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The Realized Annual Niche Space of Common Fish Species off Newfoundland

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Abstract

Data from groundfish research surveys on the continental shelf of northeast Newfoundland were used to examine the relationship between abundance of fish species at individual stations, bottom temperature, and depth in the period 1978 to 1993. The observed abundance of 24 common fishes within temperature and depth categories (-2 to +6°C, 50 to 1 000 m) was compared with the expected abundance, and preferences and avoidance were thus determined. The individual pattern of preferred categories defines the niche shape that is assumed to represent the realized niche of a species. Comparison of realized annual niche spaces showed that a pronounced shift towards deeper waters occurred in numerous fish species during the study period. These preliminary results suggest that reduction or expansion of realized niche space could be useful as an indicator for displacements and changing habitat occupation by continental shelf fishes.

Key words: abundance, depth, fish, Newfoundland shelf, niche breadth, temperature, visualization

Introduction

The aim of our study is to describe what the available data from groundfish research surveys on the continental shelf off Newfoundland convey about ecological shifts in abundant fish species. Our perspective is that of "niche space", a term introduced by Hutchinson (1957). In his concept, biotic and abiotic characteristics of the environment are represented by multi-dimensional niche axes along which each species can be located according to its specific requirements and physiological tolerances (as determined from experiments). This describes the fundamental niche space of a given species. The realized niche space is that fraction of the fundamental niche space that a species or population will actually occupy in a particular ecosystem during a determined time period. Our niche space has two axes, temperature and depth, and we use these to discriminate different realized annual niche spaces of common fish species off Newfoundland during the autumn season over the period 1978 to 1993.

Based upon Hutchinson's niche concept, we developed a graphical presentation that is rich in information. The value of publishing these sets of visualized niche space, all of which can be analysed from various different perspectives, consists in offering a tool to help interpret all kinds of other ecological and fisheries data within this geographical region. Our data sets should be useful to specialists and fisheries biologists concerned with single species and to community ecologists concerned with matters such as competition, habitat use, and predation.

Materials and Methods

The database used in this research was developed by Villagarcía (MS 1995) based on information from the annual autumn survey cruises conducted by Department of Fisheries and Oceans, Canada, from 1978 to 1993 in the Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K and 3L (Fig. 1). These surveys have been

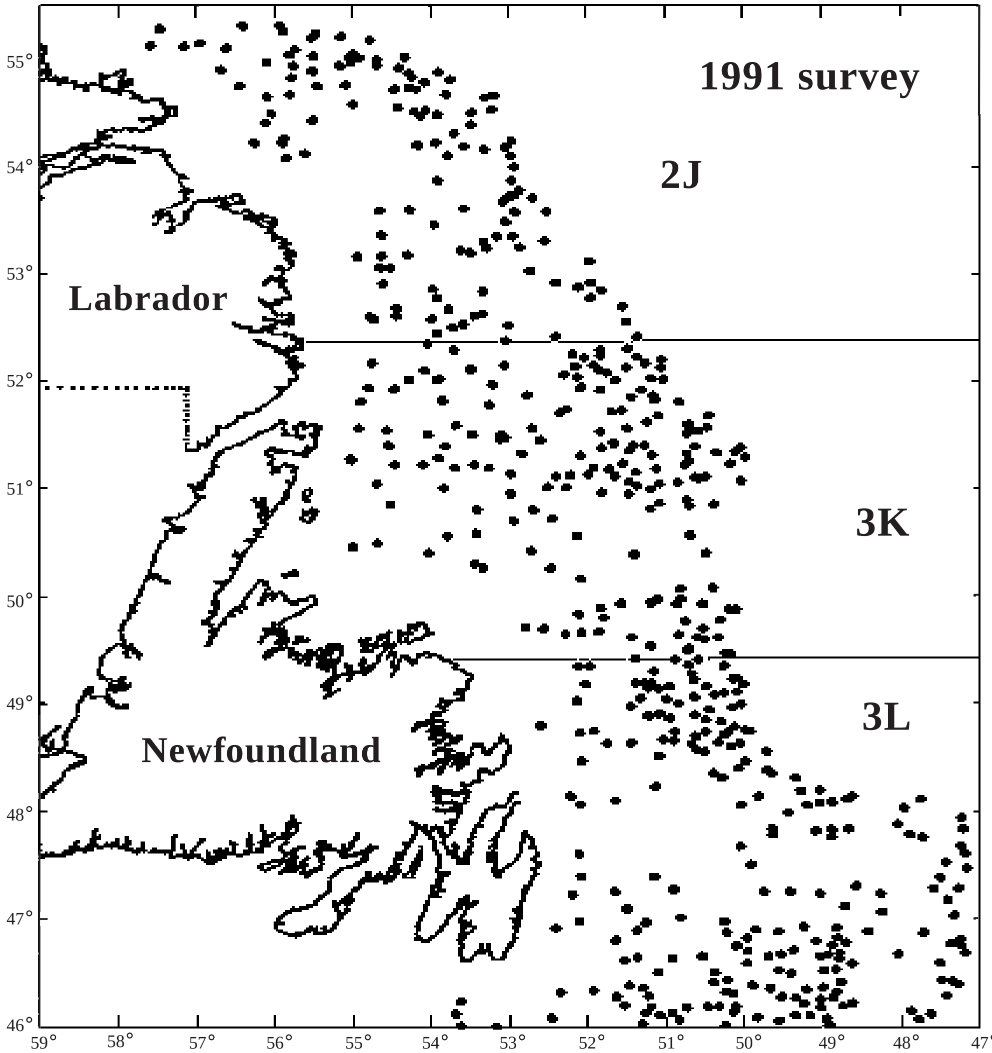


Fig. 1. NAFO Div. 2J, 3K, and 3L with an example of survey stations distribution in 1991 .

conducted by stratified random trawls (for more details see Bishop *et al.*, MS 1994). The analyses included 24 common fish species in the area (Table 1). Seven temperature categories ranging from -2 to +6°C and seven depth categories ranging from 50 to 1 000 m were established. The number of stations falling into each of the combined temperature/depth (which is described in this study as niche) categories determined the sampled niche space in regard to bottom temperature and depth. Categories with less than 3 stations were omitted from our analyses. Expected values for the abundance of every analysed fish population in each niche category (E_f) were calculated based on station distribution within the sampled niche space (where N_f is the total number of individuals of the analysed fish species, n_s is the number of stations in a particular niche category, N_s is the total number of stations considered in the analysis):

$$E_f = \frac{N_f \; n_s}{N_s}$$

The observed numbers of fish (O_f) falling into each niche category were then compared with the expected numbers and relative deviations in each cell calculated as γ-values (based on the selectivity index E_i proposed by Ivlev, 1961):

$$\gamma = \frac{\left(O_f - E_f\right)}{\left(O_f + E_f\right)}$$

TABLE 1. List of fish species included in the analyzes, their total numbers in survey catches (including all years from 1978 to 1993), their average annual *Ht* values, and *Ht* trends (correlation coefficient *r*) over the study period. Bold numbers indicate statistically significant coefficients ($\alpha = 0.05$).

	Family	Species	Common names	numbers	Average *Ht*	Trend in *Ht r*
1	Squalidae	*Centroscyllium fabricii*	Black dogfish	1 951	1.0	-0.16
2	Rajidae	*Raja radiata*	Thorny skate	41 309	5.4	-0.22
3	Rajidae	*Raja senta*	Smooth skate	2 905	3.2	**-0.68**
4	Osmeridae	*Mallotus villosus*	Capelin	122 044	3.1	0.49
5	Moridae	*Antimora rostrata*	Blue hake	2 517	1.0	-0.02
6	Gadidae	*Boreogadus saida*	Arctic cod	85 837	3.0	**0.58**
7	Gadidae	*Gadus morhua*	Atlantic cod	268 007	4.2	-0.68
8	Macrouridae	*Coryphaenoides rupestris*	Roundnose grenadier	33 411	0.9	-0.17
9	Macrouridae	*Macrourus berglax*	Roughhead grenadier	18 403	3.7	**-0.93**
10	Macrouridae	*Nezumia bairdii*	Marlin spike	3 640	1.8	-0.42
11	Zoarcidae	*Lycodes reticulatus*	Arctic eelpout	8 798	4.7	0.36
12	Zoarcidae	*Lycodes vahlii*	Checker eelpout	11 879	4.6	-0.40
13	Anarhichidae	*Anarhichas denticulatus*	Broadhead wolffish	5 582	5.4	**-0.77**
14	Anarhichidae	*Anarhichas lupus*	Atlantic wolffish	9 963	3.8	-0.36
15	Anarhichidae	*Anarhichas minor*	Spotted wolffish	2 676	5.3	**-0.77**
16	Scorpaenidae	*Sebastes marinus*	Golden redfish	16 294	2.2	0.08
17	Scorpaenidae	*Sebastes mentella*	Deep-sea redfish	556 437	2.6	-0.43
18	Cottidae	*Cottunculus microps*	Arctic deep-sea sculpin	1 072	2.9	-0.10
19	Agonidae	*Leptagonus decagonus*	Northern alligotorfish	1 636	3.6	0.45
20	Cyclopteridae	*Cyclopterus lumpus*	Lumpfish	1 375	3.7	0.04
21	Pleuronectidae	*Glyptocephalus cynoglossus*	Witch flounder	32 001	2.9	**-0.74**
22	Pleuronectidae	*Hippoglossoides platessoides*	American plaice	413 166	5.4	**0.67**
23	Pleuronectidae	*Limanda ferruginea*	Yellowtail flounder	5 388	1.1	0.33
24	Pleuronectidae	*Reinhardtius hippoglossoides*	Greenland halibut	220 550	3.5	-0.49

A positive deviation from the expected value is interpreted as preference for and a negative deviation as avoidance of that particular temperature/ depth cell. The visualisation of the realized niche space is based on the γ-values (see Fig. 2 to 13).

Linked to the variability in shape (as visualised in Fig. 2 to 13), the realized niche space has a size/width component. To facilitate comparisons, a numeric representation of the relative width of a species realized niche space (*Ht*) is determined based on chi-square (χ^2 serving as a measure of the deviation from an expected distribution and not as a statistical test for correlation). *Ht* is expressed as 1/*K*' (based upon the *K*-value of Sachs, 1988; modified); *K*' corrects χ^2 for both the total number of fish (N_f) and the number of cells (n_c):

$$K' = \sqrt{\frac{X^2}{N^f} \times \frac{1}{n_c}} \longrightarrow Ht = \frac{1}{K'}$$

A low *Ht* value (<2) indicates a relatively small realized annual niche space and a high *Ht* value (>4) points to a large realized annual niche.

Trends of a species niche width (*Ht*) on an annual basis were estimated through regression analyses and calculation of the correlation coefficient *r*.

Total numbers of species caught during surveys in each year is given with the figures (Fig. 2 to 13).

Results and Discussion

The approach used in this paper allows determining and comparing annual temperature/depth distribution of fish independent of their abundance. To examine possible changes in niche width and shape during the period of investigation, preference/ avoidance patterns were plotted for each year and annual measures of the width of the realized niche space (*Ht*) were performed (Fig. 2 to 13). When comparing the graphs for different years in any species one should keep in mind that a shift in preferred niche space does not necessarily imply that individuals of a population displayed different niche selection patterns in each year. In the situation encountered on the Newfoundland shelf where abundance of so many fish species declined from 1978 to 1993 (e.g. Haedrich and Fischer, 1996), niche space shifts might simply reflect a situation where change in environmental conditions or human predation affects some habitats more than others. This could eventually lead to a marked disappearance of individuals in once densely occupied habitats with preferred niche characteristics leaving only remnant populations in habitats with less favourable niche characteristics.

Relative to other continental shelf areas, variability in temperature off Newfoundland (ranging from approximately -2°C to +6°C) is much narrower than is variability in depth (ranging from approximately 50 m to 1 000 m). This is especially true for areas deeper than 500 m where a very narrow range of temperatures of only 4°C to 6°C is observed. As an important effect of the narrow temperature window on the Newfoundland continental shelf, thermal niche segregation in fish populations is relatively indistinct. Some species occurring in waters shallower than 500 m tend to avoid the higher temperatures within the range (Arctic cod, Arctic eelpout, and northern alligatorfish), others tend to avoid the very low temperatures (smooth skate, Atlantic cod, checker eelpout, all wolffish, both redfish, witch flounder, and yellowtail flounder), and others seem to occupy equally all temperatures within the range (thorny skate, capelin, lumpfish, and Greenland halibut). Although these temperature preferences are not very sharp, they appear to be fairly constant throughout the study period. There is not even one case in our analysis where a shift in realized temperature niche took place that was not connected to a shift in depth niche.

In contrast to the relative constancy in the realized temperature niche axis, the realized depth niche axis often changed noticeably over the 16 years of the study. In half of the species analysed, a trend towards an apparent occupation of deeper waters was observed (Fig. 2 to 13). This trend was most common in abundant species like Arctic cod, Atlantic cod, roughhead grenadier, Atlantic wolffish, golden redfish, deep-sea redfish, witch flounder, American plaice, and Greenland halibut. However, there were some less abundant species that followed the same trend, i.e. broadhead and spotted wolffish and northern alligatorfish.

Those species that did not exhibit discernible shifts in realized niche space were mostly either distinctly shallow-water fish or distinctly deep-water fish. The shallow-water category included thorny skate, capelin, Arctic eelpout, lumpfish, and yellowtail flounder. The deep-water category included mostly fish that realized a small niche space

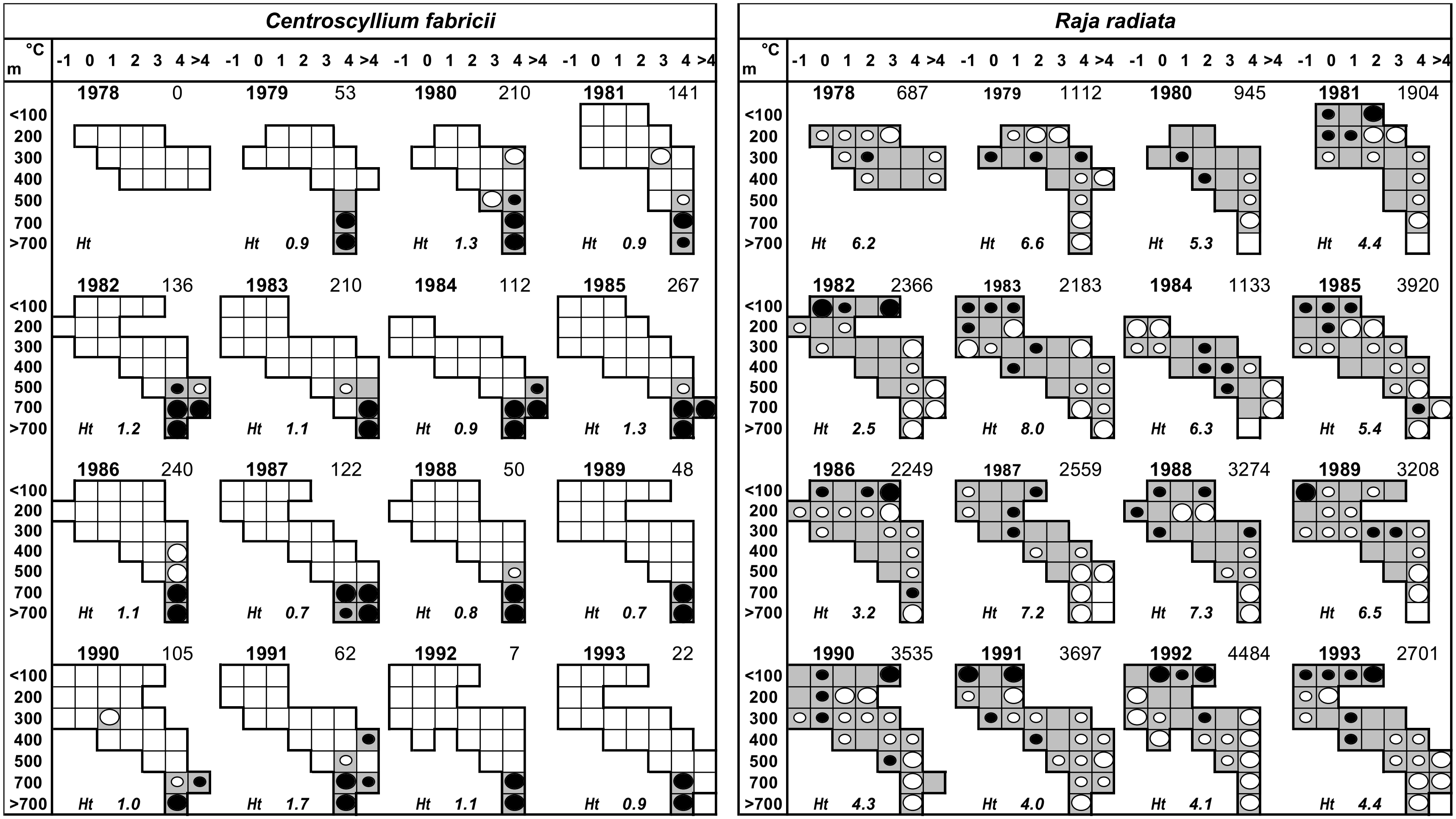


Fig. 2. Realized annual niche space of analyzed species. Temperature categories (1°C width, starting with <-1°C to >4°C) run from the left to the right corner, depth categories (100 m width, starting with <100 m to >700 m) from the upper corner down. The upper left number in each annual figure indicates years. The upper right number in each annual figure gives total catch numbers in each year. Annual *Ht* values are given at the bottom of each annual figure. Each figure has a unique shape representing the sampled niche space in a given year. White fields indicate space where the species in question was never caught. Grey fields indicate presence of the species in question. Open circles = avoidance, black circles = preference; small circles = week avoidance or preference ($\gamma < |0,2|$); large circles = strong avoidance or preference ($\gamma > |0,5|$).

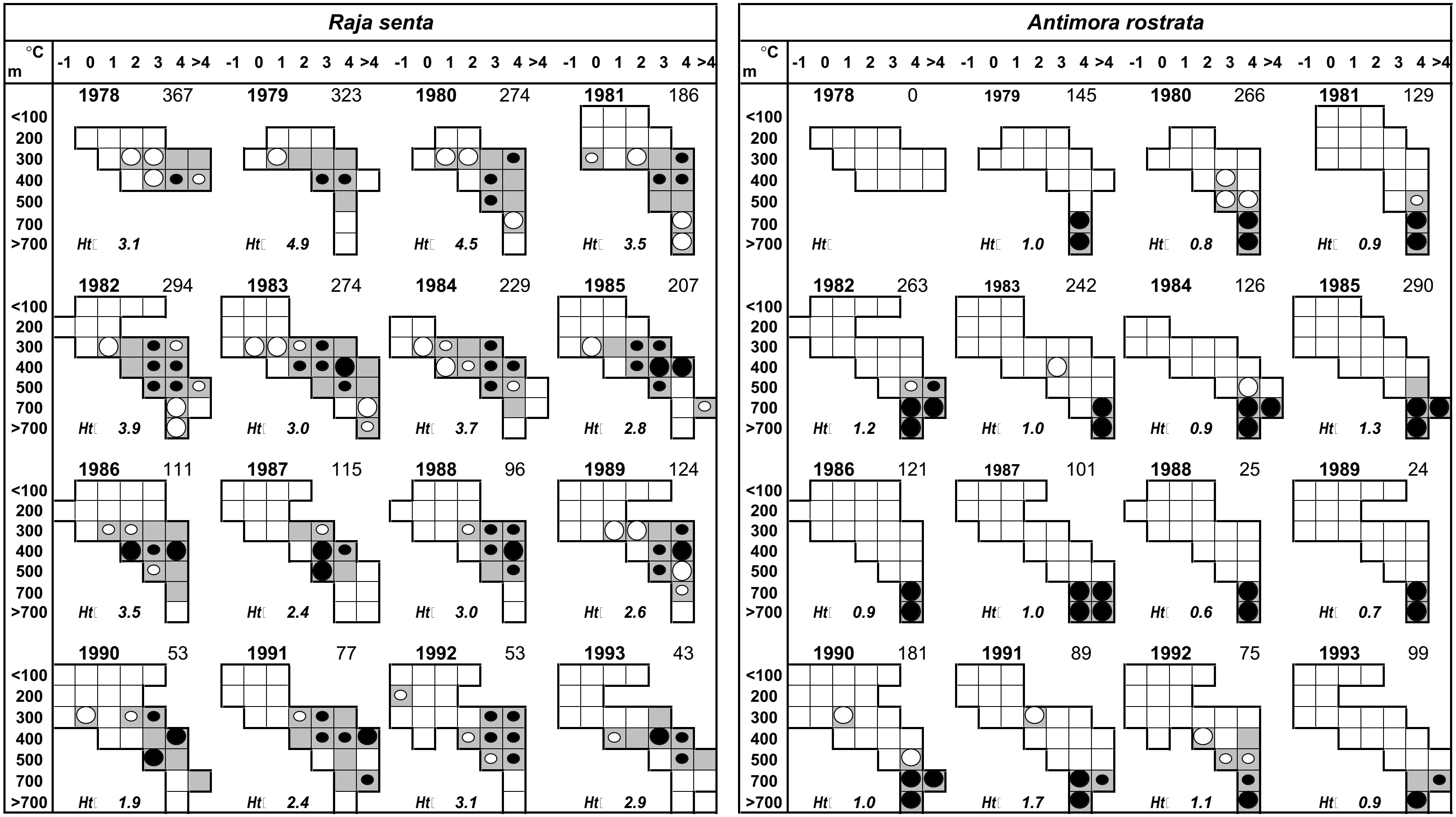


Fig. 3. Realized annual niche space of analyzed species. Temperature categories (1°C width, starting with <-1°C to >4°C) run from the left to the right corner, depth categories (100 m width, starting with <100 m to >700 m) from the upper corner down. The upper left number in each annual figure indicates years. The upper right number in each annual figure gives total catch numbers in each year. Annual *Ht* values are given at the bottom of each annual figure. Each figure has a unique shape representing the sampled niche space in a given year. White fields indicate space where the species in question was never caught. Grey fields indicate presence of the species in question. Open circles = avoidance, black circles = preference; small circles = week avoidance or preference ($\gamma < |0,2|$); large circles = strong avoidance or preference ($\gamma > |0,5|$).

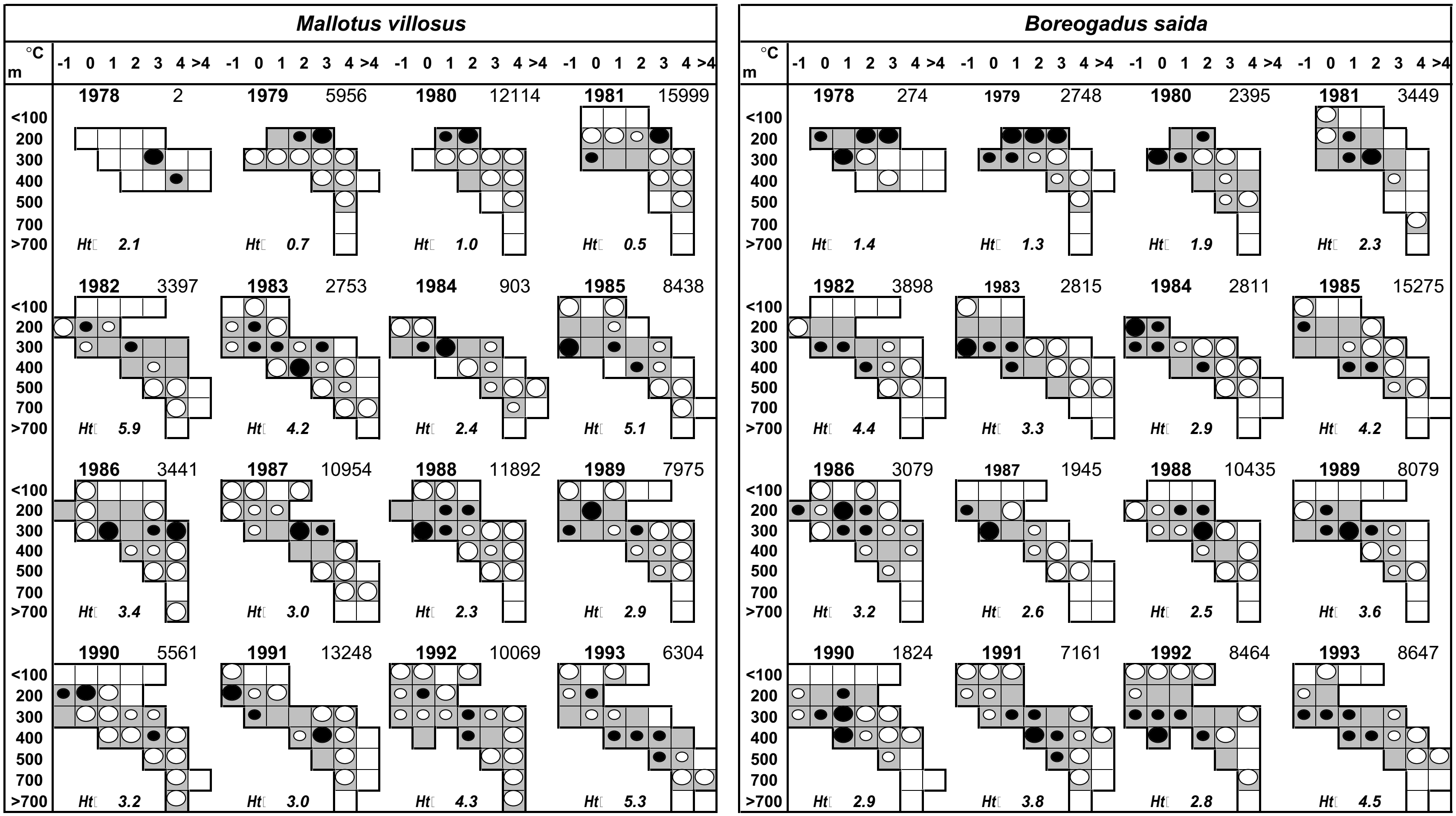


Fig. 4. Realized annual niche space of analyzed species. Temperature categories (1°C width, starting with <-1°C to >4°C) run from the left to the right corner, depth categories (100 m width, starting with <100 m to >700 m) from the upper corner down. The upper left number in each annual figure indicates years. The upper right number in each annual figure gives total catch numbers in each year. Annual *Ht* values are given at the bottom of each annual figure. Each figure has a unique shape representing the sampled niche space in a given year. White fields indicate space where the species in question was never caught. Grey fields indicate presence of the species in question. Open circles = avoidance, black circles = preference; small circles = week avoidance or preference ($\gamma < |0,2|$); large circles = strong avoidance or preference ($\gamma > |0,5|$).

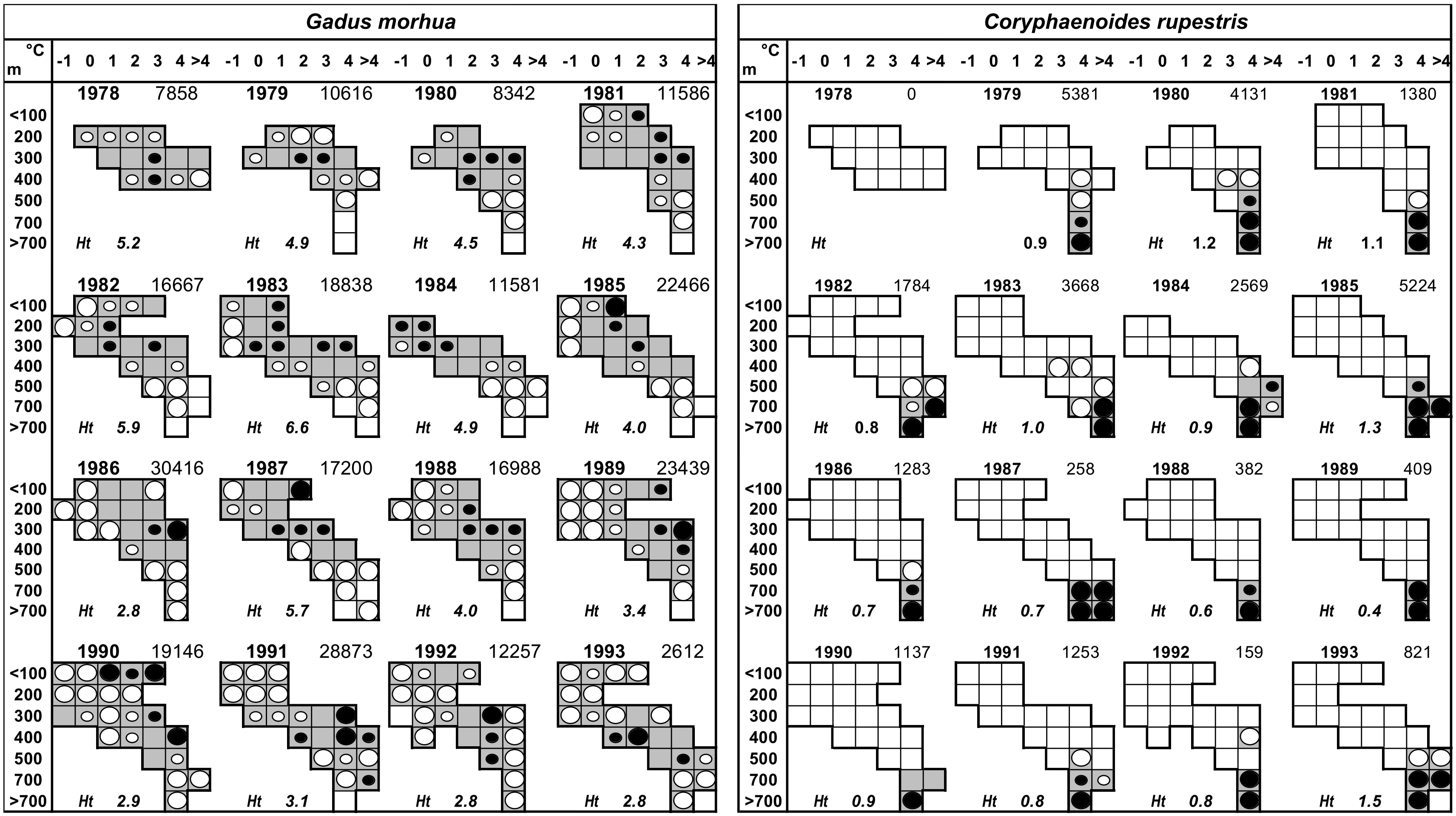
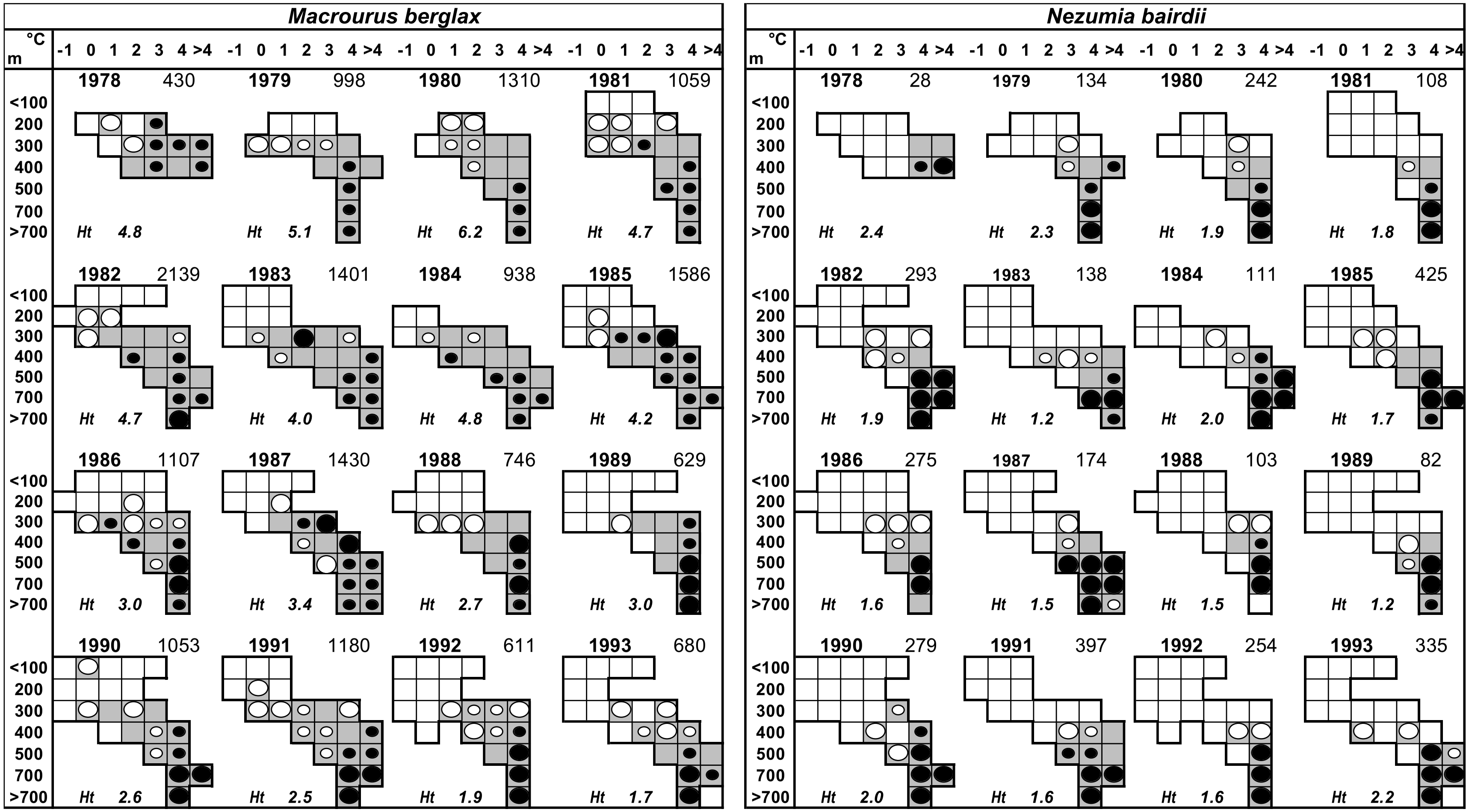


Fig. 5. Realized annual niche space of analyzed species. Temperature categories (1°C width, starting with <-1°C to >4°C) run from the left to the right corner, depth categories (100 m width, starting with <100 m to >700 m) from the upper corner down. The upper left number in each annual figure indicates years. The upper right number in each annual figure gives total catch numbers in each year. Annual *Ht* values are given at the bottom of each annual figure. Each figure has a unique shape representing the sampled niche space in a given year. White fields indicate space where the species in question was never caught. Grey fields indicate presence of the species in question. Open circles = avoidance, black circles = preference; small circles = week avoidance or preference ($\gamma < |0,2|$); large circles = strong avoidance or preference ($\gamma > |0,5|$).



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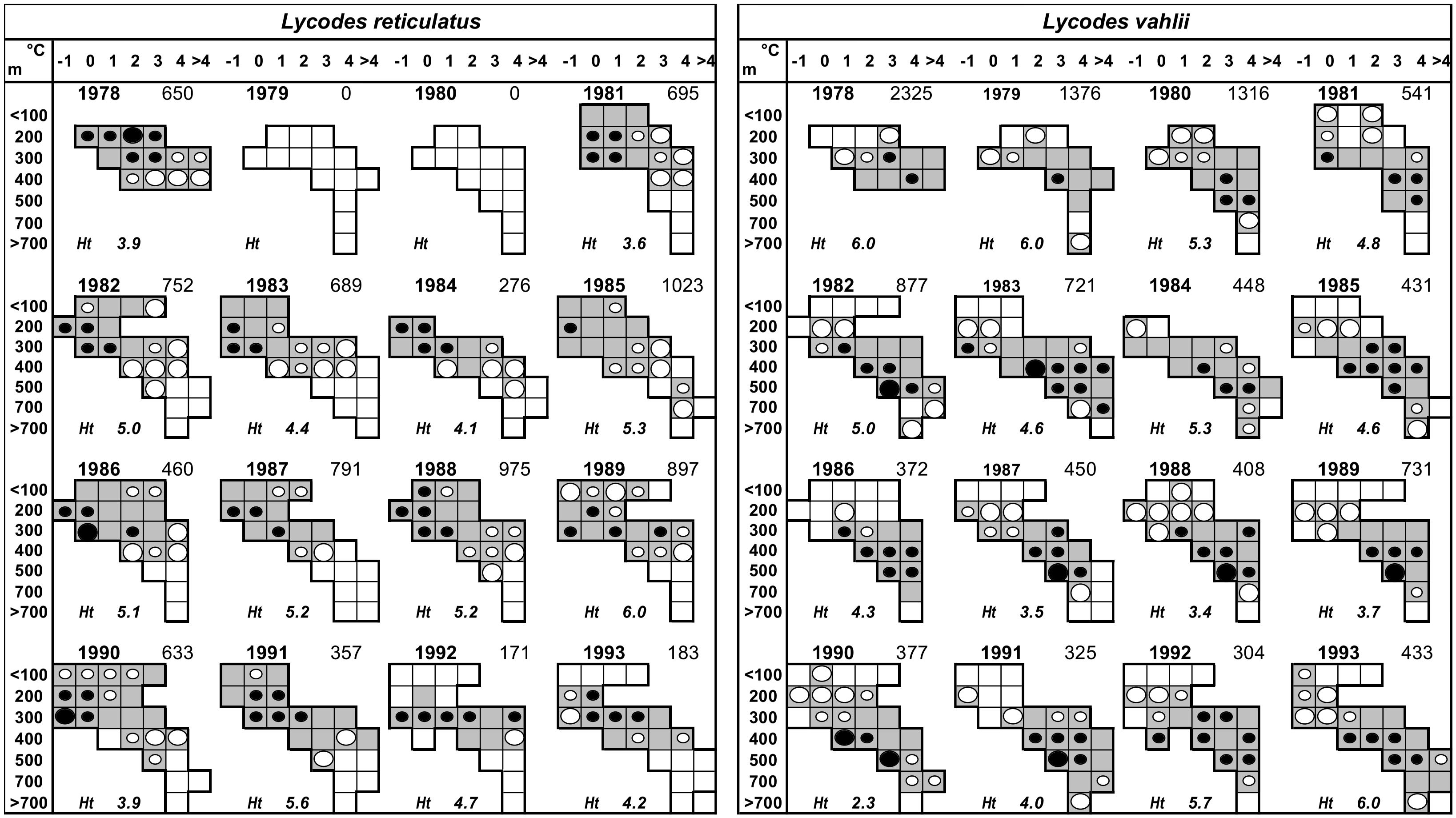

Fig. 7. Realized annual niche space of analyzed species. Temperature categories (1°C width, starting with <-1°C to >4°C) run from the left to the right corner, depth categories (100 m width, starting with <100 m to >700 m) from the upper corner down. The upper left number in each annual figure indicates years. The upper right number in each annual figure gives total catch numbers in each year. Annual *Ht* values are given at the bottom of each annual figure. Each figure has a unique shape representing the sampled niche space in a given year. White fields indicate space where the species in question was never caught. Grey fields indicate presence of the species in question. Open circles = avoidance, black circles = preference; small circles = week avoidance or preference ($\gamma < |0,2|$); large circles = strong avoidance or preference ($\gamma > |0,5|$).

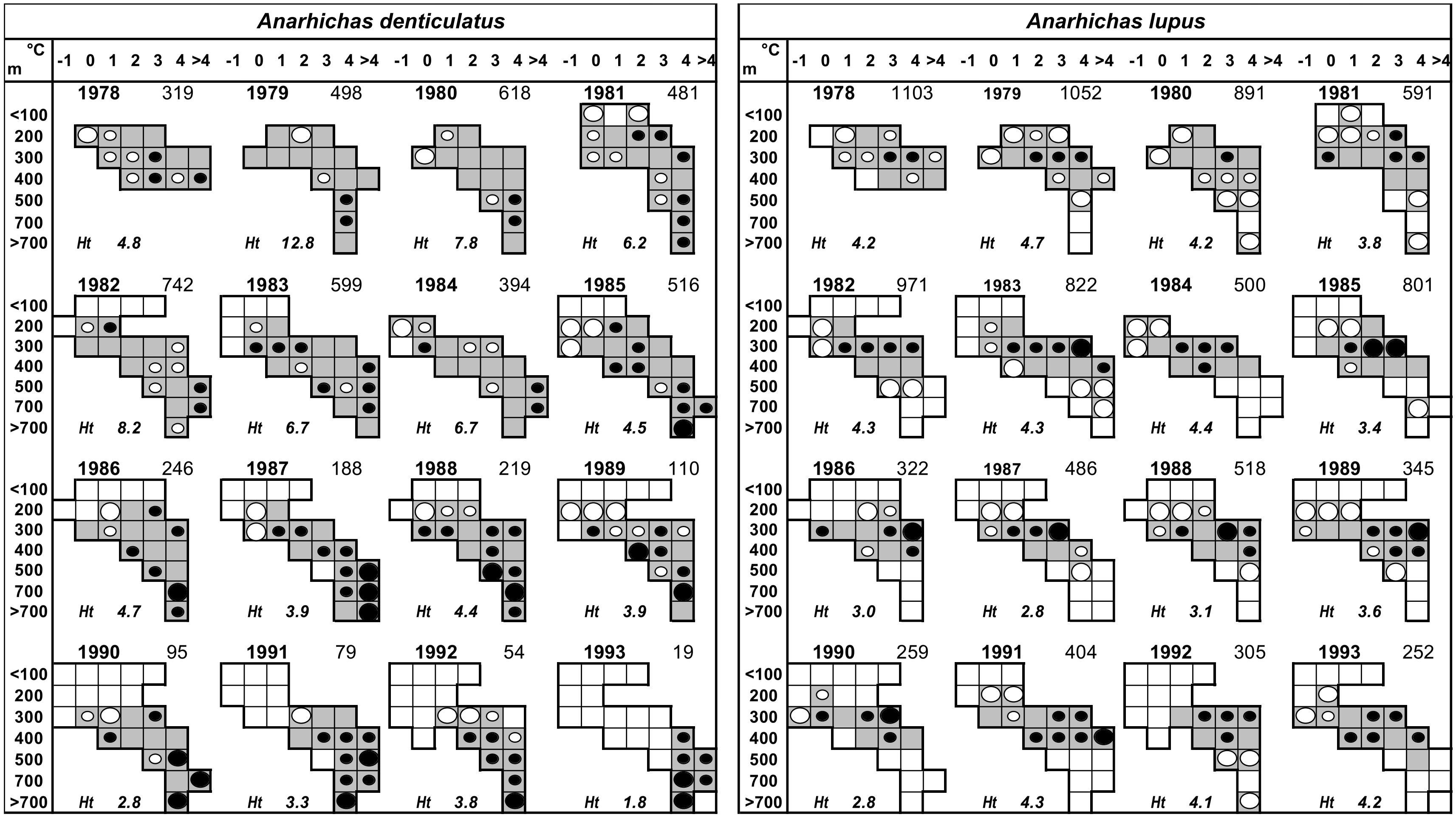

Fig. 8. Realized annual niche space of analyzed species. Temperature categories (1°C width, starting with <-1°C to >4°C) run from the left to the right corner, depth categories (100 m width, starting with <100 m to >700 m) from the upper corner down. The upper left number in each annual figure indicates years. The upper right number in each annual figure gives total catch numbers in each year. Annual *Ht* values are given at the bottom of each annual figure. Each figure has a unique shape representing the sampled niche space in a given year. White fields indicate space where the species in question was never caught. Grey fields indicate presence of the species in question. Open circles = avoidance, black circles = preference; small circles = week avoidance or preference ($\gamma < |0,2|$); large circles = strong avoidance or preference ($\gamma > |0,5|$).

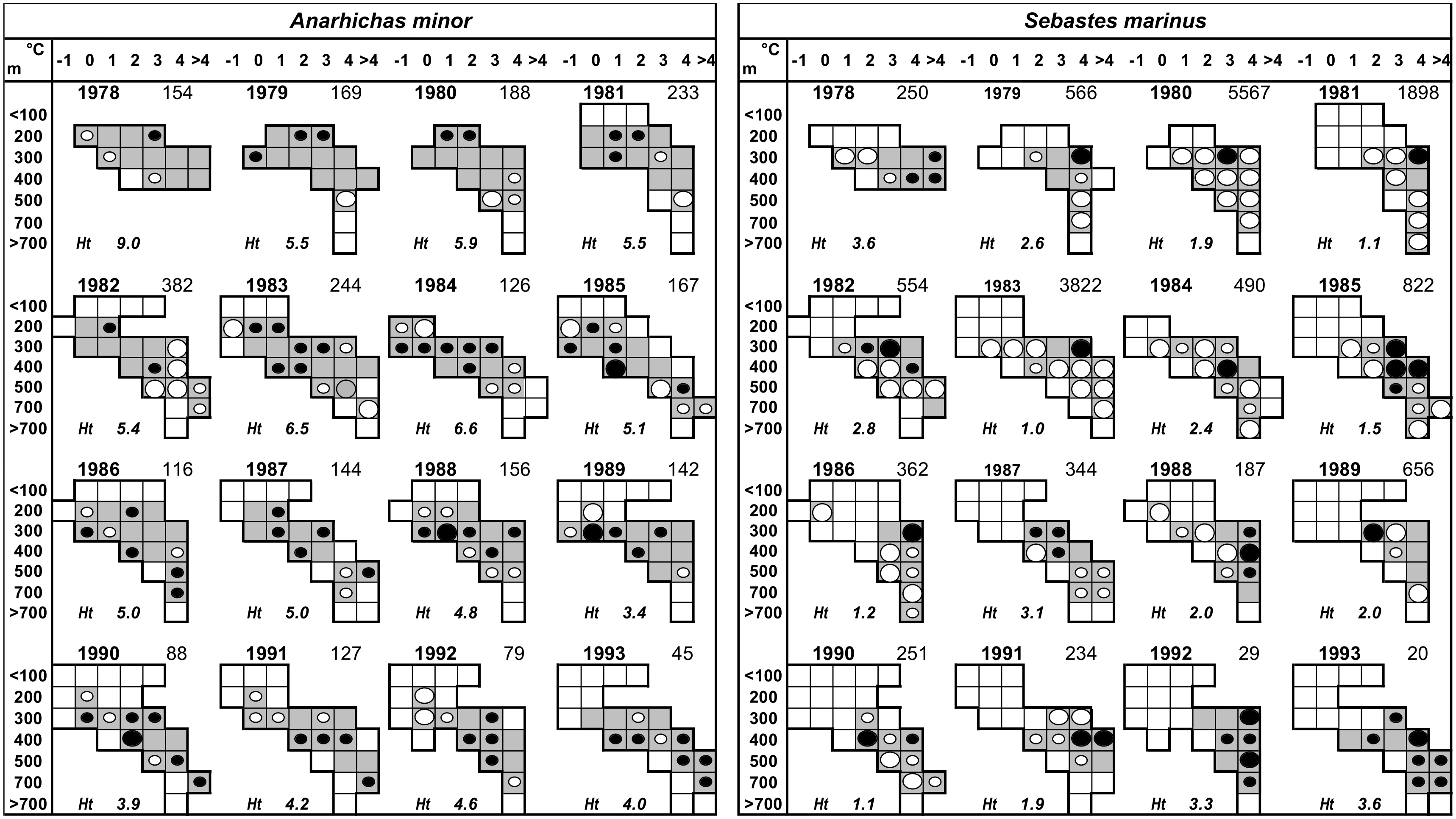

Fig. 9. Realized annual niche space of analyzed species. Temperature categories (1°C width, starting with <-1°C to >4°C) run from the left to the right corner, depth categories (100 m width, starting with <100 m to >700 m) from the upper corner down. The upper left number in each annual figure indicates years. The upper right number in each annual figure gives total catch numbers in each year. Annual *Ht* values are given at the bottom of each annual figure. Each figure has a unique shape representing the sampled niche space in a given year. White fields indicate space where the species in question was never caught. Grey fields indicate presence of the species in question. Open circles = avoidance, black circles = preference; small circles = week avoidance or preference ($\gamma < |0,2|$); large circles = strong avoidance or preference ($\gamma > |0,5|$).

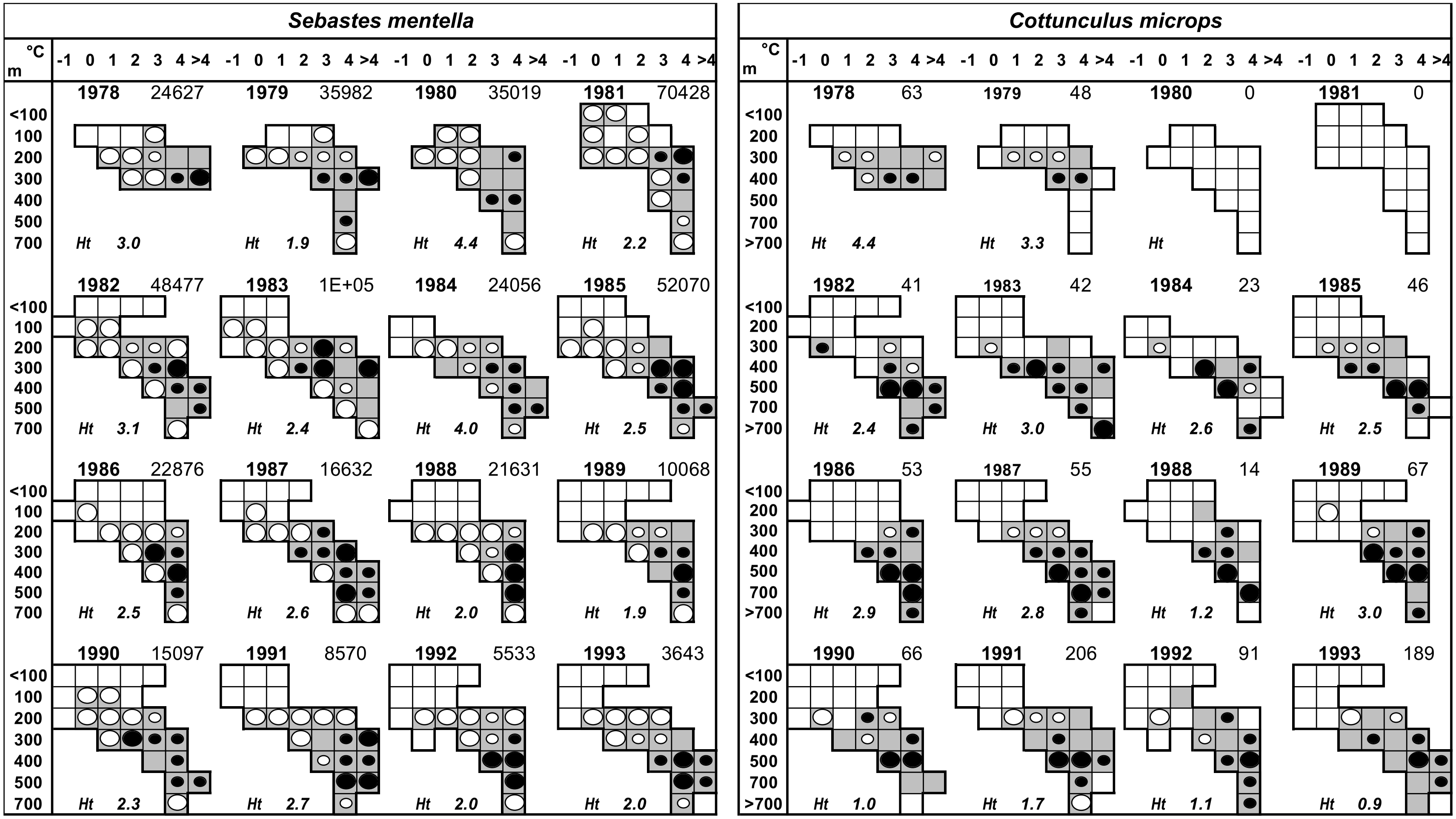

Fig. 10. Realized annual niche space of analyzed species. Temperature categories (1°C width, starting with <-1°C to >4°C) run from the left to the right corner, depth categories (100 m width, starting with <100 m to >700 m) from the upper corner down. The upper left number in each annual figure indicates years. The upper right number in each annual figure gives total catch numbers in each year. Annual *Ht* values are given at the bottom of each annual figure. Each figure has a unique shape representing the sampled niche space in a given year. White fields indicate space where the species in question was never caught. Grey fields indicate presence of the species in question. Open circles = avoidance, black circles = preference; small circles = week avoidance or preference ($\gamma < |0,2|$); large circles = strong avoidance or preference ($\gamma > |0,5|$).

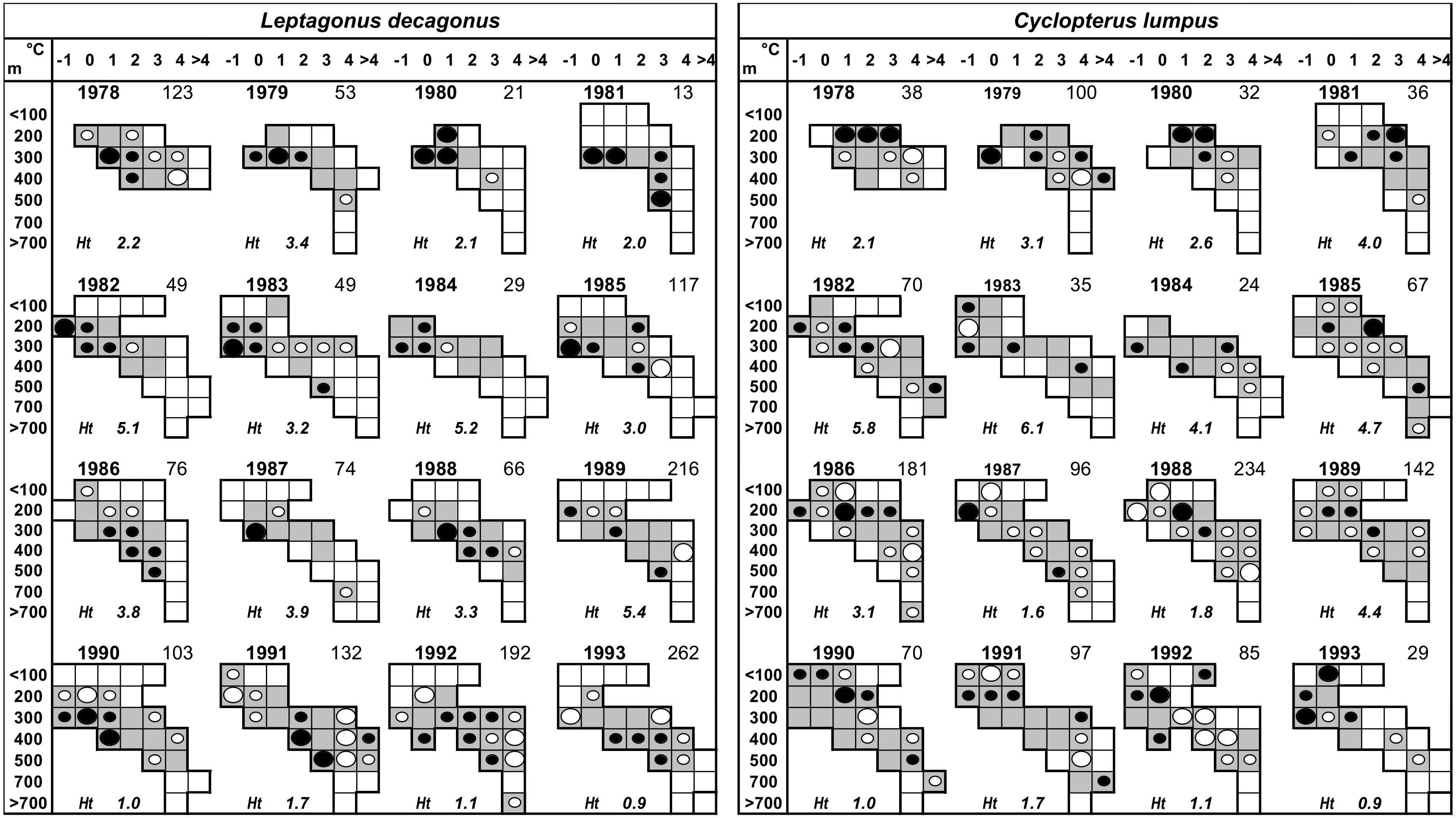

Fig. 11. Realized annual niche space of analyzed species. Temperature categories (1°C width, starting with <-1°C to >4°C) run from the left to the right corner, depth categories (100 m width, starting with <100 m to >700 m) from the upper corner down. The upper left number in each annual figure indicates years. The upper right number in each annual figure gives total catch numbers in each year. Annual *Ht* values are given at the bottom of each annual figure. Each figure has a unique shape representing the sampled niche space in a given year. White fields indicate space where the species in question was never caught. Grey fields indicate presence of the species in question. Open circles = avoidance, black circles = preference; small circles = week avoidance or preference ($\gamma < |0{,}2|$); large circles = strong avoidance or preference ($\gamma > |0{,}5|$).

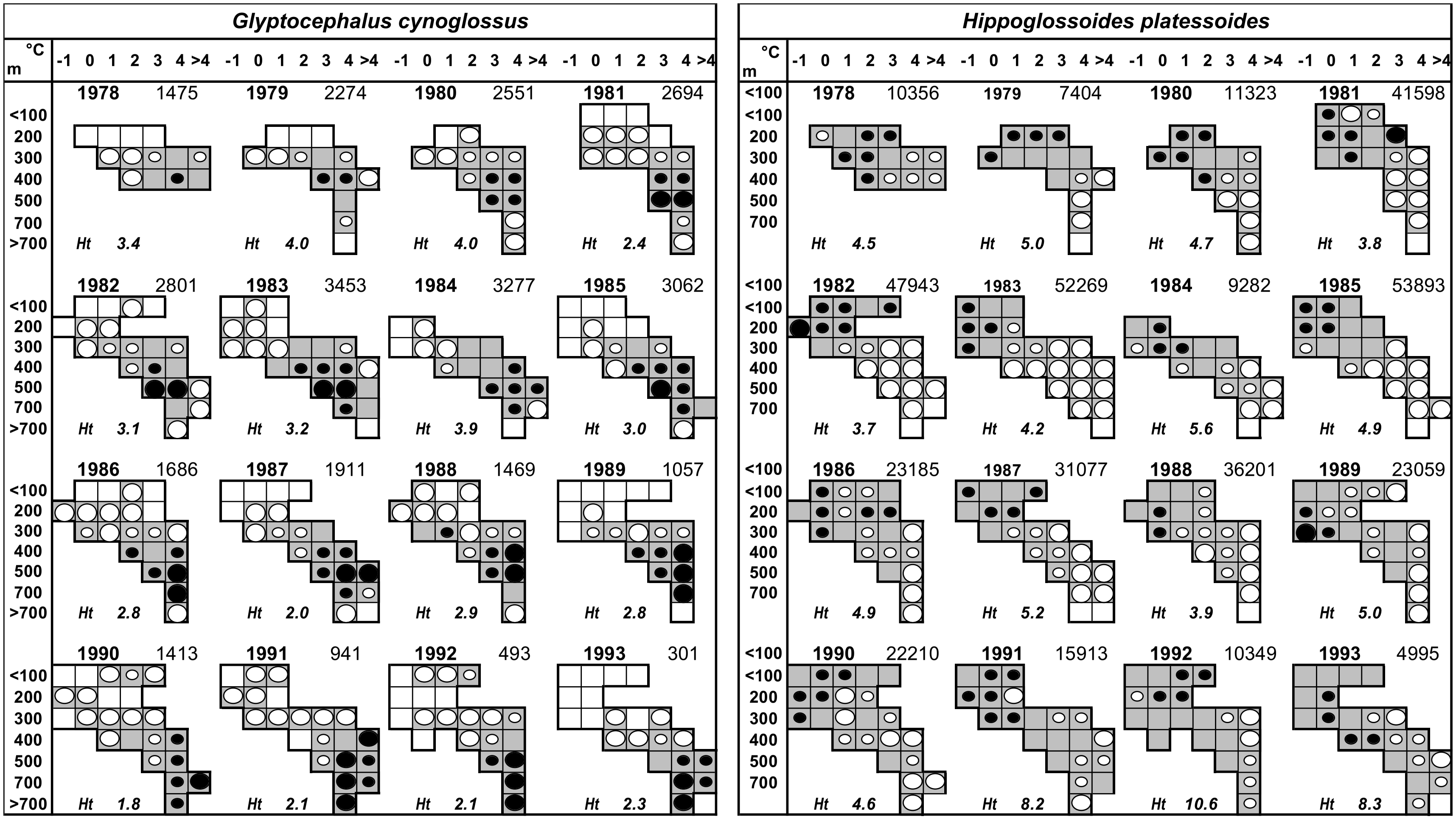

Fig. 12. Realized annual niche space of analyzed species. Temperature categories (1°C width, starting with <-1°C to >4°C) run from the left to the right corner, depth categories (100 m width, starting with <100 m to >700 m) from the upper corner down. The upper left number in each annual figure indicates years. The upper right number in each annual figure gives total catch numbers in each year. Annual *Ht* values are given at the bottom of each annual figure. Each figure has a unique shape representing the sampled niche space in a given year. White fields indicate space where the species in question was never caught. Grey fields indicate presence of the species in question. Open circles = avoidance, black circles = preference; small circles = week avoidance or preference ($\gamma < |0{,}2|$); large circles = strong avoidance or preference ($\gamma > |0{,}5|$).

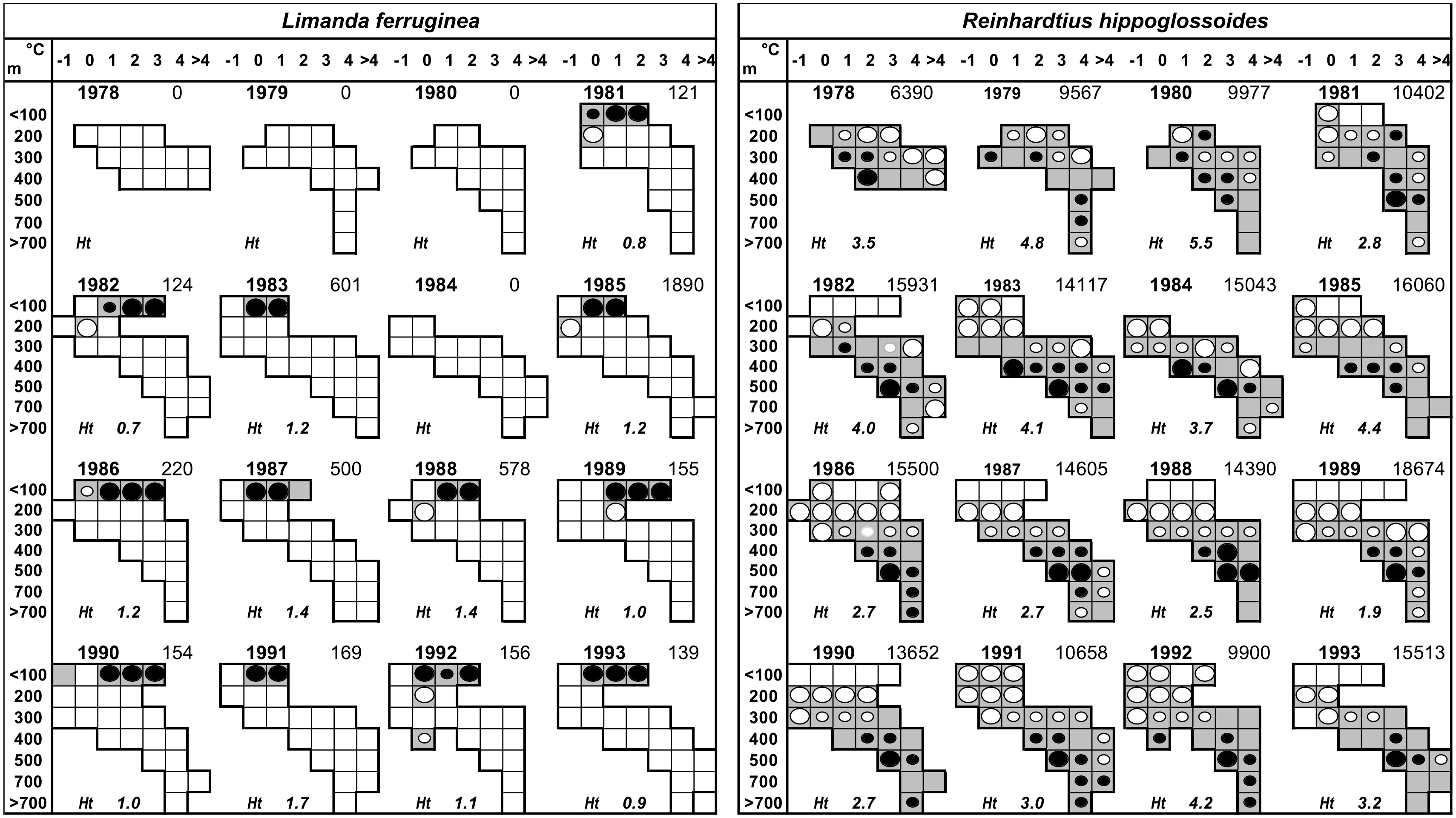

Fig. 13. Realized annual niche space of analyzed species. Temperature categories (1°C width, starting with <-1°C to >4°C) run from the left to the right corner, depth categories (100 m width, starting with <100 m to >700 m) from the upper corner down. The upper left number in each annual figure indicates years. The upper right number in each annual figure gives total catch numbers in each year. Annual *Ht* values are given at the bottom of each annual figure. Each figure has a unique shape representing the sampled niche space in a given year. White fields indicate space where the species in question was never caught. Grey fields indicate presence of the species in question. Open circles = avoidance, black circles = preference; small circles = week avoidance or preference ($\gamma < |0,2|$); large circles = strong avoidance or preference ($\gamma > |0,5|$).

like black dogfish, blue hake, roundnose grenadier, marlin spike, and Arctic deep-sea sculpin. None of these species displayed a shift towards more shallow grounds. A drift towards deeper grounds in these species would not have been detected in this study because sampling effort usually did not exceed 1 000 m.

For Atlantic cod, shifts in temperature and depth preferences on the Newfoundland shelf or neighbouring areas have been analysed before. Swain (1993) reports age-dependent density/depth correlation for Atlantic cod in the southern Gulf of St. Lawrence where younger cod were found in shallower water than were older cod. He attributed this pattern to varying strategies of resource utilisation. On the Newfoundland shelf, since 1978 the average age of Atlantic cod has declined steadily (Hutchings and Myers, 1994). Based on the results of Swain (1993), a shift in realized niche space towards more shallow waters could have been expected. However, realized niche space shifted to deeper areas, indicating that common resource use strategies probably did not apply in this case. Another important species on the Newfoundland shelf is capelin, a key prey species for many larger animals, e.g. Atlantic cod. The decline of capelin in the area since the late-1980s has been discussed as a possible factor contributing to the decline of Atlantic cod (Rose *et al.* 1994). Nakashima (1996) hypothesises that cooler water temperatures in the 1990s are the predominant reason for changes in capelin behaviour, distribution, and biology that have been observed since 1991. We therefore expected to find capelin in a relatively warm temperature niche. The contrary was true. Our data indicated that in most years a relatively large temperature-depth niche for capelin with frequently pronounced preferences for very cold temperatures below 0°C (e.g. in 1981, 1985, and 1988 to 1991) and general avoidance of temperatures above 3°C (Fig. 4).

An interesting question in connection with general deep-water shifts regards the trends over time in the *Ht* values (Table 1). The *Ht* value serves as an indicator for the size/width of the realized niche space. A large *Ht* indicates that the species in question occupies a broad temperature/depth spectrum whereas a small *Ht* points to a sharp selection of a few particular temperature/depth locales by a given species. Shifts in realized niche space such as the observed trend towards deeper waters can be the result of either niche space expansion or niche space reduction of the species concerned. An expansion of realized niche width is caused by more even distribution over the available niche space, e.g. over the total depth range, of a species and is indicated by larger *Ht* values over time. An increase of *Ht* values in connection with deep-water shifts was observed in only three cases, with statistically significant positive *Ht* trends in Arctic cod and American plaice, and non-significant but still conspicuous positive trends in northern alligatorfish. A reduction of realized niche space takes place when a species no longer occupy once preferred areas with specific habitat characteristic, e.g. shallow waters, in which case *Ht* values ought to become smaller. In two-thirds (8 out of 12) of the species exhibiting trends towards deeper grounds, the shift in realized niche space resulted in an overall reduction of its width. These trends are statistically significant in Atlantic cod, roughhead grenadier, broadhead and spotted wolffish, and witch flounder. *Ht* value trends in Atlantic wolffish, deep-sea redfish, and Greenland halibut were not statistically significant, but still suggested that the realized niche space was reduced.

Conclusions

The method described allows visualizing depth/temperature preferences (realized niche space) of fish populations in a given area independent of their abundance. Annual plots show that the realized niche space in various species does not remain fixed but varies from year to year. During the study period, a conspicuous trend towards deeper water was discernible in many species, which may be connected to changes in the environment or to declines in fish abundance. The period 1978 to 1993 was one during which disturbance, from declining sea temperature and heavy fishing effort, increased across the Newfoundland shelf ecosystem (Haedrich *et al.*, 1997, Drinkwater, 1996, Colbourne *et al.*, 1997, Borovkov and Stein, MS 1997). Most fish populations analysed, including both commercial and non-commercial species, suffered a decline in population abundance or average size of individuals, a fact that has been reported in a number of studies (e.g. Sinclair and Murawski, 1997, Haedrich and Fischer, 1996, Taggart, *et al.*, 1994, Haedrich and Barnes, 1997, Bowering and Brodie, 1995).

Ht values reflect the width/size of realized niche space. The analyses showed that the observed trends towards deeper water were mostly accompanied by a significant reduction in the size of realized niche space. We thus conclude that trends in *Ht* values can be used as an indicator for displacements and changing habitat occupancy by continental shelf fishes.

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