

Depensation, probability of fertilization, and the mating system of Atlantic cod (*Gadus morhua* L.)

Sherrylynn Rowe, Jeffrey A. Hutchings, Dorte Bekkevold, and Ana Rakitin

Rowe, S., Hutchings, J. A., Bekkevold, D., and Rakitin, A. 2004. Depensation, probability of fertilization, and the mating system of Atlantic cod (*Gadus morhua* L.). – ICES Journal of Marine Science, 61: 1144–1150.

Atlantic cod (*Gadus morhua* L.) have been severely overexploited and are currently at historic population lows, having declined 90% in the North Sea and 99% off northeast Newfoundland in recent decades. Slow rates of recovery and continuing declines may be attributable to depensation, defined as a reduction in per capita growth rate concomitant with reduced population size. Several potential causes of depensation relate to low mating success and consequent reduced production of offspring. We explore the empirical basis of one of these in Atlantic cod using egg fertilization and male abundance data obtained from 21 experimental populations generated by three independent research programmes. We find support for the hypotheses that (a) fertilization rate declines with abundance and (b) variance in fertilization rate increases as population size declines. The former identifies one potential mechanism underlying depensation in Atlantic cod. The latter has negative genetic consequences for effective population size (N_e), resulting in a decline in the ratio of N_e to census population size (N_e/N_c) with declining abundance. Our results may have general implications for the conservation biology of broadcast-spawning marine fish, particularly those with mating systems similar to that of Atlantic cod.

© 2004 International Council for the Exploration of the Sea. Published by Elsevier Ltd. All rights reserved.

Keywords: Allee effect, Atlantic cod, conservation, depensation, fertilization, mate choice, mate competition, mating system.

Received 6 June 2003; accepted 19 May 2004.

S. Rowe and J. A. Hutchings: Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada, B3H 4J1. D. Bekkevold: Danish Institute for Fisheries Research, Vejlsvøvej 39, DK-8600 Silkeborg, Denmark. A. Rakitin: Centre of Forensic Science, Toronto, Ontario, Canada. Correspondence to S. Rowe: e-mail: Sherrylynn.Rowe@Dal.Ca.

Introduction

Severe overexploitation has driven Atlantic cod (*Gadus morhua* L.) to historic low levels of abundance (Hutchings and Myers, 1994; Myers *et al.*, 1997; Smedbol *et al.*, 2002; COSEWIC, 2003). In the North Sea and adjacent waters, cod have declined by 90% since the early 1970s (ICES, 2002), a loss of more than 200 million individuals. Even more dramatic is the collapse experienced by Newfoundland's northern cod, which is estimated to have declined by 99% between 1962 and 2002, a loss of approximately 1.5 billion breeding individuals (COSEWIC, 2003). Once supporting the largest cod fishery in the world (McGrath, 1911), commercial fishing of northern cod was closed in 1992 for the first time in its 500-year history. The stock has since shown no signs of recovery (DFO, 2003). Slow or negligible rates of recovery among cod populations have been attributed to a reduction in per capita population

growth rate concomitant with reduced population size (Shelton and Healey, 1999; Frank and Brickman, 2000), an association termed depensation in the fisheries literature and Allee effect in the ecological literature (Liermann and Hilborn, 2001). However, despite increased attention to depensatory mechanisms as factors responsible for slow recovery rates in Atlantic cod, a dearth of empirical work stands as a significant barrier to assessing the potential for Allee effects in this species.

The Atlantic cod is a bet-hedging species, with a reproductive strategy in which eggs are released (broadcast) directly into the oceanic environment and for which no parental care is provided. Attaining maturity across a broad range of sizes (35–85 cm) and ages (2–7 years) throughout the species range (Brander, 1994; COSEWIC, 2003), females release their annual egg complement numbering hundreds of thousands, often millions, of 1.25–1.75 mm eggs in batches over 3–6 weeks (Chambers and Waiwood,

1996; Kjesbu *et al.*, 1996) within a 6–12-week spawning season (Myers *et al.*, 1993) in water ranging from tens to hundreds of metres in depth (Brander, 1994; Morgan *et al.*, 1997; Smedbol and Wroblewski, 1997). Successful reproduction involves complex mating interactions, including behavioural and acoustic displays by males and mate choice by females (Brawn, 1961; Hutchings *et al.*, 1999; Rowe and Hutchings, 2003). Release of sperm and eggs by Atlantic cod occurs during a ‘ventral mount’ in which the male, while grasping the female with his pelvic fins and matching her swimming speed, positions himself beneath her. The spawning couple is often quickly joined by satellite males that swim amongst the eggs and also release sperm. Accordingly, genetic work indicates that eggs from single reproductive bouts can be fertilized by more than one male (Hutchings *et al.*, 1999; Rakitin *et al.*, 2001; Bekkevold *et al.*, 2002). Thus, it is reasonable to assume that alternative mating tactics exist in male Atlantic cod.

Changes in density within Atlantic cod spawning aggregations may have been concomitant with documented changes in population size (ICES, 2002; COSEWIC, 2003), but there are no data available to assess this issue or whether locations of spawning grounds have shifted over time (detailed spawning maps do not exist for Atlantic cod). If a population falls below some critical size threshold, individuals can experience problems that adversely affect mating success and/or offspring production (Møller and Legendre, 2001). Unfortunately, for Atlantic cod, we are unable to predict the population size at which such a threshold might be situated. Although many cod populations are only small fractions of their former sizes, they still contain millions of breeding individuals (ICES, 2002; COSEWIC, 2003), and it might be difficult to argue that such a threshold has been reached. However, if reductions in population size have been accompanied by changes in density of individuals in spawning aggregations, it is quite conceivable that cod reproductive success has been affected.

At low population density, individuals will have a lower probability of encountering potential spawning partners and may either cease breeding or incur changes in reproductive behaviour that have adverse effects on fertilization rate or offspring viability. For example, individuals may experience delays in seasonal reproduction as more time might be required to find a mate. For batch-spawning fishes such as Atlantic cod, delays in release of eggs after ovulation of just a few hours can result in over-ripening of gametes and dramatically reduce viability (Kjørsvik and Lønning, 1983; Kjørsvik *et al.*, 1990). Scarcity of potential mates also lessens the potential for mate choice and individuals may resort to mating with partners of non-preferred phenotypes or genotypes, negatively affecting reproductive success (Jennions and Petrie, 1997). At the very least, size complementarity between spawning partners may be important for Atlantic cod to ensure that the urogenital openings of both fish are aligned opposite one another; pairings involving size-mismatched mates may negatively

affect fertilization rates otherwise (Hutchings *et al.*, 1999; Rakitin *et al.*, 2001). As population density declines, there may be fewer individuals near a spawning couple, and thus the number of satellite males per spawning female may also decline, resulting in reduced sperm concentration (Marconato *et al.*, 1997). This would provide another mechanism by which egg fertilization rates might decrease with declining adult density. Multiple paternity may also be important as a means for females to maximize their chance of producing viable offspring (Zeh and Zeh, 1996, 1997) and increased genetic variation improves the ability of a population to respond to future selection pressures.

Despite being of theoretical interest and practical importance, many aspects of Atlantic cod spawning behaviour are poorly understood and there is no information regarding the way that mating or reproductive success may be affected by changes in adult numbers or density (Nordeide and Folstad, 2000). Using data obtained from 21 laboratory populations, collected under three separate research programmes (Table 1), we explored the empirical basis of one potential cause of depensation in Atlantic cod. Firstly, we tested the hypothesis that fertilization rate declines with abundance. Reduced fertilization success at lower population sizes, leading potentially to reduced per capita recruitment, could produce an Allee effect. Secondly, we tested the hypothesis that variance in fertilization rate increases as

Table 1. Experimental tank volumes and sample sizes from which egg fertilization and spawner abundance data were obtained from each of the authors’ research programmes.

Research programme	Tank volume (m ³)	No. of females	No. of males	Spawning density (fish m ⁻³)	No. of egg batches
This study	2.9	3	2	1.73	11
This study	2.9	6	2	2.77	23
This study	2.9	7	4	3.81	33
This study	2.9	6	5	3.81	27
This study	2.9	3	2	1.73	16
This study	684.0	41	18	0.09	55
This study	684.0	40	27	0.10	44
This study	684.0	25	29	0.08	39
Rakitin	2.1	1	2	1.43	4
Rakitin	3.9	1	2	0.76	5
Rakitin	3.9	1	2	0.76	11
Rakitin	3.9	1	2	0.76	7
Rakitin	3.9	1	2	0.76	3
Rakitin	2.1	1	2	1.43	7
Rakitin	3.9	1	2	0.76	8
Bekkevold	8.5	4	4	0.94	22
Bekkevold	8.5	4	4	0.94	14
Bekkevold	8.5	4	4	0.94	11
Bekkevold	8.5	5	2	0.82	18
Bekkevold	8.5	4	6	1.18	11
Bekkevold	8.5	5	3	0.94	18

abundance declines. Increased variance in individual reproductive success would reduce effective population size (N_e), increasing the rate of loss of genetic variation at low levels of abundance.

While density of spawning individuals may be a more important factor influencing cod fertilization success than absolute number of individuals present in the wild, the opposite may be true within the spatial confines of a tank. In captive situations, the maximum distance between individuals, and thus the potential search time required to find a suitable mate, is very small relative to that which might occur in nature, and consequently the absolute number of mates available from which to choose may be considered more critical. Therefore, for the purpose of this study, we focused our attention on the influence of male abundance (as opposed to male density) on egg fertilization success.

Material and methods

The experimental protocols associated with two of the three aforementioned research programmes are described in detail elsewhere (Rakitin *et al.*, 2001; Bekkevold *et al.*, 2002) and will not be repeated here. We will, however, describe the methods employed in this study to examine the relationship between abundance and fertilization rate.

Atlantic cod were captured approximately 2–3 weeks before their annual spawning periods in 2001 and 2002 and transported to Dalhousie University, where they were allowed to spawn undisturbed. Upon arrival at Dalhousie in late April 2001, cod collected from the Southern Gulf of St Lawrence were assigned either to the 684 m³ Pool Tank or to one of five 2.9 m³ tanks, where they would remain for the duration of the study (Table 1). In 2002, cod were collected from both the Southern Gulf of St Lawrence (late April/early May) and the Western Scotian Shelf (January) and placed in the Pool Tank during their temporally distinct spawning periods (Table 1). In all cases, cod were maintained at densities similar to those reported in the wild [average of 0.004 fish m⁻³ (Morgan *et al.*, 1997) to a maximum of approximately 3 fish m⁻³ (George Rose, Memorial University, St John's, Canada, pers. comm.)], experienced water temperatures of approximately 8°C and natural photoperiods, and fed Shurgain® 8-mm fish feed daily.

To obtain fertilization data, each tank was outfitted with an egg collector. In the Pool Tank, eggs were collected by a plankton net covering the single tank outflow located at the surface. In the five smaller tanks, we employed an air-lift assisted egg collector located at the surface. All egg collectors were checked at approximately 16:00 every day and any eggs present were extracted. A random sample of at least 100 eggs from each daily collection was examined under a microscope to estimate the proportion of eggs fertilized (fertilization rate) and to confirm that all eggs had been spawned within the previous 24 h, based on descriptions by Hardy (1978), Davenport *et al.* (1981), and Kjærsvik

and Lønning (1983). Experimental animals were killed when no spawning had occurred in the tank for at least 5 days. Each fish was then measured and its sex and stage of maturity determined by observation of gross morphology of the gonad (Morrison, 1990) to verify that each individual was reproductively mature.

For each experimental population (Table 1), we report the median fertilization rate for the entire spawning period based on measurements of fertilization rate in daily egg collections. To control for small differences among research programmes in the timing of initial fertilization measurements, we report fertilization data for those days between the first day of the second week of spawning to the end of each spawning experiment. We initially use data from all research programmes to examine median seasonal fertilization rate in each experimental population in relation to the number of reproductive males present. Unfortunately, this relationship may be confounded by differences within or among research programmes. To address this issue, we proceeded to examine a subset of the data collected by Rakitin *et al.* (2001) and Bekkevold *et al.* (2002), in which, based on parentage analyses of daily egg collections, a single female and a known number of males had participated in spawning on a particular day. In these experiments, eggs were collected daily and a random sample was incubated until around the time of hatching, at which point it was preserved, along with tissue samples from parental fish, for parentage analysis. Only daily egg batches in which a single female had spawned and for which the number of males contributing sperm could be reliably determined are included in this component of our study. Therefore, we were able to reduce the variation in spawning density and experimental tank size (Table 1) and, based on genetic information, control for number of spawning females.

Results

Pooling all data from the three experiments, the proportion of eggs fertilized increased with total number of males (Figure 1). In addition to a positive association between proportion of eggs fertilized and number of males, the pooled data suggest that the among-brood variance in fertilization rate might decline with increased male abundance.

Similar associations between fertilization rate and male abundance appear to be evident after controlling for experimental tank size and for number of females to have contributed to daily egg batches. Based on experiments conducted by Bekkevold *et al.* (2002), as the number of males known to spawn with a single female in a spawning event increased from one to four, fertilization rate increased concomitantly (Figure 2). The data fit an asymptotic relationship with egg fertilization rate increasing rapidly with male number before levelling off at approximately 97%. The fitted equation, being forced through the origin,

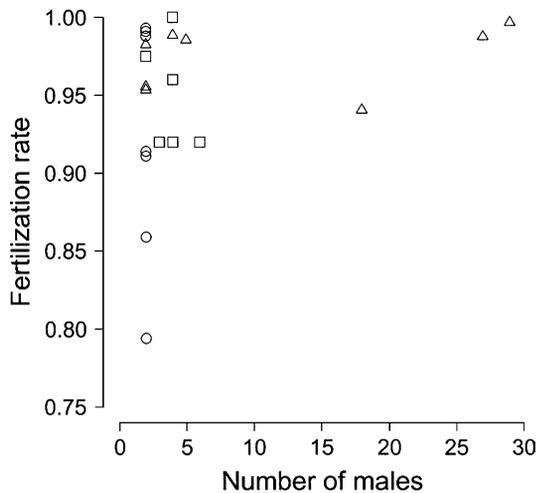


Figure 1. Median daily egg fertilization rate measured across the spawning season in captive Atlantic cod (*Gadus morhua* L.) in relation to the number of males present in each tank. Triangles represent data collected at Dalhousie University, circles represent data provided by Rakitin *et al.* (2001), and squares represent data provided by Bekkevold *et al.* (2002). Note that daily egg batches included here may have been the product of multiple spawning females engaged in multiple spawning events.

was fertilization rate = $0.97 \times (1 - e^{-2.02 \times \text{number of males}})$. The convex nature of the relationship, which is of primary interest in the present study, remains if the fitted relationship is not forced through the origin (Figure 2). Data from

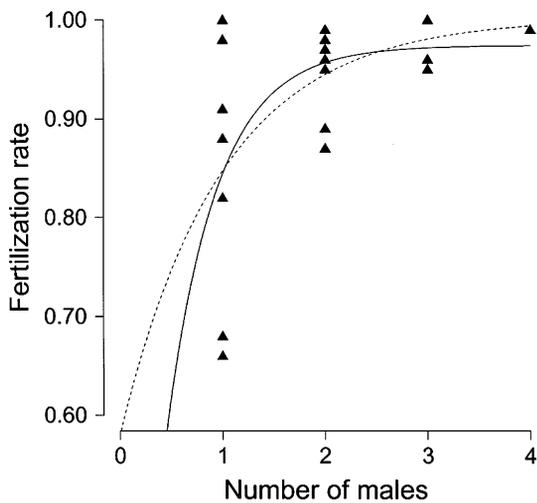


Figure 2. Atlantic cod (*Gadus morhua* L.) egg fertilization rate in individual spawning events involving a single female in relation to the number of males that contributed sperm to the event. Closed triangles represent data provided by Bekkevold *et al.* (2002), continuous line indicates the exponential asymptotic function that best described the data (fertilization rate = $0.97 \times (1 - e^{-2.02 \times \text{number of males}})$), and dashed line indicates the exponential asymptotic function not forced through the origin (fertilization rate = $1.00 - 0.42 \times e^{-1.00 \times \text{number of males}}$).

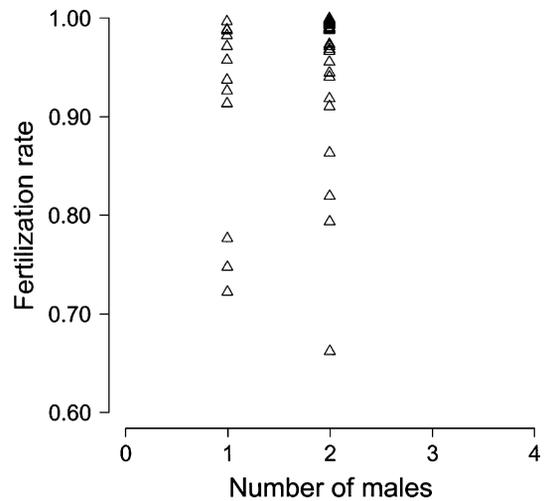


Figure 3. Atlantic cod (*Gadus morhua* L.) egg fertilization rate in individual spawning events involving a single female in relation to the number of males that contributed sperm to the event. Open triangles represent data provided by Rakitin *et al.* (2001).

Rakitin *et al.* (2001) are also indicative of higher fertilization rate within single-female broods fertilized by two males than those fertilized by one male (Figure 3; mean arcsine-transformed fertilization rate in single-female egg batches fertilized by 1 male = 74.9, 2 males = 80.2; $t_{39} = -1.72$, $p = 0.047$).

The increased among-brood variance in fertilization rate with declining male abundance suggested by the pooled data (Figure 1) was also evident from the daily egg batches for which only a single female and a known number of spawning males contributed (Figures 2, 3). Comparing three metrics of variability (variance, coefficient of variation, interquartile range), the variability in fertilization rate among batches fertilized by a single male appeared to be consistently greater than the variability among batches fertilized by two males (Table 2). However, variance ratio tests involving the arcsine-transformed data revealed that this difference was statistically significant only for the data provided by Bekkevold [Bekkevold *et al.* (2002); $F_{6,6} = 5.30$, $p = 0.031$; Rakitin *et al.* (2001): $F_{11,28} = 1.33$, $p = 0.258$].

Table 2. Metrics of variability [variance, coefficient of variation (CV), interquartile range (IQR)] in arcsine-transformed fertilization rate in single-female egg batches fertilized by either one or two males.

Reference	Spawning males	No. of egg batches	Variance	CV	IQR
Bekkevold <i>et al.</i> (2002)	1	7	171.3	0.19	21.7
	2	7	32.3	0.07	9.2
Rakitin <i>et al.</i> (2001)	1	12	98.2	0.13	15.7
	2	29	73.7	0.11	9.7

Discussion

Despite a pressing need to evaluate the potential for Allee effects to influence population growth in Atlantic cod, an empirical vacuum faces those trying to comprehend why most collapsed populations have failed to recover. In the present study, we attempted to address hypotheses relating to this issue by exploring the way that fertilization success might be affected by changes in male abundance. Because captive cod require large tanks for spawning and reproduce over a 6–12-week annual spawning season (Myers *et al.*, 1993), it is difficult to replicate spawning experiments and we opted to use data from three independent research programmes. One drawback to this approach is that experimental population differences within or among research programmes may have confounded differences observed in relation to number of males present. Nonetheless, we found a similar pattern when we controlled for number of spawning females and reduced variation in spawning density and experimental tank size by separately analysing fertilization rates in daily egg batches which involved only a single female and a known number of males.

As with any laboratory experiment, it can be difficult to evaluate the degree to which our results relate to the field conditions experienced by cod during spawning. However, notwithstanding the limited data that exist on cod spawning densities, there is reason to believe that an Allee effect of the type suggested here may be of some importance in the wild. Densities of northern cod estimated in 1992, the year in which the commercial fishing moratorium on this stock began, were measured within a shoal of reproductive fish measuring roughly 125 km² in area (Morgan *et al.*, 1997). Within-shoal densities differed by more than 2 orders of magnitude, ranging between an average of 0.004 fish m⁻³ to a maximum of 0.488 fish m⁻³. The maximum density is considerably lower than all but three of the densities included in our analysis; the average density was exceeded in all cases. Given that we found fertilization rate to decline with abundance at densities several times greater than those documented in the wild, and at a time of low overall abundance, we are persuaded that the Allee effect examined here may well be realized in the field.

The experimental work on egg fertilization rate and male abundance presented here suggests one mechanism by which depensation might be realized within populations of Atlantic cod. Specifically, there is evidence to suggest that the proportion of eggs fertilized declines with number of spawning males. If manifested as reduced number of recruits per spawner, this would provide one means by which per capita growth rate would decline, rather than increase, with reduced abundance. In addition, the data suggest that variance in fertilization success may increase as male abundance declines. This means that there may also be increased variance in individual reproductive success with declining abundance, something that would negatively affect both effective population size (N_e) and the number of

individuals contributing genes to future generations relative to the estimated census number of spawning individuals (N_c).

Reductions in fertilization rate with reductions in breeding population size, if realized in the wild, might be a product of the mating system of Atlantic cod, in which satellite males compete with primary males for egg fertilization. As population size or density declines, the number of satellite males per spawning female may decline as well, a consequence that might be particularly deleterious to fertilization success if the number of eggs fertilized depends on sperm concentration. Consistent with this hypothesis is the observation that sperm numbers and fertilization rates in multiple-male spawnings are higher than those in single-male spawnings in the bluehead wrasse (*Thalassoma bifasciatum* Bloch; Shapiro *et al.*, 1994; Marconato *et al.*, 1997).

A second proximate cause of a positive association between fertilization rate and abundance may be attributable to reduced opportunities for mate choice afforded by reduced number of males (Rowe and Hutchings, 2003). Both genetic and behavioural data are consistent with the hypothesis that mate choice is an integral part of cod spawning. Although unfertilized cod eggs and sperm remain viable for more than 1 h in seawater (Kjørsvik and Lønning, 1983; Trippel and Morgan, 1994), the sperm cells swim slowly (Trippel and Neilson, 1992; Litvak and Trippel, 1998); Brawn (1961) suggested that close alignment of the urogenital openings during the ventral mount was necessary to achieve high fertilization rate. Hutchings and Myers (1993) predicted that this should favour assortative mating, a hypothesis later supported by the genetic analyses conducted by Rakitin *et al.* (2001). In experimental competitive mating situations, they found that only males of similar length (within 13%) to the female were able to sire entire batches of offspring. Mate choice is also suggested by various behavioural interactions between spawning males and females (Brawn, 1961; Hutchings *et al.*, 1999).

Genetic complementarity may also be important insofar as various agents of intragenomic conflict and other forces acting at the suborganismal level may result in genetic incompatibility between some female and male gametes. Such genetic incompatibilities may prevent fertilization (reviewed by Wirtz, 1997) or successful development of offspring to sexual maturity (reviewed by Zeh and Zeh, 1996, 1997). Using genetic markers, Rakitin *et al.* (1999) found that when sperm from two males were combined in vitro with eggs of a single female, the relative success of males varied depending on which female was the egg donor, suggesting female 'choice' at the gamete level or perhaps genetic incompatibilities. All else being equal, we would expect genetic complementarity to increase with population size. In other words, increased opportunities for mate choice may result in increased fertilization rate because of increased phenotypic and genetic variability among potential mates.

Increased variance in individual reproductive success, reflected by increased variance in fertilization rate, will result in a reduction in effective population size (Nunney, 1993; Sugg and Chesser, 1994). Although abundance can appear high in severely depleted populations of Atlantic cod, it is important to acknowledge that census estimates of mature individuals (N_c) can poorly reflect the number of individuals that contribute genes during spawning, as represented by the effective population size (N_e). For broadcast-spawning species such as Atlantic cod, it has been estimated that N_e may be 2–5 orders of magnitude lower than N_c because of the high variance in individual reproductive success associated with this type of mating system (Hedgecock, 1994).

Empirical support for this range in N_e/N_c has recently been forthcoming from studies of marine fishes. Based on estimates of N_e from declines in heterozygosity and temporal fluctuations in allele frequency over 46–48 years, Hauser *et al.* (2002) concluded that effective population size in the New Zealand snapper (*Pagrus auratus* Forster) was 5 orders of magnitude less than census population sizes. The effective number of female red drum (*Sciaenops ocellatus* L.) in the Gulf of Mexico, estimated from both mitochondrial (Turner *et al.*, 1999) and microsatellite DNA (Turner *et al.*, 2002), has been estimated to be 3 orders of magnitude smaller than female census population size. Increased variation in fertilization rate concomitant with reductions in population size may increase the rate at which N_e declines with abundance, which would increase the rate at which genetic variation is lost from the population.

In summary, our data are consistent with the hypotheses that (a) fertilization rate declines with abundance and that (b) variance in fertilization rate increases as population size declines. The former identifies one potential mechanism underlying depensation in Atlantic cod; the latter may have negative genetic consequences for effective population size (N_e). However, it needs to be stressed that these patterns between fertilization rate and abundance are the product of exploratory analysis, and that considerably more work needs to be done before the veracity of the conclusions drawn here can be fully assessed.

Acknowledgements

We are grateful to Paty Avendaño and Jim Eddington for technical assistance in the laboratory. We also thank Tim Birkhead, Bob Latta, Marty Leonard, Ransom Myers, and three anonymous reviewers for their insightful and critical comments on this manuscript. Financial support was provided by a Natural Sciences and Engineering Research Council (NSERC) Discovery Grant and a Petro-Canada Young Innovator award to JAH, an NSERC Postgraduate Scholarship to SLR, and a European Union grant through Bergen Marine contract no. HPRI-1999-CT-00056 to DB as part of the Improving Human Potential Program.

References

- Bekkevold, D., Hansen, M. M., and Loeschcke, V. 2002. Male reproductive competition in spawning aggregations of cod (*Gadus morhua*, L.). *Molecular Ecology*, 11: 91–102.
- Brander, K. 1994. Spawning and life history information for North Atlantic cod stocks. ICES Cooperative Research Report, No. 205. 150 pp.
- Brawn, V. M. 1961. Reproductive behaviour of the cod (*Gadus callarias* L.). *Behaviour*, 18: 177–198.
- Chambers, R. C., and Waiwood, K. G. 1996. Maternal and seasonal differences in egg sizes and spawning characteristics of captive Atlantic cod, *Gadus morhua*. *Canadian Journal of Fisheries and Aquatic Sciences*, 53: 1986–2003.
- COSEWIC, 2003. COSEWIC assessment and update status report on the Atlantic cod *Gadus morhua*, Newfoundland and Labrador population, Laurentian North population, Maritimes population, Arctic population, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.
- Davenport, J., Lønning, S., and Kjorsvik, E. 1981. Osmotic and structural changes during early development of eggs and larvae of the cod, *Gadus morhua* L. *Journal of Fish Biology*, 19: 317–331.
- DFO. 2003. Northern (2J + 3KL) cod. Canadian Science Advisory Secretariat Stock Status Report 2003/018, Department of Fisheries and Oceans Canada, Ottawa.
- Frank, K. T., and Brickman, D. 2000. Allee effects and compensatory population dynamics within a stock complex. *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 513–517.
- Hardy, J. D., Jr. 1978. Development of Fishes of the Mid-Atlantic Bight. An Atlas of Egg, Larval and Juvenile Stages. Vol. II: Anguillidae Through Syngnathidae. Fish and Wildlife Service, Office of Biological Services 78/12.
- Hauser, L., Adcock, G. J., Smith, P. J., Bernal Ramírez, J. H., and Carvalho, G. R. 2002. Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). *Proceedings of the National Academy of Sciences*, 99: 11742–11747.
- Hedgecock, D. 1994. Does variance in reproductive success limit effective population sizes of marine organisms? *In Genetics and Evolution of Aquatic Organisms*, pp. 122–134. Ed. by A. R. Beaumont. Chapman and Hall, London.
- Hutchings, J. A., Bishop, T. D., and McGregor-Shaw, C. R. 1999. Spawning behaviour of Atlantic cod, *Gadus morhua*: evidence of mate competition and mate choice in a broadcast spawner. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 97–104.
- Hutchings, J. A., and Myers, R. A. 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 50: 2468–2474.
- Hutchings, J. A., and Myers, R. A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 2126–2146.
- ICES. 2002. Cod in Subarea IV (North Sea), Division VIII (Eastern Channel), and Division IIIa (Skagerrak). *In Report of the ICES Advisory Committee on Fishery Management*, 2002, pp. 219–227. ICES Cooperative Research Report, No. 255.
- Jennions, M. D., and Petrie, M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews*, 72: 283–327.
- Kjesbu, O. S., Solemdal, P., Bratland, P., and Fonn, M. 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 53: 610–620.

- Kjørsvik, E., and Lønning, S. 1983. Effects of egg quality on normal fertilization and early development of the cod, *Gadus morhua* L. *Journal of Fish Biology*, 23: 1–12.
- Kjørsvik, E., Mangor-Jensen, A., and Holmefjord, I. 1990. Egg quality in fishes. *Advances in Marine Biology*, 26: 71–113.
- Liermann, M., and Hilborn, R. 2001. Depensation: evidence, models and implications. *Fish and Fisheries*, 2: 33–58.
- Litvak, M. K., and Trippel, E. A. 1998. Sperm motility patterns of Atlantic cod (*Gadus morhua*) in relation to salinity: effects of ovarian fluid and egg presence. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 1871–1877.
- Marconato, A., Shapiro, D. Y., Petersen, C. W., Warner, R. R., and Yoshikawa, T. 1997. Methodological analysis of fertilization rate in the bluehead wrasse *Thalassoma bifasciatum*: pair versus group spawns. *Marine Ecology Progress Series*, 161: 61–70.
- McGrath, P. T. 1911. Newfoundland in 1911. Whitehead, Morris, and Co., London.
- Møller, A. P., and Legendre, S. 2001. Allee effect, sexual selection and demographic stochasticity. *Oikos*, 92: 27–34.
- Morgan, M. J., DeBlois, E. M., and Rose, G. A. 1997. An observation on the reaction of Atlantic cod (*Gadus morhua*) in a spawning shoal to bottom trawling. *Canadian Journal of Fisheries and Aquatic Sciences*, 54(Suppl 1): 217–223.
- Morrison, C. M. 1990. Histology of the Atlantic cod, *Gadus morhua*: an atlas. Part three. Reproductive tract. Canadian Special Publication of Fisheries and Aquatic Sciences, No. 110. 117 pp.
- Myers, R. A., Hutchings, J. A., and Barrowman, N. J. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecological Applications*, 7: 91–106.
- Myers, R. A., Mertz, G., and Bishop, C. A. 1993. Cod spawning in relation to physical and biological cycles of the northern North-west Atlantic. *Fisheries Oceanography*, 2: 154–165.
- Nordeide, J. T., and Folstad, I. 2000. Is cod lekking or a promiscuous group spawner? *Fish and Fisheries*, 1: 90–93.
- Nunney, L. 1993. The influence of mating system and overlapping generations on effective population size. *Evolution*, 47: 1329–1341.
- Rakitin, A., Ferguson, M. M., and Trippel, E. A. 1999. Sperm competition and fertilization success in Atlantic cod (*Gadus morhua*): effect of sire size and condition factor on gamete quality. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 2315–2323.
- Rakitin, A., Ferguson, M. M., and Trippel, E. A. 2001. Male reproductive success and body size in Atlantic cod *Gadus morhua* L. *Marine Biology*, 138: 1077–1085.
- Rowe, S., and Hutchings, J. A. 2003. Mating systems and the conservation of commercially exploited marine fish. *Trends in Ecology and Evolution*, 18: 567–572.
- Shapiro, D. Y., Marconato, A., and Yoshikawa, T. 1994. Sperm economy in a coral reef fish, *Thalassoma bifasciatum*. *Ecology*, 75: 1334–1344.
- Shelton, P. A., and Healey, B. P. 1999. Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 1521–1524.
- Smedbol, R. K., and Wroblewski, J. S. 1997. Evidence for inshore spawning of northern Atlantic cod (*Gadus morhua*) in Trinity Bay, Newfoundland, 1991–1993. *Canadian Journal of Fisheries and Aquatic Sciences*, 54(Suppl 1): 177–186.
- Smedbol, R. K., Shelton, P. A., Swain, D. P., Fréchet, A., and Chouinard, G. A. 2002. Review of population structure, distribution and abundance of cod (*Gadus morhua*) in Atlantic Canada in a species-at-risk context. Canadian Science Advisory Secretariat Research Document 2002/082, Department of Fisheries and Oceans Canada, Ottawa.
- Sugg, D. W., and Chesser, R. K. 1994. Effective population sizes with multiple paternity. *Genetics*, 137: 1147–1155.
- Trippel, E. A., and Morgan, M. J. 1994. Sperm longevity in Atlantic cod (*Gadus morhua*). *Copeia*, 1994: 1025–1029.
- Trippel, E. A., and Neilson, J. D. 1992. Fertility and sperm quality of virgin and repeat-spawning Atlantic cod (*Gadus morhua*) and associated hatching success. *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 2118–2127.
- Turner, T. F., Richardson, L. R., and Gold, J. R. 1999. Temporal genetic variation of mitochondrial DNA and the female effective population size of red drum (*Sciaenops ocellatus*) in the northern Gulf of Mexico. *Molecular Ecology*, 8: 1223–1229.
- Turner, T. F., Wares, J. P., and Gold, J. R. 2002. Genetic effective size is three orders of magnitude smaller than adult census size in an abundant, estuarine-dependent marine fish (*Sciaenops ocellatus*). *Genetics*, 162: 1329–1339.
- Wirtz, P. 1997. Sperm selection by females. *Trends in Ecology and Evolution*, 12: 172–173.
- Zeh, J. A., and Zeh, D. W. 1996. The evolution of polyandry I: intragenomic conflict and genetic incompatibility. *Proceedings of the Royal Society of London Series B*, 263: 1711–1717.
- Zeh, J. A., and Zeh, D. W. 1997. The evolution of polyandry II: post-copulatory defences against genetic incompatibility. *Proceedings of the Royal Society of London Series B*, 264: 69–75.