



Can body size parameters be used to distinguish the Kattegat cod (*Gadus morhua*) stock from the North Sea cod stock?

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Abstract

Atlantic cod is one of the world's most important commercial fish stocks and is dependent on fishing regulations for its wellbeing and survival. An important part in fisheries management is information of the stock distribution. This is needed to not cause overestimations that results in heavy overfishing. Here, Kattegat and North Sea male and female cod of the same ages (3- to 5-year-old) were distinguished using body size parameters (length, weight and condition). Parameter differences were evident between some year-classes, but when analysing the whole stock, the variance of the body size parameters was too large and could therefore not be used for stock discrimination. When the body size parameters were analysed by season (caught), the parameter variance decreased. However, not low enough for one to be able to use the parameters for stock separation. Thus, I conclude that the body size parameters length, weight and condition, could not be used to distinguish the Kattegat cod stock from the North Sea cod stock.

Background

The abundance of cod (*Gadus morhua*) outside the Swedish west coast has since decades been known to decline in areas exposed to heavy fishing (Svedäng et al., 2010; Bartolino et al., 2012; Cardinale and Svedäng, 2004) and because of the disappearance of spawning areas. (Vitale et al., 2008). This complicates the rebuilding of the cod stock. Kattegat, i.e. the water connecting Skagerrak with the Oresund and the Danish Straits, has since 1980's lost more than 90 % of its spawning stock biomass (Jonsson et al., 2016). On the contrary however, ICES (*International Council for the Exploration of the Seas*) showed that the spawning stock biomass has increased slightly since 2009 (ICES, 2016), but not reached levels near what it ones was. However, this increase suggests the importance of fishery regulations and gives a reason to continue seeking after efficient methods for stock assessments.

In the process of estimating fishing quotas, fish distribution is of great importance to achieve sustainable stock assessment and fisheries management. Assumptions of fish origin need to be scientifically proven to reduce risk of overestimations and incorrect regulations that instead could harm stocks. Different methods for stock identification have therefore been developed. Tagging individuals or by looking at the different structures of ear bones and scales can be helpful in the process of stock discrimination, not to mention genetic analysis that provide the knowledge of relatedness among fish on a DNA level. The knowledge of behavioural patterns need to be considered as well, to be able to separate stocks (Svedäng et al., 2007; André et al., 2016). Aside from that, morphometrics such as the ratio between the sizes of body parts, and life history parameters, can to some extent be used as tools in stock differentiation (Jennings et al., 2001).

Introduction

It has previously been hypothesized that differences in growth follow a countergradient variation (CnGv) where northern fish populations grow faster than those on lower latitudes (Conover, 1990; Conover and Present, 1990). This variation between the populations suggests adaptions to different growth conditions. For instance, Lambert et al. (1994) observed lower

growth in cod present in seawater compared to cod in low and intermediate salinities (7‰ and 14‰ respectively). Growth of cod has too previously been confirmed to increase with temperature (Wang et al., 2014; Righton et al., 2010) and photoperiod (Imsland et al., 2007), but can very well be supressed dependent on its thermal adaption as seen in other gadoids (Laurel et al., 2016). Moreover, fishing has proved to increase growth for highly exploited species (Swain et al., 2007). Conversely, it is known that growth rate levels off when individuals reach maturity, and start diverting energy into reproduction. (Heino et al, 2008; Pardoe et al, 2008). Growth in length and weight is however different processes (Árnason et al., 2009) and will in this study be investigated separately.

Individual length and weight are determining the condition factor that has several formulations. The Fulton K is a condition factor that assumes isometric growth (Stevenson and Woods, 2006) and show the nutritional value of a specimen. A large body mass-to-length ratio indicate good nutritional condition, while the opposite body proportions indicate poor nutritional values (Froese, 2006). It has earlier been investigated how condition may be affected by ambient environment. Rätz and Lloret (2003) suggest that North Atlantic cod in temperate waters on average had better condition than fish in colder waters, but again this relationship could differ dependent on the thermal adaption (Laurel et al., 2016). Furthermore, it is implied that cod in better condition would sustain higher exploitation (Rätz and Lloret, 2003). In line with this, low condition is suggested to have caused the decline in the number of large individuals of the Baltic cod stock (ICES, 2015). This makes it an interesting parameter to investigate because of its importance towards fishery management and close relationship with the fish length and weight. Condition is thus an estimate of the individual health and is important for the animal's performance during periods of scarcity, migration, and reproduction (Stevenson and Woods, 2006).

These findings suggest that the body size parameters; length, weight and condition, could mediate certain characteristic responses due to previous levels of fishing intensity and as effects of the ambient environment or biological processes. If differences were to be observed between fish in an area, this could suggest that they have different life histories and therefore can be proposed as belonging to separate stocks.

The purpose of this study was to investigate if body size parameters; length, weight and condition of individual cod differed between stocks. It was further investigated if body size parameters potentially could be used to distinguish between the Kattegat and the North Sea cod stocks. If so, this approach later could be used in stock assessments to give more accurate stock advices. With support from above-mentioned differences in life history traits, my hypotheses were therefore, differences in length, weight and condition can be found between the stocks and used as a separating method for the Kattegat and North Sea cod stocks.

Method

Estimating parameter differences between stocks

Genetic data of stock origin was available for cod collected by Swedish and Danish IBTS (*International Bottom Trawl Surveys*) in Kattegat executed in 2008 and 2014-2016 (n=1842). The data included individual fish total length (L), total weight (W), age, sex, and stock origin

(Kattegat and North Sea). Fish genetically identified as belonging to the Kattegat cod stock was separated from the North Sea cod stock.

Mean length and weight for each gender, age, and origin was calculated for both stocks (Figure 1). The standard error (SE) was then estimated for each parameter mean. This was in turn used to investigate if there were any difference between the parameter means of the two stocks.

Mean Fulton's condition factor (K) was calculated to retrieve the nutritional condition of the cod for each gender, age and origin (See Eq. 1). SE was too estimated for this parameter mean. Mean parameters was also calculated for cod analysed by season (Q1 and Q4).

$$K = 100 \frac{W}{L^3}$$
 (Equation 1)

K is the Fulton condition factor, W is the individual weight (g) of the fish and L (cm) is the individual length of the fish.

Parameters for cods of the same age (3-, 4- and 5-year-olds) were separately investigated between stocks for every sex using a one-way ANOVA. Obtained p-values below 0,05 would indicate a significant parameter difference between the specific age groups of the stocks, while p-values above 0,05 would indicate no difference.

Investigating body size parameters as a separating method

A χ^2 -test was carried out in Excel to establish the variance of body size parameters within stocks. First, each mean parameter SE was applied to the original data. Fish of a specific mean with parameter values within that mean SE were given a value of 1 (observed amount). Fish of that same specific mean with parameter values outside the SE was given a value of 0. The total amount of fish of that same mean (expected amount) was then estimated. Estimated observed and expected amounts of fish for each age group within every stock and gender was compared and summed to a χ^2 -value (Eq. 2).

$$\chi 2 = \sum \frac{(Obs_{Age0} - Exp_{Age0})^2}{Exp_{Age0}} + \frac{(Obs_{Age1} - Exp_{Age1})^2}{Exp_{Age1}} + \dots$$
 (Equation 2)

"Obs" is the amount of fish for each age group within a specific stock and gender that had parameter values within their mean SE. "Exp" is the total amount of fish for each age group within a specific stock and gender. The χ^2 -value is the sum of the equations.

The derived χ^2 -values was in Excel automatically compared to the critical value from a χ^2 distribution table. One single corresponding p-value was then retrieved for all fish combined of a certain stock and gender (Table 2). Significant p-values (<0,05) would propose a difference between observed and expected amounts of fish and a too big of a variance for further analysis between stocks. The body size parameters would then not be considered accurate enough to be used as a separating method between stocks.

Means (1±SE) was also calculated for each season; Q1 (Jan-Mar) and Q4 (Oct-Dec), e. g. time of the year when the fish was caught. This was calculated to investigate if any general parameter difference could be observed for fish caught in different seasons (Figure 2 and 3). It was then investigated if the season could affect the χ^2 -test results and therefore play a role in the approach to distinguish cod stocks. As before, the actual amount of fish from the original data was

counted and compared to fish derived by the SE (fish given the value of 1) using a χ^2 -test (Table 3).

Results

Parameter differences between stocks

Mean length is more linear for both stocks and sexes, while mean weight seems to increase exponentially. Fulton's condition factor is close to horizontally linear with values mostly fluctuating between 0,9-1,1 and seems to be independent on age (Figure 1). Furthermore, all fish over 6 years old that was caught in the surveys were Kattegat cod.

When divided into seasons, Q1 and Q4 showed similar trends as when not divided by season (Figure 2 and 3). The only exception was for mean length of Q4 that instead of being linear, displayed a logistic curve shape (Figure 3a).

Comparisons of parameters with the one-way ANOVA revealed significant differences between the stocks mean length and weight for 3-year-old fish of both sexes (females [Length]: F = 4,03, P < 0,05., female [Weight]: F = 4,61, P < 0,05; males [Length]: F = 14,35, P < 0,001., male [Weight]: F = 17,41, P < 0,001). A significant difference in condition was also observed between the stocks for 4-year-old females (F = 5,50, P < 0,05) (Table 1). For the cod with significant parameter differences, the North Sea cod expressed higher parameter values than Kattegat cod regardless of age-group and sex.

Splitting the means into season (Figure 2 and 3) did not reveal any evident divergence between stocks compared to the original graphs (Figure 1). This led to no further test with an ANOVA.

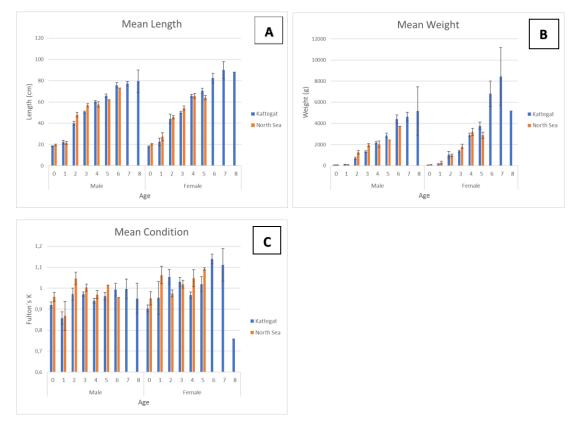


Figure 1. Mean A) length, B) weight, and C) condition between the Kattegat and the North Sea cod stock. Bars represents standard errors.

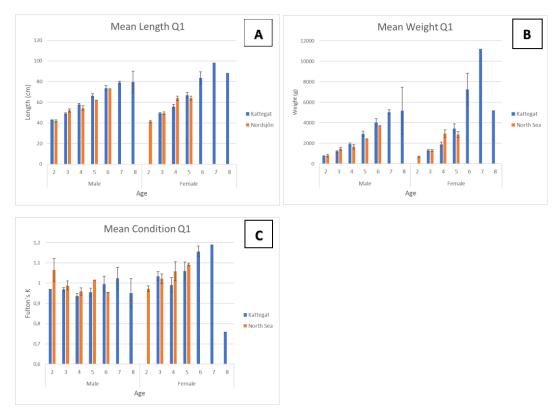


Figure 2. Mean A) length, B) weight, and C) condition between the Kattegat and the North Sea cod stock of season 1 (Jan-Mar). Bars represents standard errors.

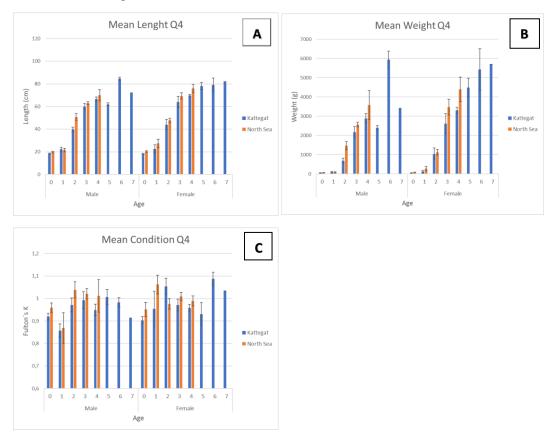


Figure 3. Mean A) length, B) weight, and C) condition between the Kattegat and the North Sea cod stock of season 4 (Oct-Dec). Bars represents standard errors.

Table 1. Table showing F-, and p-values derived from the one-way ANOVA when investigating stock parameter differences. Values under the column "Amount" represent amount of Kattegat cod (no parenthesis) and North Sea cod (with parenthesis). Grey cells are observed significant differences. Where parameter differences could be found, North Sea cod displayed higher parameter values than Kattegat cod.

| | | Lengtl | Length (cm) | | Weight (g) | | Condition | |
|--------|-----|----------|-------------|-------|------------|-------|-----------|----------|
| | Age | F | P | F | P | F | P | (N) |
| Female | 3 | 4,03 | 0,0484 | 4,61 | 0,0350 | 0,144 | 0,705 | 47/ (29) |
| | 4 | 6,72E-06 | 0,998 | 0,667 | 0,417 | 5,50 | 0,0218 | 54/ (19) |
| | 5 | 0,731 | 0,403 | 0,632 | 0,437 | 0,398 | 0,536 | 19/(2) |
| Male | 3 | 14,3 | 2,95E-04 | 17,4 | 7,69E-05 | 3,10 | 0,0824 | 54/ (27) |
| | 4 | 1,05 | 0,309 | 0,263 | 0,610 | 1,23 | 0,270 | 70/ (15) |
| | 5 | 0,204 | 0,656 | 0,146 | 0,707 | 0,347 | 0,562 | 22/(1) |

Body size parameters as a separating method

Low χ^2 p-values (<0,05) were observed for all parameters for fish both divided and not divided into seasons (Table 2 and 3). However, clustering fish according to seasons decreased the significance of the χ^2 -test.

All Kattegat cod showed a lower χ^2 p-value than North Sea cod did. When not divided into seasons, all North Sea females had lower p-values than the males, while the opposite relationship was observed for the Kattegat cod (Table 2). When instead divided into season (Q1 and Q4), Q1 displayed the same relationship as when not divided into seasons (Table 3). For Q4, North Sea females had higher χ^2 p-values than the males in length and weight, but not in condition. Kattegat females also had higher χ^2 p-values than males in weight (Table 3).

Table 2. Derived p-values from χ^2 -test that show the relationship between the total amount of cod and the amount of cod with parameter values within the confidence interval (SE). Values represent relationship for males (no parenthesis) and females (parenthesis).

| All | Length | Weight | Condition |
|-----------|------------|------------|------------|
| | 3,46E-32/ | 1,23E-34/ | 5,13E-31/ |
| Kattegat | (2E-25) | (4,86E-25) | (6,06E-24) |
| | 1,03E-8/ | 3,92E-09/ | 2,06E-07/ |
| North Sea | (1,83E-10) | (1,28E-09) | (2,93E-10) |

Table 3. Derived p-values from χ^2 -test when fish were analysed by season. Values show the relationship between the total amount of cod and the amount of cod with parameter values within the confidence interval (SE). Values represent relationship for males (no parenthesis) and females (parenthesis).

| Season | Origin | Length | Weight | Condition |
|--------|-----------|------------|------------|------------|
| Q1 | | 5,47E-19/ | 4,47E-20/ | 5,77E-18/ |
| | Kattegat | (2,59E-12) | (3,15E-11) | (3,39E-10) |
| | | 4,26E-04/ | 1,94E-04/ | 9,42E-04/ |
| | North Sea | (1,27E-06) | (6,10E-06) | (6,18E-06) |
| Q4 | | 1,39E-12/ | 5,30E-14/ | 1,45E-12/ |
| | Kattegat | (4,04E-13) | (9,72E-14) | (1,05E-13) |
| | | 1,05E-05/ | 1,05E-05/ | 1,17E-04/ |
| | North Sea | (7,27E-05) | (1,12E-04) | (2,50E-05) |

Discussion

Parameter differences between stocks

From the one-way ANOVA one could conclude that there were parameter differences between the stocks for some fish of the same age groups (Table 1). This strengthened the first hypothesis stating that parameter differences could be found between the stocks. The fish that showed differences, indicated greater mean parameters values for North Sea cod than the Kattegat cod. However, there were no consistent significant differences in body size parameters across all ages that supported my first hypothesis, leading to its rejection.

The observed differences and similarities between the stocks might be explained by the fish adaption towards prevailing environmental factors. For example, despite that increased temperature has shown to positively affect fish growth (Wang et al., 2014) the differences between areas might not be enough for supporting different growth rates. In accordance to Conover and Present (1990) the latitudinal difference between the study areas would lead to increased growth of North Sea cod in comparison to Kattegat cod because the area stretches further north. Conversely, the southern and northern North Sea have both higher respectively lower prevailing temperatures than Kattegat (Righton et al., 2010). However, the original data left no possibility to investigate from which area the North Sea fish came from. This might even out the difference between the Kattegat and North Sea stocks if the fish in the North Sea express different growth depending on where it resides. Furthermore, though cod is an euryhaline species that can sustain in a wide range of salinities it is known to have increased growth at low and intermediate salinity conditions (e.g. 7‰ and 14‰ respectively) compared to when in seawater (Lambert et al., 1994). These findings suggest a decrease in the growth of fish as one move from Kattegat towards the North Sea.

Interestingly, Righton et al. (2010) identified Skagerrak (a part of the North Sea cod stock) and Kattegat as having similar ecosystems in the respect to historical and existing commercial cod fisheries. If Skagerrak have been caused by similar fishing intensities to Kattegat, and is unified with the remaining North Sea stock, as in this study, this might decrease the difference between the North Sea and Kattegat stock. This leads to the conclusion that they could display the same body size parameters. The cod abundance in both the North Sea and Kattegat has been severely

reduced in the recent decades (Jonsson et al., 2016). This too suggests that they could display similar growth (Swain et al., 2007), that may explain the few differences found in the ANOVA. Moreover, early life environment (e.g. salinity and temperature) has been shown to affect cod biomass later in life (Imsland et al., 2011). This might explain the similar mean lengths, weight and condition received in this study.

Body size parameters as a separating method

In the χ^2 -test, the observed distribution of fish within the parameter SE differed too much from the expected outcome suggesting one could only determine the origin on a small amount of cod by using the body size parameters. The low p-values proved that the parameter variance of fish within the stocks was too high for one to be able to use the data in further analysis between the stocks. This goes against the second hypothesis stating that the body size parameters could be used in stock separation.

From the χ^2 derived p-values, one can also observe a greater significance (lower p-value) for all Kattegat cod compared to the North Sea cod. This suggests that the parameter variance within the North Sea cod stock was smaller than that of the Kattegat cod stock. This could be because of the fewer North Sea individuals in the data. As the number of replicates in a sample increases, SE will become narrower. Lower SE will cause fewer individuals to fit with their parameter values within the confidence intervals, leading to less significant p-values in the χ^2 -test for the Kattegat cod in comparison to North Sea cod. On the contrary, a greater sample size tends to lead to more accurate estimations of the real stock means. Similar differences also apply between sex for each stock.

When the body size parameters were analysed by seasons, χ^2 p-values was higher compared to when seasons were clustered. (Table 1 and 2). The higher p-values suggest a less varied parameter distribution when fish were analysed by season compared to when not analysed by season. The results highlight the importance of seasonality and suggest it as having an additional explanatory power in stock discrimination. Furthermore, no ANOVA was carried out for cod analysed by season. The observed parameter values (Figure 2 and 3) suggested that the differences between stocks were small. An ANOVA would therefore not bring any additional information about the parameter differences. It would instead risk II errors (e.g. finding no differences between parameters although there is one).

It is however obvious that cod in similar seasons would be found to express a less varied parameter distribution compared to cod caught in separate times of the year. Female cod caught in Q4 (Oct-Dec) could for example channel their energy into egg production in preparation for the spawning season (Jan-Apr), which will increase their weight. When spring arrives, Q1 (Jan-Mar) cod that have not yet spawned can though express a higher weight than Q4 cod because it has been producing eggs for a longer period of time. On the contrary, Q1 cod that already spawned before getting caught can display a considerably lower weight than Q4 cod because the eggs have been released.

In this study, although differences were small, Q4 cod mediated slightly higher weight than the Q1 cod (Figure 2 and 3). This difference is mostly evident for 3- and 4-year-old cod that is a common age of spawning. If Q1 cod were only to consist of cods after spawning, the difference

in weight between Q1 and Q4 cod would be expected to be greater than it displays in the graphs. This suggests that the data may contain Q1 cod caught both before and after spawning.

The difference in body size and condition values between the Q1 and Q4 cod can therefore be suggested to be dependent on the spawning period. This may explain why there was a proposed lower parameter variance when the stocks were analysed by season compared to when not analysed by season. The χ^2 p-values however, never exceeded 0,05 (Table 3), indicating that one could determine the origin for only a few cods by using the body size parameters. Hence, the parameter variance was too high for one to be able to use the data in further analysis between stocks.

Future studies

Stock dynamics is a complex network of interacting elements, which suggest that it rarely can be explained by just one single factor. It would therefore be interesting in future studies within the subject of body size parameters used for cod stock separation, to combine the length, weight or condition with other parameters as well as with each other. By considering more than one parameter this might minimize the variance between stocks and make it easier to find differences, much in the same way, as seasonality in this study seemed to play a role in stock discrimination. Until then, stock assessment has to rely on trustworthy separating methods like genetics and otolith chemistry.

Conclusion

To conclude, the parameter variance between the stocks were too big for one to be able to use these parameters to separate stocks, although differences were found between some age groups. In contrast to the hypotheses, the only conclusion that can be drawn is that the body size parameters; length, weight, and condition cannot be used to distinguish cod stocks of Kattegat and the North Sea. Even though these parameters cannot be used as a separating method, this study has provided an additional knowledge of what factors that may or may not be relevant to use when investigating stock distinction. It further proves that studies of body size parameters under controlled conditions might not always mediate the same outcome as seen in nature, which is the case when performing stock assessment. However, these results do not say anything about parameter differences between other stocks, or between stocks of other species. This reveals an interesting field of science ready to be explored in the future.

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References

- André, C., Svedäng, H., Knutsen, H., Dahle, G., Jonsson, P., Ring, A. -K., Sköld, M., Jorde, P. E. 2016. Population structure in Atlantic cod in the eastern North Sea-Skagerrak-Kattegat: early life stage dispersal and adult migration. *BMC Research Notes*. 9: 63.
- Árnason, T., Björnsson, B., Steinarsson, A. 2009. Allometric growth and condition factor of Atlantic codconover (Gadus morhua) fed to satiation: effects of temperature and body weight. *J. Appl. Ichthyol*. 25: 401-406.
- Bartolino, V., Cardinale, M., Svedäng, H., Linderholm, H.W., Casini, M., Grimwall, A. 2012. Historical spatiotemporal dynamics of eastern North Sea cod. *Can. J. Fish. Aquat. Sci.* 69: 833-841.
- Cardinale, M. and Svedäng, H. 2004. Modelling recruitment and abundance of Atlantic cod, Gadus morhua, in the eastern Skagerrak-Kattegat (North Sea): evidence of severe depletion due to a prolonged period of high fishing pressure. *Fish. Res.* 69: 263-282.
- Conover, D. O. 1990. The Relation between Capacity for Growth and Length of Growing Season: Evidence for and Implications of Countergradient Variation. *Trans. Am. Fish. Soc.* 119: 416-430.
- Conover, D. O. and Present, T. M. C. 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia*. 83: 316-324.
- Froese, R. 2006. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *J. Appl. Ichthyol.* 22: 241-253.
- Heino, M., Baulier, L., Boukal, D. S., Dunlop, E. S., Elisassen, S., Enberg, K., Jörgensen, C., Varpe, O. 2008. Evolution of growth in Gulf of St Lawrence cod?. *Proc. R. Soc. B-Biol. Sci.* 275: 1111-1112.
- ICES. 2016. Report of the Baltic Fisheries Assessment Working Group (WGBFAS). 12-19 April 2016. Copenhagen, Denmark. ICES ICES CM 2016/ACOM:11. p. 85-116.
- ICES. 2015. Report of the benchmark workshop on Baltic cod stocks (WKBALTCOD). 2–6 March 2015. Rostock, Germany. ICES CM 2015/ACOM:35. 172 p.
- Imsland, A. K., Koedijk, R., Stefansson, S. O., Foss, A., Hjorleifsdottir, S., Hreggvidsson, G. O., Otterlei, E., Folkvord, A. 2011. A retrospective approach to fractionize variation in body mass of Atlantic cod Gadus morhua. *J. Fish. Biol.* 78: 251-264.
- Imsland A. K., Foss, A., Koedijk, R., Folkvord, A., Stefansson, S. O., Jonassen, T. M. 2007. Persistent growth effects of temperature and photoperiod in Atlantic cod Gadus morhua. *J. Fish. Biol.* 71: 1371-1382.
- Jennings, S., Kaiser, M. J., Reynolds, J. D. 2001. Getting the data: stock identity and dynamics. Marine Fisheries Ecology. Oxford: Blackwell Science Ltd. p. 178-204.
- Jonsson, P. R., Corell, H., Andre C., Svedäng, H., Moksnes, P. O. 2016. Recent decline in cod stocks in the North Sea–Skagerrak–Kattegat shifts the sources of larval supply. *Fish. Oceanogr.* 25: 210-228.
- Lambert, Y., Dutil, J.-D., Munro, J. 1994. Effects of Intermediate and Low Salinity Conditions on Growth Rate and Food Conversion of Atlantic Cod (Gadus morhua). *Can. J. Fish. Aquat. Sci.* 51: 1569-1576.
- Laurel, B. J., Spencer, M., Iseri, P., Copeman, L. A. 2016. Temperature-dependent growth and behavior of juvenile Arctic cod (Boreogadus saida) and co-occurring North Pacific gadids. *Polar Biol.* 39: 1127-1135.

Pardoe, H., Vainikka, A., Thordarson, G., Marteinsdotter, G., Heino, M. 2009. Temporal trends in probabilistic maturation reaction norms and growth of Atlantic cod (Gadus morhua) on the Icelandic shelf. *Can. J. Fish. Aquat. Sci.* 66: 1719-1733.

Righton, D. A., Andersen, K. H., Neat, F., Thorsteinsson, V., Steingrund, P., Svedäng, H., Michalsen, K., Hinrichsen, H., -H., Bendall, V., Neuenfeldt, S., Wright, P., Jonsson, P., Huse, G., van der Kooij, J., Mosegaard, H., Hussy, K., Metcalfe, J. 2010. Thermal niche of Atlantic cod Gadus morhua: limits, tolerance and optima. *Mar. Ecol. -Prog. Ser.* 420: 1-U344.

Rätz, H. J. and Lloret, J. 2003. Variation in fish condition between Atlantic cod (Gadus morhua) stocks, the effect on their productivity and management implications. *Fish. Res.* 60: 369-380.

Stevenson, R. D. and Woods, W. A. 2006. Condition indices for conservation: new uses for evolving tools. *Integr. Comp. Biol.* 46: 1169-1190.

Svedäng, H., Righton, D., Jonsson, P. 2007. Migratory behaviour of Atlantic cod Gadus morhua: natal homing is the prime stock-separating mechanism. *Mar. Ecol. -Prog. Ser.* 345: 1-12.

Swain, D. P., Sinclair, A. F., Hanson, J. M. 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proc. R. Soc. B-Biol. Sci.* 274: 1015-1022.

Vitale, F., Börjesson, P., Svedäng, H. and Casini, A. 2008. The spatial distribution of cod (Gadus morhua L.) spawning grounds in the Kattegat, eastern North Sea. *Fish. Res.* 90: 36-44.

Wang, HY., Botsford, L. W., White, J. W., Fogarty, M. J., Juanes, F., Hastings, A., Holland, M. D., Brander, K. 2014. Effects of temperature on life history set the sensitivity to fishing in Atlantic cod Gadus morhua. *Mar. Ecol. -Prog. Ser.* 514: 217-229.