Indications of a negative impact of herring on recruitment of Norway pout

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Introduction

The mortality of marine fish larvae is generally high and variable in space and time (Hjort, 1926; McGurk, 1986; Chambers and Trippel, 1997). Several hypotheses have been advanced to explain heavy larval mortality (reviewed by Chambers and Trippel, 1997), including predation by planktivorous fish owing to their potentially high densities and efficient foraging on fish larvae (Bailey and Houde, 1989). It has been hypothesized that predation by juvenile Norwegian spring-spawning (SSS) herring (Clupea harengus) on Barents Sea capelin (Mallotus villosus) larvae is the cause for the poor recruitment of the capelin stock in some years (Hamre, 1994). This hypothesis is supported by observations of negative correlations between herring abundance in the Barents Sea and capelin recruitment (Gjøsæter and Bogstad, 1998), and by observations of capelin larvae in herring stomachs (Huse and Toresen, 2000; Godiksen et al., 2006). Three recent collapses in Barents Sea capelin have been attributed to herring predation (Gjøsæter, 1998; Gjøsæter and Bogstad, 1998; ICES, 2006).

Recruitment of many fish stocks in the North Sea (Figure 1) has been exceptionally poor recently (ICES, 2007b), and this has led to a re-examination of the hypotheses about different factors affecting fish recruitment. A negative relationship between pelagic fish abundance and recruitment of demersal fish has been suggested for the North Sea, specifically because the so-called “gadoid outburst” during the 1960s coincided roughly with a collapse in North Sea herring and mackerel stocks (Cushing, 1980; Daan et al., 1985, 1994). However, the timing of various events in the 1950s and 1960s does not fully support a negative relationship between biomass levels of pelagic fish and recruitment of gadoids (Hislop, 1996). On the other hand, the recent poor recruitment to many North Sea stocks has coincided with a large herring stock, which again raises the question of predatory interactions. The picture is now even more complicated because the spawning-stock biomass (SSB) of many stocks is very low, which obviously should have a negative effect on recruitment (Myers and Barrowman, 1996). However, the stock of Norway pout (Trisopterus esmarkii) in the North Sea has experienced several years of poor recruitment, despite its initially large spawning stock (ICES, 2007b). This could be due to predation by herring, because there is potential for spatial overlap between the two stocks, although there is no information available on stomach content analysis to suggest such an interaction. Verifying that predation takes place and has the magnitude needed to induce high rates of mortality is costly, because it entails extensive use of ship time and manpower. Moreover, it is difficult to detect predation of fish larvae by fish because of the rapid digestion of larval tissue (Folkvord, 1993). It is therefore valuable to utilize existing data to look for signs of predatory interactions between planktivorous fish and larvae. As spatial overlap is a prerequisite for a predatory interaction, maps of spatial distributions of species can provide information about the potential for predatory effects on recruitment. However, there is no standardized means of incorporating spatial overlap information into stock–recruit models. Gjøsæter and Bogstad (1998) showed that excluding years with the presence of herring in the Barents Sea...
from the analysis substantially improved the fit between the stock–recruit model and data for the Barents Sea capelin. Similarly, Fiksen and Slotte (2002) showed that the fit between the stock–recruit model and observations for NSS herring was improved by including a temperature term. Such examples illustrate the potential benefit that lies in modifying stock–recruit relationships to understand better and quantify the dynamics of fish stocks.

The distribution of Norway pout in the North Sea is indicated in Figure 1. The species is preyed upon by cod (Gadus morhua), whiting (Merlangius merlangus), saithe (Pollachius virens) and other fish in the North Sea (ICES, 1997). Herring are generally widespread, and there is considerable potential for overlap with Norway pout. The objectives of this study were to investigate whether there are patterns in spatial and population dynamics of Norway pout and herring in the North Sea that indicate interactions between the two stocks. We initially look for correlative evidence of predatory interactions, then estimate the extent of spatial overlap. Finally, we investigate the potential for using spatial information to improve the stock–recruit relationship of Norway pout. These analyses are complemented by correlations between prey abundance and abundance of juvenile Norway pout.

**Material and methods**

For herring, estimated total-stock biomass was taken from the final assessment in the Report of the Herring Assessment Working Group for the Area South of 62°N (ICES, 2007a). For Norway pout, estimates of SSB, recruitment (numbers of fish aged 0 in quarter 3), proportion mature-at-age, mean weights-at-age, and stock numbers-at-age in the North Sea and Skagerrak were taken from ICES (2007c; the working group report that was the basis for the ICES advice in spring 2007).

The spatial distributions of herring and Norway pout were estimated based on abundance indices per ICES rectangle, derived from the quarter 1 International Bottom Trawl Survey (IBTS) for the period 1982–2006. The IBTS data are archived and updated by ICES (see ICES database http://www.ices.dk/datacentre/datras/datras.asp). The survey takes place in February just before the peak in hatching of Norway pout, in early April (Heath, 2007), and is therefore relevant to estimating overlap between Norway pout eggs and larvae and potential predators. To include the herring distribution in the Norway pout stock–recruit relationship, we estimated the SSB of Norway pout occupying ICES rectangles with no herring for each year. This was done by spatially resolving the estimates of Norway pout abundance based on virtual population analysis (VPA) to obtain a spatial SSB distribution, then summing the SSB from ICES rectangles without herring (age 1 and older):

$$SSB_{\text{free}} = \sum_{i} \sum_{a=1}^{4} N_i P_{ai} M_a W_a,$$

where the index $i$ represents ICES rectangles without herring (i.e. no catch of herring in these rectangles during the IBTS quarter 1 survey), $P_{ai}$ the proportion of Norway pout aged $a$ caught in rectangle $i$ (estimated from IBTS data), $M_a$ the proportion of mature fish aged $a$, $W_a$ the individual fish weight-at-age $a$, and $N_i$ the estimated number of individuals at age $a$ in the stock (taken from the ICES stock assessment). This was used to generate a “herring-free” stock–recruit relationship, which could then be contrasted with the total SSB and used to calculate the extent of overlap with herring:

$$\text{Overlap} = 1 - \frac{SSB_{\text{free}}}{SSB}.$$

If the entire Norway pout spawning stock overlaps with herring, $SSB_{\text{free}}$ will be 0 and the overlap will be 1. Conversely, if there are no herring in the rectangles with Norway pout SSB, $SSB_{\text{free}}$ will be equal to SSB and the overlap will be 0.

A Beverton–Holt (Beverton and Holt, 1957) model was fitted to the SSB and recruitment data for Norway pout. The Beverton–Holt spawner–recruit curve relates recruitment ($R$) to SSB ($S$) using the equation:

$$R = \frac{aS}{b + S},$$

where $a$ is the maximum number of recruits produced, and $b$ the SSB needed to produce (on average) recruitment equal to $a/2$. The Beverton–Holt curve increases towards an asymptote as spawning stock increases. To estimate the parameters, $a$ was set to the maximum number of recruits produced in the available dataset, then the value of $b$ was estimated using a least-squares method (Table 1).

Although this work focuses on potential predation effects (i.e. top–down), limitation in prey availability (i.e. bottom–up effects) is often regarded as a key factor in determining the rate of survival of fish larvae (Cushing, 1990; Chambers and Trippel, 2007).
In the North Sea, the copepod *Calanus finmarchicus* is the main prey of fish larvae that hatch during spring (Sundby, 2000). We therefore explored the relationship between the estimated relative abundance of *C. finmarchicus* collected by the Continuous Plankton Recorder (CPR) and recruitment and survival (recruitment per SSB) of Norway pout. Monthly CPR indices of total *C. finmarchicus* abundance (average number of individuals per sample per month) from the geographical area 57–0°N, 1°W–6°E from January to June of the period 1984–2004 were used. These data were kindly provided by the Sir Alistair Hardy Foundation for Ocean Science (SAHFOS). Monthly indices and indices averaged over longer periods (e.g. January–March) were investigated.

**Results**

There was a significant, but not very strong, negative relationship between Norway pout recruitment and total-stock biomass (TSB) of herring (linear regression = $-0.033 x + 17,432$, $r = -0.44$, $p < 0.05$; Figure 2a and b). The overlap between Norway pout and herring varied substantially over time (Figure 2c), and there was a significant negative relationship between the overlap and Norway pout recruitment (linear regression = $-135.44 x + 189.56$, $r = -0.52$, $p < 0.01$). The variation in overlap is illustrated for a year with low degree of overlap in Figure 3a, and for one with a high degree of overlap in Figure 3b. The pattern between herring and Norway pout recruitment is also seen with time-lags, and there was a strong negative correlation between the total-stock biomass (TSB), (b) annual Norway pout recruitment and SSB of Norway pout 2 years later (linear regression = $-144.2 x + 4 \times 10^6$, $r = -0.68$, $p < 0.01$). Moreover, the SSB of Norway pout is dominated by 2-year-olds, which typically constitute 60–80% of the biomass, and there is a strong negative relationship between herring TSB and SSB of Norway pout 2 years later (linear regression = $-9 \times 10^{-5} x + 409.4$, $r = -0.79$, $p < 0.01$; Figure 4).

The Beverton–Holt model did not fit the stock–recruit data for Norway pout well ($r^2 = 0.04$; Figure 5). However, when only the part of the Norway pout SSB not overlapping with herring (SSB$_{\text{free}}$) is included (see Figure 3), the fit of the model to the stock–recruit data improved substantially ($r^2 = 0.31$; Figure 5). The SSB$_{\text{free}}$ stock–recruit relationship in Figure 5 is influenced by 3 years with very high SSB$_{\text{free}}$. When these points are removed, the Beverton–Holt model maintains a good fit to the data ($r^2 = 0.25$).

*Calanus finmarchicus* abundance estimated by the CPR was generally poorly correlated ($p > 0.1$) to Norway pout recruitment and survival, on both a natural and a log–log scale. The only exception was a significant positive relationship between *C. finmarchicus* abundance in January and subsequent Norway pout recruitment (Figure 6; linear regression $= 16.323 x + 6.1691$, $r = 0.47$, $p < 0.05$). For log–log scale, the relationship was slightly weaker.

**Discussion**

Our results demonstrate that taking into account the distribution of a suspected predator can improve the stock–recruit relationship for Norway pout substantially. Further, our analysis strengthens the suspicion that herring might influence recruitment of Norway pout. This was indicated both by a simple correlation analysis of herring biomass against Norway pout recruitment and through a modified stock–recruit relationship. Moreover, there was a strong negative correlation between the total biomass of herring and Norway pout SSB 2 years later. The analyses were based on partially independent data, the IBTS time-series and stock assessment estimates. The herring stock assessment utilizes catch per unit effort from the IBTS time-series to tune the VPA for the younger age groups, but the rest of the assessment is driven by landings data and other tuning series. This independence in the data used for our correlation and stock–recruit analyses strengthens the hypothesis that Norway pout recruitment can be impeded by herring. Estimates of recruitment and SSB of Norway pout rely on the VPA analysis and are therefore not completely independent.

In principle, the negative influence of herring on recruitment of Norway pout can be explained in terms of both food competition and predation (Hislop, 1996). Although herring and Norway pout larvae eat similar planktonic food, it seems rather unlikely that competition would result in the type of inverse pattern found here, because plankton availability will depend on a number of...
other factors, such as the annual productivity and the abundance of other food competitors. Predation by herring on Norway pout larvae, on the other hand, is a plausible explanation for the inverse pattern in population dynamics we have seen. Frederiksen et al. (2007) hypothesized that herring predation is important in regulating sandeel abundance around the Shetlands, based on negative correlations between local herring and sandeel abundance. Field studies have shown that herring feed on fish eggs (Daan et al., 1985; Ellis and Nash, 1997; Segers et al., 2007) and can be a major predator of fish larvae (Huse and Toresen, 2000; Godiksen et al., 2006; Halfredsson et al., 2007), but further studies in the North Sea in the areas of overlap between herring and Norway pout are needed to verify that the proposed predation actually takes place to a marked degree. Episodes of massive predation by fish on fish have been witnessed in some instances (Godiksen et al., 2006; Temming et al., 2007), and an episodic view of predation might be a fruitful paradigm to improve our understanding of fish recruitment and natural mortality of fish in general.

Although our results indicate that recruitment of Norway pout could be influenced by herring, other environmental factors could impact recruitment. Hislop (1996) tried to disentangle the causes of the gadoid outburst in the 1960s in a retrospective analysis. He found that no single factor was responsible for the increase in gadoid abundance during that period, when examining various effects related to climate, predators, and prey. The North Sea is a warmer, more diverse ecosystem than the Barents Sea, which appears to be more strongly affected by interannual climate variation both directly and indirectly through cascading climatic effects. There, herring recruitment is strong typically in warm years (Toresen and Østvedt, 2000; Fiksen and Slotte, 2002; Sætre et al., 2002), and results in herring being widespread in the

Figure 3. Distribution of herring (green), showing overlap between herring and Norway pout (blue), and Norway pout only (red) in (a) 1983 and (b) 2002.

Figure 4. Total-stock biomass (TSB) of herring in year “t” plotted against Norway pout SSB 2 years later for the period 1982–2006.

Figure 5. Beverton–Holt stock–recruit relationship for total Norway pout SSB (triangles) and for the part of the spawning stock not overlapping with herring (SSBfree squares) for the period 1985–2006.
Figure 6. Relationship between the abundance of Calanus finmarchicus during January in the northern North Sea and Norway pout recruitment for the period 1984–2004.

southern Barents Sea, where they overlap with and prey on capelin larvae (Huse and Toresen, 2000; Godiksen et al., 2006). This interaction has resulted in three recent collapses in the Barents Sea capelin stock, in 1986, 1994, and 2003 (ICES, 2006). In the Barents Sea, an inflow of warm water gives a positive direct effect on growth and recruitment, but it is also associated with better inflow of Calanus-rich water masses from the Norwegian Sea (Skjoldal et al., 1992). This results in a strong positive association between temperature and recruitment being seen for many stocks in the Barents Sea (Settersdal and Loeng, 1987; Ottersen et al., 1994; Sundby, 2000). In the North Sea, inflow of water rich in C. finmarchicus from the cold Norwegian Sea is associated with low temperature (Reid et al., 2003). Bromley et al. (1997) found that C. finmarchicus made up the most of the diet of 0-group Norway pout. There has been a major change in the composition of copepods in the North Sea during the past few decades (Planque and Fromentin, 1996). The decrease in Calanus abundance and shift from C. finmarchicus to C. helgolandicus has therefore been used to explain the poor recruitment of North Sea fish stocks in recent years (ICES, 2007b, c). We investigated the relationship between Norway pout recruitment and abundance of C. finmarchicus by using the data from the CPR from the northern North Sea. The only significant relationship we found was between Norway pout recruitment and C. finmarchicus abundance in January (Figure 6). However, the relationship was not really strong and only provided modest indications of bottom–up control of Norway pout recruitment.

The stock–recruit relationship for Norway pout improved substantially when the SSB was modified by taking the herring distribution into account. Similar analyses can easily be made for other stocks, and might provide insight into stock dynamics. A more dynamic approach would be to move the Norway pout larvae using a hydrodynamic model, and simulate the herring movements. However, this would require a substantial increase in effort and model complexity. Our analyses indicate that herring have a negative effect on recruitment of Norway pout. The most plausible cause for this is herring predation on Norway pout larvae, but field studies are needed to verify this hypothesis. We note that the biomass of herring in the North Sea is currently declining, so we anticipate that this might lead to improved conditions for Norway pout soon.

Acknowledgements

We thank Geir Ottersen and two anonymous referees for valuable comments on an earlier version of the manuscript. The Sir Alistair Hardy Foundation for Ocean Science kindly provided the Calanus data. The work was supported by the Research Council of Norway through the projects RECNOR and INFERNO.

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doi:10.1093/icesjms/fsn074

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