COMMENT

Did signals from seabirds indicate changes in capelin biology during the 1990s? Comment on Davoren & Montevecchi (2003)

J. E. Carscadden*

Department of Fisheries and Oceans, PO Box 5667, St John's, Newfoundland A1C 5X1, Canada

In a recent paper, Davoren & Montevecchi (2003a) reported on the interactions between a seabird, the common murre *Uria aalge*, and one of its prey, the capelin *Mallotus villosus*, a forage fish in boreo-arctic waters throughout the northern hemisphere. The authors described common murres as capelin specialists and stated that murres are robust samplers of capelin biology. Although common murres feed intensively on capelin during the murre breeding season when capelin are available, it should be noted that in the absence of capelin, murres can adopt alternate foraging strategies and reproduce successfully (see Carscadden et al. 2002). Davoren & Montevecchi (2003a) examined various biological attributes of capelin collected from common murres when they returned to the breeding colony, and concluded that 'consistent among all data sources, including signals from murres shown here, are declines in capelin condition and size and delays in spawning times throughout the 1990s' (p. 259). Davoren & Montevecchi (2003a) contains weaknesses in both data collection and data analyses; as a result, these conclusions are not supported by the data analyses. Furthermore, the authors drew several conclusions about capelin biology and the physical environment, based partly on published studies, which require clarification. The authors also develop hypotheses that were not supported by the data available.

BIOLOGY OF CAPELIN AND MURRES

Data collection

The annual sampling periods for capelin were short in Davoren & Montevecchi (2003a, their Table 1) compared to the potential residency period of capelin in a given spawning area. For example, at Bellevue Beach, a major capelin spawning area (see e.g. Nakashima & Wheeler 2002), the residency period of mature capelin ranges over at least 3 wk. In 2000, capelin spawned over a period of about 3 wk (Nakashima & Wheeler 2002) and in 1993, capelin spawned over a 40 d period (Carscadden et al. 2002, their Fig. 2). These ranges represent only the beginning and end of actual spawning events, as capelin are resident inshore for longer periods (e.g. Atkinson & Carscadden 1979). In contrast, Davoren & Montevecchi (2003a) collected capelin over periods ranging from a low of 3 d in 1991 to a high of 13 d in 1998 (their Table 1). Thus, the duration of sampling was probably significantly shorter than the time period during which capelin were available to foraging murres, and there is no indication in the paper when the samples were collected relative to the capelin maturation and spawning cycle. These data must be considered in the context of the breeding cycle of murres, a point made by the authors. As the chick rearing period lasts about 3 wk, capelin sampling as described was inadequate relative to the murre breeding cycle. Thus, the results reported by Davoren & Montevecchi (2003a) may have reflected the diets of the birds on the days of sampling, but probably did not reflect the total diet nor describe the characteristics (length, weight and condition) of the capelin delivered to the chicks throughout the entire murre breeding season. In the 'Discussion' (p. 258) the authors noted that 'the variability in the percentage of gravid capelin delivered to murre chicks is consistent with the increased irregularity in the timing of major spawning events of capelin, as well as the protracted spawning period throughout the 1990s (Nakashima 1996, Carscadden & Nakashima 1997).' However, the variability in the percentages of gravid capelin may have been an artifact of sampling duration and timing rather than a reflection of capelin spawning variability.

*Email: carscaddenj@dfo-mpo.gc.ca

Davoren & Montevecchi (2003a) stated that fish were categorized as belonging to one of 2 maturity stages, either gravid or spent-immature. Spent and immature capelin were grouped into 1 category because it was not always possible to discriminate between these 2 stages. There is no problem with this, since it is indeed difficult to discriminate between spent female capelin and immature capelin (spent males are easy to identify because they retain the secondary sexual characteristics for some time after spawning). Males were virtually ignored since they were reported to have been present only in small proportions among the capelin recovered from the birds. The authors never explain how the spent-immatures were sexed, which must have been done to determine the sex ratios reported in the paper. The determination of sex in immature capelin is often difficult.

Davoren & Montevecchi (2003a, their Table 2) presented results for female capelin, gravid capelin and spent-immature capelin. In the 4th paragraph of the 'Results', there were references to the decline in the size of 'all female capelin' and the decline in 'condition of female capelin' (their Table 2 and Fig. 4b). If, as stated, samples were grouped into 2 maturity stages, namely gravid and spent-immature, it is not clear what fish were included in the analysis of 'female capelin'. Two possibilities exist to explain this grouping: (1) The female category was composed of gravid and spent-immature combined; if so, this combination has the possibility of including immature males. (2) There was another maturity category for female capelin that was not defined in the paper, and analyses were reported for this category; if this was the case, what was this maturity category and how was it determined? Most probably it was comprised of females that contained visible eggs and were therefore maturing to spawn in that spawning season, but they were not as ripe as those individuals assigned to the gravid category. If this interpretation is correct, then that maturity category should have been defined, with an explanation of the criteria used to categorize gravid female capelin and those females that were less ripe but maturing nonetheless. In summary, there should have been a clear definition of the term 'female' capelin and the sample sizes for this category should have been provided.

The short data collection period during an unknown part of the capelin maturation period, as well as the inadequately defined maturation stages and their grouping in the subsequent analyses severely weaken the results of Davoren & Montevecchi (2003a) and cast doubts on the conclusions drawn later.

The data on murre chick metrics were also collected over a short time period, and this sampling deficiency equally led to potential biases in the results on murre biology. Growth in murre chicks is rapid. They are reared for about 3 wk (Davoren & Montevecchi 2003a), growing from 55 to 95 g at hatching to 170 to 290 g at fledging (Harris & Birkhead 1985), Thus, if body measurements are used to assess interannual differences in condition, the comparisons should be made using the same point on the growth curve each year. Ideally, these measurements should be collected throughout the entire chick period, but lacking this, measurements at a single point in time could be compared as long as the measurements were taken at the same time in the chick growth period. Davoren & Montevecchi (2003a) measured chicks on 1 d each year, between August 4 and 15, over 7 years. However, they did not indicate that the measurements taken on that day were at the same time during the chick rearing period. In fact, this was highly unlikely, given that the murre breeding time shifted towards later in the season in the course of the 1990s, while the sampling periods remained temporally fixed.

Data analysis

Davoren & Montevecchi (2003a) calculated condition for all capelin females, although—as already noted—it is not clear what is meant by 'all females'. As the authors stated, Carscadden & Frank (2002) concluded that Fulton's K was a good descriptor of capelin condition. However, Carscadden & Frank (2002) calculated K using somatic weight (total body weight–gonad weight). This approach was used because gonads develop rapidly during maturation and gonad weight can account for a significant portion of total weight of the female (see Carscadden et al. 1997, their Fig. 2, and Fig. 1 here). Carscadden & Frank (2002) did not include spent fish in their estimations of capelin condition. In contrast, Davoren & Montevecchi (2003a) calculated capelin condition using total body weight including the weight of the gonads. This is inappropriate, since there is no indication that they knew the timing of their sampling in relation to the maturation cycle of capelin. It is plausible that the decline in capelin female condition in Davoren & Montevecchi (2003a, their Fig. 4b) was due to the presence of females with low or zero gonad weight (depending on whether females were in early maturity stages or spent) along with gravid females having higher gonad weights. The proportion of gravid females decreased (as shown in their Fig. 4a) meaning that the proportion of maturing or spent-immature females increased with time, and this could result in a decline in the estimates of condition over time.

This conclusion is supported by their description of the trends in length, mass and condition, all of which declined with time (Davoren & Montevecchi 2003a). If condition declined with time, then weight must have
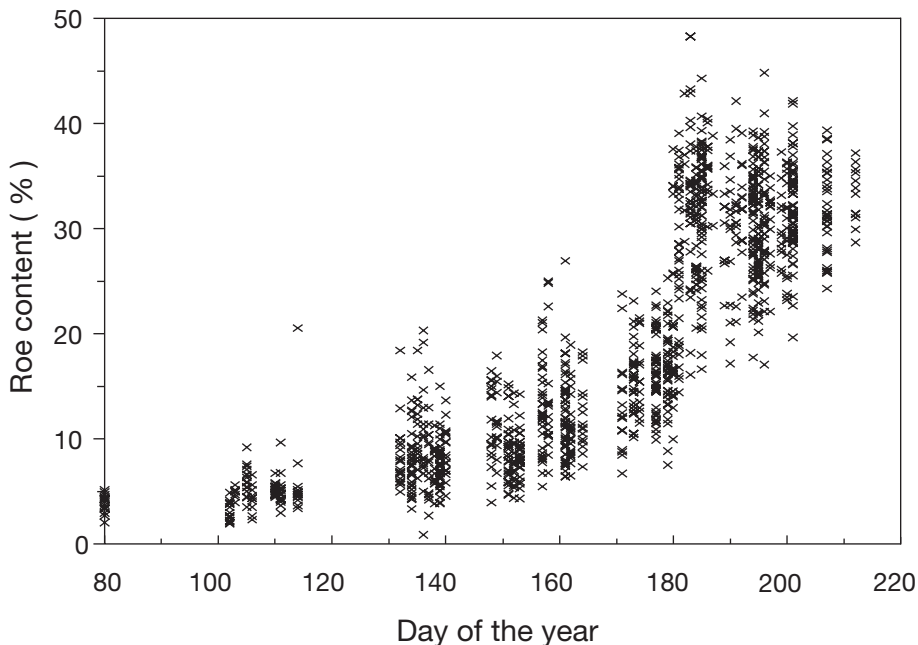
Fig. 1. *Mallotus villosus.* Daily percent roe content [(weight of roe/total weight of fish) × 100] of maturing female capelin off eastern and northeastern Newfoundland in 1998 (data are available for several years; 1998 was chosen randomly)

declined proportionately faster than length, given the method of calculating condition [weight (g)/length (cm)^3]. This relatively rapid decrease in weight over time is consistent with the reported decline in proportion of gravid females coincident with an increase in proportion of maturing and/or spent females.

The declining proportion of gravid females over time in Davoren & Montevecchi (2003a, their Fig. 4a) was probably the main reason why energy per capelin declined over time (their Fig. 4c). Gravid females have large stores of energy-rich eggs and since there was no significant trend of female lengths over time, the declining proportions of gravid females in the samples would be the most likely explanation for the declines in energy per capelin over time.

Davoren & Montevecchi (2003a) also noted that energy per capelin declined throughout the 1990s, coincident with a decline in murre chick condition. The concept that chick condition was declining with declining food energy is a biologically plausible relationship, yet the authors did not attempt to test the relationship for statistical significance (also note the later discussion here on the derivation and biological significance of chick condition in Davoren & Montevecchi 2003a). Perhaps this test was not performed because the energy per capelin calculated did not represent the total energy being delivered to the chicks each year. Although the authors reported that there was no statistically significant trend in proportions of capelin in murre diets over the study period, the actual propor-

tions varied from 74 to 99% annually. Only this range was provided, but even so it is clear that in 1 yr at least a substantial portion of the diet (26%) was composed of food items other than capelin, and the exclusion of these items from the energy calculations will have introduced a degree of bias.

Murre chick condition was expressed as the ratio of chick mass over wing length (Davoren & Montevecchi 2003a), but there is concern regarding the biological significance of this metric. The authors reported a positive linear relationship when data for all years were combined, and they concluded that this ratio provided a robust condition index. It would have been informative for the reader to see the full statistics for the regressions and a plot of the data. It is not clear, for example, that a linear relationship was the most appropriate and a plot of the data would have aided the reader in evaluating such a possibility. Annual tests of the relationships would also be useful to ensure that the relationships did not change annually and that they were significant each year. The authors stated that chick body mass declined and wing length increased throughout the time period. This implies that there was a trend in the residuals of the regression, further strengthening the argument that plots and associated regression statistics should have been presented on a yearly basis, as well as for the entire series.

Perhaps the presentation of a ratio (body mass:chick length) was an attempt to correct for the fact that measurements were made on only 1 d during the chick stage and that there was uncertainty concerning the period in that growth phase in which the samples were collected. However, if this were the case, it was not explicitly stated and Davoren & Montevecchi (2003a) did not present enough data on the body mass:wing length relationship to support the conclusion that it is a robust condition index. Therefore, the chick condition trends in their Fig. 4d should be viewed with caution.

Plots of mass and wing length for fledglings from Funk Island for 2000 were available from Davoren & Montevecchi (2003b, their Fig. 3), as opposed to the nestlings in Davoren & Montevecchi (2003a). The statistics provided for the body mass:wing length relationship were: slope = 2.9 g mm^{-1}, $r^2 = 0.079$, n = 43. This relationship is not statistically significant and the low value of r^2 indicates that very little of the variation in body mass was explained by wing length at the fledg-

ling stage. While it is possible that the body mass:wing length relationship is a good descriptor of chick condition, the lack of detail in Davoren & Montevecchi (2003a) and the lack of a relationship at the fledgling stage raise concerns that this ratio may not be a robust index of chick condition.

Corroboration from other sources

Davoren & Montevecchi (2003a, p. 259) made the point that 'consistent among all data sources, including signals from murres shown here, are declines in capelin condition and size and delays in spawning times throughout the 1990s'. However, there is little support for this generalization. Carscadden & Frank (2002) did show a decline in capelin condition during the 1990s, but the estimation of capelin condition calculated by Davoren & Montevecchi (2003a) may be compromised by inappropriate treatment of the data. As a result, the reported trend (their Fig. 4b) may be an artifact and should be viewed with caution.

Davoren & Montevecchi (2003a, p. 256) also stated that 'the size (length and mass) of all female capelin tended to decline throughout the 1990s'. However, those data were not provided and the regressions of female length and year, and female mass and year (their Table 2) were not statistically significant. On p. 258–259 they stated that 'declining trends in size and condition of capelin delivered to murre chicks through the 1990s were corroborated independently by Fisheries and Oceans data on spawning and juvenile capelin (Carscadden & Nakashima 1997, Ander-
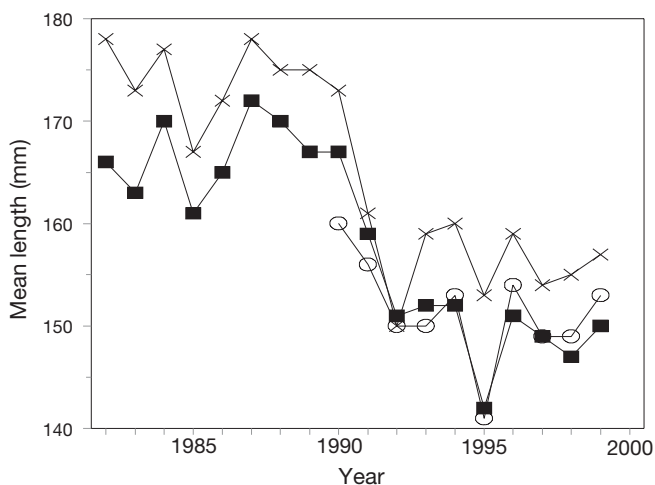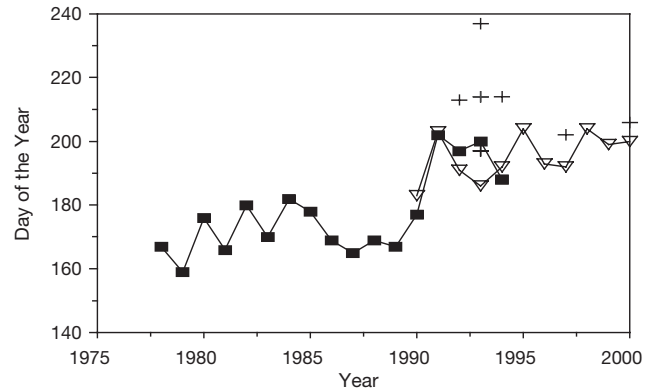

Fig. 3. *Mallotus villosus.* Time of spawning 1978 to 2000. (■) from Carscadden et al. (1997); (▽) earliest spawning of capelin at Bellevue Beach, a major capelin spawning area and site of ongoing research on capelin (e.g. Nakashima & Wheeler 2002); (+) later spawning times at Bellevue Beach

son et al. 2001, Carscadden & Frank 2002)'. Only Carscadden & Frank (2002) presented data on condition factors of capelin. Anderson et al. (2001) presented only length frequencies for larval 1 yr old and 2 yr old capelin, whereas Davoren & Montevecchi (2003a) presented data for predominantly mature capelin delivered to murre chicks. Furthermore, the length frequency plots in Anderson et al. (2001) are embedded in larger figures, making the length frequencies very difficult to read; moreover, mean lengths were not provided and it is impossible to visually estimate mean lengths each year and trends through time from these plots. Carscadden & Nakashima (1997) presented mean lengths only up to and including 1993. Thus, the 'corroboration' of the capelin data from the murre diets with mean length data in the referenced papers was, in reality, not possible.

However, mean lengths of mature capelin were available in studies not cited by Davoren & Montevecchi (2003a). Mean lengths of female capelin were available from Bellevue Beach for 1990 to 1999 (Nakashima & Slaney 2001) and for female capelin from the inshore fishery for 1982 to 1999 (Carscadden et al. 2001a; see Fig. 2 here). In addition, mean length of capelin in the inshore fishery in 1982 to 1999 was also available for both sexes combined (Carscadden et al. 2002; Fig. 2 here). In the longer term data sets, there were obvious differences in mean length between the 1980s and 1990s (discussed below), but during the 1990s no trends are obvious.

The information from previous studies indicates that capelin spawning was delayed throughout the 1990s, compared to earlier periods (Carscadden et al. 2002, their Fig. 2; data reproduced in Fig. 3 here). Davoren & Montevecchi (2003a) showed order of magnitude differences in abundances of breeding murres (their

Fig. 2. *Mallotus villosus.* Mean lengths (mm) of mature capelin. (×) Males and females combined, same data as in Carscadden et al. (2002); (■) females, from Carscadden et al. (2001a). (○) females, from Nakashima & Slaney (2001)

Fig. 3) and attributed the change in 1993 to a change in breeding time, which they explained as an adaptation of the murres to the later spawning of capelin. They further indicated that breeding did not appear to have been delayed in 1991 and 1992, which suggested that the murres could not forecast the timing of capelin spawning in any given year, but that they must have gone through a learning period once prey conditions changed. Thus, if one accepts the links between abundance of murres in early August and breeding time, then the delay in murre breeding first observed in 1993 did not parallel the onset of delayed capelin breeding, which was first evident from direct observations of capelin spawning in 1991 (Carscadden et al. 1997). In fact, the entire argument is somewhat circular. On one hand, the authors suggested that murres learned to delay their breeding within a few years of the onset of late capelin spawning. In 2 other places in their paper, Davoren & Montevecchi stated that the signals from murres indicated the delayed spawning of capelin. It is inappropriate to conclude that murre breeding was delayed by the late spawning of capelin and then use the same data to conclude that the delayed murre breeding was indicative of the late spawning of capelin.

Many aspects of capelin biology changed during the early 1990s and the changes have persisted for several years. Annual variations in each biological character have been small during the 1990s, compared to the differences between the 1990s and earlier periods. In particular, since the early 1990s there have been large and persistent changes in capelin areal distribution (Frank et al. 1996, Carscadden et al. 2001b), vertical distribution (Mowbray 2002), time of spawning (Carscadden et al. 1997, 2002), mean size (Carscadden et al. 2002), and condition (Carscadden & Frank 2002). Davoren & Montevecchi (2003a) provided data relevant to capelin size, condition and spawning time, and while they acknowledged that large changes in capelin biology had occurred, most of their data were collected during the 1990s only. The exception was their conclusion of later capelin spawning derived indirectly from the observations of large numbers of breeding adults present at the colony later in the season. There were no data for capelin length or weight from murre sampling prior to 1991 that would allow comparison to other sources of capelin data. Thus, the authors were unable to demonstrate that the capelin caught by murres reflected the large and significant changes in length and condition that occurred in the early 1990s. Consequently, the information in Davoren & Montevecchi (2003a) does not reflect trends in capelin biology during the 1990s, nor was there information in their study that would show the dramatic changes in capelin biology, which began in the early 1990s.

Conclusions

Davoren & Montevecchi (2003a) state that 'we analyze a 10 yr data series of breeding times, diets and condition of common murres at the largest colony of common murres in eastern North America' and 'we compare these data with other biological and physical indices and use these comparisons to assess the status of capelin in the NW Atlantic' (p. 254). However, the weaknesses in data collection and analyses outlined above cast serious doubts on their conclusions. This is true for conclusions relating to each biological character of capelin discussed, namely, size, timing of spawning and condition. In addition, the conclusions that trends in the capelin data for the 1990s were corroborated by independent data do not withstand closer scrutiny. And finally, because most of their data do not span the time period when the biology of capelin changed most dramatically, they were unable to show that the capelin delivered by murres to their chicks reflected the important changes in biology exhibited by capelin documented elsewhere (size and timing of spawning in Carscadden et al. 2002; condition in Carscadden & Frank 2002) collected from other sources.

The stated purpose of Davoren & Montevecchi (2003a) was 'to assess the status of capelin stocks in the NW Atlantic' by comparing breeding times, diets and condition of common murres with other biological and physical indices. However, it is not clear that the trends in murre condition were ever related to the status of capelin stocks, and the authors never derived any conclusions regarding the status of capelin stocks from the trends in condition of common murres. The one comparison that was made, a regression between chick condition and energy delivered per fish, was not statistically significant. Despite this, the authors devoted an entire section of their paper to chick condition, including speculation on the possible consequences of reduced chick condition to the murre colony.

PREVIOUS STUDIES

Davoren & Montevecchi (2003a, p. 259) stated that 'integration of this information with widely divergent biomass estimates of capelin throughout the 1990s has led to conflicting statements on current stock status (Carscadden et al. 2001b, Rose 2001).' (The information to which the authors referred included the declines in capelin condition, length and spawning times, and reasons for declining size). The 2 papers cited dealt with different topics, and Rose (2001) did not discuss stock status of capelin or abundance of capelin. He made the point that during the period from 1997 to 2000, cod (sampled in inshore Newfoundland)

that had capelin in their diets exhibited higher liver condition (a measure of cod well-being) than cod (sampled on offshore banks of Newfoundland) that did not contain capelin in their diet. Using potential contact analysis, Rose (2001) found that cod on the offshore shelf have had virtually no contact with capelin, whereas in one coastal area (Trinity Bay), cod have maintained contact with capelin and have shown signs of recovery. He concluded that 'a diet high in capelin is likely to be crucial for the recovery of cod stocks in Newfoundland waters'. In this one page report, Rose (2001) provided background references; the full scientific report is in Rose & O'Driscoll (2002).

In an extensive review of capelin in the NW Atlantic ecosystem, Carscadden et al. (2001b) provided the most recent analysis of relative yearclass strengths at that time (their Fig. 3), showing that yearclass strength was at least as strong during the 1990s as during the 1980s. They also noted that there were large statistical uncertainties in the estimates and that there were discrepancies between the trends in the analysis presented, and information from offshore acoustic surveys and inshore trap fishers.

It is unclear to what Davoren & Montevecchi (2003a, p. 259) referred when they mentioned 'divergent biomass estimates of capelin throughout the 1990s'. There was a dramatic and unexpected decline in biomass estimates from Canada's Department of Fisheries and Oceans spring offshore acoustic surveys from the high 1990 to the low 1991 estimate. Biomass estimates from these acoustic surveys have remained low throughout the 1990s, although some caution is in order, since survey coverage has been highly variable (recent information can be accessed in a series of Research Documents and Stock Status reports at www.dfo-mpo.gc.ca/csas/Csas/English/Publications/Index_Pub_e.htm; information on earlier periods can be obtained directly from J.E.C.) However, a decline within a survey series does not warrant the word 'divergence'.

There has been a divergence between the biomass estimates derived from the offshore acoustic surveys and other indicators of abundance (not biomass) collected inshore. When the biomass measured offshore declined between 1990 and 1991, these other indices of abundance did not decline to the extent that would have been expected based on the acoustics results. This dichotomy continued throughout the 1990s. It is not known why offshore acoustic estimates suddenly declined, nor why there was a continuing divergence between the acoustic estimates and the inshore indices of abundance. Nevertheless, the uncertainties surrounding the abundance indices, both offshore and inshore, have been identified (e.g. Anonymous 1998, 1999, 2000) and Carscadden et al. (2002) have called for the resolution of the divergence.

Returning now to the juxtaposition of the Carscadden et al. (2001b) and Rose (2001) references, it can be argued that the results in Rose (2001) and Rose & O'Driscoll (2002) were consistent with the results from the offshore acoustic surveys. The observations that capelin consumption by cod and proximity of cod and capelin in the offshore sector was low (Rose 2001) did not contradict the low acoustic biomass estimates of capelin offshore.

Davoren & Montevecchi (2003a, p. 259) referred to Carscadden & Nakashima (1997) to support the statement that 'the inshore fishery for capelin targets older and larger gravid capelin that arrive first at spawning beaches'. In fact, there is no such statement or allusion to this practice in the referenced paper. The use of the term 'targets' implies that fishermen could selectively harvest larger individuals, while at the same time avoiding the capture of smaller individuals. There is no evidence to indicate that this was or is possible. In fact, during the 1990s, the tendency for larger capelin to arrive prior to small ones lessened (Nakashima 1996; noted by Davoren & Montevecchi 2003a). This meant that there was less likelihood of catching greater proportions of large individuals by fishing early in the spawning run of capelin. The most likely way that fishermen could optimize their returns was to check their catches for marketability of capelin based on size, and then release or discard catches that did not meet market size requirements. This practice of discarding and provoking unnecessary mortality was recognized by management authorities, and fishing was not allowed until a test fishery determined the fish to be acceptable for the market (Carscadden & Nakashima 1997).

HYPOTHESES

Davoren & Montevecchi (2003a) stated that the mass, length and condition factor of female capelin in their study declined with time, although, as previously noted, they did not show the annual mean lengths and weights of capelin. In addition, the relationships between female length and year, and female weight and year were not significant (their Table 2), indicating that there were no significant trends over time. Nevertheless, the authors asserted that the declines they observed were counterintuitive because higher growth would be expected under warm water conditions. While this may be a reasonable hypothesis (however, see the discussion later relating to factors affecting growth), the fact is that during the 10 yr study period (1991 to 2000), temperatures were below normal in 7 of those years and had been below normal since 1984. Although the negative temperature anomalies (their Fig. 2) decreased after 1991 (the year of the most

extreme temperature anomaly), temperatures remained below normal until 1996, slightly below normal during 1997 and 1998 and were above normal during 1999 and 2000. The mature female capelin that the authors sampled would have been at least 2 yr old and the lengths they measured would have represented the culmination of growth up to the time of sampling. Positive water temperature anomalies occurred in 1996, 1999 and 2000. If growth were positively linked to water temperatures then it is only in these years that better growth might be expected. It is plausible that any significant growth associated with the 1996 positive temperature anomaly would not be detectable, given the low sampling frequency in this study and the below-average water temperatures in adjacent years. Any above-average growth in 1999 and 2000 resulting from the influence of the above average temperatures would not become obvious in the mean lengths and weights until after those years.

Davoren & Montevecchi (2003a) presented the hypothesis that larger, older capelin have been removed from the population and that the present population contains a lower proportion of the larger genotype. They further suggested that high fishing mortality in the mid-1970s could have 'influenced the size and age structure of the population' (p. 259) (They acknowledge that fishing quotas have been low since the 1970s, implying that fishing has not been a problem since then.) Is there evidence in the literature to support or refute the hypothesis that high fishing mortality during the 1970s influenced the population structure during the 1990s?

Carscadden et al. (2001b) reviewed the effects of exploitation since the start of the commercial fishery in the 1970s on the stock of capelin occurring in Northwest Atlantic Fisheries Organization (NAFO) statistical Subarea 2 and Divisions 3KL and concluded that exploitation has been minimal. They noted that during the 1970s, fishing mortality rates had been estimated at < 0.1.

Mean length of capelin fluctuated between 160 and 180 mm during 1980 to 1990, then declined abruptly and have fluctuated below 160 mm during 1991 to 1999 (Fig. 2 here). It is clear from the data that capelin were larger in the 1980s, compared to the 1990s. If larger individuals had been removed from the population during the 1970s in large enough quantities to affect the hypothetical genetic structure that determines length, why did this effect not manifest itself until the early 1990s, several generations after the peak of the fishery in the 1970s?

Finally, capelin in the Gulf of St Lawrence also exhibited a decline in mean size during the 1990s, yet the commercial capelin fishery there did not begin until 1978 (Anonymous 2003). During the late 1970s, catches there were less than 10 % of the average catch in NAFO Divisions 2J3KL, 1972 to 1979 inclusive. The similar trends in mean lengths over these wide geographical areas suggest that large-scale environmental changes, rather than exploitation, have been exerting an influence on growth.

Davoren & Montevecchi (2003a, p. 259) stated that 'the changes in capelin biology are not consistent with environmental factors or density-dependent responses, because environmental conditions have returned to pre-perturbation levels and because spawning capelin are both smaller and younger.' Based on the information presented in their paper, it would appear that the authors' reference to 'environmental factors' applies to water temperatures. Based on their Fig. 2 and assuming that they interpret 1991 as the perturbation year, water temperatures were above normal in only 3 of the 9 following years (1996, 1999 and 2000). Furthermore, temperatures were below normal beginning in 1984 and the low temperatures in 1991 represented the nadir of below normal temperatures. On a decadal basis, temperatures in the 1990s were reported to have been below average and the most variable on record (Colbourne 2002). It is, therefore, not clear what the authors meant by 'environmental conditions have returned to pre-perturbation levels'. Given that fish are poikilotherms, the use of environmental variables such as water temperature to explain changes in capelin biology is reasonable. Although Davoren & Montevecchi (2003a) included water temperatures in their statistical testing, there are other environmental variables that might also be important but were not addressed, even as a point of discussion.

One such variable is salinity. The trends in salinity since the early 1990s have been unusual. While ocean temperatures were beginning to warm after the nadir in 1991, surface waters remained fresher than normal. This pattern of warmer, fresher water during the late 1990s and into the 2000s, which is contrary to historical observations (where warmer water temperatures and higher salinity values usually occurred together), has not been explained (Colbourne 2002). The reduced surface salinities during the 1990s have been identified as a cause of increased stratification (Craig et al. 2001), which in turn can reduce vertical mixing, transport of nutrients to the surface, and thereby reduce productivity. Although the potential relationships between capelin biology and changes in salinity and/or stratification have not been investigated, the fact that these physical changes have existed coincident with the changes in capelin biology should not be ignored.

It appears as if the authors equated environmental factors to temperatures, but the food supply of capelin should also be considered as a subset of environmental factors. Unfortunately, the data on zooplankton distribution or abundance in the NW Atlantic are not exten-

sive. The only record with a historical perspective (1959 to 1986, 1991 to 1998) is the database from the Continuous Zooplankton Recorder surveys (cf. Beaugrand et al. 2004), but there are no data for 1987 to 1990 inclusive. These data indicate that the trends in relative abundance of *Calanus finmarchicus*, Stages 1 to 4, and total euphausiids were similar over large geographical areas from the Scotian Shelf to the Grand Banks. During the 1990s these zooplankton groups had lower abundances than during the earlier periods (D. Sameoto, pers. comm., quoted in Carscadden et al. 2001b).

In summary, while the inclusion of many environmental variables in the analysis by Davoren & Montevecchi (2003a) may have been challenging, it would have been appropriate for the authors to at least acknowledge that other environmental variables have been changing coincident with the changes in capelin biology, and that these additional environmental changes might form the basis for reasonable hypotheses to test in future studies.

In the second part of the statement cited above, Davoren & Montevecchi (2003a, p. 259) indicated that ' changes in capelin biology are not consistent with … density-dependent responses, because … spawning capelin are both smaller and younger'. While this general observation about capelin size and age is true for all ages combined, the trend in length has not been obvious when examined for each age. Between 1981 and 1993 inclusive, the mean length of mature 2 yr old capelin did not change, while the length of mature 3, 4 and 5 yr old capelin declined, beginning as early as 1987, with some variation between sexes and among geographical areas (Nakashima 1996). Thus, at least until 1993, growth appeared to have been similar up to Age 2 but had declined at the older ages. It may be that changes in the zooplankton community have been affecting feeding, and ultimately growth, especially when capelin attained a larger size.

Studies on Icelandic capelin suggest that the relative influences of density-dependent and density-independent factors on capelin growth are not clear. Gudmundsdottir & Vilhjalmsson (2002) reported that there was an inverse relationship between the weight-at-age of maturing capelin in autumn and the numbers of adults in the total stock. This observation suggests a density-dependent relationship. However, Vilhjalmsson (2002) reported that capelin average weight, weight-at-age and capelin biomass are higher in warm years, as is zooplankton biomass. In the Barents Sea, where capelin growth has been studied extensively (reviewed in Gjosaeter 1998), various factors, including stock size, water temperature and geographical distribution, are correlated with growth. It appears from the numerous studies on growth of both Icelandic and Barents Sea capelin that there is probably no sin-

gle factor that determines capelin growth and that both density-dependent and density-independent factors are influential.

In the case of Newfoundland capelin, the reasons for the combination of small sizes and younger ages in the spawning stocks are not known. There may be many factors that are contributing to these changes. These may include biological changes such as later spawning of capelin, changes in abundance of zooplankton, changes in capelin distribution (vertical: Mowbray 2002; horizontal: Frank et al. 1996, Carscadden et al. 2002) and changes in the physical environment. It is possible that many of these factors are themselves inter-related, and clear identification of the most influential factors will remain a challenge.

LITERATURE CITED

Anderson JT, Dalley E, Davis D (2001) Year-class strength of Northwest Atlantic capelin (2J3KLNO) estimated as 0-Group (larval), 1-Group and 2+ Group stages from the pelagic juvenile fish surveys, 1994–1999. In: Anonymous (ed) Capelin in SA2+Div. 3KL during 1999. Research Document 2001/161, Canadian Department of Fisheries and Oceans, St. John's, NF, p 209–230

Anonymous (1998) Stock status report capelin in Subarea 2+Div.3KL. Stock status report B2–02, Department of Fisheries and Oceans, Science, Ottawa

Anonymous (1999) Stock status report capelin in Subarea 2 + Div. 3KL. Stock status report B2–02, Department of Fisheries and Oceans, Science, Ottawa

Anonymous (2000) Capelin in SA2+Div 3KL. Stock status report B2–02, Department of Fisheries and Oceans, Science, Ottawa

Anonymous (2003) Capelin in the estuary and the Gulf of St Lawrence (4RST) in 2002. Stock status report 2003/09, Department of Fisheries and Oceans, Science, Ottawa

Atkinson DB, Carscadden JE (1979) Biological characteristics of inshore capelin, *Mallotus villosus* (Muller), June-July 1977. Fish Mar Serv Tech Rep No. 881, Department of Fisheries and the Environment, St John's, NF

Beaugrand G, Edwards M, John A, Lindley A (eds) (2004) Continuous plankton records: plankton atlas of the North Atlantic Ocean 1958–1999. Mar Ecol Prog Ser Suppl 2004: 1–75

Carscadden JE, Frank KT (2002) Temporal variability in the condition factors of Newfoundland capelin (*Mallotus villosus*) during the past two decades. ICES J Mar Sci 59:950–958

Carscadden JE, Nakashima BS (1997) Abundance and changes in distribution, biology and behavior of capelin in response to cooler waters of the 1990s. In: Forage fishes in marine ecosystems. Proc Int Symp Role of Forage Fishes in Alaska. Alaska Sea Grant College Program Rep No 97–01, Fairbanks, AK, p 457–468

Carscadden JE, Nakashima BS, Frank KT (1997) Effects of fish length and temperature on the timing of peak spawning in capelin (*Mallotus villosus*). Can J Fish Aquat Sci 54: 781–787

Carscadden J, Evans GT, Nakashima, BS (2001a) Predicting

mean lengths of female capelin in SA2+Div. 3KL. In: Anonymous (ed) Capelin in SA2+Div. 3KL during 1999. Res Doc 2001/161, Canadian Department of Fisheries and Oceans, St. John's, NF, p 178–182

Carscadden JE, Frank KT, Leggett WC (2001b) Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. Can J Fish Aquat Sci 58:73–85

Carscadden JE, Montevecchi WA, Davoren GK, Nakashima BS (2002) Trophic relationships among capelin (*Mallotus villosus*) and marine birds in a changing ecosystem. ICES J Mar Sci 59:1027–1033

Colbourne E (2002) Decadal changes in the ocean climate in Newfoundland waters from the 1950s to the 1990s. SCR Doc. 02/33, Serial No N4644, North Atlantic Fisheries Organization, Dartmouth

Craig JDC, Colbourne EB, Maillet GL (2001) Preliminary studies of density stratification and fluorescence on the Newfoundland shelf. Res Doc 2001/085, Can Sci Adv Sec, Department of Fisheries and Oceans, Ottawa

Davoren GK, Montevecchi WA (2003a) Signals from seabirds indicate changing biology of capelin stocks. Mar Ecol Prog Ser 258:253–261

Davoren GK, Montevecchi WA (2003b) Consequences of foraging trip duration on provisioning behaviour and fledging condition of common murres. J Avian Biol 34:44–53

Frank KT, Carscadden JE, Simon JE (1996) Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions. Can J Fish Aquat Sci 53:1473–1486

Gjosaeter H (1998) The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. Sarsia 83: 453–496

Gudmundsdottir A, Vilhjalmsson H (2002) Predicting total allowable catches for Icelandic capelin, 1978–2001. ICES J Mar Sci 59:1105–1115

Harris MP, Birkhead TR (1985) Breeding biology of the Atlantic Alcidae. In: Nettleship DN, Birkhead TR (eds)The Atlantic Alcidae. The evolution, distribution and biology of the auks inhabiting the Atlantic Ocean and adjacent water areas. Academic Press, London

Mowbray FK (2002) Changes in the vertical distribution of capelin (*Mallotus villosus*) off Newfoundland. ICES J Mar Sci 59:942–949

Nakashima BS (1996) The relationship between oceanographic conditions in the 1990s and changes in spawning behaviour, growth and early life history of capelin (*Mallotus villosus*). NAFO Sci Counc Stud 24:55–68

Nakashima BS, Slaney BW (2001) The 1999 inshore capelin (*Mallotus villosus*) fishery in NAFO Div. 3KL. In: Anonymous (ed) Capelin in SA2+Div. 3KL during 1999. Research Document 2001/161, Canadian Department of Fisheries and Oceans, St. John's, NF, p 35–52

Nakashima BS, Wheeler JP (2002) Capelin (*Mallotus villosus*) spawning behaviour in Newfoundland waters—the interaction between beach and demersal spawning. ICES J Mar Sci 59:909–916

Rose GA (2001) Can Newfoundland cod stocks recover without capelin? ICES Newsl 38:8

Rose GA, O'Driscoll RL (2002) Capelin are good for cod: can the northern stock rebuild without them? ICES J Mar Sci 59:1018–1026

Vilhjalmsson H (2002) Capelin (*Mallotus villosus*) in the Iceland-East Greenland-Jan Mayen ecosystem. ICES J Mar Sci 59:870–883