Exploitation drives an ontogenetic-like deepening in marine fish

Kenneth T. Frank[a,1], Brian Petrie[a], William C. Leggett[b], and Daniel G. Boyce[a,2]

[a]Ocean and Ecosystem Sciences Division, Bedford Institute of Oceanography, Dartmouth, NS, Canada B2Y 4A2; and [b]Department of Biology, Queen's University, Kingston, ON, Canada K7L 3N6

Virtually all studies reporting deepening with increasing size or age by fishes involve commercially harvested species. Studies of North Sea plaice in the early 1900s first documented this phenomenon (named Heincke's law); it occurred at a time of intensive harvesting and rapid technological changes in fishing methods. The possibility that this deepening might be the result of harvesting has never been evaluated. Instead, age- or size-related deepening have been credited to interactions between density-dependent food resources and density-independent environmental factors. Recently, time-dependent depth variations have been ascribed to ocean warming. We use a model, initialized from observations of Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf, where an age-dependent deepening of ~60 m was observed, to assess the effect of size- and depth-selective exploitation on fish distribution. Exploitation restricted to the upper 80 m can account for ~72% of the observed deepening; by extending exploitation to 120 m, all of the deepening can be accounted for. In the absence of fishing, the model indicated no age-related deepening. Observations of depth distributions of older cod during a moratorium on fishing supported this prediction; however, younger cod exhibited low-amplitude deepening (10–15 m) suggestive of an ontogenetic response. The implications of these findings are manifold, particularly as they relate to hypotheses advanced to explain the ecological and evolutionary basis for ontogenetic deepening and to recent calls for the adoption of evidence of species deepening as a biotic indicator or "footprint" of warming seas.

ontogeny | fishing mortality | deepening | Heincke's law | cod

A progressive deepening of exploited marine fish species with increasing age or size is commonly observed throughout the oceans. This phenomenon was first brought to scientific attention through field studies of North Sea plaice (*Pleuronectes platessa*) conducted in the early 1900s (1, 2). There, 2-y-old plaice were located at an average depth of 20 m and a progressive size-based deepening occurred such that by age 15 individuals predominantly inhabited depths of about 85 m (*SI Appendix*, Fig. S1). The amplitude of this deepening is similar to that subsequently observed for other North Atlantic species including cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius pollachius*), and several flatfish species (Fig. 1). This "ontogenetic deepening" has been observed so frequently (*SI Appendix*, Table S1) that it has been designated as Heincke's law (2, 3). Indeed, it has been argued (4) that, given the generality of this pattern, it can be considered a fundamental characteristic of fish life history having important evolutionary implications.

Several hypotheses have been advanced to explain Heincke's law, one of which entails a life-history strategy that involves a trade-off between age- or size-dependent growth and metabolism. This growth/metabolism hypothesis assumes that increased longevity and greater energy allocation to reproduction will accrue, and ultimately produce, a higher fitness advantage if larger individuals selectively occupy cooler temperatures, leading to lower metabolic costs (4). A second hypothesis invokes density-dependent habitat selection in which fish occupy the highest-quality habitat available when populations are low. As population density increases, larger individuals move differentially into less-productive

habitat where intraspecific competition is lower (5). In support of this hypothesis, it has been found that larger cod occupied deeper waters when abundance was high, whereas when abundance was low larger cod were found in the shallowest depths and the age-specific bathymetric pattern was weak (6). A third hypothesis argues that predator–prey dynamics involving the interaction between adults and juveniles generates ontogenetic deepening as smaller, younger individuals seek refuge in shallower waters from adults (7). These hypotheses rest on several untested assumptions that can lead to apparent paradoxes. For example, under the second hypothesis, when cod abundance is low and intraspecific competition is reduced, all sizes would be expected to prefer habitats with the highest resource level, typically in shallow water (8–10). However, why would only larger cod shift to deeper, less-productive waters when abundance and competition for resources increases?

Recently, several researchers have hypothesized that a progressive deepening (range from 5–10 m per decade) and/or a poleward redistribution (10–80 km per decade) of exploited fish assemblages in the extratropical regions of the North Atlantic is a response to their efforts to maintain thermally optimal habitats during climate-driven ocean warming (refs. 11–17 and *SI Appendix*, Table S2). Reports of correlations between deepening and temperature increases are so widespread that it is now being advanced as a biotic indicator or "footprint" of warming seas (18, 19).

Significance

The occupation of progressively deeper waters with increasing size and age of fish is common among commercially exploited species, a behavior attributed to evolved ontogenies. Recently deepening has been attributed to ocean warming. We evaluated the possibility, ignored in previous analyses, that these patterns result from selective exploitation of larger individuals. We found that size-selective exploitation accounted for >70% of the deepening of cod on the Scotian Shelf (Northwest Atlantic). This deepening declined dramatically when exploitation was banned. Ontogeny contributed to the remaining variance. The claim that deepening can be used as an index of ocean warming should be exercised with caution; the overarching effect of exploitation should be specifically addressed in all such analyses.
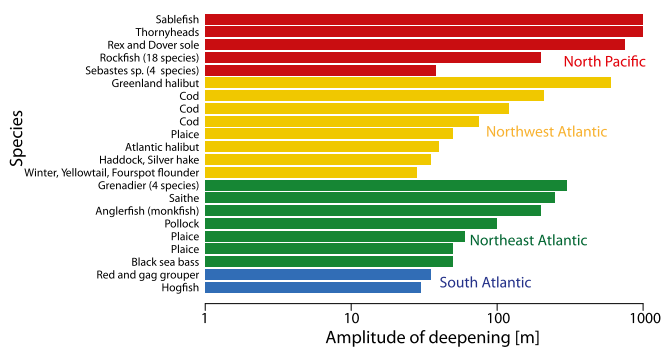
Fig. 1. Amplitude of deepening among fish species/species complexes distributed across the North Pacific, Northwest Atlantic, Northeast Atlantic, and South Atlantic commonly interpreted as being due to ontogeny. In some instances, where a range of depths is reported, averages are shown. Typically the deepening is based on the difference in depth distribution of juveniles and adults involving several age and/or size groups. See *SI Appendix*, Table S1 for details.

Notable among the studies above is a focus on extrinsic forcing and a general failure to consider intrinsic processes associated with ontogeny despite the long history of published studies on ontogenetic migrations. Barbeaux and Hollowed (20), who argued that when it comes to the analysis of climate variability and fish distributions "ontogeny matters," recently highlighted this oversight. A further limitation is that the more recent climate-centric interpretations of such distributional shifts are based on bulk biomass or abundance estimates that preclude the analysis of age- or size-related factors (*SI Appendix*, Table S2). This bulk biomass approach could yield a reliable indicator of a climate response if the population age/size structure remains constant. However, this is unlikely given the periodic development of anomalously strong or weak year classes and the reduction of older age classes in populations subjected to high fishing pressure (21). It is possible, though, that recent climate change dominated by a general warming of ocean temperatures could generate a deepening response of fish stocks complementary to ontogenetic deepening.

The assessments of changes in age- or size-specific depth distributions due to ontogeny and/or climate change may be confounded by fishing effects that are size-selective. In this connection, it is noteworthy that all of the reported ontogenetic distributional shifts by marine fishes reported to date involve commercially exploited species. Indeed, even Garstang's (1) and Heincke's (2) defining studies were conducted in an era of major technological change involving a transition to motorized fishing vessels and from beam trawls to much larger otter trawls towed at greater speeds (22). As a consequence, plaice fishing mortalities (F) during the early 1900s ranged from 0.54 to 0.71, levels considerably higher than those currently experienced by the stock. Consequently, any assumption, whether explicit or inadvertent, that even Heincke's observations and the "law" that resulted were unaffected by the potentially biasing effects of exploitation would appear to be unwarranted.

Is it possible that the reported pattern of deepening is a manifestation of size- and age-selective fishing pressure? All of the species reported to exhibit progressive deepening with age have been exploited, and the majority have been subjected to size-selective fishing, largely driven by minimum landing size regulations and reinforced by unit pricing standards. The resulting selective removal of larger, older individuals from shallower waters where fishing is disproportionately concentrated may produce a relationship between age or size and the depth of occupancy (Fig. 2). Here, we evaluate the hypothesis that the apparent age-related deepening of fish depth distributions is a consequence of intensive size-/age-specific exploitation that selectively and differentially

reduces the numbers of older, larger fish from the most heavily fished, typically shallower, waters.

Our primary focus for this evaluation is the cod stock resident on the eastern Scotian Shelf (ESS). It is for this region that Sinclair (23) used 20 y of abundance-at-age observations (1970–1989), before a fishing moratorium on cod exploitation initiated in 1993, to establish a positive relationship between age and depth. He reported that younger cod predominantly inhabited the shallower banks (~80 m) and older cod occurred at greater depths (>120 m; *SI Appendix*, Table S1). He discussed this change in age-specific depth of occurrence in terms of age- (size-) related depth or temperature preferences of cod, or other related variables such as prey distribution, and noted that this age segregation would allow the commercial fishery to selectively target year classes by changing fishing locations. In this area where the commercial fishery is dominated by otter trawls, it is not until age 4 y that cod become broadly susceptible to capture (23).

We evaluated our hypothesis in two ways: (*i*) empirical analysis of 20 y of scientific survey data of ESS cod (*Materials and Methods* and *SI Appendix*, Figs. S2 and S3), the same database employed by Sinclair (23), and (*ii*) a population dynamic model simulating the effects of varying levels of F across different depth ranges and a constant, depth-independent natural mortality (M) on the age-specific depth distribution of cod (*Materials and Methods*).

Results

Empirical Analysis of Age-Specific Depths. Our analyses indicated that during the 1970–1989 period covered by Sinclair, age-specific depth distributions of cod were highly variable. Each age group (ages 4–12 y) occupied a broad range of depths and there was considerable overlap among groups (Fig. 3 and *SI Appendix*, Fig. S4). Four- and 5-y-old cod were, however, more abundant in relatively shallow waters and older cod were distributed across all depths to a maximum of ~370 m with a tendency toward progressively higher abundances in deeper waters. The center of mass
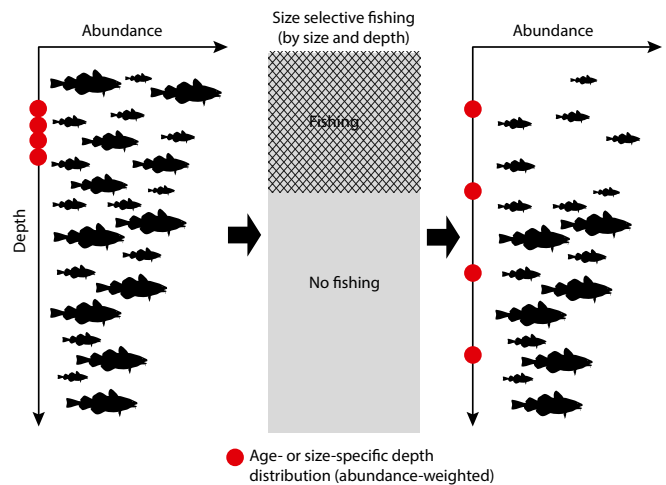

Fig. 2. Schematic illustrating that in the absence of fishing (*Left*) there is a weak or no strong pattern of deepening with size or age in bottom-dwelling fish species. Given that resources are normally higher at shallower depths all sizes of fish, including larger (older) fish, would tend to preferentially inhabit these areas. Fishing has been most often concentrated at shallower depths (e.g., on banks, plateaus, reefs, etc.) and has most often been size-selective (*Middle*). The outcome of this selective fishing (or filtering) can produce an apparent deepening with size or age given the selective removal of larger (older fish) from the shallower regions, whereas at deeper locations only M operates (*Right*). The red circles show the approximate CM of the depth distributions by age or size, illustrating a deepening with age after selective fishing and no strong trend in its absence.
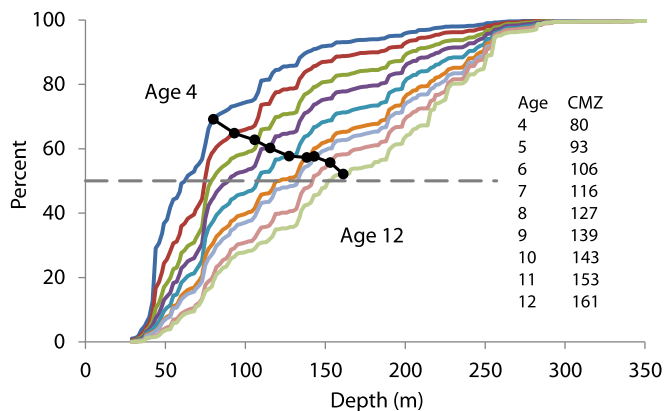
Fig. 3. Cumulative frequency distributions of abundance (number per standardized tow) of ESS cod with the depth of capture for age groups 4 y, the age at which cod become available to the fishery, to 12 y. The curves progress serially from ages 4–12. Data were derived from fishery independent surveys conducted during 1970–1989 (1,691 standardized tows). The black dotted line denotes the depths of the CM; the numerical values are given in the inset.

(CM; *Materials and Methods*) deepened progressively with age from 80 m at age 4 y to 161 m at age 12 y (Fig. 3), consistent with the results reported by Sinclair (ref. 23 and *SI Appendix*, Fig. S5). He also noted that preliminary analyses of the more temporally limited spring (1979–1983) and fall (1978–1982) surveys indicated a pattern of older fish occupying deeper waters (23).

Empirical Analysis of Age-Specific Temperature. There was no appreciable difference in the distributions of cod aged 2 y and older with respect to temperature. The median temperature occupied averaged 3.3 °C with an interquartile range of 2.3–5.0 °C (*SI Appendix*, Figs. S6 and S7 and Table S3). Ages 0 and 1 y were associated with warmer temperatures (median of 7.2 °C and 6.0 °C, respectively), although these age groups are not well-sampled by the survey due to off-bottom behavior and/or residency inshore of the survey area (*SI Appendix*, Table S4). From 1970 to 1989, the bottom temperature on the ESS averaged 5.4 °C with a range of 4.4 °C to 6.8 °C, well within the temperatures associated with cod aged 4–12 y (*SI Appendix*, Fig. S8). These findings too are consistent with those of Sinclair (23), who reported that the median temperatures of capture for cod ages 4–12 y were consistently between 2.4 °C to 3.3 °C with no apparent trend. While the pattern of deepening with age by cod in this ecosystem is consistent with an ontogenetic response, it is also clear that there would be little or no metabolic advantage to such behavior given the absence of any evidence of selective occupancy of progressively colder temperatures with age. The variability of shelf-bottom temperature from 1970 to 1989 was within the range preferred by cod. This precluded the investigation of deepening related to climate warming beyond the cod's preferred temperature range with these data.

Simulation Model Output of Age-Specific Depth at Varying F Levels. The model was initialized with F = 0.52 (1970–1989 average F, ref. 24) applied from 0 to 80 m, M = 0.2 at all depths, and with the observed depth distribution of age 4 cod (Fig. 4 *A* and *B*). Application of the model shows progressive deepening of cod with age to a maximum depth of 136 m for age 12 (Fig. 4 *C* and *D*). Subsequent runs were set up with varying magnitudes of F. At each age the CM of the depth distribution deepened progressively as F increased, the one exception being F = 0, for which no age-related response occurred (Fig. 5*A*). The difference in the CM depth between age 4 and 12 cod varied with F and ranged from 32 m at F = 0.2 to 58 m at F = 1. At F = 0.52, the average

cod mortality during the interval 1970–1989, the difference in the depth of CM between age 4 and 12 was 56 m. These model outcomes are highly consistent with our empirical findings and with those reported by Sinclair (ref. 23 and *SI Appendix*, Fig. S5).
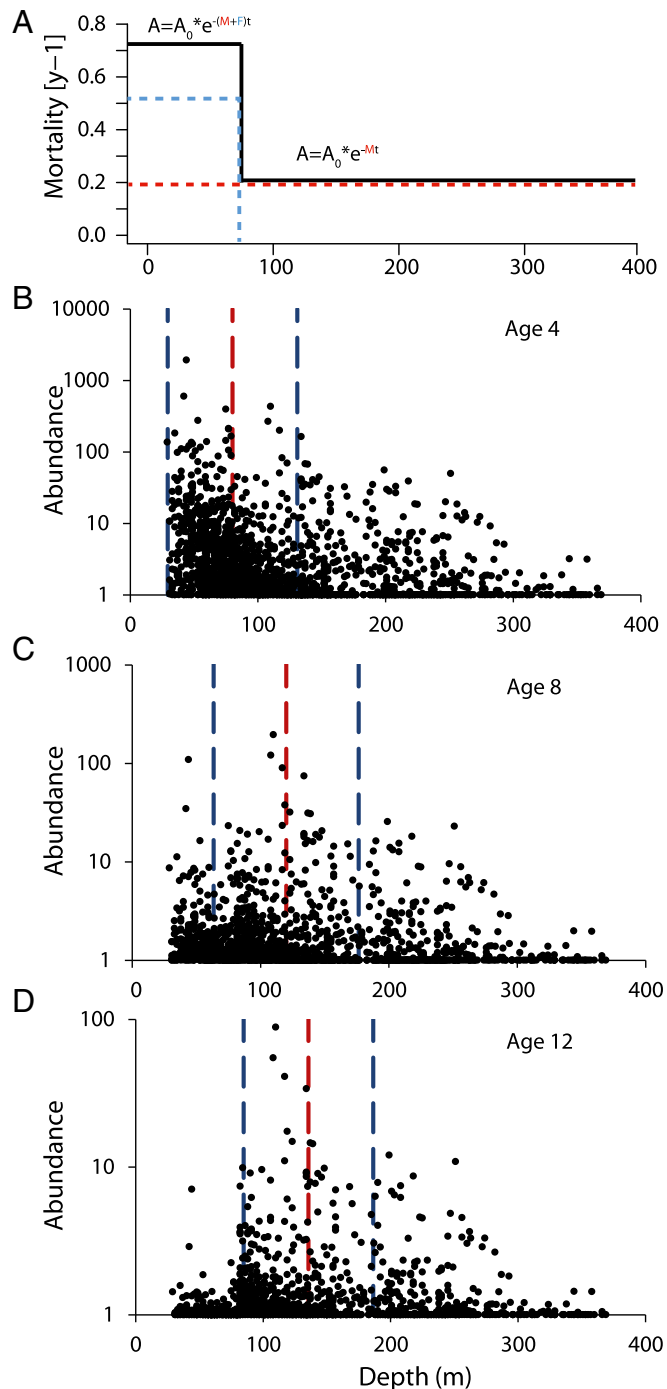

Fig. 4. Description of the simulation model with initial conditions and modeled abundances. (*A*) Schematic of the natural (M = 0.2 at all depths, red dashed line) and fishing (F = 0.52, blue dashed line) mortalities employed in the model. F was applied from the minimum depth of occurrence of cod to 80 m. (*B*) The observed abundances of age-4 ESS cod from the July groundfish surveys 1970–1989 (the initial conditions for the application of the model) and the modeled abundances for (*C*) age-8 and (*D*) age-12 cod after the successive application of the model. The CMs (red) and 95% CI (blue) are indicated by vertical lines. The y axes in *B*–*D* are logarithmic to better illustrate the data. For these plots, 1 was added to the each of the observed abundances.
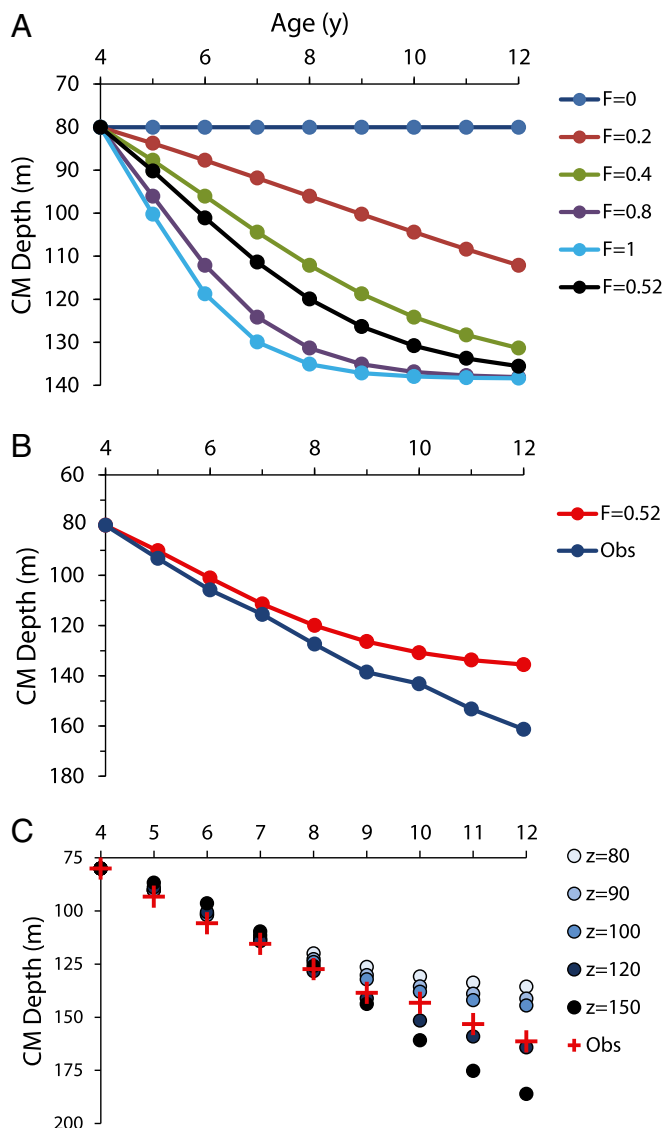
Fig. 5. Simulation model runs and comparison with observations. (*A*) The output of the model showing the CM by age for ESS cod as a function of differing levels of F. (*B*) Comparison of the observed age-specific CM (blue line, dots) and predicted (red line, dots) for the simulation model run with F = 0.52 from 0 m to 80 m during the interval 1970–1989. The modeled CM accounts for 72% of the observed deepening (CM$_{model}$ = 0.72*CM$_{obs}$ + 25, R^2 = 0.98). (*C*) The output from the simulation model showing the effect of extending the depth range over which F = 0.52 applies incrementally to 150 m. The plus signs show the observed age-specific CMs.

Comparison of Observed and Model-Predicted Age-Specific Depths.

The results of our modeling exercise indicated that fishing alone, at F = 0.52 to a depth of 80 m, could account for 72% of the observed age related deepening of ESS cod (Fig. 5*B*). The discrepancy between the observed and simulated CM increases with age (Fig. 5*B*). This is expected given that the abundance of age 4 cod is 14 times greater than that at age 8 and 353 times greater than at age 12, thereby giving rise to greater uncertainty in the estimates of the CM for older age classes. Moreover, it is probable that this error would increase with successive applications of the model as any error at age 5 would propagate through all other age groups. However, the average value of F (0.52) was based on the entire depth range surveyed within the management unit. Consequently, applying this value to the upper 80 m alone would likely underestimate the impact of exploitation. However, increasing

the value of F in our model did not result in a better overall agreement between the observed and simulated results.

Model Output When Extending the Depth Range of F.

Decreased landings over several decades forced fishing fleets to exploit stocks at ever-increasing depths. The annual average fishing depths across the entire North Atlantic increased from 5.5 m per decade during the interval 1950–1989 to 32.1 m per decade thereafter (25). A similar pattern occurred on the Scotian Shelf. From 1970 to 1977 the otter trawl fishery, the dominant contributor to total cod landings, was primarily focused on the shallow banks, whereas the longline fishery, the second-largest component and accounting for 11% of cod landings, was characterized by greater effort in deeper waters. During the interval 1978–1989, the contribution of the longline fishery to total landings had increased to 20% (ref. 23 and *SI Appendix*, Fig. S9). In addition, reported depths of cod catches by commercial trawlers operating on the ESS revealed an increase in the average set depth from 73 m in 1986 to 132 m in 1989 (*SI Appendix*, Fig. S10). It is also apparent that some fishing occurred at depths up to ~150 m.

We therefore examined the effect of this deepening of the fishing effort on estimates of the age-specific CMs of the ESS cod stock. These simulations revealed that moving the fishery into progressively deeper waters resulted in a deepening of the CMs (Fig. 5*C*). Extending F of 0.52 from the minimum depth of cod occurrence to 120 m resulted in a slight overestimation of the observed deepening by about 10% (the slope of the linear fit is 1.1, R^2 = 0.99; best fit at ~110 m, slope = 1.01, intercept = −2.8 m, and R^2 = 0.996), which improved the correspondence between simulation output and empirical observations (Fig. 5*C*).

Empirical Support for Depth Response When F = 0.

No changes in the age-dependent cod depth distributions were evident in the simulation employing F = 0 and a constant, depth-independent M (Fig. 5*A*). We therefore analyzed data on cod distributions derived from the 2006–2016 surveys, during which F = 0 and when the cod population was exhibiting the first signs of recovery from its near-total collapse in 1992 (26). The systematic, well-separated cumulative abundance distributions of 1970–1989 when F = 0.52 differed markedly from the compressed, overlapping distributions of 2006–2016 (Figs. 3 and 6). The progressive deepening from 80 to 161 m
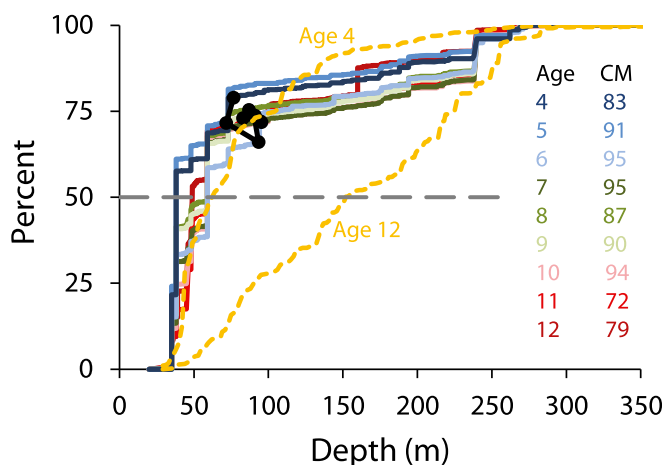

Fig. 6. Cumulative frequency distributions of abundance (number per standardized tow) of ESS cod with depth of capture for age groups 4 y to 12 y. Data were derived from fishery independent surveys conducted during 2006–2016 (969 standardized tows). The black dotted line denotes the depths of the CM; the numerical values are given in the inset. The two broken yellow lines are the envelope (age 4 and 12) of the cumulative percent distribution for 1970–1989 (time interval of high exploitation) from Fig. 3.

Age	CM
4	83
5	91
6	95
7	95
8	87
9	90
10	94
11	72
12	79

(ages 4–12, slope = 10 ± 0.4 m·y⁻¹ based on CM depths) of the earlier period contrasts with the overall shallowing (slope = −1.5 ± 1 m·y⁻¹) during the 2006–2016 period. Moreover, we note that the more complex response for the later period could be decomposed to a weaker deepening from 83 to 95 m for the younger fish (ages 4–7, slope = 3.9 ± 1.4 m·y⁻¹) and a tendency for shallowing with increasing age for ages 7–12. The deepening response of the younger fish could be a manifestation of ontogeny, whereas for the older fish it might reflect a repopulation of the more productive shallower ESS waters after a prolonged period without recovery following the initiation of the moratorium (26, 27).

Discussion

Heincke (2) concluded that "the size and age of the plaice in a definite part of the North Sea are inversely proportional to the density of their occurrence, but directly proportional to the distance of the locality from the coast, and to its depth." Repeated observations of a similar nature for a wide variety of fish species have led to the conclusion that this pattern represents a universal ontogenetic trait that has come to be known as Heincke's law (3).

Our analyses provide strong support for our hypothesis that the widespread reports of age-/size-related deepening of larger fishes characterized as Heincke's law can be, in large measure, of size-selective exploitation. By extension, these findings call into question the veracity of the several hypotheses advanced to date which invoked an evolved, selective basis for the development of age-/size-specific patterns of deepening. The tendency for larger fish to be present at all surveyed depths, albeit at lower densities in shallower waters relative to smaller fish, as revealed in our study and others (28–32) provides further support for the selective fishing effect hypothesis.

Our modeling and empirical evaluations of the expected and realized distribution of cod on the Scotian Shelf when F = 0, the condition prevailing during the moratorium imposed on exploitation of this species from 1993 to present, suggest that there may also be ontogenetic component to the deepening, at least for younger fish, of as much as 3.9 m·y⁻¹, compared with the earlier period (1970–1989) when the deepening rate was much greater (10 m·y⁻¹) and both ontogeny and fishing were factors driving the depth distribution of cod.

In further support of the size-selective exploitation hypothesis, direct observations of habitat occupation derived from data storage tags deployed on individuals of several discrete cod stocks distributed across the North Atlantic indicate that cod often occupy water temperatures shown experimentally to be suboptimal for growth (33, 34). They also frequently fail to move systematically closer (vertically or horizontally) to thermal optima as defined by laboratory studies (35). Further, our analyses of the temperature distributions of ESS cod revealed that the cod aged 2–12 y occupied essentially the same temperatures, thus revealing no tendency toward age-specific temperature preferences that would lead to ontogenetic differences in depth distributions and enhanced metabolic benefits. The median temperature occupied varied by only 0.5 °C and ~80% of all cod occupied temperatures ranging from 1.3 °C to 7 °C (*SI Appendix*, Figs. S6 and S7 and Tables S3 and S4). It should be noted also that some cod of all ages occupied temperatures ranging from below 0 °C to the low to mid teens.

We note that our primary dataset from 1970 to 1989 was during a period when ocean bottom temperature remained within the cod's preferred range. Consequently, we could not explore the potential of long-term warming in particular to drive a deepening response in the stock as a whole. Even if a warming were observed our analysis indicates, given the survey design, that 13–14 y of data (*SI Appendix*, Table S5) are required to achieve reliable estimates of biomass-related parameters such as the CM.

It is also notable that the seasonal temperature variations at depths ≥65 m during the North Sea studies of plaice depth distributions during the early 1900s (1, 2) were also small, from 0.7 °C to 1.8 °C (*SI Appendix*, Fig. S1). As was the case for 2- to 12-y-old cod on the ESS (*SI Appendix*, Fig. S7), plaice ranging in weight from ~500–900 g were all found in this nearly isothermal environment (*SI Appendix*, Figs. S1 *B* and *C*). It thus would appear that the hypothesis that these plaice were exhibiting an age-/size-specific search for preferred temperatures is questionable. Collectively, direct in situ behavioral observations (33–35) of cod distributions with respect to temperature, our detailed empirical observations of the pre- and postmoratorium temperature related distributions of cod on the ESS (*SI Appendix*, Fig. S7), and the results of our simulation studies raise serious questions regarding the assumption, common to virtually all contemporary studies of distributional changes of commercially exploited demersal fish species (*SI Appendix*, Table S2), that individual species, and indeed individual age/size classes within species, actively seek to remain within their thermal optima, in the latter case leading to ontogenetic deepening.

Given the greater availability of food resources in shallower waters (8–10), the model result that cod depth distributions, regardless of age, were uniform with depth when F was set at 0 was generally supported by our analysis of the depth distributions of cod during the recovery era when a fishing moratorium on the ESS existed. The estimated average CM across age groups was 87 m with a range of 23 m (Fig. 6). This result favors the hypothesis that all age/size classes would seek to exploit the feeding advantage associated with shallow bank habitats (36) and that, in the absence of size-selective exploitation, relatively uniform size/depth distributions should prevail. A recent analysis of 16 y of annual bottom trawl survey data from the Rockall Trough (Northeast Atlantic), coincident with a time of greatly reduced fishing effort, revealed a reoccupation of large-bodied fishes within the shallowest depth zone where most of the fishing pressure had been concentrated (37).

Moreover, and perhaps most importantly, our findings, which demonstrate that the age-/size-related deepening frequently observed in commercially exploited species can be a direct result of size-selective harvesting, call into serious question the assertion that species-specific deepening is, and therefore can be used as, an indicator/index of biological effects of ocean warming linked to climate change. Ontogenetic factors, fisheries exploitation, and climate variability must be considered before deepening or any other spatial adjustment of populations/assemblages can be attributed to any of these mechanisms.

Materials and Methods

ESS Cod Observations. We approached this question by first reviewing 20 y of annual Department of Fisheries and Oceans Canada scientific survey data (1970–1989). The survey is based on standardized tows, a stratified random design, and has been conducted on the ESS (Northwest Atlantic Fisheries Organization division 4VsW) of the Northwest Atlantic off Nova Scotia every summer (July) since 1970 (38). Sampling occurred at bottom depths ranging from ~29–369 m (*SI Appendix*, Fig. S2A). The average number of sets per year is 85 ± 9 (SD), with a range of 43. This can lead to significant spatial gaps in any 1 y with large areas not sampled, for example, the central inshore area and the outer bank in the southeast quadrant in 1971 (*SI Appendix*, Fig. S2B). The depth distribution of bottom trawl sets across the ESS closely reflects the distribution of depths from bathymetric mapping (*SI Appendix*, Fig. S3).

Evaluation of Cod Depth Distribution Based on the CM. Several different metrics have been used to determine a characteristic depth for the fish species under investigation. Dulvy et al. (12) used the center of the distribution estimated as the mean latitude/depth weighted by the natural log of the mean abundance in their defined areas (*SI Appendix*, Table S1). Sinclair (23) used catch-per-tow adjusted to a standard tow length of 3.24 km; numbers at age of cod were calculated on a tow-by-tow basis. Abundances were weighted by the ratio of stratum area and the number of tows in each stratum on an annual basis. Our metric differs from that of ref. 23; we use the CM of the distribution to characterize the depth of cod-at-age (Eq. **1**). Moreover, we take each set as an independent measure of the population density and accord it a weight of 1:

$$CM = \left\{ \sum_{n=1}^{1,691} A_n * Z_n \right\} \Big/ \left\{ \sum_{n=1}^{1,691} A_n \right\}, \qquad [1]$$

where A_n (Z_n) is the abundance (depth) for set n. There were 1,691 standardized sets.

Modeling the Effect of Exploitation. We used a simple population dynamic model to generate successive abundances at age and the age-specific CMs at depth as a function of instantaneous F (Fig. 4*A*). The model was defined as

$$dA/dt = -(M + F)A, \qquad [2]$$

where A is abundance and t time. Eq. **2** has the solution

$$A(age + 1) = A(age) * e^{-(M+F)t}, \qquad [3]$$

where age = 4–11. The model was initialized to reflect (*i*) the depth distribution of the age-4 population, the youngest cod available to the fishery on the ESS, as assessed in annual research surveys and (*ii*) the age-specific selectivity of the dominant gear type (trawlers) for cod (ref. 23 and *SI Appendix*, Fig. S9). The distribution of age-4 cod available to the fishery over the period 1970–89 was based on all (1,691) standardized sets used by ref. 23. The population model solution (Eq. **3**) was applied successively to all sets using the observed age-4 distributions as the initial conditions. In the model, we used a constant M of 0.2 over all depths sampled in the research surveys. A sample solution is provided in *SI Appendix*, Fig. S11. The depth of the ESS banks, where the mobile gear fishery predominantly operates, averages ~80 m (23). Fs of 0, 0.2, 0.4, 0.52 (the average F for 1970–1989; ref. 24), 0.8, and 1.0 were used to generate successive cod abundances by age (Fig. 4*B*) over all depths to a maximum of 80 m. The value of F was set at 0 for all depths >80 m. The model simulation yielded a prediction of the depth of the CM for each individual age group (ages 5–12) for each of the F values evaluated. The effect of extending the depth range to 90, 100, 120, and 150 m over which F = 0.52 applies was also evaluated.

1. Garstang W (1909) The distribution of the plaice in the North Sea, Skagerrak and Kattegat, according to size, age and frequency. *Rapp Cons Perm Int Explor Mer* 1: 136–138.
2. Heincke F (1913) Investigations on the plaice. General report 1. Rapports et Procès-Verbaux des Réunions (International Council for the Exploration of the Sea, Copenhagen), Vol 17.
3. Cushing DH (1975) *Marine Ecology and Fisheries* (Cambridge Univ Press, Cambridge, UK).
4. MacPherson E, Duarte CM (1991) Bathymetric trends in demersal fish size: Is there a general relationship? *Mar Ecol Prog Ser* 71:103–112.
5. MacCall AD (1990) *Dynamic Geography of Marine Fish Populations* (Univ of Washington Press, Seattle).
6. Swain BP (1993) Age- and density-dependent bathymetric pattern of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. *Can J Fish Aquat Sci* 50: 1255–1264.
7. Methratta ET, Link JS (2007) Ontogenetic variation in habitat associations for four flatfish species in the Gulf of Maine-Georges Bank region. *J Fish Biol* 70:1669–1688.
8. Tumbiolo ML, Downing JA (1994) An empirical model for the prediction of secondary production in marine benthic invertebrate populations. *Mar Ecol Prog Ser* 114: 165–174.
9. Kedra M, Renaud PE, Andrade H (2017) Epibenthic diversity and productivity on a heavily trawled Barents Sea bank (Tromsøflaket). *Oceanologia* 59:93–101.
10. Bolam SG, Barrio-Frojan CRS, Eggleton JD (2010) Macrofaunal production along the UK continental shelf. *J Sea Res* 64:166–179.
11. Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science* 308:1912–1915.
12. Dulvy NK, et al. (2008) Climate change and deepening of the North Sea fish assemblage: A biotic indicator of warming seas. *J Appl Ecol* 45:1029–1039.
13. Nye JA, Link JS, Hare JA, Overholtz WJ (2009) Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Mar Ecol Prog Ser* 393:111–129.
14. Lenoir S, Beaugrand G, Lecuyer E (2011) Modelled spatial distribution of marine fish and projected modifications in the North Atlantic Ocean. *Glob Change Biol* 17: 115–129.
15. Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA (2013) Marine taxa track local climate velocities. *Science* 341:1239–1242.
16. Hollowed AB, Sundby S (2014) Ecology. Change is coming to the northern oceans. *Science* 344:1084–1085.
17. Kleisner KM, et al. (2016) The effects of sub-regional climate velocity on the distribution and spatial extent of marine species assemblages. *PLoS One* 11:e0149220.
18. Scheffers BR, et al. (2016) The broad footprint of climate change from genes to biomes to people. *Science* 354:aaf7671.
19. Pecl GT, et al. (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* 355:1–9.
20. Barbeaux SJ, Hollowed AB (2017) Ontogeny matters: Climate variability and effects on fish distribution in the eastern Bering Sea. *Fish Oceanogr* 27:1–15.
21. Anderson CNK, et al. (2008) Why fishing magnifies fluctuations in fish abundance. *Nature* 452:835–839.
22. Rijnsdorp AD, Millner RS (1996) Trends in population dynamics and exploitation of North Sea plaice (*Pleuronectes platessa* L.) since the late 1800s. *ICES J Mar Sci* 53: 1170–1184.
23. Sinclair AF (1992) Fish distribution and partial recruitment: The case of eastern Scotian Shelf cod. *J Northwest Atl Fish Sci* 13:15–24.
24. Sinclair AF (1996) Recent declines in cod species stocks in the Northwest Atlantic. *Northwest Atl Fish Organ Sci Counc Stud* 24:41–52.
25. Morato T, Watson R, Pitcher TJ, Pauly D (2006) Fishing down the deep. *Fish Fish* 7: 24–34.
26. Frank KT, Petrie B, Fisher JAD, Leggett WC (2011) Transient dynamics of an altered large marine ecosystem. *Nature* 477:86–89.
27. Ellingsen KE, et al. (2015) The role of a dominant predator in shaping biodiversity over space and time in a marine ecosystem. *J Anim Ecol* 84:1242–1252.
28. Jacobson LD, Vetter RD (1996) Bathymetric demography and niche separation of thornyhead rockfish: *Sebastolobus alascanus* and *Sebastolobus altivelis*. *Can J Fish Aquat Sci* 53:600–609.
29. Van Keeken OA, van Hoppe M, Grift RE, Rijnsdorp AD (2007) Changes in the spatial distribution of North Sea plaice (*Pleuronectes platessa*) and implications for fisheries management. *J Sea Res* 57:187–197.
30. Head M, Keller AA, Bradburn M (2014) Maturity and growth of sablefish, *Anoplopoma fimbria*, along the U.S. west coast. *Fish Res* 159:56–67.
31. Mitchell WA, et al. (2014) Depth-related distribution of post-juvenile red snapper in southeastern U.S. Atlantic Ocean waters: Ontogenic patterns and implications for management. *Mar Coast Fish* 6:142–155.
32. Bacheler NM, Ballenger JC (2015) Spatial and temporal patterns of black sea bass sizes and catches in the southeastern United States inferred from spatially explicit non-linear models. *Mar Coast Fish* 7:523–536.
33. Björnsson B, Steinarsson A (2002) The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 59:494–502.
34. Lafrance P, Castonguay M, Chabot D, Audet C (2005) Ontogenetic changes in temperature preference of Atlantic cod. *J Fish Biol* 66:553–567.
35. Righton DA, et al. (2010) Thermal niche of Atlantic cod *Gadus morhua* limits, tolerance and optima. *Mar Ecol Prog Ser* 420:1–13.
36. Sherwood GD, Grabowski JH (2016) A comparison of cod life-history parameters inside and outside of four year-round groundfish closed areas in New England, USA. *ICES J Mar Sci* 73:316–328.
37. Mindel BL, Neat FC, Webb TJ, Blanchard JL (2018) Size-based indicators show depth-dependent change over time in the deep sea. *ICES J Mar Sci* 75:113–121.
38. Chadwick EMP, et al. (2007) History of annual multi-species trawl surveys on the Atlantic coast of Canada. *Atl Zonal Monit Program Bull* 6:25–42.

ECOLOGY