The effect of temporal changes in life-history traits on reproductive potential in an exploited population of Pacific cod, Gadus macrocephalus

Yoji Narimatsu, Yuji Ueda, Takehiro Okuda, Tsutomu Hattori, Kunihiro Fujiwara, and Masaki Ito


The population size of Pacific cod (Gadus macrocephalus) in the northeastern Pacific has fluctuated at high levels during the past 10 years, despite heavy exploitation from the juvenile stage. Annual changes in growth, age, and standard length (SL) at maturity, potential fecundity (PF), and total egg production are evaluated in relation to the population fluctuations. Most 4-year-old females were mature, and the SL at which 50% of 3-year-old females matured fluctuated very little over the years. However, the proportion of mature 3-year-old females varied significantly among years. The values of PF-at-age also varied among years and were explained by a model containing SL, condition factor, and oocyte diameter. The population size was negatively correlated with the proportion of mature females and the PF of females 3 years old, so the range of total egg production was smaller than that of spawning-stock biomasses. Eggs were produced mainly by young adults (3 and 4 years of age). The age of adult females did not affect recruitment success. It is suggested that plasticity of life-history traits allowed for compensation of total egg production and that the compensation contributed to maintaining the abundance of a population consisting mainly of young fish.

Keywords: maturity-at-age, potential fecundity, recruitment, total egg production.

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Introduction

Rigorous assessment of a fish population relies on understanding its reproductive potential. The spawning-stock biomass (SSB) is often used as an index of reproductive potential, based on the assumption that SSB is directly correlated with egg production. However, recent studies have questioned the correlation between SSB and reproductive potential (Marshall et al., 1998; Scott et al., 1999, 2006; Murawski et al., 2001; Morgan and Brattey, 2005, Marshall, 2009), primarily because of variability in reproductive and life-history traits (Trippel et al., 1997; Marteinsdottir and Begg, 2002). Those studies emphasized the importance of estimating total egg production and the viability of the progeny in the population.

Heavy fishing removes the larger, older members of a population, and a decrease in the number of large fish results in an increase in the relative abundance of small and immature fish (Trippel et al., 1997). Continued fishing pressure often removes even small and immature members of a population, so that only a small percentage of fish attain the body size and age necessary for maturation. In such populations, reproductive traits such as body size, age at maturity, and fecundity-at-age are variable, and this variability is likely to have a greater effect on egg production than it would in unexploited populations. Moreover, larger or older members of a population may contribute differently to the reproductive potential of a population, relative to smaller or younger members. There is also evidence that the size of populations composed of young fish fluctuates more than unexploited populations (Ottersen et al., 2006; Anderson et al., 2008). Therefore, knowledge of the fecundity and the age composition of egg-producing adults is important. In addition, the effect of adult age on recruitment is important when considering population dynamics, especially in populations consisting primarily of small and young fish.

Pacific cod (Gadus macrocephalus) are distributed throughout the North Pacific (Bakkala et al., 1984; Stark, 2007). Commercially, it is one of the most important species for bottom trawlers along the Pacific coast of the northern mainland of Japan (the so-called Tohoku population). The cod there have a lifespan of up to 8 years (Hattori et al., 1992a). Mature females deposit demersal eggs over shallow, sandy substrata once between December and February (Hattori et al., 1992b; Yoseda et al., 1992; Sakurai and Hattori, 1996). Recently, harvesting of the population has intensified and now includes 1-year-old fish (Narimatsu et al., 2009) and, as a consequence, the population currently consists mainly of young fish (Ueda et al., 2006; Narimatsu et al., 2009). The size of the cod population has fluctuated considerably during the past 30 years, but has remained high for the past 10 years (Narimatsu et al., 2009). The fluctuations may
have been accelerated by changes in the age composition and age at maturity of the population, but there is no information on annual variation in life-history traits and their effects on age composition, egg production, and recruitment.

The objectives of this study were to document temporal variation in growth and reproductive traits in the exploited Tohoku population of Pacific cod and to evaluate the influence of life-history traits on annual egg production. In addition, the contribution of each age class to egg production was estimated and used to determine the effect of adult age on recruitment success. Based on the results, we discuss the processes that have maintained the abundance of this population despite the heavy fishing pressure.

**Methods**

Pacific cod were collected from the fish market at Hachinohe, Aomori Prefecture, Japan, and from bottom-trawl surveys in the North Pacific off Japan. Trawl surveys and sample collection from the market were conducted between October and December of 1996–2007. The fish samples had been caught by bottom trawl in the waters next to Hachinohe (40°00′–41°20′N 141°25′–142°20′E; Figure 1), and bottom-trawl surveys were conducted at depths of 100–1000 m in the Tohoku region (36°25′–41°00′N 140°57′–142°35′E; Figure 1). Pacific cod that are distributed throughout the Tohoku area are considered to be part of a single population (the Tohoku population; Saito, 1998), so the survey and market sample data were pooled for analysis.

The total number of trawl survey sites in each year ranged from 57 to 150. The standard length (SL) of each fish was measured to the nearest 0.1 cm. Cod of SL <38.0 cm were aged using an SL frequency distribution and were assigned to either the 0+ or the 1+ age classes (Narimatsu et al., 2009). Cod of SL ≥38.0 cm were aged by sectioning their otoliths (Hattori et al., 1992a). Pacific cod spawn from December to February in Japanese offshore waters (Hattori et al., 1992b). For this study, January was defined as the month of spawning and used as time 0 for age determination. The ages of cod caught from October to December were rounded up to the next full year.

Whole body weight (BW) and gonad weight (GW) were recorded to the nearest 1 g for cod of SL ≥38.0 cm. The ovaries were removed and preserved in 10% buffered formalin, and the gonadosomatic index (GSI) and Fulton’s condition factor (K) for females calculated from

\[
GSI = \frac{100 \times GW}{BW},
\]

\[
K = \frac{100 \times BW}{SL^2}.
\]

Female cod begin vitellogenesis for the following spawning season in September (Hattori et al., 1992b). The frequency distributions of GSI values were determined for October samples and for November/December samples, and based on these values, some samples were defined as mature or immature (see below). The reproductive status of the other females was determined by histological observation. A section of the ovary tissue was removed, dehydrated, embedded in paraffin, sectioned (8 µm slices), and stained with Mayer’s haematoxylin and eosin. The sections were then examined under a light microscope. Females with vitellogenic oocytes were defined as mature, and those without vitellogenic oocytes as immature.

We used a logistic regression analysis to estimate maturity ogives by age for each of the 1997–2005 year classes using the formula

\[
\text{logit}(m) = \log \left(\frac{m}{1 - m}\right) = c_0 + c_1 \times \text{SL}.
\]

where \(m\) is the probability of being mature, SL the standard length at each age, and \(c_0\) and \(c_1\) the constants. Model parameters were estimated by maximum likelihood. The likelihood-ratio test was then used to determine the significance of the explanatory variables. We estimated the SL at which 50% of each female age class matured (L_{50}) using a logistic regression model, and the proportion of each female age class that matured was estimated by adapting the model to the SL frequency distribution for each year class. In addition, temporal changes in the values of L_{50} and the probability of maturation were evaluated with the model.

The specific growth rate (SGR, % year\(^{-1}\)) was estimated according to the equation of Ricker (1979), using the SL for each age class:

\[
\text{SGR} = \frac{\ln \text{SL}_2 - \ln \text{SL}_1}{t_2 - t_1},
\]

where SL\(_1\) and SL\(_2\) are the mean standard lengths at times \(t_1\) and \(t_2\), respectively. We calculated three SGRs for each year class, from age 0 to 1 (G\(_1\)), from age 1 to 2 (G\(_2\)), and from age 2 to 3 (G\(_3\)). The body length at hatching was assumed to be 0.41 cm (Narimatsu et al., 2007). To evaluate the effects of SL and growth rate on the probability of maturation, the SL at a given age and the SGR

![Figure 1. Tohoku area, Japan. Sampling locations by trawl survey and by commercial fishery are dotted and hatched, respectively.](https://example.com/image-url)
(G_1-G_3) were compared with the proportion of females that matured in each year class. The relationship between the SGR and the population size at 1-year old was also evaluated.

A few small pieces of the fixed ovary tissue were removed from each mature female. The tissue was then washed, dehydrated, and weighed to the nearest 0.0001 g. The number of vitellogenic oocytes in each piece was determined under a binocular microscope. The mean number of vitellogenic oocytes per 1 g of ovary and coefficient of variation (CV) were calculated. Using that mean number of vitellogenic oocytes, the predicted potential fecundity (PF) of each fish, i.e. the number of vitellogenic oocytes, was estimated gravimetrically. In addition, the predicted PF per 1 g body weight (relative fecundity, RF) was also estimated.

Ovary samples were preserved before the spawning seasons of 2001–2008, i.e. October–December of the years 2000–2007, but not between 1997 and 2000. In addition, fish samples used in the study were not always caught just before the spawning season. PF is generally defined as the number of vitellogenic oocytes, was estimated gravimetrically. In addition, the predicted PF per 1 g body weight (relative fecundity, RF) was also estimated.

The mean number of vitellogenic oocytes per 1 g of ovary and coefficient of variation (CV) were calculated. Using that mean number of vitellogenic oocytes, the predicted potential fecundity (PF) of each fish, i.e. the number of vitellogenic oocytes, was estimated gravimetrically. In addition, the predicted PF per 1 g body weight (relative fecundity, RF) was also estimated.

The long axis (LD) and the short axis (SD) of 30 oocytes in each piece was determined under a binocular microscope. The mean oocyte diameter of each fresh ovary (Do) was estimated from

\[ \text{Do} = \frac{(\text{LD} + \text{SD})}{2} \times 1.025 - 0.0039, \]

where \( n = 45, r^2 = 0.999, p < 0.001, \) and \( 0.484 < \text{Do} < 0.866. \)

We used generalized linear models (GLMs) to perform the regression of PF on SL and \( K, \) and of PF on SL, \( K, \) and Do. These factors were accounted for in the GLM by fitting models with a Poisson distribution as follows:

\[ \text{PF} = \exp(a + b \times \text{SL} + cK), \]

\[ \text{PF} = \exp(a + b \times \text{SL} + cK + d \times \text{Do}), \]

where \( a, b, c, \) and \( d \) are the parameters estimated by regression coefficients. We used the Akaike’s information criterion (AIC) to select the model with the best fit. We also conducted a generalized linear mixed model (GLMM) analysis to test whether the estimated parameters varied among years. The estimated parameters were similar for both the GLMM and the GLM. Moreover, there was little variance among years, so we used the parameters obtained from the GLM analysis only.

The PF of the population (potential total egg production, PEP) was estimated using population size indices and maturity ogives for the age and SL distributions from the spawning seasons between 1997 and 2008 in the function

\[ \text{PEP} = \sum_{i=2}^{5+} \frac{N_i}{2} \bar{F}_i M_i, \]

where \( N_i \) is the estimated population size index at age \( i, \bar{F}_i \) the mean PF at age \( i, \) and \( M_i \) the proportion of mature females at age \( i. \) Cod aged 5 years and older were treated as a plus age group. The \( \bar{F}_i \) values were estimated using the PF model. The CV between the PEP and SSB was compared to evaluate the compensating effect of population size on the PEP. Recruitment per PEP (RPS) was estimated using PEP and population size indices at 1 year old. To evaluate the effect of adult age on recruitment success, we compared the RPS with the proportion of adults in each age class contributing to PF. The predictive variables (age classes) were chosen by stepwise regression in a multiple regression analysis.

The population size indices and weight-at-age from 1997 to 2008 were estimated using the swept-area method based on data from the bottom-trawl surveys conducted in October and November from 1996 to 2007 (Ueda et al., 2006; Narimatsu et al., 2009). Mean fishing mortality of all ages (1–7) was estimated to be 0.66, much higher than what is generally recommended (e.g. \( F_{\text{max}} = 0.45 \)). Population size was known to have been strongly correlated with annual catch between 1997 and 2007 (Narimatsu et al., 2009; Figure 2). Recent levels of population abundance appear to be higher than between 1975 and 1996, based on a comparison of annual catches. The size of the cod population 1-year old was used as an index of recruitment and compared with SSB or PEP. The number of 1-year-old cod varied widely, from 3 million to 206 million.

**Results**

**Maturation**

Values of GSI in the 1997–2008 samples were bimodally distributed, with peaks of \(<1.0 \) and \( >4.0 \) in both October and November/December samples (Figure 3). Based on the

![Figure 2](https://academic.oup.com/icesjms/article-abstract/67/8/1659/605408)

**Figure 2.** Annual changes in population size (weight) and harvest of Pacific cod in the Tohoku area.

![Figure 3](https://academic.oup.com/icesjms/article-abstract/67/8/1659/605408)

**Figure 3.** Frequency distributions of the GSI of female Pacific cod caught in October, or November and December, from 1996 to 2007.
distributions, we used the GSI value as an index to define mature (≥3.4) or immature cod (≤1.2) for the forthcoming spawning season. The reproductive status of the remaining fish (GSI values of 1.3–3.3) was determined histologically. As a result, all females with GSI values of 1.3–2.2 and 2.6–3.3 were immature and mature, respectively. Both reproductive stages were included in samples with a GSI of 2.3–2.5. Atretic oocytes were found along with vitellogenesis, but reabsorbing (ripe but not released; Rideout et al., 2005) and retaining (vitellogenesis started but being reabsorbed) ovaries were not in the histological observations.

The age at maturity of Pacific cod in the Tohoku population varied. Between 1997 and 2008, all 2-year-old fish were immature and all 5+-year-old fish were mature. The proportion of mature 3-year-old females fluctuated among years, ranging from 18 to 73%, with a mean (± s.d.) of 43% (±16%). In contrast, there was less variation among 4-year-old females, ranging from 78 to 96% (88±6%; Table 1). There were no obvious temporal trends in the proportion of mature fish aged 3 and 4 (Table 1).

The logistic regression analysis suggested that SL influenced the probability of maturation in age 3 females in all years except 2002 (Table 1). In contrast, there was no correlation in several years for 4-year-old fish, perhaps partly because of the smaller number of immature 4-year-old cod sampled in those years (Table 1). The SL at which 50% of the 3-year-old females matured ($L_{50}$) varied within a small range, without any consistent trend among years (Table 1).

**Fecundity and egg production**

The mean CV of the predicted PF was 0.059 (range 0.003–0.13). There was a negative relationship between RF and Do (Figure 4). The RF varied mainly in the samples where Do was ≥0.500 mm (Figure 4), so we used only the samples with values of Do ≥0.500 mm to construct the PF models. The PF of females was fitted to two models, one including two explanatory variables (SL and K) and the other containing three explanatory variables (SL, K, and Do). The AIC of the latter model was lower than that of the former for all age classes (ages 3, 4, and 5+; Table 2). We employed the model containing SL, K, and Do as explanatory variables to describe PF. The mean SL and K of the samples caught in December (1997–2000) or the samples with Do ≥0.500 mm (2001–2008) and a mean Do at the maturation developmental stage of oocyte (0.800 mm; Hattori et al., 1992b).

Table 1. Parameters and significance (p) of maturity ogives for female Pacific cod aged 3 and 4 from 1997 to 2008.

<table>
<thead>
<tr>
<th>Year</th>
<th>n</th>
<th>% mature</th>
<th>$c_0$</th>
<th>$c_1$</th>
<th>$L_{50}$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>32</td>
<td>36</td>
<td>23.36</td>
<td>-0.61</td>
<td>51.51</td>
<td>0.003</td>
</tr>
<tr>
<td>1998</td>
<td>17</td>
<td>35.5</td>
<td>0.35</td>
<td>-0.17</td>
<td>48.68</td>
<td>0.275</td>
</tr>
<tr>
<td>1999</td>
<td>34</td>
<td>63.6</td>
<td>0.64</td>
<td>-0.14</td>
<td>51.13</td>
<td>0.270</td>
</tr>
<tr>
<td>2000</td>
<td>62</td>
<td>46.0</td>
<td>0.49</td>
<td>0.07</td>
<td>41.78</td>
<td>0.175</td>
</tr>
<tr>
<td>2001</td>
<td>106</td>
<td>20.6</td>
<td>0.43</td>
<td>0.05</td>
<td>46.96</td>
<td>0.143</td>
</tr>
<tr>
<td>2002</td>
<td>11</td>
<td>11.1</td>
<td>0.51</td>
<td>0.12</td>
<td>47.56</td>
<td>0.312</td>
</tr>
<tr>
<td>2003</td>
<td>53</td>
<td>40.7</td>
<td>0.36</td>
<td>0.07</td>
<td>50.92</td>
<td>0.134</td>
</tr>
<tr>
<td>2004</td>
<td>36</td>
<td>27.8</td>
<td>0.53</td>
<td>0.08</td>
<td>44.68</td>
<td>0.143</td>
</tr>
<tr>
<td>2005</td>
<td>252</td>
<td>19.7</td>
<td>0.21</td>
<td>0.06</td>
<td>45.35</td>
<td>0.312</td>
</tr>
<tr>
<td>2006</td>
<td>100</td>
<td>24.1</td>
<td>0.19</td>
<td>0.05</td>
<td>49.22</td>
<td>0.281</td>
</tr>
<tr>
<td>2007</td>
<td>11</td>
<td>24.3</td>
<td>0.22</td>
<td>0.05</td>
<td>48.29</td>
<td>0.306</td>
</tr>
<tr>
<td>2008</td>
<td>53</td>
<td>25.5</td>
<td>0.27</td>
<td>0.05</td>
<td>49.19</td>
<td>0.306</td>
</tr>
</tbody>
</table>

The probability of maturation was represented by the function logit $(m) = \log\left(\frac{m}{1 - m}\right) = c_0 + c_1 SL$. $L_{50}$ represents the standard length at which 50% of fish mature.

**Figure 4.** Relationship between Pacific cod oocyte diameter and RF (all age classes included).
Temporal changes in life history and reproductive potential of Pacific cod

Table 2. Results of a GLM fit to data from 2000 to 2007.

<table>
<thead>
<tr>
<th>Age</th>
<th>n</th>
<th>Variations</th>
<th>Coefficients</th>
<th>s.e.</th>
<th>p-value</th>
<th>Variations</th>
<th>Coefficients</th>
<th>s.e.</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>87</td>
<td>a</td>
<td>11.280</td>
<td>0.002</td>
<td>&lt;0.001</td>
<td>a</td>
<td>11.779</td>
<td>0.002</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>b</td>
<td>0.052</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>b</td>
<td>0.053</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>c</td>
<td>0.108</td>
<td>0.001</td>
<td>&lt;0.001</td>
<td>c</td>
<td>0.647</td>
<td>0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>d</td>
<td>-1.847</td>
<td>0.002</td>
<td>&lt;0.001</td>
<td>d</td>
<td>-1.847</td>
<td>0.002</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>4</td>
<td>155</td>
<td>a</td>
<td>11.446</td>
<td>0.001</td>
<td>&lt;0.001</td>
<td>a</td>
<td>11.534</td>
<td>0.060</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>b</td>
<td>0.045</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>b</td>
<td>0.052</td>
<td>0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>c</td>
<td>0.251</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>c</td>
<td>0.400</td>
<td>0.021</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>d</td>
<td>-1.207</td>
<td>0.001</td>
<td>&lt;0.001</td>
<td>d</td>
<td>-1.207</td>
<td>0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>5</td>
<td>107</td>
<td>a</td>
<td>11.508</td>
<td>0.001</td>
<td>&lt;0.001</td>
<td>a</td>
<td>11.805</td>
<td>0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>b</td>
<td>0.041</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>b</td>
<td>0.043</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>c</td>
<td>0.427</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>c</td>
<td>0.583</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>d</td>
<td>-1.062</td>
<td>0.001</td>
<td>&lt;0.001</td>
<td>d</td>
<td>-1.062</td>
<td>0.001</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Two models were tested, one using the explanatory variables SL (cm) and condition factor (K) and one SL, K, and oocyte diameter (Do, mm) on PF (number of yolked oocytes × 10⁶).

were adopted to estimate the mean PF-at-age in each year. Mean PF values were estimated to range from 79 × 10³ to 114 × 10⁴ (mean ± s.d. 95 ± 13 × 10³) at age 3, from 119 × 10³ to 170 × 10³ (mean ± s.d. 151 ± 14 × 10³) at age 4, and from 200 × 10⁴ to 312 × 10⁴ (mean ± s.d. 251 ± 33 × 10³) at age 5 between 1997 and 2008.

The estimated PEP for 3-year-old females ranged from 1.12 × 10¹⁵ to 18.1 × 10¹⁵ between 1997 and 2008 (mean ± s.d. 6.4 ± 4.9 × 10¹⁵; Figure 5). There was a 16-fold difference in the maximum PEP for 3-year-olds, considerably less than the range in SSB among years for this age class (159-fold; Figure 5). Moreover, the CV of the PEP (0.77) was lower than that of the SSB for 3-year-old females (0.88).

The PEP was attributed to young adult fish aged 3 and 4 years (Figure 6). In addition, the primary contributor to PEP fluctuated among years between these two age classes (Figure 4). The values of RPS ranged from 0.9 × 10⁻⁶ to 168 × 10⁻⁶ individuals (Figure 6; mean ± s.d. = 50 ± 54 × 10⁻⁶). To evaluate the effect of adult age on RPS, we used RPS as a response variable and the PEP values for each age class (3, 4, and 5+) as explanatory variables. None of the explanatory variables were significant in the analysis (F < 4.0).

Interactions among year-class strength, probability of maturation, and PF

The proportion of mature 3-year-old females varied among years (Table 1). The stepwise multiple regression revealed that the lengths at 3 years old (SL₃) and the SGR from 2 to 3 years (G₁) had a significant effect on the probability of maturation at age 3. Conversely, SL₁, SL₂, G₁, and G₂ had no effect on the probability of maturation for this age class (Table 3).

We compared the population size of the Tohoku population aged 1 to the SGR, mean PF, and the proportion of mature 3-year-old females. The linear regression analyses suggest that population size at age 1 was negatively correlated with G₁ (r² = 0.505, p < 0.01; Figure 7a), but not with G₂ (p = 0.878) or G₃ (p = 0.145). Population size at age 1 was also negatively correlated with the mean PF at age 3 (r² = 0.557, p < 0.01; Figure 7b), and the proportion mature at the same age (r² = 0.365, p < 0.05; Figure 7c).

Figure 5. Annual changes in SSB and estimated total egg production of age 3 female Pacific cod.

Figure 6. Temporal changes in PEP (bars) and RPS (circles) from 1997 to 2008.

Discussion

The SSB has traditionally been used to predict the reproductive potential and the adult–progeny relationship for fish populations. Reproductive potential is the ability of a fish stock to produce offspring that may recruit to adulthood or to the fishery (Trippel, 1999; Morgan and Brattey, 2005). In a broad sense, this implies that stock reproductive potential includes both total egg production and the viability of the progeny. The SSB was one of
Table 3. Results of a stepwise regression to explain the probability of maturation in age 3 female Pacific cod.

<table>
<thead>
<tr>
<th>Variables</th>
<th>s.e.</th>
<th>Adjusted $r^2$</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>SL$_3$</td>
<td>2.77</td>
<td>0.876</td>
<td>0.006</td>
</tr>
<tr>
<td>G$_3$</td>
<td>91.6</td>
<td>0.624</td>
<td>0.017</td>
</tr>
</tbody>
</table>

Standard length at age 1 (SL$_1$), 2 (SL$_2$), and 3 (SL$_3$), and SGR during ages 0–1 (G$_1$), 1–2 (G$_2$), and 2–3 (G$_3$) were used as explanatory variables. SL$_3$, SL$_2$, G$_3$, and G$_1$ were not significant predictors of the probability of maturation.

Figure 7. Relationships between (a) population size at age 1 and SGR at age 0–1 ($G_1$), (b) mean PF at age 3, and (c) proportion mature at age 3. All response variables were negatively correlated with population size. SGR: $r^2 = 0.505$, $p < 0.01$; PF: $r^2 = 0.557$, $p < 0.005$; Proportion mature: $r^2 = 0.365$, $p < 0.05$.

Several parameters included in our models of PEP, but interestingly, it was not always a good predictor of PEP (e.g. 2001 and 2007; Figure 5). This underscores the risk of using SSB to predict reproductive potential and the importance of understanding the components of reproductive potential in assessing and managing exploited populations.

The values of RF decreased with development of the oocytes. The RF at given oocyte size was highly variable in ovaries containing oocytes of diameter $\leq 0.5$ mm compared with those containing oocytes of diameter $>0.5$ mm (Figure 4). Similar results were reported for Atlantic cod (Gadus morhua) by Thorsen et al. (2006). Those authors suggested that samples containing advanced yolked oocytes ($\leq 0.6$ mm) are adequate to estimate PF and to construct a fecundity model. In Pacific cod, the oocyte diameter at advanced developmental stages such as the late yolk formation and migratory nucleus phases ranged from 0.5 to 0.7 mm (Hattori et al., 1992b). Therefore, we used only the samples with oocytes $>0.5$ mm to construct our PF model. In addition, as the oocyte diameter at maturation of Pacific cod around Japan ranges from 0.7 to 0.9 mm (Hattori et al., 1992b), we used 0.8 mm as the standard size to estimate PF.

SGR, SL, and PF at a given age were related to year-class strength. Although these factors were significant, a number of other unexamined factors, such as water temperature and/or food availability, might also affect the response. The results of the analysis here suggest that correlations were only present in populations fluctuating in size, not in a population that was merely increasing or decreasing over time. In addition, several fish populations react to density-dependence (Lorenzen and Enberg, 2001; Armstrong et al., 2004), a factor thought to play an important role in compensating for fishing pressure (Rochet, 2009). Taken together, these results suggest that the year-class strength of the Tohoku Pacific cod population is one of the key factors explaining the variation in life-history traits.

Population size at 1 year of age influenced the SGR at ages 0–1 ($G_1$), but not at ages 1–2 ($G_2$) or 2–3 ($G_3$). This suggests that changes in growth depended on the abundance of cod <1-year old, but not of cod aged 1 and 2. Age-related fishing pressure is one explanation for the ontogenetic difference in the relationship between year-class strength and SGR, i.e. the negative correlation between abundance and $G_1$ and the absence of any correlation between abundance and $G_2$ or $G_3$. As fish attain 1 year of age, their exploitation by commercial fisheries commences, and because of the heavy fishing pressure, the density of fish decreases over time. Moreover, as the fish grow, they distribute themselves vertically and horizontally over a wider range and utilize a greater variety of food resources (Fujita et al., 1995; Kitagawa et al., 2002). Such ontogenetic niche shifts and anthropogenic influences may explain why growth changed in conjunction with population size only in the early life stages.

In some instances, fish will mature if the rate of acquisition of surplus energy during a critical period exceeds a genetically determined threshold (Thorpe, 2007). Growth rate (Godo and Haug, 1999; Morita et al., 2006) and SL are likely cues to predict the probability of maturation. Laboratory experiments indicate that life-history traits such as SL and growth rate can change between pre- and post-decision to mature (Yoneda and Wright, 2005; Wright, 2007). Therefore, it is important to determine the timing of the decision to mature and then to examine the relationship between the probability of maturation and life-history traits (Wright, 2007). In Pacific cod, the probability of maturation for 3-year-old females depends on the SL at 3 years old (SL$_3$) and the growth rate between 2 and 3 years of age ($G_3$), but is independent of SL$_1$, SL$_2$, $G_1$, and $G_2$.

Pacific cod in the region studied begin vitellogenesis in September (Hattori et al., 1992b), so the fish used in the current study had already made the decision of whether to mature in the forthcoming reproductive season. Our results suggest that SL and SGR are available to predict maturation within a year of the maturation taking place, but not earlier in life. However, the timing of the decision to mature and the changes in life-history traits at that time remain unclear.

Maturity- and PF-at-age were negatively correlated with population size at age 1, showing that the expected productivity per female varied with the abundance of the same year class, high in poor year classes and low in strong year classes. In fact, the range in PEP was considerably less than the range in SSB for females aged 3. Moreover, the CV of the PEP was also lower than that of the SSB for 3-year-old females (Figure 5). Together, these results suggest that the variation in the probability of maturation and PF in the first mature age class compensated for total egg production of poor year classes.
Moderate or strong year classes of Pacific cod have been frequent recently (Figure 2). This is partly explained by the stable supply of eggs that resulted from compensatory egg production. In addition to the quantity of eggs, their quality is likely an important factor in determining recruitment. The eggs of younger or virgin females are generally more vulnerable than the eggs of older or experienced females (Solemldal, 1997; Trippel, 1998; Berkeley et al., 2004a, b). This is particularly true in unfavourable environments, where the eggs and larvae of young females have poorer rates of survival than older females (Ottersen et al., 2006). Although the quality of eggs produced by young adults was not evaluated, there was no relationship between RPS and PEP for each adult age class in the Tohoku population of Pacific cod. This fact and recent population levels imply that the progeny of younger and virgin females contribute to recruitment at the same rate as the progeny of older females in the population.

In recent years, the size of the Tohoku population has remained as high as it was at the peak levels observed during the past 30 years, although heavily exploited from the juvenile stage. It appears that this population has produced a robust response to fishing pressure. Our results suggest that these high population levels have been achieved through good recruitment. Females of the population reach sexual maturity quickly after recruitment and have flexible growth rates, ages at maturity, and PF, depending on year-class strength. Such traits make it easier to increase or recover population numbers in favourable environments. However, very poor year classes were generated in 1999 and 2007. If unsuitable conditions continue for more than one generational cycle, the traits described here will not prevent declines in recruitment. The population may then lose the opportunity to generate a strong year class because of a shortage of adults. Hence, despite the ability of the population to remain abundant, the increased fishing pressure has the potential to cause a substantial decrease in population size over a short period, if not closely monitored and managed.

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