

REPLY COMMENT

Did signals from seabirds indicate changes in capelin biology? Reply to Carscadden (2004)

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Carscadden (2004, this issue) contends that Davoren & Montevecchi (2003a) 'contains weaknesses in both the data collection and the data analyses; as a result, these conclusions are not supported ... drew several conclusions about capelin biology and the physical environment, based partly on published studies, which require clarification', and 'develop hypotheses that were not supported by the data available (p. 289). We address these criticisms and engage Carscadden's broader discussion of recent changes in the biology of capelin *Mallotus villosus* in the NW Atlantic.

BIOLOGY OF CAPELIN AND MURRES

Common murres as capelinivores

Carscadden (2004) questions whether common murres *Uria aalge* are robust samplers of capelin and whether they can be considered as capelin specialists.

Among the seabirds breeding in the NW Atlantic region, common murres are the major consumers of capelin (Piatt 1990, Burger & Piatt 1990, Bundy et al. 2000), and capelin dominates their prey consumption in other regions of the North Atlantic (e.g. Anker-Nilssen et al. 1997). Common murres in the North Atlantic will at times reproduce successfully when capelin is in limited availability (Bryant et al. 1999), but at times they cannot (Vader et al. 1990). At the species' largest colony on Funk Island, as well as elsewhere, common murres provision their chicks almost exclusively on capelin, and it is reasonable to regard them as capelin specialists.

Davoren & Montevecchi (2003a) reported that the percentage of capelin in murre chick diets ranged from 74 to 99% between 1991 and 2000. Detailed information on the other fish species that comprise the diet is presented in Table 1. Only in 1995 did the percentage of capelin delivered to chicks fall below 95%, due to a higher proportion of sand lance. Clearly, capelin was

Table 1 *Uria aalge*. Prey species delivered (% of individuals) to common murre chicks on Funk Island from 1991 to 2000. From Davoren & Montevecchi (unpubl. data)

	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
Capelin	97.9	95.2	99.3	97.8	72.1	97.4	95.2	95.0	98.4	98.7
Sandlance	0	0.6	0	0	23.8		0.3	4.0	1.6	0.6
Sandlance and capelin larvae	0	0	0	0	0	0	0.6	0	0	0
Sculpin	0	0.6	0.7	0	1.7	1.3	0.9	1.0	0	0.6
Gadid	2.1	1.8	0	0	1.2		0	0	0	0
Cod	0	0	0	2.2	0	0	0	0	0	0
Arctic cod	0	0.6	0	0	1.2	1.3	0.9	0	0	0
Blenny and rockfish	0	0.6	0	0	0	0	0.6	0	0	0
Ratfish and hake	0	0	0	0	0	0	0.6	0	0	0
Other (wolfish, rockling)	0	0.6	0	0	0	0	0.6	0	0	0

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the primary prey of murres at Funk Island during the study period.

Dietary sampling relative to capelin residency and maturation cycles in the study area

We prefer to use long sampling periods as much as Carscadden. We obtained as many samples as possible within the logistical constraints of (1) minimizing disturbance at this globally significant colony, (2) adjusting to weather conditions that often limited the length of research visits and extent of sampling (e.g. catching food-carrying murres with long-poled nets as they fly into the colony depends on wind speed and direction), and (3) conducting a research

program on several different seabird species simultaneously during research visits. The long-term sampling regime was designed to provide annual indices of the diets of common murre chicks and of chick condition during a consistent period each year. Owing to the short chick-rearing period of murres (~3 wk) in relation to the longer residency time of capelin in the study area (>2 mo; Davoren et al. 2003), it was not our intention to cover the entire duration of capelin residency. If capelin of different age or size groups and maturation stages moved through the study area at different times, then the short sampling period in relation to capelin residency time could potentially weaken the conclusions drawn. Historically, large mature capelin moved into spawning areas first (Templeman 1948, Nakashima 1996).

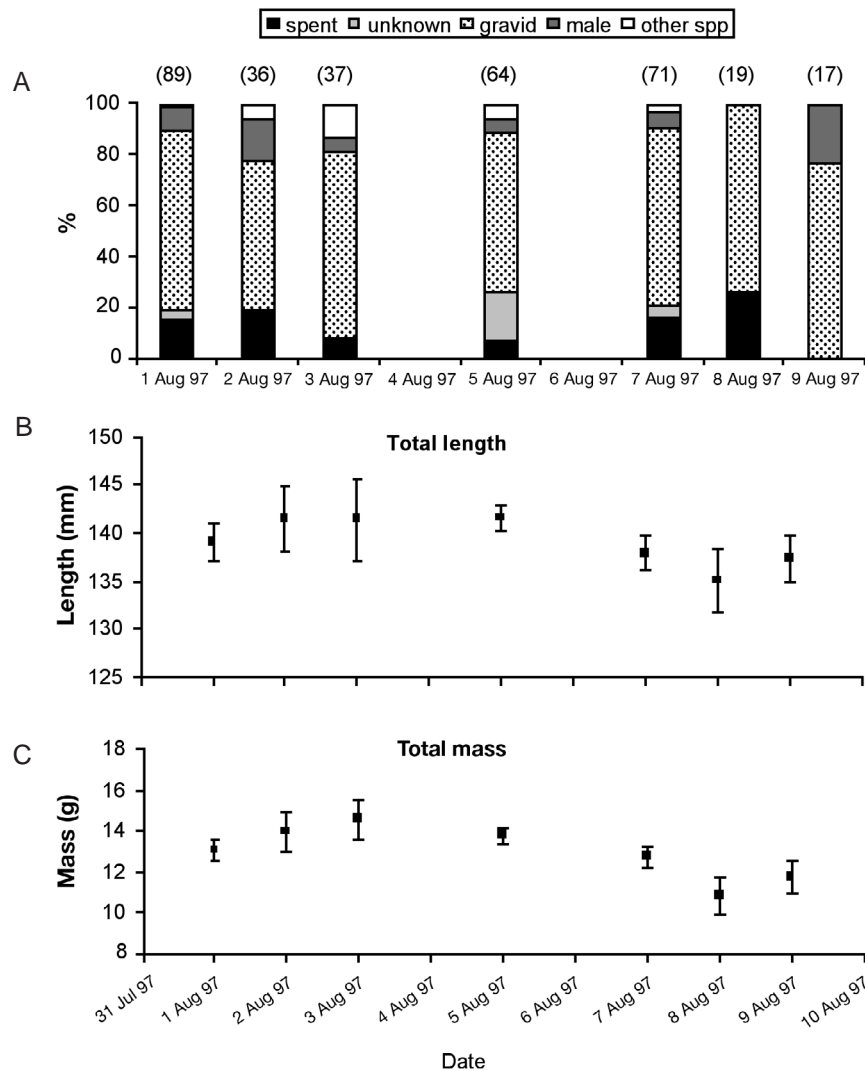


Fig. 1. *Uria aalge* and *Mallotus villosus*. (A) Percentages of spent female, gravid female, male and unknown capelin and other species as well as the (B) total length and (C) total mass of capelin (mean \pm SE) delivered to common murre chicks per day during all samples days in 1997. Sample sizes in parentheses

Therefore, if capelin spawned later throughout the 1990s, compared to the murre chick rearing period, our samples would have been biased towards larger fish, because our samples would have been taken earlier, relative to the capelin spawning period. Since 1990, however, the historical pattern of large immature capelin arriving to spawn first has not occurred (Nakashima 1996) and, therefore, our comparatively short sampling period, relative to capelin residency, made little difference.

We assumed that murre preferentially select gravid capelin, owing to their higher energy content (Montevecchi & Piatt 1984) and owing to the high energetic costs of raising a chick. We hypothesized that the percentage of gravid capelin delivered to murre chicks would reflect their availability within the murre's foraging ranges around Funk Island. The sampling would thus indicate inter-annual variability in the timing of capelin spawning. Therefore, we see temporally consistent dietary sampling as a more informative method for studying the inter-annual variability in capelin behaviour (e.g. timing of spawning) than one based on a variable annual reproductive chronology of fish (and birds), as Carscadden (2004) suggests. This is a biologically important issue because the spawning behaviour of capelin has not been studied extensively in our study area, and thus, the maturation and spawning cycles of capelin were unknown during our study. Owing to the temporal consistency of our sampling, we expect changes in the murre's biology and feeding ecology to be consequences of physical and biological environmental circumstances, including that of their primary prey, capelin.

Dietary sampling relative to the chick-rearing period

Carscadden (2004, p. 289) contends that our sampling 'probably did not reflect the total diet nor describe the characteristics (length, weight and condition) of the capelin delivered to the chicks' that is needed to make inferences about dietary changes, and that '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.' Dietary samples from chicks showed little variation among days within a year. For example, in 1997, a representative year, dietary samples taken on any given day likely represent the

Table 2. *Uria aalge* and *Mallotus villosus*. Re-analysis of statistical relationships (linear regressions) in Davoren & Montevecchi (2003a). **Bold** entries indicate statistically significant relationships

	b	r	p
Proportion of gravid female capelin versus day of the year	-0.425	0.029	0.840
Year versus			
Spent capelin mass	0.047	0.023	0.949
Spent capelin length	-0.109	0.269	0.452
Spent capelin condition	3.150	0.393	0.261
All female capelin (gravid and spent) mass	-1.049	0.637	0.047
All female capelin (gravid and spent) length	-0.107	0.269	0.452
All female capelin (gravid and spent) condition	-2.276	0.325	0.360
Chick condition versus energy delivered per fish	0.028	0.870	0.011

diets on other days and, hence the diet during the entire chick rearing period (Fig. 1). Additionally, when data from sampling days were combined for all years, there was no relationship between the proportion of gravid females and Julian day (Table 2 & Fig. 2), revealing that variability in the proportion of gravid females delivered to murre chicks did not increase or decrease over the sampling periods. Therefore, our diet samples accurately describe the species composition and the characteristics of capelin delivered to chicks during the entire chick rearing period, not only for the days when samples were collected.

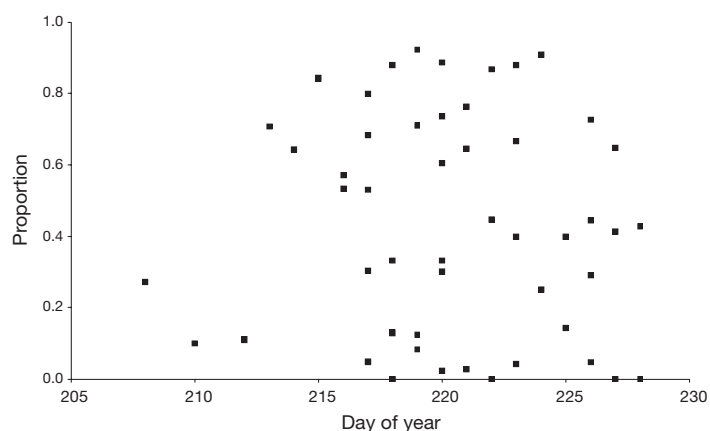


Fig. 2. *Uria aalge* and *Mallotus villosus*. The proportion of gravid capelin delivered to common murre chicks at Funk Island on each sampling day from 1991 to 2000

Table 3. *Uria aalge* and *Mallotus villosus*. Percentage of capelin, and within this, the percentages of mature males, mature (gravid) females, spent females and unknown capelin in the diets of common murre chicks on Funk Island, 1991 to 2000. N is the total number of fish collected from adult murre chicks arriving at the colony

Year	Capelin (%)	Mature male (%)	Mature (gravid) female (%)	Spent female (%)	All females ^a (%)	Unknown ^b (%)	N
1991	98	4	47	49	96	0	48
1992	96	11	71	7	78	11	166
1993	99	8	83	8	92	1	151
1994	99	18	45	25	70	12	96
1995	74	11	58	20	78	11	187
1996	98	1	7	92	99	0	83
1997	95	10	71	18	88	2	339
1998	95	4	22	51	73	23	101
1999	98	0	15	83	98	2	61
2000	99	2	6	76	82	16	133

^aAll females refers to the combined percentage of gravid and spent female capelin
^bThis percentage represents capelin with an unknown sex/maturity

Sex and maturity categories of capelin

Gravid capelin were defined as having a gonad sac full of eggs. Spent females were identified on the basis of unfirm undersides and gonad sacs that were empty or contained very few eggs (<10). When we were not certain about the status of a fish, we classified it as 'unknown'; this was the case for 0 to 15 fish per year. We combined this unknown category with capelin classified as spent in the inclusive category of 'spent-immature' for our analyses and did not have another maturity category as Carscadden (2004 p. 290) questions. The 'all female capelin' category was a summation of the gravid and spent-immature categories, and due to this combination, the all female category could contain some immature male fish. The percentage of unknown fish, however, was low (Table 3). Therefore we do not consider that this categorization influenced the results of our chick diet or condition data.

Fulton's K and somatic condition

Carscadden (2004, p. 290) indicates that Fulton's K should be calculated by subtracting gonad weight from total body weight, because the former can account for a significant portion of a gravid female's total weight. We weighed whole fish in the field without removing gonadal tissue, and we concur with Carscadden (2004) that the change in Fulton's K and in total body mass of all female capelin across years could indicate a declining percentage of gravid capelin. We attempted to derive an alternative measure of somatic condition from spent females, because their gonad weight is likely negligible and their somatic condition similar to that of gravid capelin. Exclusion of fish of unknown

maturity reveals no significant trends in the condition of spent females (Table 2 & Fig. 3), confirming our original analysis (e.g. Table 2 in Davoren & Montevecchi 2003a). Similarly, trends in the size of spent female capelin were not significant (Table 2). For all female capelin (gravid and spent), there was a significant decline in mass, whereas declines in length and condition were not significant (Table 2 & Fig. 3). Overall, there were significant declines in the mass of female capelin, either separately as gravid capelin or combined as gravid and spent fish, revealing a trend towards smaller sized female capelin being delivered to chicks of murre chicks at Funk Island (Fig. 3). Conversely, trends in condition were variable.

Measurement of murre chick metrics

Carscadden (2004, p. 290) stated that for our index of chick condition 'comparisons should be made using the same point on the growth curve each year', because of the rapid growth of murre chicks. Due to the limited frequency of visits to the colony, laying and hatching dates were unknown, and we collected a single measurement of chick condition per year to reduce disturbance to the colony. To limit variability in development among chicks measured, analyses of metrics were restricted to chicks within a range of 25 to 65 mm wing length, which corresponds approximately to the first 14 d post-hatch, when growth in mass approaches linearity (Gaston & Jones 1998). This resulted in the deletion of data on 1 to 5 chicks in each year. Davoren & Montevecchi (2003a) specifically discuss the restriction in data interpretation. The use of mass at a specific wing length, or the mass of a bird at a given linear size, has been used to describe inter-annual differences at

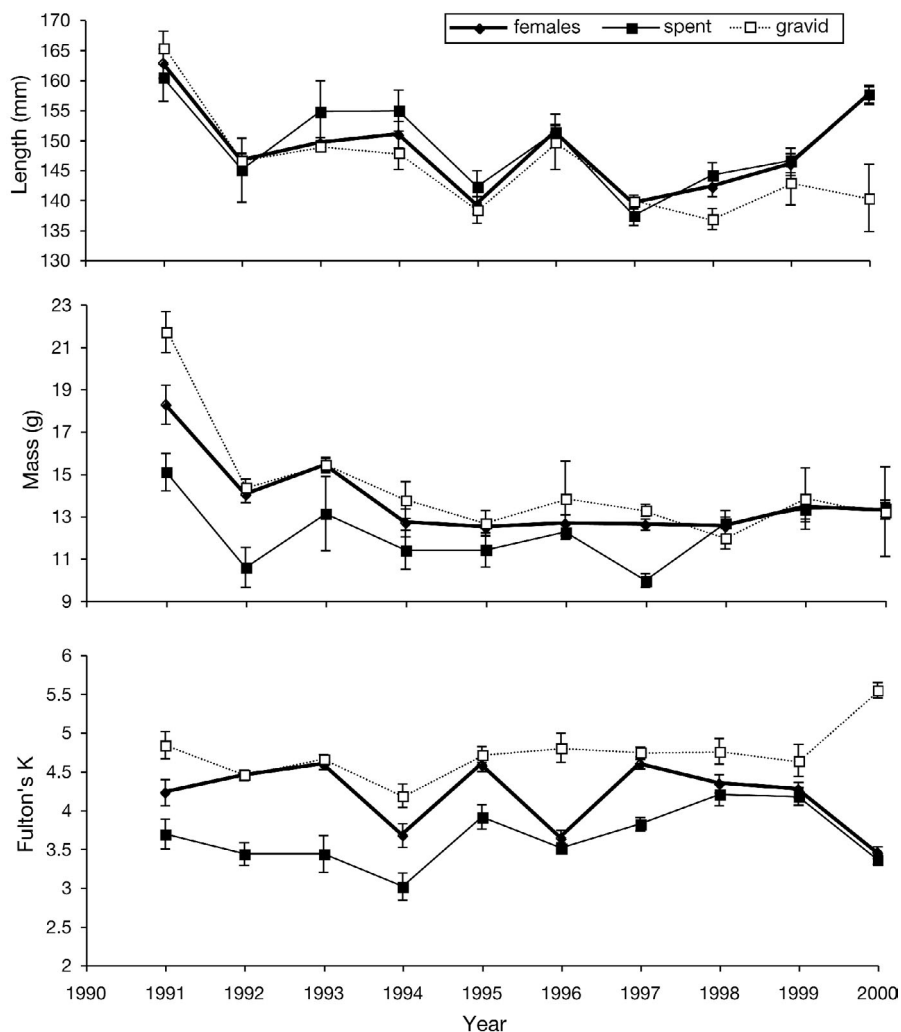


Fig. 3. *Uria aalge* and *Mallotus villosus*. Mass, length and condition mean (Fulton's K) (mean \pm SE) of gravid female, spent female, and all female capelin (gravid and spent) delivered to common murre chicks at Funk Island from 1991 to 2000

the same colony and among colonies (e.g. Bertram et al. 2002). Despite limitations of this method, such as developmental responses to food variability (Kitaysky 1999), these simple mass and wing measurements yield results similar to more intensive sampling programs (Bertram et al. 2002). These indices reflect chick condition at the time of sampling, yet because murrens rear their chicks for only ~3 wk, sampling near the middle of their rearing cycle likely reflects the condition of chicks in a given year.

Biological significance of chick condition index

Contrary to Carscadden's (2004) contention, Davoren & Montevecchi (2003a, 'Materials and methods') did provide the full statistics of the regression showing the positive linear relationship between wing

length and body mass in chicks for all years combined. This relationship was best described by a linear equation and was highly significant in all years (Table 4). The relationship between fledgling mass and wing length for murrens at the same colony in the same years

Table 4. *Uria aalge*. Linear regressions of chick mass on wing length

Year	Linear regression	R ²	p	N
1991	$Y = 3.2x + 26.0$	0.664	<0.001	39
1992	$Y = 4.8x + 35.2$	0.743	<0.001	20
1993	$Y = 3.3x + 17.3$	0.675	<0.001	36
1994	$Y = 3.1x + 3.2$	0.815	<0.001	28
1995	$Y = 3.2x + 5.0$	0.838	<0.001	41
1997	$Y = 2.0x + 53.5$	0.577	<0.001	31
1998	$Y = 2.1x + 57.8$	0.379	<0.02	31

can break down (Davoren & Montevecchi 2003b), owing to different fledging decisions (e.g. Ydenberg 1998, Gaston 1998) and pre-fledging mass loss (e.g. Bertram et al. 2002). We discussed these ideas in Davoren & Montevecchi (2003b) and did not see the need of repeating this in Davoren & Montevecchi (2003a).

Energy delivered per fish, and chick condition

Carscadden (2004) questions whether other fish species in chick diets could have contributed to declining chick condition. In only one year (1995, the mid-point of the data series) did capelin fall below 95% of the prey deliveries (Table 1). In 1995, sand lance, a fish with similar or higher energy density than capelin (Montevecchi et al. 1984, Anthony et al. 2000), comprised most of the other prey. Hence, it is unlikely that changes in chick condition related to diet were associated with any prey other than capelin. We concur with Carscadden (2004) that the declining percentage of gravid capelin in the diets of murre chicks was one of the primary factors resulting in a decline in the energy delivery per fish through the 1990s. To illustrate this, Davoren & Montevecchi (2003a, p. 259) stated: 'The changing biology and behaviour of capelin throughout the 1990s resulted in a substantial decline in the energy delivered per capelin to murre chicks'. This refers to the declines in capelin size (biology) as well as the timing of spawning (behaviour), which as stated previously is likely due to a mismatch in the temporal overlap of chick rearing and the arrival of pre-spawning, gravid capelin in the murre's foraging range.

Carscadden (2004, p. 291) writes '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.' We did test this relationship and reported the statistics in the 'Results' ($b = 0.018$, $r = 0.594$, $n = 7$, $p = 0.160$; Davoren & Montevecchi 2003a, p. 256). Although in one year (1995) the energy per capelin would not represent the total energy being delivered to chicks, due to the higher percentage of sand lance in the diets, this is clearly not an issue in other years of the study (see Table 1). When the data are re-analyzed using only known spent females (rather than the criticized spent-immature category), and including the energy densities and proportions of males, the relationship between chick condition and energy delivered per fish is significant (Table 2). Males are heavier (19.9 ± 0.5 g, all years combined) than females (gravid: 13.8 ± 0.2 g; spent: 12.4 ± 0.2 g), but comprised only a small proportion of the chicks' diets.

A conspicuous aspect of reproductive conditions of

the common murre colony on Funk Island is that the number of birds has not increased during the 1990s, while increases at other large colonies appear substantial (Canadian Wildlife Service unpubl. data). These increases are likely due to reductions in adult mortality associated with the extensive removal of gill nets (see Piatt et al. 1984, Troke 2004), following closure of the eastern Canadian ground fishery in 1992. It is paradoxical that the murre's largest colony on Funk Island, where the birds are not limited by nesting space or predators, has not increased. A reasonable and plausible explanation for this is that declining chick condition, owing to lower energy delivered per fish, is resulting in lower fledgling condition and chick survival at Funk Island, relative to other colonies (Davoren & Montevecchi 2003b).

Corroboration from other sources

Carscadden (2004) contends there is little corroboration from other sources for our generalization about declines in capelin size and condition through the 1990s, but rather that the literature primarily shows dramatic changes in capelin metrics in the 1990s, compared to the 1980s (e.g. Carscadden & Frank 2002). We are aware that major differences in capelin metrics occurred between the 1980s and 1990s (Carscadden et al. 2002); however, it was clearly not our objective to compare murre diets between these decades as we did not have dietary information in the 1980s. Instead, our aim was to assess capelin biology (i.e. length, mass, condition) and behaviour (i.e. timing of capelin spawning) through the 1990s and use other independently collected data to show that capelin biology and behaviour has not returned to pre-perturbation levels. We did this in Davoren & Montevecchi (2003a) by referring readers to previous studies. For instance, Fig. 4 in Carscadden & Nakashima (1997), as referenced in Davoren & Montevecchi (2003a), shows the mean lengths of mature capelin for the period spanning from 1978 to 1994. Additionally, we referred readers to Anderson et al. (2001), whose Fig. 7 unmistakably shows a tri-modal length frequency distribution of capelin in a 1999 survey (modes at ~30, 100 and 125 mm; range: ~5 to 184 mm), similar to the size range of capelin delivered to murre chicks (58 to 190 mm). We were aware of the mean lengths of mature capelin from Bellevue Beach for 1990 to 1999 presented in Nakashima & Slaney (2001a; not Nakashima & Slaney 2001b, as indicated by Carscadden 2004). We assessed our data in relation to these and other data from federal government research documents (e.g. Davoren et al. 2001). The Bellevue Beach data set collected by Fisheries & Oceans Canada researchers began in the

1990s and these data are generally presented alongside those from other sources to show the dramatic change in capelin biology and behaviour (e.g. Carscadden & Nakashima 1997). We provide a similar plot here (Fig. 4). The mean length of capelin obtained from murre diets clearly follows the same pattern as data collected during the inshore fishery (Carscadden et al. 2001a) and on Bellevue Beach (Nakashima & Slaney 2001b), showing that capelin mean length has not returned to pre-perturbation levels. An exception was during 1997, when capelin collected by murre were considerably smaller than in the other 2 studies. The mean length of capelin collected by murre are likely biased by active selection, as foraging theory predicts that murre would 'select' the richest, largest fish available to them during the energetically demanding chick rearing period (Davoren & Montevecchi 2003b). Therefore, the murre data likely reflect a continued decline in capelin length within their foraging range at Funk Island, where the biology and spawning activity of capelin has received little research attention. Overall, we show clearly that capelin have continued trends precipitated in the early 1990s, despite the fact that the low water temperatures have returned to pre-perturbation levels. We fundamentally disagree with Carscadden (2004, p. 293) that '... the information in Davoren & Montevecchi (2003a) does not reflect the trends in capelin biology during the 1990s...'

Prior to the 1990s, too few murre were rearing chicks at Funk Island during our temporally fixed visits to collect dietary and chick condition data. We contend that this strengthens the validity of the dramatic population response of delayed breeding by murre on

Funk Island in the early 1990s. In contrast, Carscadden (2004, p. 292) writes '... if one accepts the links between abundance of murre 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 ... in 1991'. Only in the most extreme of circumstances would a major shift in the population activity of a long-lived vertebrate respond immediately to environmental perturbation and changes in prey bases (e.g. Schreiber & Schreiber 1984, Cairns 1987, Vader et al. 1990). Lagged responses are to be expected (e.g. Montevecchi & Berruti 1991, Francis et al. 1998). Yet this is no reason not to view the order of magnitude shift in the presence of breeding common murre at their largest colony as an indication of a pervasive shift in ecosystem circumstances during the 1990s. Due to this population response, we predict that shifts in the timing of breeding of murre were due to delayed spawning of capelin and, therefore, delayed breeding of murre could indicate future shifts in capelin spawning schedules in regions where little or no systematic research is conducted, as was the case for our study area during the 1990s.

PREVIOUS STUDIES

To clarify 'divergent biomass estimates of capelin throughout the 1990s' (Davoren & Montevecchi 2003a, p. 259), we referred to the decline in biomass estimates found between the 1990 and 1991 spring offshore acoustic surveys, in contrast to the abundance indica-

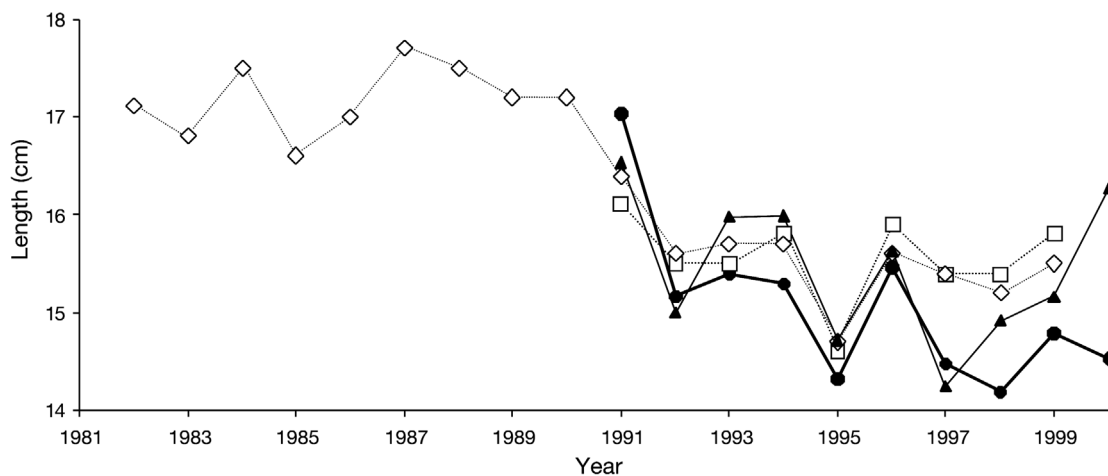


Fig. 4. *Mallotus villosus*. Mean length of gravid (●) and spent (▲) female capelin from Davoren & Montevecchi (2003a) along with the mean length of mature capelin (□) from Nakashima & Slaney (2001b) and mature capelin (◇) from Carscadden et al. (2001a)

tors derived from inshore spawning beaches (see Fig. 5 in Carscadden & Nakashima 1997). The offshore acoustic estimates of capelin indicate a decline in capelin biomass from 7 million t in 1990 to 100 000 t in 1991 (Carscadden & Nakashima 1997). Acoustic biomass estimates have remained low through the 1990s (Carscadden 2004), and regardless of variability in survey coverage, many researchers conducting acoustic surveys have observed very few notable schools of capelin in Newfoundland waters during various acoustic surveys in the 1990s (F. Mowbray, R. O'Driscoll, G. Rose pers. comm.). Even though there has been an appearance of a 'capelin carpet' (fish near the seabed, where they are not reliably detected or recognized by acoustic processors), it is unlikely that these fish could make up for the capelin biomass 'missing' from hydroacoustic estimates (e.g. O'Driscoll et al. 2001). Bottom-trawl surveys have also noted a decline in the biomass of capelin in the early to mid-1990s (Lilly & Simpson 2000). The fact that offshore cod *Gadus morhua* (the major predator of capelin in the NW Atlantic; Bundy et al. 2000) showed little evidence of capelin consumption during the 1990s (capelin found in 0.2% of cod stomachs; Rose 2001, Rose & O'Driscoll 2002) provides indirect support for the low acoustic biomass estimates of capelin. Taken together, evidence for a major decline in the capelin population and for a shift in the regional ecosystem during the 1990s, as alluded to by Mowbray (2002), is compelling. Conversely, Carscadden et al. (2001b) went so far as to suggest that smaller capelin during the 1990s may have resulted from an overabundant population, caused by declining predator populations (primarily Atlantic cod) in conjunction with decreased zooplankton biomass (density-dependent response, trophic cascade). Empirical evidence for these conjectures is equivocal at best. We agree with Carscadden (2004) and others (e.g. Mowbray 2002) that resolutions of these inconsistencies are needed.

Carscadden (2004) questions our statement that the capelin fishery was able to target older and larger gravid capelin. Larger capelin are usually the first components of the population to move inshore (Templeman 1948, Nakashima 1996 for the 1990s). Although gear used to capture capelin (i.e. primarily purse seines) is not size selective, fishers concentrate on the large, early run of capelin to meet Japanese market demands. Smaller female capelin during the 1990s could have increased the number of discards (due to 'high-grading'). Beginning in 1994, the fishery was not permitted to open until female capelin exceeded a critical size in each quota area. These management measures were initiated to avoid high-grading, but fishers still received more money for larger gravid females, due to their higher roe contents

and, consequently, likely still sampled catches to ensure that they would provide an adequate profit before bringing them aboard. We agree that fishers' ability to catch larger capelin deteriorated during the 1990s, because the tendency for larger capelin to arrive first had weakened (Nakashima 1996). Most fisheries biologists and commercial fishers, however, are well aware that size selection is still a major factor in the capelin fishery. There is also considerable unaccounted mortality in the capelin fishery, as there is for all fisheries directed at forage fishes.

HYPOTHESES

Carscadden (2004) questions the hypothesis that the loss of larger fish due to fishing mortality could have resulted in a population now composed of smaller and younger fish that spawn later. Others also suggested that the later spawning of capelin has been due to a shift in cohort strength, although mechanisms for this shift were not offered (e.g. Therriault et al. 1996). Capelin population dynamics could have been influenced by excessive catches of the offshore factory fishery during the 1970s and by the inshore fishery since then, as well as by increased natural mortality of adults, larvae and eggs due to the 1991 oceanographic perturbation (Bundy 2001). Carscadden et al. (2001b) contend that capelin exploitation in the NW Atlantic region has been low relative to capelin fisheries in other regions of the world. This is primarily based on estimates of spawner biomass and predator consumption in the NW Atlantic. Repeated impacts on larger, earlier-spawning females, however, could influence stock genetics and phenotypes (Barot et al. 2002). The highest catches of the roe-based fishery during 1988 to 1990 (79 000 to 83 000 t; Carscadden & Nakashima 1997) immediately precede the abrupt decline in size, in acoustic biomass estimates and with the later spawning of capelin in the early 1990s.

We agree with Carscadden (2004) that environmental factors may have contributed to continued changes in biology and behaviour of capelin through the 1990s; as stated in Davoren & Montevecchi (2003a, p. 259) 'This indicates that factors other than simply ocean temperature (e.g. low zooplankton biomass in the 1990s) are responsible for these declines in capelin size and conditions (Carscadden & Frank 2002).' We considered that referencing a paper where these other environmental factors were discussed in detail, as well as providing references to other studies, would be adequate, given the scope of our manuscript. The overriding environmental influences on capelin biology appear to be (1) a physically forced systemic bottom-up perturbation (e.g. cold water in 1991), coupled with (2)

food web shifts and (3) a potential top-down influence of fishing mortality on large, early-spawning gravid capelin.

Carscadden et al. (2001b, p. 76) stated that '... estimates of relative year-class strength, derived from several independent sources combined into a multiplicative model (Fig. 3; Anonymous 1999b), indicate that year-class strengths during the 1990s have been at least as strong as those observed during the 1980s...' and that 'Capelin abundance has increased, with improved annual recruitment and several strong year-classes during the 1990s.' (p. 82) These statements were qualified because indices used to determine year-class strength had high uncertainty and some data that did not follow these trends were not included (Anonymous 1999). Of the 12 indices used to generate these estimates, the offshore acoustic estimates of capelin, which indicate a decline by an order of magnitude in capelin biomass from 1990 to 1991 (Carscadden & Nakashima 1997), were not included. The reasoning was that 'Abundance estimates derived from the acoustic survey cannot be considered an indicator of stock status', because 'only a part of the stock distribution area can be surveyed in the time available and the proportion of the stock found therein is unknown and probably highly variable' (Anonymous 2001, p. 2). Although a similar concern was raised with regard to autocorrelated abundance indicators from a single spawning beach, these indicators were included in the model (Anonymous 1999).

Acoustic research surveys within the traditional area that the stock occupied were resumed in 1999, but scientific assessments of capelin stock status have not been performed. This termination of stock status assessments was due to a lack of available indices for estimating year-class strength, owing to a reduction in funding. Given that only 2 indices remained, both of which were derived from the same spawning beach, Anonymous (2001) stated that '... it is not possible to judge the impact of the present exploitation levels in the absence of knowledge regarding stock status' (p. 4) and acknowledged that '... the abrupt decline in offshore acoustic densities between 1990 and 1991, the continuing low offshore acoustic densities and the discrepancies between the acoustic indices and other indices have never been explained (p. 5)'. Subsequently, Anonymous (2003, p. 13) contended that 'Whatever the present circumstances, there remains concern that there may not be sufficient capelin to support a recovery of the cod stock, especially in the offshore and in the north'. Since this publication and the acceptance of Davoren & Montevecchi (2003a), the total annual allowable catch of capelin has been reduced by 40% in NAFO Division 2J3KL in an effort to mitigate further declines in northern cod stocks. So

despite Carscadden et al.'s (2001b) contention that the exploitation of capelin in Newfoundland is low, compared to other capelin and pelagic fisheries worldwide, we and various members of the Canadian government believe that capelin fishing mortality should be minimized due to the importance of this species as a forage fish in the NW Atlantic ecosystem (Lavigne 1996).

The capelin fishery is being continued in the absence of baseline biomass estimates, and this is difficult to justify in terms of conservation policy. In the present circumstances, with the commercial extinction of northern cod in eastern Canada (Hutchings & Myers 1994) and its designation as a threatened and potentially endangered population (Hutchings 2004), the rationale for fishing any of its potential food base is obscure. Inordinate attention is directed at seals, relatively minor cod predators (Bundy et al. 2000), but virtually none at the cod's principal prey—capelin. Finally, trophic models estimated that millions of tons of capelin were consumed by cod in the mid 1980s (Bundy et al. 2000). With the cod population significantly reduced — where are all the capelin?

CONCLUSIONS

Carscadden (2004, p. 293) concludes that 'weaknesses in data collection and analyses outlined above cast serious doubts on their conclusions ...'. On the basis of our above arguments and discussions of the limitations of seabird data to indicate the biology and behaviour of their fish prey (Davoren & Montevecchi 2003a), we stand by our conclusions.

There are conflicting ways of interpreting the data for capelin. We are continuing collaborative efforts with fisheries researchers and fishers in a multi-species, ecosystem initiative to help unravel discrepancies among biomass and abundance indices of capelin, as well as to further an understanding of the basic biology and behaviour of capelin. This research is only possible by the collaboration among Canadian universities, Newfoundland and Labrador commercial fishers and Fisheries and Oceans Canada. Only through inter-disciplinary and inter-institutional collaboration and critiques of each others' work will important resolutions to conservation questions be achieved. We agree with Carscadden (2004) that this research is an ongoing challenge.

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