

Do haddock select habitats to maximize condition?

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Haddock *Melanogrammus aeglefinus* in the North sea increased their distributional range when more abundant, but this density dependent habitat selection (DDHS) explained only a small part of the year-on-year variation in distribution patterns. The condition of haddock was examined at 24 sites in the North Sea in August and September 2004 and related to their abundance, to examine if the ideal free distribution theory (IFD), which assumes that organisms select habitats that maximize their rate of food intake, can be used to explain this variation in large scale distribution patterns. At a given temperature, condition (hepato-somatic index, I_H) was better at stations where haddock were most abundant. Therefore, haddock were not distributed perfectly according to the IFD in 2004. The positive correlation between abundance and I_H , however, indicated there was some habitat selection by haddock, as in the total absence of habitat selection no correlation between I_H and abundance, and no spatial variation in abundance was expected. DDHS may only explain a small part of the yearly variation in the distribution because haddock did not equalize and maximize their fitness at the scale of the North Sea. In addition, stable isotope analysis of muscle samples showed that haddock did not avoid competition for food when at high abundance by feeding at a lower or wider range of trophic levels.

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Key words: density dependence; habitat selection; ideal free distribution.

INTRODUCTION

Many studies that describe correlations between environmental variables and fish distribution do not explore the mechanistic basis for these correlations (*e.g.* Zheng *et al.*, 2002; Hedger *et al.*, 2004). To predict how changes in the environment and abundance affect distribution, however, an understanding of the key behavioural, physiological or environmental mechanisms is required. The ideal free distribution (IFD) was developed as a mechanistic explanation of the manner in which changes in density affect habitat use given known available resources (Fretwell & Lucas, 1970). The IFD assumes that all individuals try to optimize their net rate of energy gain. Thus, if they have perfect knowledge of resource distribution (they are ideal) and can move without cost (they are free), individuals should be distributed in proportion to resources and fitness, which should be equal among habitats.

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Body condition may be used as a proxy of fitness and depends on the balance of energy intake and expenditure. In ectotherms, metabolic rate increases with temperature. When food availability limits energy intake, organisms use proportionally more of the acquired energy for metabolism. At low temperatures, the same amount of food leaves a surplus because metabolic rate is lower (Brett, 1979). Thus, when organisms compete over the same quantity of resource, organisms can concentrate in larger numbers at lower rather than at higher temperatures without incurring negative effects of competition on condition. Therefore, food availability and temperature are likely to interact in habitat selection of ectotherm organisms (Hughes & Grand, 2000). For fishes, temperature may be more important than food in driving short-term habitat selection (Wildhaber & Crowder, 1990; Krause *et al.*, 1998).

Large scale distribution patterns in some marine fishes appear to be indicative of density-dependent habitat selection (Swain & Wade, 1993; Marshall & Frank, 1995) and therefore are assumed to support the underlying IFD theory. Observed patterns, however, may be the result of other causes (Morris, 1989), and modelling work by Tyler & Hargrove (1997) indicates that the IFD is unlikely to be good predictor of animal distributions on large scales. Tests for the presence of density-dependent habitat selection using only temporal variations in distribution patterns, and no information about the spatial distribution of fitness, do not evaluate the prediction of the IFD that fitness is equalized across habitats. The present study examined whether the IFD-prediction that organisms equalize fitness across habitats is applicable at large scales. In this study the distribution and the relationship with the abundance and condition of haddock *Melanogrammus aeglefinus* (L.), a demersal gadoid that primarily feeds on benthic invertebrates and to a lesser extent on small fishes (Adlerstein *et al.*, 2002), were examined.

Condition is a measure of energy that can be invested in life history decisions such as growth or reproductive output. Condition may be used as a proxy of fitness although Koops *et al.*, (2004) suggest that mass at age may be just as useful and haddock egg production is correlated to condition (Marshall & Frank, 1999; Blanchard *et al.*, 2003). Density dependent habitat selection (DDHS) has been shown in previous studies that have examined the distribution of haddock (Crecco & Overholtz, 1990; Marshall & Frank, 1994, 1995). In the North Sea, the 1999-year class was abundant, and therefore offers an opportunity to examine the effect of habitat selection on condition, as fish are likely to occupy a larger variety of habitats due to intraspecific competition (Swain & Sinclair, 1994; Shepherd & Litvak, 2004). Tests were conducted to determine whether or not haddock show DDHS in the North Sea, and if the spatial variation in haddock condition reflects expectations based on the IFD. If the distribution of the year class is consistent with the IFD, then the condition of haddock will be equal at all sites, because fish will distribute themselves in proportion to resources. If fish show no habitat selection at all, fish will be distributed homogeneously in space and condition will be proportional to resource levels. If the fish are not completely ideal and free but the fish do show some habitat selection, then richer sites are expected to be underused and poorer sites overused in relation to IFD predictions (Kennedy & Gray, 1993). Because a fraction of the available energy is lost in every step in a food chain,

theoretically, haddock can increase the amount of food available to them by feeding at a lower or wider range of trophic levels. Therefore, the current study also investigated whether differences in trophic level of fish at different abundances might explain deviations from the IFD.

METHODS

SAMPLING AND ABUNDANCE

Haddock were caught during the 2004 North Sea Ground Fish Survey (GFS), which sampled demersal fishes at 75 stations during August and September (Fig. 1) using a grande ouverture verticale (GOV) trawl that catches fishes living on or close to the seabed. At each station, the trawl was towed for 30 min. The catch was sampled to determine the total catch mass and length distributions for all fish species caught. Abundances were standardized to numbers per 1 h tow. Temperature was recorded at the midpoint of each tow using a SAIV micro CTD unit attached to the headline of the trawl. Haddock spawn in early spring in the North Sea, hence the distributions of fish reported will not be affected by spawning behaviour or migration (Thompson, 1929; Pedersen & Hislop, 2001).

DENSITY DEPENDENT HABITAT SELECTION

If DDHS occurs, the area occupied by a population should increase with abundance (Shepherd & Litvak, 2004). To test for DDHS, the area occupied by the haddock population between 30 and 40 cm total length (L_T) was estimated in relation to their abundance. Haddock abundance and distribution over a 20 year period (1985–2004) were obtained from the yearly GFS (CEFAS, 2003). The area occupied was estimated as the relative number of the ICES rectangles that contained >95% of the population. This adjustment to the total number of rectangles sampled was necessary to account for year to year differences in spatial coverage of the survey.

CONDITION INDEX

Condition of haddock was compared at 24 stations that covered a large range of abundances. All haddock caught in the size range 30–40 cm L_T , up to a maximum of six individuals, were collected at each station and frozen whole in sealed bags to -20° C. Fish were defrosted in the laboratory within 2 months of collection. Total body mass (M_T , g) and L_T to the nearest cm below were measured. Total liver mass (M_L), mass of the stomach contents (M_S) and gonad mass (M_G) (of sufficient size) were measured (g). The hepato-somatic index was calculated as: $I_H = 100 M_L (M_T - M_S)^{-1}$

In statistical analyses the average condition per station was used. The I_H had to be used in this study because there were insufficient fish in the samples to predict the M_T or M_L at L_T from M_T and L_T and M_L and L_T relationships. While such indices may not be suitable for making comparisons among populations, they are suitable for the one-off spatial comparisons made in this study (Cone, 1989). The I_H is a measure of the capacity for fitness, but not a measure of fitness itself. A life history trade-off between growth and reproduction may preclude a positive relationship between condition and fecundity (Koops *et al.*, 2004), so the I_H should be seen a measure of the life-history options.

ENERGY RESERVES

The energy content of 17 fish, chosen to cover a wide range of conditions based on I_H , was analysed to determine how this measure of condition related to energy content.

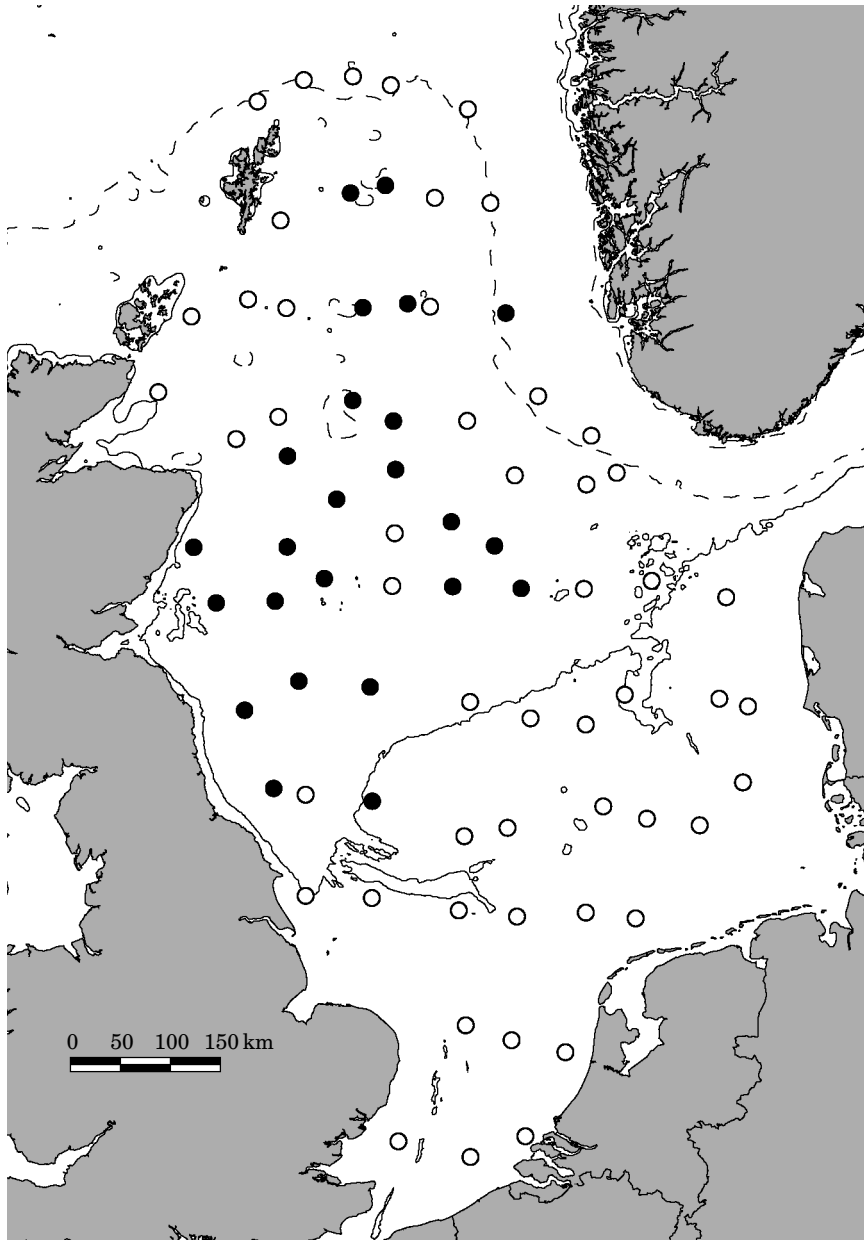


FIG. 1. Sampling stations in the North Sea in 2004. (○, stations that were sampled for abundance only; ●, stations where fish were collected for condition analysis in addition to abundance data. The 50 (—) and 150 m (- - -) depth contours are shown.

Water content of a muscle sample (>7 g wet mass) was estimated by freeze drying to constant mass. Muscle energy content was determined by combusting dried tissue samples in an oxygen bomb calorimeter (IKA Calorimeter C2000 Control). The high lipid content of the liver samples (>7 g wet mass) made freeze drying impossible, and

therefore liver water content was determined by drying in an oven at 65° C. After 1 h at this temperature a layer of oil formed at the surface of the sample, which prevented drying of the underlying liver tissue. This oil was decanted and dried in a separate weighed cup. Mass of the oil and liver tissue was recorded after drying for 72 h. Liver water content was calculated for the total sample including the oil fraction. Total fish energy stores were calculated assuming that white muscle composed 70% of fish mass, excluding liver and stomach content masses (Waterman, 1975). Liver oil and water content were negatively correlated (Pearson correlation, $n = 130$, $r = -0.786$, $P < 0.001$) and as gadoids store most energy as lipids, water content can be used as a predictor of liver energy content as shown in cod *Gadus morhua* L. (Lambert & Dutil, 1997). As the composition of cod and haddock tissue is similar (Holland *et al.*, 1993; Pedersen & Hislop, 2001), it was assumed that the relationship between water content and energy content for cod livers was also valid for haddock [liver energy content (kJ g^{-1} wet mass) = $36.6 - 0.39$ water content (%), Lambert & Dutil, 1997]. Energy contents of other tissues were not included in the energy store, as liver and white muscle are believed to contain the majority of energy reserves in gadoids (Lambert & Dutil, 1997).

TROPHIC LEVEL

Trophic level was estimated by nitrogen stable isotope analysis (Post, 2002). Approximately 1 g of white muscle tissue was removed from each fish, immediately frozen to -20° C and subsequently freeze dried. The dried tissue was powdered with a pestle and mortar to a grain size of <60 μm . Samples of powder (1 mg) were weighed into a tin capsule, and the ^{15}N composition was determined using continuous flow isotope ratio mass spectrometry (Europa Scientific Roboprep-CN sample preparation module and a Europa Scientific 20–20 IRMS operated by Iso-analytical Ltd, Sandbach, Cheshire, U.K.). Two samples of reference material (powdered bovine liver) were analysed after every five tissue samples to calibrate the system and compensate for drift. The ^{15}N composition was expressed in conventional delta notation, relative to the level of ^{15}N in atmospheric N_2 . Experimental precision (based on the s.d. of replicates of the internal standard) was $<0.07\%$. Trophic level (I_L) was estimated as: $I_L = (\delta^{15}\text{N}_i - \delta^{15}\text{N}_{\text{ref}}) (\Delta\delta^{15}\text{N})^{-1} + 2.5$ where $\delta^{15}\text{N}_i$ is the $\delta^{15}\text{N}$ of the tissue of fish i and $\delta^{15}\text{N}_{\text{ref}}$ is the $\delta^{15}\text{N}$ of an appropriate isotopic baseline (Post, 2002) and $\Delta\delta^{15}\text{N}$ is the trophic transfer shift for ^{15}N , which was assumed to be 3.4‰. The estimated $\delta^{15}\text{N}$ of queen scallops *Aequipecten opercularis*, a filter feeding bivalve, was used as $\delta^{15}\text{N}_{\text{ref}}$, they were assumed to have a trophic level of 2.5. The $\delta^{15}\text{N}$ of queen scallops, in the ICES rectangles (*c.* 56×56 km) where the samples were taken, was estimated using an equation for the same season and area, linking $\delta^{15}\text{N}$ to temperature, salinity and depth from Jennings & Warr (2003): $\delta^{15}\text{N}_{\text{ref}} = 208.51 - 0.009617 D + 6.7729 T_s - 0.31562 T_s^2 + 1.888 T_b - 0.06505 T_b^2 - 13.7488S + 0.18969S^2$ where D is the depth (m), T_s is the annual mean surface temperature ($^{\circ}$ C), T_b is the annual mean bottom temperature ($^{\circ}$ C) and S is the mean salinity in August. No information is available about year-on-year spatial variation of the $\delta^{15}\text{N}$ of baseline organisms, but given that the yearly variations in salinity and its associated terrestrial nitrogen are small in the examined offshore areas, it is expected that this equation is accurate to predict isotope baselines in this study. The $\delta^{15}\text{N}_{\text{ref}}$ was calculated using long-term temperature and salinity data from Jennings & Warr (2003). Analysis was carried out using the average trophic level per station.

To avoid competition at a given site, the haddock present may feed at a wider range of levels; on an individual basis; thereby reducing intraspecific competition. The question of whether haddock fed at a wider range of trophic levels when abundant was examined by linear regression of the s.d. of the trophic level of all six fish at a station against abundance. Two stations where less than six fish were collected were excluded from this analysis.

RESULTS

SIZE, ABUNDANCE AND RELATIONSHIP WITH ABIOTIC VARIABLES

Sixty six per cent of haddock between 30 and 40 cm L_T consisted of 1999-year class fish. This size range contained 84% of all 1999-year class fish. Haddock were most abundant between 75 and 125 m depth; the shallowest record was at 32 m. The temperature at the stations for the entire groundfish survey ranged from 7.5 to 19.5° C, but haddock was only caught at stations with a temperature <13° C.

DENSITY DEPENDENT HABITAT SELECTION

The area used by haddock was significantly positively related to the abundance of haddock, although there remained a lot of unexplained variation around this relationship ($r^2 = 0.21$, $F_{1,18}$, $P = 0.040$) (Fig. 2).

CONDITION INDEX

Gonads that were well developed were found in only one fish that was dissected for condition analysis. Mean muscle energy content was 5.28 ± 0.70 kJ g⁻¹ wet mass, while mean liver energy content for the same fish, calculated based on the water content, was higher and more variable at 21.79 ± 8.20 kJ g⁻¹ wet mass. Livers could have a high oil content (up to 66% wet mass or 82% dry mass), and liver oil content correlated with I_H ($r = 0.909$, $P < 0.001$). The I_H was strongly correlated with the energy density of the whole fish [(kJ g⁻¹ wet mass); ($r = 0.947$, $P < 0.001$; Fig. 3(a))]. Total energy stores per fish (kJ) also correlated significantly with I_H ($r = 0.844$, $P < 0.001$). Total energy stores in the liver and muscle were significantly correlated [$r = 0.906$, $P < 0.001$; Fig. 3(b)]. The intercept with the x -axis in Fig. 3(b) suggests that haddock only stored energy in the liver when at least 1000 kJ had been stored in muscle tissue. Because I_H correlated closely with fish energy content, it was used as an index of condition in subsequent analyses.

CONDITION ABUNDANCE AND TEMPERATURE RELATIONSHIPS

Haddock condition was highest at the stations where they were most abundant and where temperature was low (linear regression, $r^2 = 0.54$, abundance: $F_{1,21}$, $P = 0.0014$; temperature $F_{1,21}$, $P = 0.0036$; interaction $F_{1,21}$, $P = 0.48$; Fig. 4). As the interaction between temperature and abundance was not significant, at a given temperature I_H was greater at the stations where haddock were more abundant. Because of the positive correlation between abundance and condition, however, <26% of the total number of fish had a I_H lower than the median value.

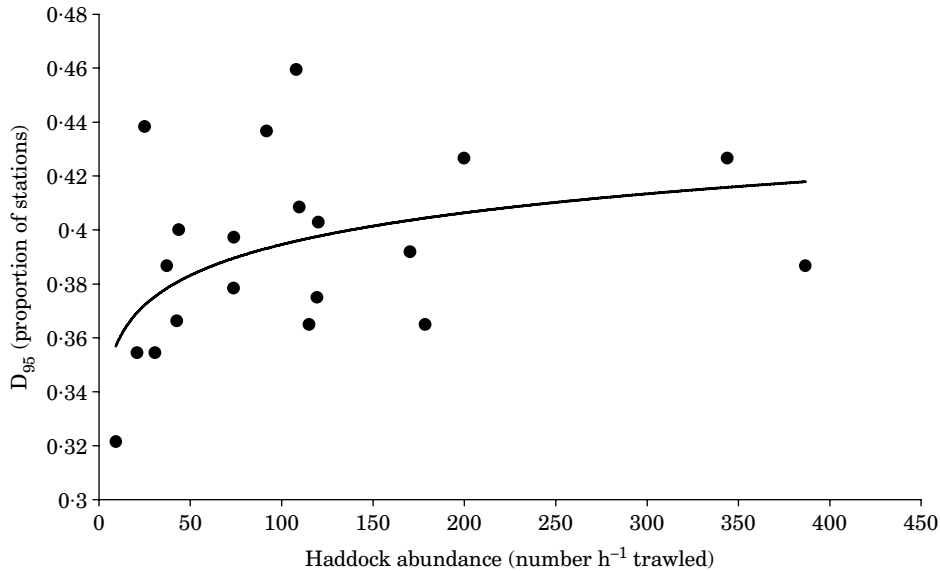


FIG. 2. The relationship between the proportion of stations occupied by 95% of 30–40 cm total length haddock D_{95} and abundance in the North Sea over a 20 year period. Every data point represents 1 year. The curve was fitted by: $y = 0.325x^{0.042}$.

TROPHIC LEVEL

The average isotope composition of haddock white muscle was -18.7‰ $\delta^{13}\text{C}$ and 10.6‰ $\delta^{15}\text{N}$. The trophic level of haddock was 4.0 ± 0.3 (mean \pm s.d.). There was no relationship between abundance, I_L and the mean trophic level at which fish fed, or its s.d. (Pearson correlation, $P > 0.05$, Fig. 5).

DISCUSSION

If individuals select habitats in order to maximize fitness, then the fitness of individuals should be equal among habitats and should remain equal under changing population abundance (Shepherd & Litvak, 2004). The results show that DDHS explained a small part ($r^2 = 0.22$) of the year-on-year variation in haddock distribution patterns. In 2004 haddock, however, were not distributed according to the IFD, as haddock had a better condition at low temperatures and at stations where they were more abundant. These results show that haddock under-utilized the best sites and over-utilized poorer sites in comparison with the IFD. There was, however, some indication of habitat selection by haddock, as in the absence of habitat selection no correlation between condition and abundance, and no spatial variation in abundance was expected. Therefore, DDHS may explain only a small part of the yearly variation in the distribution of fish based on basin-scale surveys. The DDHS of haddock had a limited role in determining their spatial distribution as, according to the IFD, they did not equalize and maximize their fitness at the scale of the North Sea. This suggests that their range did not contract enough when rare and did not expand enough when abundant according to the IFD. Large scale distribution patterns in

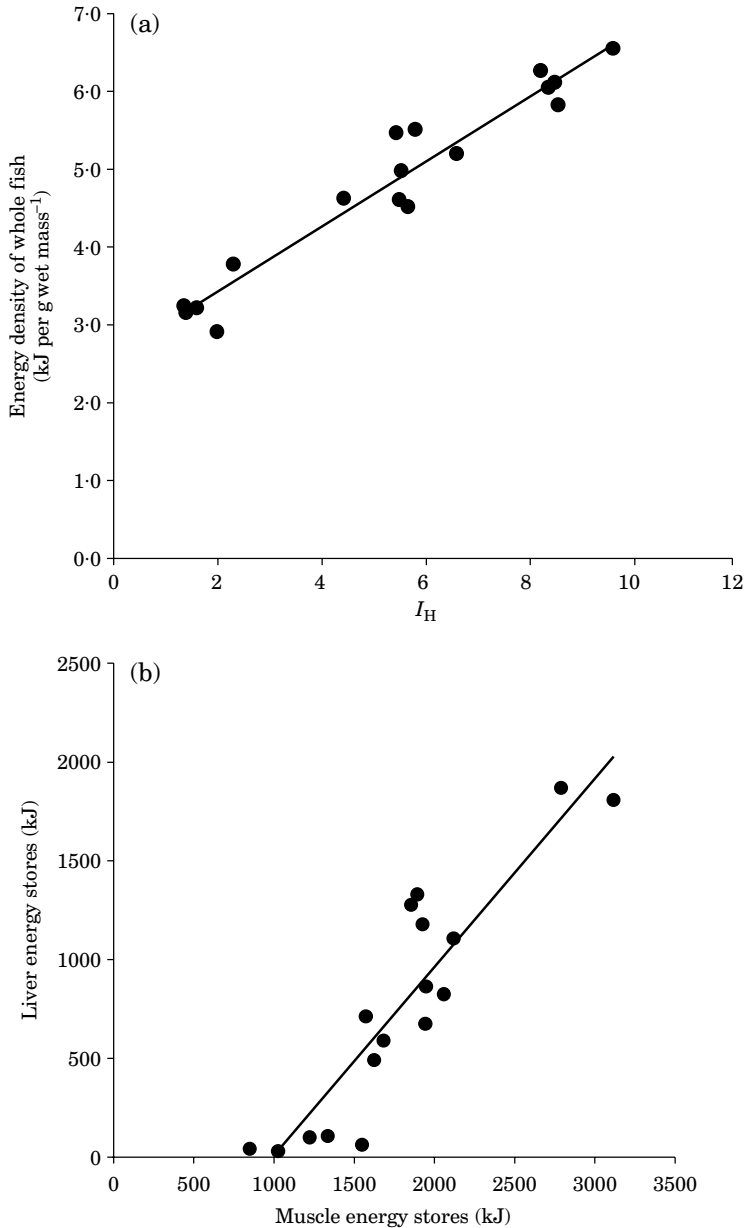


FIG. 3. The relationship between haddock (a) hepatosomatic index and energy density of whole fish and (b) muscle and liver energy content. The curves were fitted by: (a) $y = 41.8x + 2.6$ and (b) $y = 0.95x - 945.64$.

marine fishes that appear to be indicative of density-dependent habitat selection, but that are not supported by spatial patterns in fitness, therefore do not necessarily support all the assumptions of the IFD, as observed patterns may occur as the result of other factors (Morris, 1989). Ideally, a direct test of

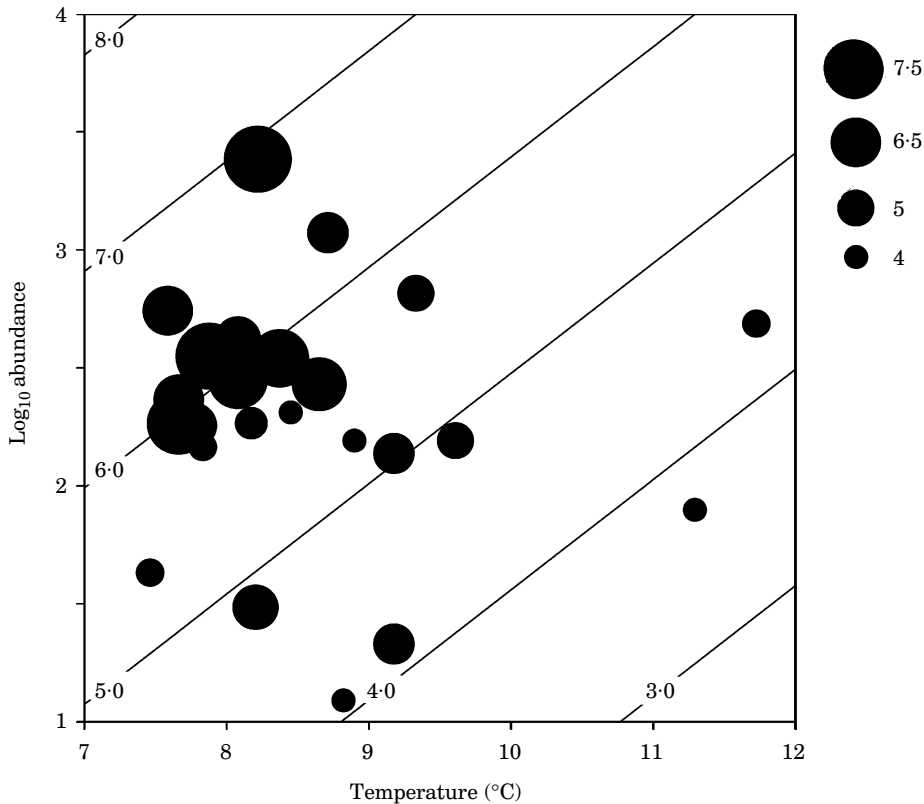


FIG. 4. Haddock condition (hepato-somatic index, ●) in relation to temperature and abundance. Bubble size indicates magnitude of I_H . The fitted regression of I_H is plotted as contour lines.

density-dependent habitat selection should simultaneously examine the fitness of individuals between habitats when population abundance is changing (Tyler & Hargrove, 1997). This is illustrated by a study of density-dependent habitat selection of juvenile haddock on the Scotian Shelf and Bay of Fundy (Marshall & Frank, 1995). There was a relationship between local density and total abundance at age that could be interpreted as a confirmation of IFD theory, but that there also was a spatial gradient in length at age, which did not conform to the IFD theory (Marshall & Frank, 1995).

As condition was significantly higher at stations where haddock were more abundant at a given temperature, this better condition could not be explained by the effects of temperature alone. This deviation from the IFD means haddock under-utilized sites that provide richer feeding grounds and over-utilized poorer sites. Therefore, haddock utilized sites of poor resource value to a greater extent than might be predicted by the IFD and would have a better condition in locations with high resource availability. The distribution of many organisms is consistently less extreme than the distribution of resources (Kennedy & Gray, 1993). Reasons for this deviation from the IFD may be that animals are not 'ideal', as they are unlikely to have total knowledge of the profitability and whereabouts of all resources, interfere during foraging or are unequal

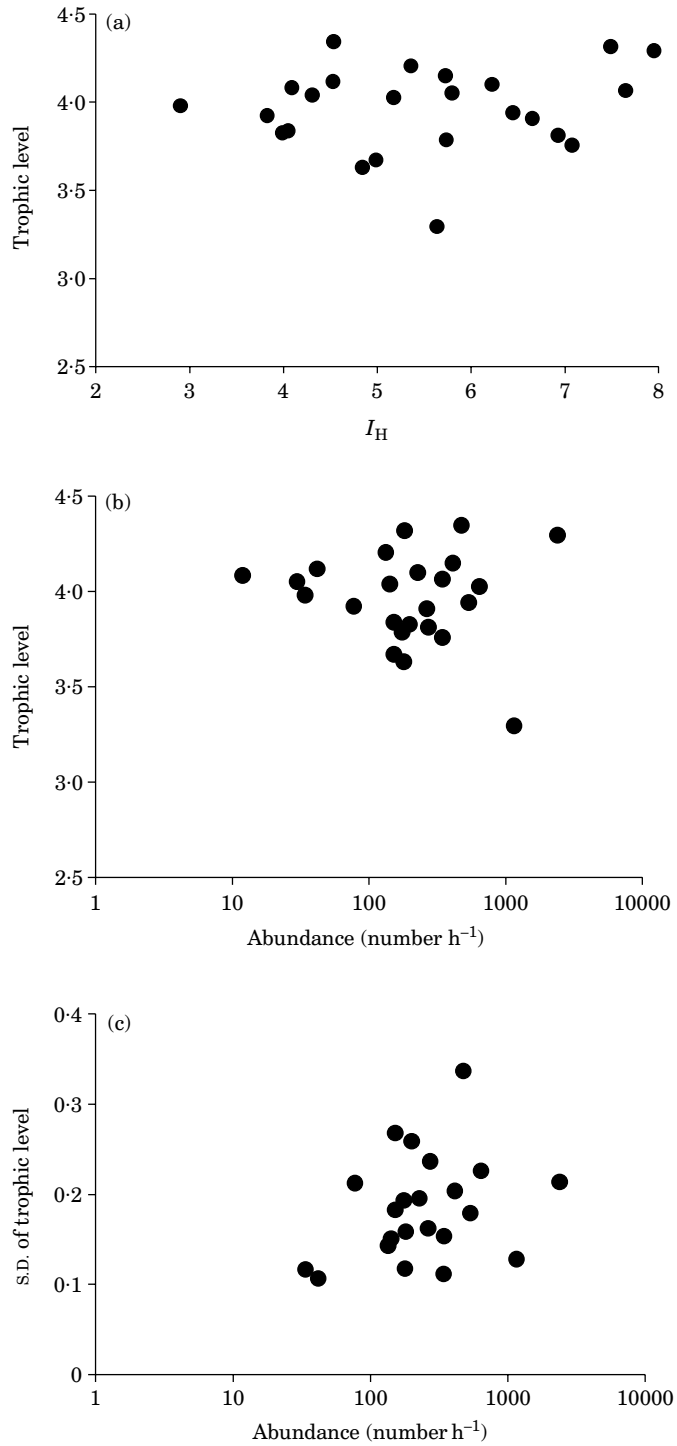


FIG. 5. The relationship between (a) trophic level and haddock condition (I_H), (b) trophic level and abundance and (c) s.e. of trophic level and abundance.

competitors (Kennedy & Gray, 1993; Yates *et al.*, 2000). The highest abundance of fish in this study compares with a density of *c.* one fish per 200 m², at which interference between foraging fish may occur, such that it would cause deviations from the predictions of IFD. Furthermore, the stations in this analysis were distributed over a very large area (>600 km), which means fish are unlikely to have perfect knowledge about the distribution of food resources at the scale of the study and 'travel costs' cannot be neglected. This means fish were neither 'ideal' nor 'free' at the scale of the present study.

The present study was complicated by the fact that there was no information about the spatial distribution of food resources and no conclusive information about the optimum temperature for growth for haddock. The temperature dependence of growth for larval and small juvenile haddock has been studied (Peck *et al.*, 2003), but studies for other fishes show that the temperature dependence of growth can be different for small and large fishes (*e.g.* cod, Bjornsson & Steinarsson, 2002). In unpublished sources it was found that the optimal temperature for growth for haddock >25 cm is probably 9–12° C, although they continue to grow well at temperatures up to 16° C and their cortisol stress response is not stimulated at a temperature of 15° C (C. Frantsi, pers. comm; S.C. Johnson, pers. comm.). At 6° C growth is poor and haddock become highly stressed (Havbruk, 2001), while >18° C growth stops (C. Frantsi, pers. comm.). In the North Sea, however, the vast majority of fish were found at temperatures <9° C and the optimum condition was reached at *c.* 8° C. This substantiates the conclusion that haddock are food limited and may try to minimize the effect of food limitation by selecting habitats where the temperature reduces respiration rate (Brett, 1979).

Haddock did not appear to alleviate the competition for food at high abundances by feeding at lower or a wider range of trophic levels where more food might be available. Haddock had a relatively low trophic level (4.0), which using a trophic fractionation of 3.4‰, indicates that haddock feed extensively on benthic invertebrates (trophic level ≥ 2.5). Perhaps poor condition fish cannot shift to more abundant resources at lower trophic levels, because haddock already feed at the lowest trophic level food sources available to them. McCutchan *et al.* (2003), however, showed that the trophic fractionation, $\Delta\delta^{15}\text{N}$, is smaller when feeding on invertebrates (1.4‰) than when feeding on other high protein diets (3.3‰). For the correct interpretation of $\delta^{15}\text{N}$, the food chain with all the trophic fractionation coefficients for each step leading to haddock should be known. This requires not only a study of the diet of haddock, but also of the diets of the prey of haddock. This was beyond the scope of this study, and suggests that using stable isotopes to compare trophic levels between areas and species can only be done if it is assumed that the food chain contains the same fraction of invertebrate steps. This does not affect the conclusion, however, that haddock do not feed at a lower trophic level at higher densities if it was assumed that they fed on benthic invertebrates to the same extent at all stations.

No data describing food availability for haddock were collected, but as the better condition could not be explained by less energy expenditure in relation to temperature, energy intake must have been higher at the high abundance locations. Therefore, it is likely that more food was available per fish on the high-abundance locations. Bottom trawling negatively affects biomass and

production of benthic communities (Jennings *et al.*, 2001; Hermsen *et al.*, 2003) that are the main food source for haddock (Hoines & Bergstad, 1999; Adlerstein *et al.*, 2002). As a result, bottom trawling has the potential to affect the condition and distribution of haddock. This is particularly important as trawl fisheries are most likely to target the areas where fish are abundant, thereby modifying important fish habitat. The strength of the impact of otter trawling on benthic production in the areas where haddock were sampled, however, is yet to be studied. Given that otter trawling effects are probably less than the effect of beam trawling and scallop dredging (Collie *et al.*, 2000), reductions in production due to trawling may not limit haddock, especially as the direct effects of fishing on the stock have currently reduced it to a small proportion of its 'virgin' biomass. Therefore, it is not possible to draw unequivocal conclusions about the indirect effects of trawling on fish stocks without determining the large scale effects of otter trawling on benthic production and determining at what level of benthic production levels begins to limit haddock population size.

Haddock were not distributed perfectly according to the IFD in 2004. There was, however, some indication of habitat selection by haddock, as in the total absence of habitat selection no correlation between condition and abundance and no spatial variation in abundance was expected. Therefore, DDHS may only explain a small part of the year-on-year variation in the distribution because haddock did not equalize and maximize their fitness at the scale of the North Sea.

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References

- Adlerstein, S. A., Temming, A. & Mergardt, N. (2002). Comparison of stomach contents of haddock (*Melanogrammus aeglefinus*) from the 1981 and 1991 North Sea International Stomach Sampling Projects. *ICES Journal of Marine Science* **59**, 497–515.
- Bjornsson, B. & Steinarsson, A. (2002). The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 494–502.
- Blanchard, J. L., Frank, K. T. & Simon, J. E. (2003). Effects of condition on fecundity and total egg production of eastern Scotian Shelf haddock (*Melanogrammus aeglefinus*). *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 321–332.
- Brett, J. R. (1979). Environmental factors and growth. In *Fish Physiology. Bioenergetics and Growth*, Vol. **8** (Hoar, W. S., Randall, D. J. & Brett, J. R., eds), pp. 599–677. Orlando, FL: Academic Press.
- Collie, J. S., Hall, S. J., Kaiser, M. J. & Poiner, I. R. (2000). A quantitative analysis of fishing impacts on shelf-sea benthos. *Journal of Animal Ecology* **69**, 785–798.
- Cone, R. S. (1989). The need to reconsider the use of condition indices in fishery science. *Transactions of the American Fisheries Society* **118**, 510–514.
- Crecco, V. & Overholtz, W. J. (1990). Causes of density-dependent catchability for Georges Bank haddock *Melanogrammus aeglefinus*. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 385–394.
- Fretwell, S. D. & Lucas, H. L. (1970). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**, 16–36.
- Hedger, R., McKenzie, E., Heath, M., Wright, P., Scott, B., Gallego, A. & Andrews, J. (2004). Analysis of the spatial distributions of mature cod (*Gadus morhua*) and

- haddock (*Melanogrammus aeglefinus*) abundance in the North Sea (1980–1999) using generalised additive models. *Fisheries Research* **70**, 17–25.
- Hermesen, J. M., Collie, J. S. & Valentine, P. C. (2003). Mobile fishing gear reduces benthic megafaunal production on Georges Bank. *Marine Ecology Progress Series* **260**, 97–108.
- Hoines, A. S. & Bergstad, O. A. (1999). Resource sharing among cod, haddock, saithe and pollack on a herring spawning ground. *Journal of Fish Biology* **55**, 1233–1257. doi: 10.1006/jfbi.1999.1122
- Holland, B., Brown, J. & Buss, D. H. (1993). *Fish and Fish Products: the Third Supplement to McCance & Widdowson's The Composition of Foods*, 5th edn. London: HMSO.
- Hughes, N. F. & Grand, T. C. (2000). Physiological ecology meets the ideal-free distribution: Predicting the distribution of size-structured fish populations across temperature gradients. *Environmental Biology of Fishes* **59**, 285–298.
- Jennings, S. & Warr, K. J. (2003). Environmental correlates of large-scale spatial variation in the $\delta^{15}\text{N}$ of marine animals. *Marine Biology* **142**, 1131–1140.
- Jennings, S., Dinmore, T. A., Duplisea, D. E., Warr, K. J. & Lancaster, J. E. (2001). Trawling disturbance can modify benthic production processes. *Journal of Animal Ecology* **70**, 459–475.
- Kennedy, M. & Gray, R. D. (1993). Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the ideal free distribution. *Oikos* **68**, 158–166.
- Koops, M. A., Hutchings, J. A. & McIntyre, T. M. (2004). Testing hypotheses about fecundity, body size and maternal condition in fishes. *Fish and Fisheries* **5**, 120–130.
- Krause, J., Staaks, G. & Mehner, T. (1998). Habitat choice in shoals of roach as a function of water temperature and feeding rate. *Journal of Fish Biology* **53**, 377–386.
- Lambert, Y. & Dutil, J.-D. (1997). Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of Atlantic cod (*Gadus morhua*)? *Canadian Journal of Fisheries and Aquatic Science* **54** (Suppl. 1), 104–112.
- Marshall, C. T. & Frank, K. T. (1994). Geographic responses of groundfish to variation in abundance: methods of detection and their interpretation. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 808–816.
- Marshall, C. T. & Frank, K. T. (1995). Density-dependent habitat selection by juvenile haddock (*Melanogrammus aeglefinus*) on the southwestern Scotian Shelf. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 1007–1017.
- Marshall, C. T. & Frank, K. T. (1999). The effect of interannual variation in growth and condition on haddock recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 347–355.
- McCutchan, J. H., Lewis, W. M., Kendall, C. & McGrath, C. C. (2003). Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* **102**, 378–390.
- Morris, D. W. (1989). Density-dependent habitat selection: testing the theory with fitness data. *Evolutionary Ecology* **3**, 80–94.
- Peck, M. A., Buckley, L. J., Caldarone, E. M. & Bengtson, D. A. (2003). Effects of food consumption and temperature on growth rate and biochemical-based indicators of growth in early juvenile Atlantic cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*. *Marine Ecology Progress Series* **251**, 233–243.
- Pedersen, J. & Hislop, J. R. G. (2001). Seasonal variations in the energy density of fishes in the North Sea. *Journal of Fish Biology* **59**, 380–389. doi: 10.1006/jfbi.2001.1649
- Post, D. M. (2002). Using stable isotopes to estimate trophic position: models, methods and assumptions. *Ecology* **83**, 703–718.
- Shepherd, T. D. & Litvak, M. K. (2004). Density-dependent habitat selection and the ideal free distribution in marine fish spatial dynamics: considerations and cautions. *Fish and Fisheries* **5**, 141–152.

- Swain, D. P. & Wade, E. J. (1993). Density-dependent geographic distribution of Atlantic Cod (*Gadus morhua*) in the southern Gulf of St-Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 725–733.
- Swain, D. P. & Sinclair, A. F. (1994). Fish distribution and catchability – what is the appropriate measure of distribution? *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 1046–1054.
- Thompson, H. (1929). Haddock biology (North Sea). A brief survey of recent data, methods and results. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **54**, 135–163.
- Tyler, J. A. & Hargrove, W. W. (1997). Predicting spatial distribution of foragers over large resource landscapes: A modeling analysis of the Ideal Free Distribution. *Oikos* **79**, 376–386.
- Waterman, J. J. (1975). The haddock. *Torry Advisory Note 67*. Aberdeen: Torry Research Station.
- Wildhaber, M. L. & Crowder, L. B. (1990). Testing a bioenergetics-based habitat choice model: bluegill (*Lepomis macrochirus*) responses to food availability and temperature. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 1664–1671.
- Yates, M. G., Stillman, R. A. & Goss-Custard, J. D. (2000). Contrasting interference functions and foraging dispersion in two species of shorebird (Charadrii). *Journal of Animal Ecology* **69**, 314–322.
- Zheng, X., Pierce, G. J., Reid, D. G. & Jolliffe, I. T. (2002). Does the North Atlantic current affect spatial distribution of whiting? Testing environmental hypotheses using statistical and GIS techniques. *ICES Journal of Marine Science* **59**, 239–253.

Electronic References

- CEFAS (2003). *The English 3rd Quarter North Sea Groundfish Survey*. Available at <http://www.cefas.co.uk/fishinfo/Surveys.htm>
- Havbruk (2001). *Haddock: Farming haddock*. Available at <http://www.havbruk.no/bla-det/infoeng/infoeng2001/aquacult/0113haddock.html>