Journal of FISH BIOLOGY

Published for the Fisheries Society of the British Isles

Journal of Fish Biology (2013) **82**, 2141–2146
doi:10.1111/jfb.12140, available online at wileyonlinelibrary.com

Habitat complexity affects how young of the year Atlantic cod *Gadus morhua* perceive predation threat from older conspecifics

P. Theodorou*†, S. S. Snorrason† and G. Á. Ólafsdóttir*‡

**Research Centre of the Westfjords, University of Iceland, Adalstraeti 21, 415 Bolungarvík, Iceland and †Department of Biology, University of Iceland, Askja, Sturlugata 7, 101 Reykjavík, Iceland*

(Received 21 November 2012, Accepted 25 March 2013)

The response of age 0+ year juvenile Atlantic cod *Gadus morhua* to the presence of age 1+ and age 3+ year conspecifics was measured with and without cover available. Juveniles reacted by aggregating more closely and maintaining distance from older conspecifics in an experimental setting without cover but only to age 3+ year conspecifics when cover was available. The results indicate that prior residence of older juveniles can affect age 0+ year juveniles during benthic settlement and highlights the conservation value of structurally complex nursery habitats.

Key words: cannibalism; intercohort competition; recruitment; schooling; territory defence.

Conspecifics commonly compete for limited resources, and intraspecific competition poses strong selection pressure on species (Claessen & Dieckmann, 2002). Body size is a major predictor of competitive ability in intraspecific competition for food and space (Johnsson *et al*., 1999; Schmitt & Holbrook, 1999). Although different sized conspecifics sometimes specialize on discrete niches (Einum & Kvingedal, 2011) asymmetrical competitive ability of size classes, *i.e*. cohorts influence year-class survival and recruitment in many fishes, including Atlantic cod *Gadus morhua* L. 1758 (Bjørnstad *et al*., 1999; Kaspersson *et al*., 2012).

After the first few months as pelagic larvae and juveniles, *G. morhua* shift to benthic habitats (Fahay, 1993; Lomond *et al*., 1998). Both field observations and theory suggest that this shift is adaptive, optimizing survival and growth (Svåsand & Kristiansen, 1990; Salvanes *et al*., 1994). During the shift, juveniles suffer high mortality rates and are found to prefer substrata that offer cover from predators (Tupper & Boutilier, 1995*a*, *b*). Predation pressure is high and age 0+ year juvenile *G. morhua* are known to be predated by older juveniles as young as age 1+ years (Gotceitas & Brown, 1993; Grant & Brown, 1998). There is also considerable

‡Author to whom correspondence should be addressed. Tel.: +354 456 1221; email: gaol@hi.is

competition for space and food both among and within age classes of juvenile *G. morhua* (Nordeide & Fossa, 1992; van Duren & Glass, 1992). Therefore, both competition and the risk of predation from older juveniles can be expected to influence the survival of *G. morhua* juveniles during benthic settlement.

In nature, age 0+ year juvenile *G. morhua* aggregate in response to perceived threat. Both field and laboratory studies have shown that age 0+ year *G. morhua* juveniles aggregate more in open than in structured habitats and increase schooling in the presence of a predator (Laurel *et al*., 2004; Laurel & Brown, 2006). The effect of older juveniles on the behaviour of benthic settlers is much less known. In the current study, the aggregation of age 0+ year juvenile *G. morhua* and their avoidance of age 1+ and age 3+ year conspecifics was examined in experimental tanks with and without available cover.

Age 0+ year juveniles were caught in September 2008 in north-west Iceland (66° 06′ N; 25° 53′ W). The experimental aquarium consisted of six tanks ($100 \times 110 \times 30$ cm) with a salinity of 30–35 and temperature of 9° C (range ±0·5° C). In three tanks, stones placed throughout the tanks provided cover (complex environment) while the other three were empty (simple environment). Each tank was given a partial water change (*c*. one third) and cleaned every day. *Gadus morhua* were held under a 12L:12D regime and hand fed daily to saturation with commercial pellets. At the beginning of each experiment groups of six age 0+ year juveniles were randomly caught from different holding tanks, transferred with hand-nets and released as a group into the test environment. They were allowed to acclimatize for 20 min prior to 20 min behaviour recording. The first test consisted of only age 0+ year juveniles in simple and complex environments. In the second test age 0+ year *G. morhua* juveniles were in the presence of an age 1+ year conspecific and finally in the presence of an age 3+ year *G. morhua*. The experimental tanks were continuously monitored to ensure that age 0+ year juveniles were not harmed. Ten groups of six age 0+ year juveniles went through each of the three tests in both environments, a total of 60 trials. The study used 360 age 0+ year individuals (mean ± S.D. total length, $L_T = 9.15 \pm 1.46$ cm), 10 age 1+ year juveniles ($L_T = 20.27 \pm 0.23$ cm) and four age 3+ year *G. morhua* ($L_T = 48.86 \pm 0.80$ cm). The trials were performed in October 2008. To minimize handling time of each age 1+ and age 3+ year individual, treatments were run subsequently. Digital video recordings were obtained by a camera positioned above each tank. From the video, mid eye distances (cm) between all individuals were determined on a series of snapshots (5, 10, 15 and 20 min). Distance measures were done in the image analysis software ImageJ version 1.42q (http://rsb.info.nih.gov/ij/) (Rasband, 2009).

Linear mixed effects model was used to examine: (1) the effect of older conspecific presence on age 0+ year juvenile aggregation (inter individual distances) and (2) age 0+ year juvenile avoidance of older conspecifics (age 0+ year juvenile distances to age 0+, age 1+ and age 3+ year conspecifics respectively). In both models, treatment (control, age 1+ and age 3+ year conspecifics) and environment (complex and simple) formed the fixed factors with an interaction term. To avoid pseudo-replication, trial was included as a random-effect factor to account for the repeated measurements of the same group of *G. morhua* within each trial (at 5, 10, 15 and 20 min). Significant interaction terms were further analysed with Tukey HSD *post hoc* tests. All distances were $\log_{10}$ transformed prior to analysis to meet assumptions of normality. The mixed effects model analyses were conducted in

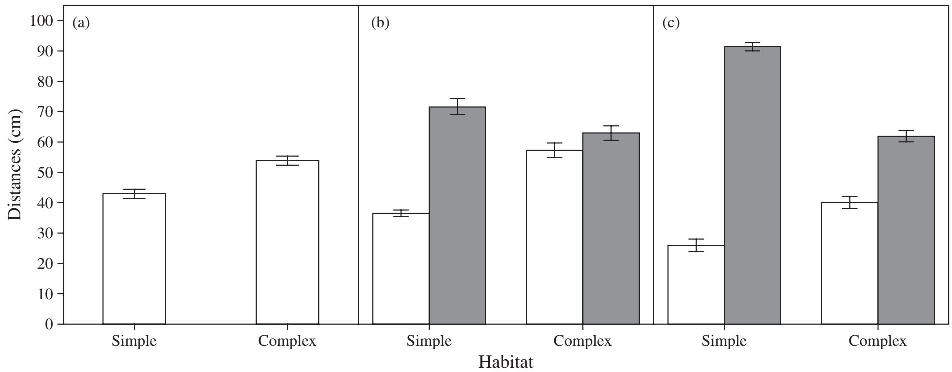

FIG. 1. Distances (cm) between age 0+ year juveniles (□) and between age 0+ year juveniles and older conspecifics (■) in each of the three tests (treatments): mean ± S.E. aggregation distances (a) between age 0+ year groups when alone, (b) with age 1+ year juvenile and (c) with age 3+ year juvenile.

the package lme4 0.99 (Bates *et al*., 2012). *Post hoc* tests were performed using the package Multcomp 1.2-8 in R (Hothorn *et al*., 2011). Both are part of the R statistical programme 2.15.1 (R Core Team; www.r-project.org).

Environment significantly explained variation in the interindividual distances of age 0+ year juveniles ($\chi^2 = 37{\cdot}20$, d.f. = 1, $P < 0{\cdot}001$) as did the presence of older conspecifics ($\chi^2 = 25{\cdot}29$, d.f. = 2, $P < 0{\cdot}001$) (Fig. 1). Specifically, juveniles were more aggregated in the spatially simple than in the more complex environment both with age 1+ year juvenile (Tukey HSD, $P < 0{\cdot}001$) and with age 3+ year *G. morhua* (Tukey HSD, $P < 0{\cdot}001$). Juveniles aggregated more closely in the presence of a age 3+ year *G. morhua* than when alone and this was consistent for both environments (Tukey HSD, simple, $P < 0{\cdot}001$; complex, $P < 0{\cdot}001$) but although age 0+ year juveniles tended to aggregate more closely in the presence of a age 1+ year juvenile in the simple environment (mean ± S.D. distance between age 0+ year individuals alone was $42{\cdot}91 \pm 9{\cdot}39$ cm and mean ± S.D. distance between age 0+ year individuals and age 1+ year olds was $36{\cdot}61 \pm 6{\cdot}54$ cm) this was not significant.

Distances between age 0+ year juveniles and the older conspecifics also varied with both environment ($\chi^2 = 28{\cdot}11$, d.f. = 1, $P < 0{\cdot}001$) and conspecific presence and type ($\chi^2 = 4{\cdot}42$, d.f. = 1, $P < 0{\cdot}05$) and there was a significant interaction effect between the two ($\chi^2 = 12{\cdot}69$, d.f. = 1, $P < 0{\cdot}001$) [Fig. 1 (b), (c)]. Age 0+ year juveniles stayed further away from both age 1+ and age 3+ year conspecifics in the simple compared to the complex environment (Tukey HSD, simple, $P = 0{\cdot}05$ and complex, $P < 0{\cdot}001$). Age 0+ year juveniles maintained significantly longer distances to the age 1+ year juvenile than between themselves in the simple environment (Tukey HSD, $P < 0{\cdot}001$) and from the age 3+ year fish in both environments (Tukey HSD, simple, $P < 0{\cdot}001$ and complex, $P < 0{\cdot}001$).

The benthic settlement of juvenile *G. morhua* is a critical time in their life stage and their survival depends in part on their response to environmental factors such as habitat complexity, predation risk and the level of competition. Strong consecutive year classes of *G. morhua* are uncommon (Bjørnstad *et al*., 1999). This has been attributed to both resource competition and potential cannibalism of age 1+ year olds on age 0+ year olds in nursery grounds (Gotceitas & Brown, 1993, Gotceitas *et al*., 1997). Although the extent of cannibalism on benthic settlers by older juveniles in nature is not well known, results from farmed *G. morhua* indicate that juvenile cannibalism is common even within cohorts (Folkvord & Otterå, 1993). In this study age 0+ year juveniles aggregated more closely and avoided the age 3+ year *G. morhua* in both environments (Fig. 1). This was expected as first year juvenile *G. morhua* are known to shoal more cohesively in the presence of a predator (Laurel *et al*., 2004; Laurel & Brown, 2006). The presence of an age 1+ year conspecific also affected both shoaling and dispersal of the age 0+ year juveniles. Specifically, they stayed further away from the age 1+ year juvenile than from other age 0+ year juveniles and aggregated more closely in the presence of an age 1+ year juvenile than when alone in the simple environment (Fig. 1). Wild age 0+ year and age 1+ year juvenile *G. morhua* commonly coexist in their preferred habitats (Methven & Bajdik, 1994) but laboratory experiments have shown that age 0+ year juveniles tend to avoid habitats already occupied by their older conspecifics (Fraser *et al*., 1996). From the current results it can be concluded that age 0+ year juveniles perceived predation threat from both age 3+ and age 1 +year conspecifics and that predation risk by older juveniles, in addition to post-settlement competition, may result in the exclusion of younger settlers from preferred habitats.

The presence of an age 1+ year juvenile, however, had negligible effects on age 0+ year juvenile aggregation distances and avoidance in the complex environment and much less than the presence of an age 3+ year *G. morhua* (Fig. 1). Complex environments provide better shelter from predation (Savino & Stein, 1982, 1989) and fishes are generally more likely to shoal in open habitats (Krause & Ruxton, 2002). Accordingly, structurally complex environments are known to have higher density of juveniles (Gotceitas *et al*., 1997, Grant & Brown, 1998, Laurel *et al*., 2003) and a recent study found that complex habitats optimize resource quality, foraging and predation avoidance for juvenile *G. morhua* (Persson *et al*., 2012). To conclude, the current results show although the immediate response of age 0+ year juveniles to both age 1+ and age 3+ year conspecifics in open habitats is predator avoidance, habitat complexity can act to moderate the deterring effect of age 1+ year conspecific prior residence on age 0+ year benthic settlers.

We are grateful to Gunnvör hf. for providing the experimental fish. We thank H. Reynisson, B. Þórisson and A. Andreou for their assistance during the experiments. This project was funded by AVS R&D fund of the Ministry of Fisheries.

References

Bjørnstad, O. N., Fromentin, J. M., Stenseth, N. C. & Gjøsæter, J. (1999). Cycles and trends in cod population. *Proceedings of the National Academy of Sciences of the United States of America* **96,** 5066–5071.

Claessen, D. & Dieckmann, U. (2002). Ontogenetic niche shifts and evolutionary branching in size-structured populations. *Evolutionary Ecology Research* **4,** 189–217.

van Duren, L. A. & Glass, C. W. (1992). Choosing where to feed – the influence of competition on feeding behavior of cod, *Gadus morhua L. Journal of Fish Biology* **41,** 463–471.

Einum, S. & Kvingedal, E. (2011). Relative importance of size-based competitive ability and degree of niche overlap in inter-cohort competition of Atlantic salmon juveniles. *Canadian Journal of Fisheries and Aquatic Sciences* **68,** 969–976.

Fahay, M. P. (1993). Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. *Journal of Northwest Atlantic Fisheries Science* **4,** 1–423.

Folkvord, A. & Otterå, H. (1993). Effects of initial size distribution, day length and feeding frequency on growth, survival and cannibalism in juvenile Atlantic cod (*Gadus morhua* L.). *Aquaculture* **114,** 243–260.

Fraser, S., Gotceitas, V. & Brown, J. A. (1996). Interactions between age-classes of Atlantic cod and their distribution among bottom substrates. *Canadian Journal of Fisheries and Aquatic Sciences* **53,** 305–314.

Gotceitas, V. & Brown, J. A. (1993). Substrate selection by juvenile Atlantic cod (*Gadus morhua*) effects of predation risk. *Oecologia* **93,** 31–37.

Gotceitas, V., Fraser, S. & Brown, J. A. (1997). Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **54,** 1306–1319.

Grant, S. M. & Brown, J. A. (1998). Diel foraging cycles and interactions among juvenile Atlantic cod (*Gadus morhua*) at a nearshore site in Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 1307–1316.

Johnsson, J. I., Nöbbelin, F. & Bohlin, T. (1999). Territorial competition among wild brown trout fry: Effects of ownership and body size. *Journal of Fish Biology* **54,** 469–472.

Kaspersson, R., Höjesjö, J. & Bohlin, T. (2012). Habitat exclusion and reduced growth: a field experiment on the effects of inter-cohort competition in young-of-the-year brown trout. *Oecologia* **169,** 733–742.

Krause, J. & Ruxton, G. D. (2002). *Living in Groups*. Oxford: Oxford University Press.

Laurel, B. J. & Brown, J. A. (2006). Influence of cruising and ambush predators on 3-dimensional habitat use in age 0 juvenile Atlantic cod *Gadus morhua*. *Journal of Experimental Marine Biology and Ecology* **329,** 34–46.

Laurel, B. J., Gregory, R. S. & Brown, J. A. (2003). Settlement and distribution of age-0 juvenile cod, *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation. *Marine Ecology Progress Series* **262,** 241–252.

Laurel, B. J., Gregory, R. S., Brown, J. A., Hancock, J. K. & Schneider, D. C. (2004). Behavioural consequences of density-dependent habitat use in juvenile cod *Gadus morhua* and *G-ogac*: the role of movement and aggregation. *Marine Ecology Progress Series* **272,** 257–270.

Lomond, T. M., Schneider, D. C. & Methven, D. A. (1998). Transition from pelagic to benthic prey for age group 0–1 Atlantic cod, *Gadus morhua*. *Fishery Bulletin* **96,** 908–911.

Methven, D. A. & Bajdik, C. (1994). Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences* **51,** 78–90.

Nordeide, J. T. & Fossa, J. H. (1992). Diet overlap between two subsequent year-classes of juvenile coastal cod (*Gadus morhua L.*) and wild and reared cod. *Sarsia* **77,** 111–117.

Persson, A., Ljungberg, P., Andersson, M., Götzman, E. & Nilsson, P. A. (2012). Foraging performance of juvenile Atlantic cod *Gadus morhua* and profitability of coastal habitats. *Marine Ecology Progress Series* **456,** 245–253.

Salvanes, A. G. V., Giske, J. & Nordeide, J. T. (1994). Life history approach to habitat shifts for coastal cod. *Aquaculture and Fisheries Management* **25,** 215–228.

Savino, J. F. & Stein, R. A. (1982). Predator–prey interaction between largemouth bass and bluegills as influenced by simulated submerged vegetation. *Transactions of the American Fisheries Society* **111,** 255–266.

Savino, J. F. & Stein, R. A. (1989). Behavioral interactions between fish predators and their prey: effects of plant density. *Animal Behaviour* **37,** 311–321.

Schmitt, R. J. & Holbrook, S. J. (1999). Mortality of juvenile damselfish: implications for assessing processes that determine abundance. *Ecology* **80,** 35–50.

Svåsand, T. & Kristiansen, T. S. (1990). Enhancement studies of coastal cod in western Norway. Part II . Migration of reared coastal cod. *ICES Journal of Marine Science* **47,** 13–22.

Tupper, M. & Boutilier, R. G. (1995*a*). Effects of habitat on settlement, growth, and post settlement survival of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **52,** 1834–1841.

Tupper, M. & Boutilier, R. G. (1995*b*). Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. *Marine Ecology Progress Series* **118,** 295–300.

Electronic References

Bates, D., Maechler, M. & Bolker, B. (2012). *lme4: Linear Mixed-effects Models Using S4 Classes*. Available at http://CRAN.R-project.org/package=lme4/ (last accessed 19 February 2013).

Hothorn, T., Bretz, F. & Westfall, P. (2011). *Multcomp: Simultaneous Inference in General Parametric Models*. Available at http://cran.r-project.org/web/packages/multcomp/index.html/ (last accessed 19 February 2013).

Rasband, W. S. (2009). *ImageJ*. Bethesda, MD: U.S. National Institutes of Health. Available at http://rsb.info.nih.gov/ij/ (last accessed 19 February 2013).

