mh}, population density in marginal habitat under low and high population abundance respectively; d_{ol} and d_{oh}, population density in optimal habitat under low and high population abundance respectively; Δd_o and Δd_m, change in population density because of change in total population abundance in optimal and marginal habitat respectively. Solid line represents optimal habitat while the dotted line represents marginal habitat.

The variety of suitability curves definable is only limited by imagination. MacCall (1990) discusses at some length various parameterization options for the logistic function and describes a major benefit of the variable r, variable K model as 'graphic convenience'. Nonlinear habitat suitability curves (Fretwell and Lucas 1970; Fretwell 1972) and habitat-specific curves which may both diverge and converge at different points along their trajectories (Holt 1985; Morris 1987; MacCall and Tatsukawa 1994; Morris 1994) are also possible. Other factors can influence how suitability changes with density such as Allee effects (Greene and Stamps 2001), interference competition (Kennedy and Gray 1993), conspecific attraction (Muller *et al.* 1997), genetic relatedness (Morris *et al.* 2001), aggregation level (Sutherland 1983), phenotype (Ruxton *et al.* 2001), perceptual

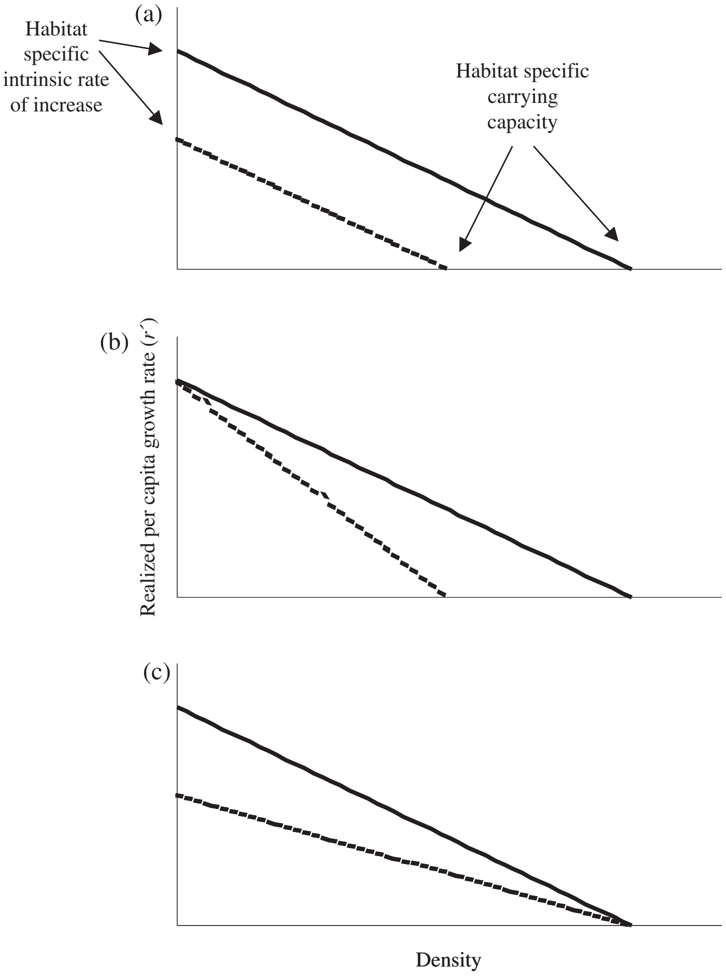

Figure 4 Graphical representation of three possible forms of the logistic model used in ideal free theory. Solid and dotted lines represent relationships between realized per capita growth rate and density for optimal and marginal habitats respectively.
(a) variable r, variable K model;
(b) constant r, variable K model;
(c) variable r, constant K model.

constraints (Gray and Kennedy 1994) and travel costs (Kennedy and Gray 1997).

Given the variety of forms possible for habitat-suitability curves, both within and between habitats, it becomes apparent that for any set of habitat-specific population growth rates, an ideal free distribution can be defined. Thus, density-dependent habitat selection can be shown to exist for any pattern of local population growth rates. Whether the key spatial models in marine fish ecology are in fact all expressions of the ideal free distribution under different forms of density-dependent effects on suitability is unknown. However, this demonstrates how *a priori* information on the form of the suitability density functions can greatly change inferences made based on habitat-specific growth rates (Morris 1987). The necessity of having *a priori* knowledge of how suitability changes with density is also explicit to the model of Fretwell and Lucas (1970) in which they included unique suitability density functions for each habitat. This information is in fact necessary for proper hypothesis construction in tests for density-dependent habitat selection using distributional data.

Does density-dependent habitat selection exist in marine fish?

Distributional patterns in many marine fish appear to be indicative of density-dependent habitat selection. However, tests for the presence of density-dependent habitat selection using only distributional patterns are always indirect. These tests do not evaluate the underlying assumptions of the theory, and observed patterns may be the result of other causes (Morris 1989). We have shown in the preceding discussion how these patterns may arise in marine fish populations from mechanisms other than density-dependent habitat selection. That being said, how then can we evaluate whether density-dependent habitat selection exists in marine fish?

Density-dependent habitat selection and the ideal free distribution are active processes in which individuals select the most suitable habitats in order to maximize their fitness (Fretwell and Lucas 1970; MacCall 1990). The resulting distribution should result in average fitness being equal between habitats (Morris 1989). Thus, a direct test of density-dependent habitat selection should examine the fitness of individuals between habitats when population abundance is changing (Tyler and Hargrove 1997). If individuals are selecting habitats in order to maximize fitness, then the fitness of individuals should be equal between habitats and it should remain equal under changing population abundance. As habitats are arranged in space, evaluating a group of animals for spatial variation in some measure of fitness should be a reasonable test of the theory.

In marine fish, spatial variation in measures such as size at age (Marshall and Frank 1995; Stokesbury *et al.* 1999; Taylor and Stefánsson 1999), condition factor (Brodeur *et al.* 2000) and reproductive success (Marteinsdottir *et al.* 2000) appears relatively common. Lloret *et al.* (2002), in a study on the condition of various north-western Mediterranean groundfish found spatial variation in both morphometric and physiological measures of condition for many species. They concluded that these species were not distributed according to an ideal free distribution. While the fact, as to whether the measures such as length at age and condition factor are suitable measures of fitness can be debated, it is generally accepted that larger fish at a particular age have higher reproductive success (Trippel *et al.* 1997) and thus are more likely to pass on their genes to successive generations. The study by Marshall and Frank (1995) provides a good example of how distributional patterns can be misleading. In juvenile haddock, on the Scotian Shelf and Bay of Fundy, they found patterns in the relationship between local density and total abundance at age, which they stated were indicative of density-dependent habitat selection. At the same time they describe a spatial gradient in length at age for these same fish, which is not indicative of density-dependent habitat selection. In their defence, they recognized that a spatial gradient in size at age was probably present because individuals are not free to move between habitats (i.e. not able to select between the three geographical areas they studied). Unfortunately, the haddock cannot be exhibiting density-dependent habitat selection while they are not able to select between habitats.

Effect of spatial scale

Much of what is discussed with regard to the relative importance of density-dependent effects will be strongly influenced by the spatial scale of observation and study. For density-dependent habitat selection to truly exist, individuals must make informed decisions on optimal habitat suitability between an array or along a gradient of habitats available. At the scale over which most marine fish populations are distributed (hundreds of kilometres), it is unlikely that individuals would be adequately informed much beyond their immediate perceptual range. Further, even if they could make informed decisions about optimal suitability over the population's range of distribution, the energetic costs of travelling to the optimal habitat may outweigh any benefit. Others have warned against applying habitat selection theory when a population is examined at a scale beyond the 'maximum daily movement' of individuals (Tyler and Hargrove 1997) and against trying to extrapolate small-scale tests of the ideal free distribution to habitat scale studies (Kennedy and Gray 1997). It is possible that habitat selection may occur over a larger scale than the perceptual range of individuals through the orientation and movement of fish along a preference gradient. While this mechanism was proposed by MacCall (1990) for highly mobile, schooling fish, it is not clear as to whether this may be viable for real populations. This mechanism may be important for species such as the Atlantic bluefin tuna (*Thunnus thynnus*, Scombridae) which travel thousands of kilometres each year and inhabit pelagic environments with smooth environmental gradients. However, demersal fish are often closely associated with benthic substrates (Scott 1982), which may be highly heterogeneous and thus preclude the presence of a clearly defined preference gradient along which individuals can align and move.

In an attempt to help resolve these scale-related issues, we suggest that density-dependent habitat selection can exist and be an important determinant in marine fish distribution on a relatively small scale. This scale would be relevant to the natural dispersive ability of the species in question. Conceptually, we suggest a model of marine fish spatial dynamics where habitat-selection (density-dependent) and

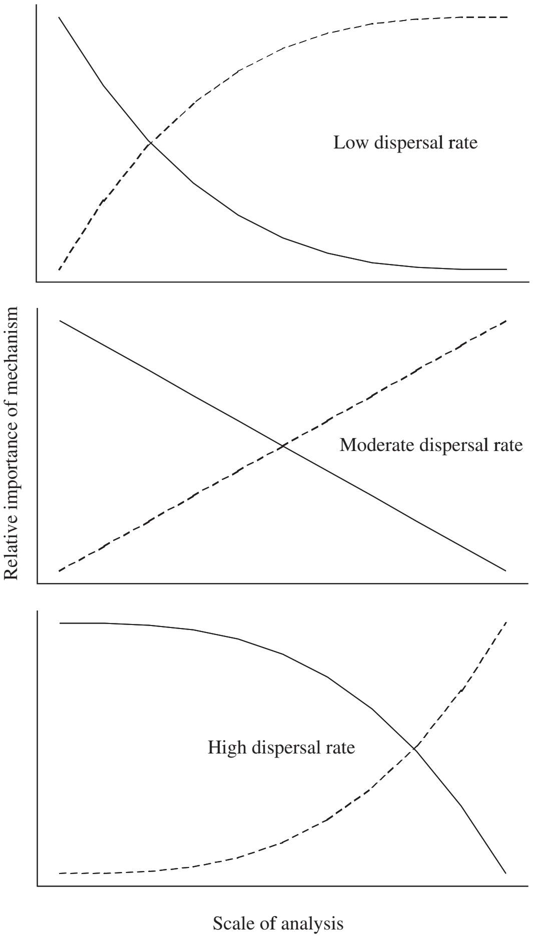

Figure 5 Conceptual model of relative contribution of both habitat selection and environmental mechanisms to the observed spatial dynamics of marine fish exhibiting various dispersal rates. Solid line represents habitat selection mechanism while dotted line represents environmental mechanism.

environmental (density-independent) mechanisms are both contributing and interacting factors in determining population distribution. The nature of the interaction would depend on the dispersive nature of the species and the scale at which patterns of habitat usage are observed (Fig. 5). Our model is similar to extensions of hierarchy theory (O'Neill *et al.* 1986) in that it recognizes that multiple mechanisms may generate observed patterns and the relative importance of these mechanisms may change across spatial scales. Others have shown how the applicability of the ideal free distribution will occur over a smaller scale for low mobility animals compared with those with high mobility (Tyler and Hargrove 1997). We believe, as others have (Mason and Brandt 1999), that issues of scale cannot be ignored and the explicit consideration of scale can lead to an improved understanding of the relationships between biological and physical processes and advance the management of fisheries resources.

Conclusion

The popularity of the ideal free distribution is partially the result of its ability to explain and predict a wide array of spatial patterns. This is in part because of the fact that an ideal free distribution can be defined regardless of the underlying patterns of the suitability-density functions within and among habitats. Currently implemented tests for the presence of density-dependent habitat selection, which examine differences in local population per capita growth rates, intrinsically assume something about how habitat-specific suitability responds to density-dependent pressures. However, without *a priori* knowledge of the form of the habitat suitability functions among and between habitats, it is difficult to access what mechanisms may lead to an observed spatial pattern. Likewise, without an appropriate expectation of the pattern, the presence of density-dependent habitat selection cannot be resolved. However, these problems are not insurmountable. Through an examination of the spatial variation in a proxy of fitness and consideration of how multiple factors may interact across spatial scales, further insight may be gained into how marine fish utilize habitat. The utility of our conceptual model (Fig. 5) remains to be seen, but we hope that it will begin to address a central problem in ecology as it applies to fisheries ecology, the problem of pattern and scale (Levin 1992). Ideally this will further lead to narrowing the gap between behavioural and landscape level ecology which has plagued other disciplines studying habitat selection (Lima and Zollner 1996).

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