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Shrimps and Cod in West Greenland, and How Many of the One are Eaten by the Other

by

Michael C. S. Kingsley

Pinngortitaleriffik, Greenland Institute of Natural Resources
Box 570, DK-3900 Nuuk, Greenland

Summary

The function for calculating the predation on shrimps by cod in the surplus-production model used for the assessment of the West Greenland stock of *P. borealis* has two parameters, one of which has heretofore been treated as known. The intended two-parameter sigmoidal relationship between shrimp biomass and predation rate has thus been converted into a single-parameter, nearly linear, relationship. If the assessment model is allowed to fit values for both parameters, a sigmoidal relationship results, with lower predation rates at high shrimp biomasses.

Introduction

The surplus-production model adopted by NAFO Scientific Council for the assessment of the West Greenland stock of the Northern Shrimp *Pandalus borealis* includes a term for predation by Atlantic cod in its definition of the dynamics of the stock and indices of cod biomass among the input data series (Hvingel and Kingsley 2002). The expression relating predation to biomass of both shrimps and cod is written into the model as 'Holling type III' (Holling 1959). This is a sigmoidal relationship between predation by unit quantity of predator and quantity of available prey. An accelerating initial phase when prey is scarce indicates the predator switching to this prey as it becomes more plentiful; a decelerating phase when prey is abundant indicates that the predator is satiated:

$$C(P | m, q) = \frac{mP^2}{P^2 + q^2}$$

where the quantity C is that taken by unit quantity of predator when the quantity of prey available is P . m is a scaling parameter on the amount taken, the limiting amount reached when P becomes large. q is a scaling parameter on P , specifying the value of P when predation rate is half of its maximum m . Its only parameters being scalars, the expression is inflexible as to its shape¹. Sigmoidal curves are often difficult to fit unless the data clearly shows a point of inflection and fixes its position. If it doesn't, the parameters of the curve depend on uncertain extrapolation of poorly determined curvatures.

¹ Its point of inflection is at $(q/\sqrt{3}, m/4q)$ and its maximum slope $3\sqrt{3}m/8q$; all the action is at the left-hand end, with a long right-hand tail slowly converging on the asymptote m (Figure 1).

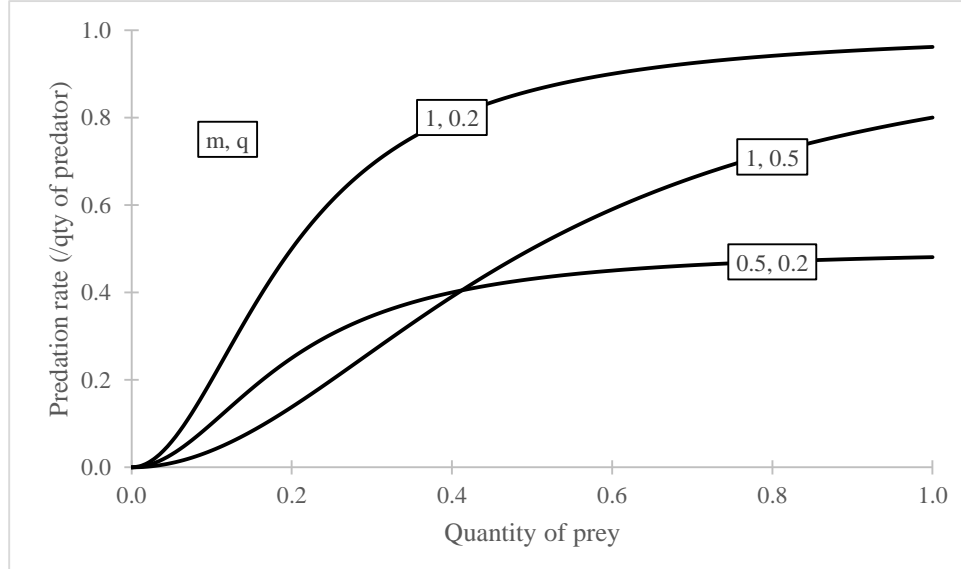


Figure 1. Examples of Holling type III functional relationships between quantity of prey and predation rate.

When P is much less than q , the expression becomes approximately

$$C(P | m, q) = \frac{mP^2}{q^2}$$

and predation rate is proportional to P^2 with m and q^2 both acting as scalars; i.e. the function acts like a one-parameter curve.

Problem

The surplus-production model adopted by NAFO for the assessment of the West Greenland shrimp stock is fitted by Bayesian methods, which require prior distributions for parameter values. The parameter m (O_{max} in the model code) has been given a prior distribution $N(3, 0.1)$ limited also to values between 1 and 5. This distribution is very tight—‘highly informative’ in Bayes-speak. There was a reason behind this construction: laboratory studies had shown that cod were unlikely to eat much more than three times their body weight of shrimps in a year (Björnsson and Steinarsson 2002). The parameter q^2 ($P50.sqr$ in the model code) has been given an uninformative log.-Normal prior distribution such that $\ln(q^2)$ is $N(-1.36, 1/0.11)$; this gives q a prior median value of close to 0.5.

The distribution of m is not updated in the fitting of the model to the data, as, indeed, it was not intended to be. The distribution of q^2 is strongly updated to a nearly symmetrical distribution with a median value (2014 results) of 7.2 (Kingsley 2014) (Table 1). The 2014 median estimates of thirty years’ values of P^2 range from 0.56 to 3.7, but half the values are below 1.2. This is the situation described by the second equation above, with a value of q^2 that is large relative to values of P^2 . As a result, q^2 and m are both trying to do the same thing: scale the predation rate to the quantity of prey. Because the prior on m is informative and that for q^2 uninformative, q^2 is updated to high values; once q^2 finds high values, it has taken over m ’s job and there is then no incentive to update m . The two-parameter Holling type III predation relationship that we started with has thus been reduced to a one-parameter function.

Table 1. *Pandalus borealis* in West Greenland: prior and posterior quartiles of the distributions of parameters of a Holling type III function relating cod predation to shrimp biomass, using existing prior distributions.

	$m (O_{max})$			$q^2 (P50.sqr)$		
	Lower	median	Upper	lower	Median	Upper
prior	2.775	2.988	3.203	0.08188	0.41	2.306
posterior	2.777	2.992	3.203	4.933	7.181	10.4

The prior distribution of m is not being updated, while that for q^2 is strongly updated—the posterior lower quartile point is over twice the prior upper quartile—to quite well defined values, which are, however, outside the relevant range and so large that q^2 and m are both acting only as scalars on the predation rate (Table 1). They are both trying to do the same job; q^2 is succeeding, because its uninformative prior allows it to, while m is functioning as an arbitrarily chosen constant value. The tight prior distribution on m is reflected in the small range of the posterior distribution of q^2 , as the two parameters are tied together.

Solution

What we need to do is to provide prior distributions for both the parameters in the predation function that will allow a more flexible fit, and ideally would result in q^2 values that are within the working range. Therefore, I tried the effect of changing the priors. I gave both parameters log-normal priors with medians at 1 and log-space variances of 10. m was in addition limited to the interval (0.1,10).

Results

Then, when the model was fitted, both these parameter distributions were updated:

Table 2. *Pandalus borealis* in West Greenland: prior and posterior quartiles of the distributions of parameters of a functional relationship between shrimp biomass and cod predation, using revised prior distributions.

	$m (O_{max})$			$q^2 (P50.sqr)$		
	Lower	median	upper	lower	median	upper
prior	0.3465	1.016	2.871	0.1205	1.062	9.126
posterior	0.3162	0.6875	2.017	0.1961	1.267	5.102

The posterior median for m is lower than the prior median and it is not evidently trying to reach its former value of about 3 (Table 2). The posterior median for q^2 , although higher than its prior, is nowhere near its former value of 7. Both the upper quartile points of these long-tailed and highly skewed distributions have been brought down in the updating. With either set of priors, the posterior median for m is about twice that for q^2 , and the cod predation rate is about the same for either set when P is not large, and so is its rate of change as P changes. As P increases, the results diverge as the smaller q^2 obtained using the revised priors is overpowered by P and the predation rate levels off (Figure 2). For the largest shrimp biomass values experienced in recent decades, modelling with the revised prior distributions allows cod predation to be estimated at not much over half the rates estimated using the original priors.

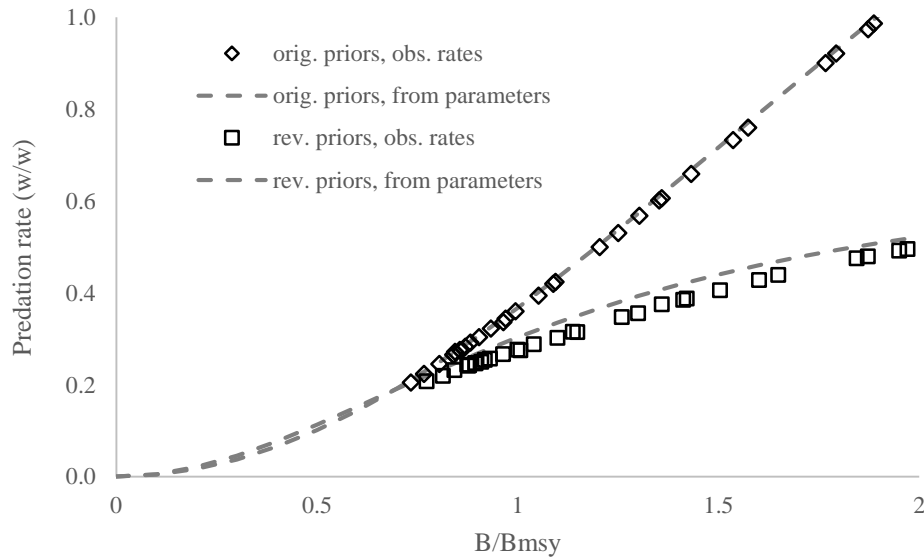


Figure 2. *Pandalus borealis* in West Greenland: estimated cod predation rate vs shrimp biomass 1985–2014, using original and revised priors on the parameters of a predation relationship.

Since both the revised priors are significantly updated, and to apparently sensible values far removed from the former posterior values, it would seem reasonable to draw the conclusions firstly that predation by cod does—as we already thought—have a detectable, and determinable, influence on the stock dynamics of the Northern shrimp in West Greenland waters, and secondly that there is no reason not to adopt the revised priors.

However, the error variances in the model fit do not show any great differences due to changing the priors:

Table 3. *Pandalus borealis* in West Greenland: median estimates of uncertainty CVs in a surplus production model of shrimp stock dynamics under two sets of prior distributions for the parameters of a predation function.

	CV CPUE	CV survey	CV process	CV cod
Original priors	18.9	15.9	12.1	115.2
Revised priors	18.9	15.9	12.2	124.7

The fit cvs for the process and for the biomass index series are the same, and that for the cod-predation fit increases (Table 3). However, this is a slightly larger cv on a smaller—in some cases much smaller—estimate and the i.q.r. of the weight eaten under the revised priors is between 61% and 107% of that estimated under the original priors, with a mean ratio of 83%. I.e. the effect of cod on the stock dynamics of the shrimps appears less uncertain with the revised priors.

Estimates of stock-dynamic parameters are also affected (Table 4). Cod predation being overall estimated lower with the new values of the predation parameters, the productivity of the stock is lowered to compensate. The present status of the stock is estimated slightly better with less predation in the recent few years with large cod stocks. However, the risk levels for future management options do not change a great deal; they go down a bit because with the high cod-stock levels we expect, forecasting a lower predation rate is a bonus. (If we were expecting low cod stocks, we would expect that risk levels would increase with the revised priors, owing to the smaller estimate of MSY.) The uncertainty of stock-dynamic parameters tends overall to increase a little bit. This is perhaps because the original priors on the predation relationship expressed a great deal of confidence in one of the values— O_{max} was essentially fixed at 3. Even though that confidence was misplaced, it was reflected in narrower posterior distributions on perhaps slightly dubious values of stock-dynamic parameters. The revised priors are less certain about the values to be adopted and this shows up in wider posterior distributions.

Table 4. *Pandalus borealis* in West Greenland: posterior estimates of some parameters of stock dynamics and of the state of the stock in 2014, using existing and revised prior distributions on the parameters of a predation function.

	Original priors		Revised priors	
	median	i.q.r.	median	i.q.r.
MSY (Kt/yr)	130.9	57.8	128.3	66.0
Biomass ratio, end 2014, %	95.9	36.1	100.3	38.4
Biomass risk, end 2014, %	56.2		49.6	
Mortality ratio, 2014, %	103.7	90.8	99.5	92.5
Mortality risk, 2014, %	52.6		49.7	
Effective cod biomass, 2014, Kt	44.3	42.0	43.8	41.7
Mortality risk 2015, %:				
60 Kt catch and 50 Kt effective cod	32.8		31.7	
70 Kt catch and 30 Kt cod	33.5		32.0	

Conclusions

The function relating cod predation on shrimps to biomasses of predators and prey is constrained by tight prior distributions on the parameters. Replacing the tight priors with wider prior distributions shows that the function has been restricted to regions that are not the best fit to the stock-trajectory data. Doing so also generates lower estimates of predation, especially when shrimp biomass is estimated as high. The wider priors produce slightly different estimates of stock-dynamic parameters; differences in advice will vary with expected cod biomass. It is expected that the wider prior distributions on predation-function parameters will be taken into use in the assessment in 2015.

References

- Björnsson, B. and A. Steinarsson. 2002. The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 59:494–502.
- Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91: 385–398.
- Hvingel, C. and M.C.S. Kingsley. 2002. A framework for the development of management advice on a shrimp stock using a Bayesian approach. NAFO SCR Doc. 02/158, Ser. No. N4787.
- Kingsley, M.C.S. 2014. A provisional assessment of the shrimp stock off West Greenland in 2014. NAFO SCR Doc. 14/059, Ser. No. N6361. 21 pp.