Density and Mortality in a Harvested Population of Quahog (*Mercenaria mercenaria*) in Nova Scotia, Canada

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**Abstract**  
Innovative Fishery Products Inc. has managed a 1,682 ha quahog (*Mercenaria mercenaria*) lease in St. Mary’s Bay, Nova Scotia, Canada, since 1997. A management strategy based on population modeling is desired to optimize production on a long-term basis. This requires a description of life history parameters, and data on the quahog population and its commercial exploitation. The objectives of this study were to describe the data collected on the commercial fishery, estimate quahog densities, and calculate preliminary mortality rates for the population. Mean densities ranged from 48.3 to 88.4 individuals per m² during surveys conducted in June 2001 and 2002, and May 2003. Densities were higher than those typically described for commercially harvested quahog beds. The mean age to market was 7 years. Spat recruitment was variable and age frequency graphs suggest immigration of juvenile quahogs between the ages of 3 and 6 years onto the intertidal portion of the lease area. Survival was estimated between 24 and 37% for 7-8 year old quahogs using catch curve and analysis of covariance techniques, where commercial exploitation only represented 5-10% of the loss. Causes of apparent high natural mortality are unclear, but winterkill due to ice abrasion or scouring, predation, and the movement of quahogs from the lease appear reasonable.
Introduction

Quahog population distribution in Atlantic Canada

The northern quahog (*Mercenaria mercenaria*) is a bivalve found in shallow coastal waters from the Gulf of Mexico to its northern limit in the southern Gulf of St. Lawrence. These bivalves are found in small patches or large beds in both intertidal and subtidal reaches of coastal embayments, from muddy sand to sand-based sediments (Grizzle et al. 2001). The geographical distribution of this species in Atlantic Canada is limited to areas where summer water temperature exceeds 20ºC (Landry and Sephton 1996), and therefore wild quahog populations typically occur in the southern portions of the Gulf of St. Lawrence (Fig. 1). Two populations have been documented in the Bay of Fundy region of Atlantic Canada, one of which in St. Mary’s Bay, Nova Scotia, Canada. However, details on their origin and actual population structure have never been described (Whiteaves 1901, Dillon and Manzi 1992). Innovative Fishery Products Inc. (IFP) manages this population, which represents the only commercially viable quahog stock in the Bay of Fundy. This paper represents the first study of the St. Mary’s Bay population.

Lease production and fishery management

Quahogs are harvested in St. Mary’s Bay from May to November with the peak harvest period occurring from June to September. The annual harvest has ranged from 95 to 370 t since commercial harvesting began in 1997 (Fig. 2). Lease management is based on (1) routine visual inspections for quahogs of the intertidal portion of the lease prior to the harvest season; (2) harvest rotation whereby the lease area is harvested in plots and plots may not be harvested every year; (3) a minimum shell length of ≥50 mm, although the harvest may include a small percentage of individuals between 45 and 49 mm; (4) daily harvest monitoring; (5) a harvest season from May to November; and (6) active lease enforcement throughout the year where IFP reports illegal lease harvesting to Department of Fisheries and Oceans (DFO) enforcement officers. IFP and DFO entered into a four-year partnership to evaluate the use of population models to develop long-term management strategies to optimize quahog harvesting on the lease. St. Mary’s Bay was considered to be ideal for population modeling. The St. Mary’s Bay population appears to be an isolated population whereby immigration or emigration are currently considered negligible, the population can be readily surveyed, the lease area is managed by one user group, and good data on daily harvest and fishing effort are available. A precursor to population modeling is the requirement for a clear understanding of the life cycle of the population and basic population parameters. The objectives of this study were to describe the quahog population in relation to commercial harvesting in St. Mary’s Bay and to estimate preliminary mortality rates using basic fisheries techniques.
Figure 1. Northern quahog lease located in St. Mary's Bay, Nova Scotia, Canada. Sam Orr's Pond, near St. Andrews, New Brunswick, is represented by the star. The northern quahog is typically found in the Gulf of St. Lawrence as described by dashed oval.
Materials and methods

Population surveys

The study area includes the entire lease, which has a surface area of 1,682 ha with a maximum intertidal zone of 628 ha where the quahog is the dominant bivalve. The intertidal zone gradually slopes from the high to low tide mark and the substrate is largely mud and a mud-sand mixture. Pre-harvest population intertidal surveys were conducted in collaboration with IFP in June 2001 and 2002, and in May 2003. In June 2001 and 2002, surveys consisted of one sampling station per 500 × 500 m sampling unit for a total of 45 stations. A sampling grid 500 m east by 250 m south was used during the 2003 intertidal survey for a total of 95 stations. However, only the 45 traditional stations used in the June 2001 and 2002 surveys were used for survey comparisons with the May 2003 survey. During the May 2003 survey, 10% of randomly selected stations were also resampled.

At each sampling site, the upper sediment layer was collected to a depth of 25 mm from a 0.25 m² quadrat with small garden shovels and rinsed through a 2 mm mesh sieve, as spat and juvenile clams are typically found at this depth. Samples were bagged and frozen at −30°C until sample processing. All clams were then removed from the sediment by hand to a maximum depth of 15 cm. All clams were bagged and frozen at −30°C until sample processing. Shell length was measured to the nearest 1 mm with digital calipers. Whole frozen weight was measured to the nearest 0.1 g with a top loading digital balance.

Commercial harvest data

IFP measured the daily weight of quahogs harvested by each clam digger from 1997 to 2003. The harvested quahogs were sampled twice weekly.
during 2003. For each sample \((n = 200)\), the length frequency, to the nearest millimeter, and the sample weight, to the nearest 0.01 kg, were recorded.

**Age determination**

Quahogs \((n = 362)\) from the June 2002 survey were aged using techniques developed for surf clams, *Spisula solidissima* (Ropes and O’Brien 1979, Jones et al. 1990, Sephton and Bryan 1990). Thin sections were excised from the right-hand valve of specimens ranging from 25 to 110 mm shell length. The valve was secured to the manipulative support of an Isomet low speed geological saw and a 2 mm section was sliced between two diamond wafer cutting blades, one of the blades cutting just anterior of the umbo, yielding a highly polished thin section. The umbo side of the section was glued to a glass slide and viewed under a dissecting microscope at 25x. The number of annuli was counted within the outer and middle shell layers in the radial section from the umbo to the ventral margin.

Few quahogs older than 10 years were collected from the survey; thus the growth curve could not be properly estimated. Also, bivalves typically have highly variable growth rates whereby length frequency intervals of larger animals may encompass several age groups. Therefore, an age-length matrix coupled with the length frequency of the population was used to estimate the age composition rather than using a deterministic relationship between age and length (Hilborn and Walters 1992). Lengths for which age could not be determined were assigned to an unspecified group.

First the age-length matrix derived from the 2002 survey was used to calculate the proportion at age of quahogs for each 1 mm shell length interval. This age-length key was used in conjunction with the respective length frequencies for the June 2001 and 2002 and May 2003 population surveys. The numbers obtained for each age class were expanded to the survey area by multiplying the numbers at age by the ratio of the total survey area to the sampled area. The same age-length key was used to obtain an estimate of the age composition of the 2003 commercial harvest up to September 15, which made up most of the harvest.

**Preliminary estimates of mortality rates and survival**

Total instantaneous mortality rates \((Z)\) were estimated from catch curve analyses on the yearly age compositions for the surveys and commercial harvest (Ricker 1975). This analysis assumes that recruitment and mortality rates are constant over the period determined by the number of age-groups used in the calculation. The slope of the descending limb of the natural logarithm of numbers at age is an estimate of \(Z\). Only ages 7-10 years were used in the analysis because few individuals older than 10 years were collected.
Estimates of $Z$ also can be obtained from catch curve analyses conducted along individual cohorts. This approach removes the assumption that cohorts are of similar abundance but requires data over several years. For the time series of pre-harvest surveys (2001-2003), a modified catch curve analysis was used. Sinclair (2001) used this approach to estimate total mortality rates of southern Gulf of St. Lawrence cod ($Gadus morhua$). The method is essentially an analysis of covariance and assumes that mortality rates in 2001-2002 and 2002-2003 were similar. We note that fishing effort over the lease area in 2001 and 2002 were relatively constant (3,145 and 3,198 harvester days respectively). This would imply that at least the fishing portion of the mortality rate may have been constant. The statistical model used was

$$\ln A_{ij} = \beta_0 + \beta_1 Y + \beta_2 I + \varepsilon$$

where $A_{ij}$ is the number of quahogs of age $i$ in year $j$; $Y$ is a class variable indicating year class, and $I$ is the covariate age. $\beta_1$ are year-class effects and $\beta_2$ is the estimate of total mortality in the time period.

For 2003, an exploitation rate for the fishery up to September 15 could be calculated because the harvest had been sampled. The exploitation rate was the ratio of the numbers of quahogs harvested to the numbers of quahogs estimated from the May 2003 pre-harvest survey for quahogs with shell length >45 mm. In addition, the fraction of the biomass removed by the fishery was estimated for all three years by dividing commercial landings by the estimated biomass of animals with shell-length >45 mm from spring surveys.

Finally, estimates of survival rate, $S$, were calculated using the standard equation $S = e^{-Z}$.

**Results**

**Population surveys and age to market**

Mean quahog densities ranged from 50 to 90 individuals per m$^2$ from 2001 to 2003 (Table 1). A comparison of mean densities with and without spat (quahogs with shell length $\leq$ 5 mm) suggested variable recruitment in 2002 and 2003 (Table 1). Few quahogs $\geq$10 years old were collected during the 2001-2003 surveys (Tables 2 and 3, Fig. 3).

The age composition of quahogs larger than 25 mm, sampled in the surveys of June 2001 and 2002 and May 2003, showed a similar age structure in the three years of the surveys (Fig. 3). Age 7 was the dominant age class. In 2003, age 7 was also the dominant age class of the commercial harvest, and the 258 t of harvested quahogs was equal to 4.2 million individuals.
Estimates of mortality rates

Catch curve analyses of the 2001-2003 surveys (Fig. 4) as well as the fishery harvest (Fig. 5) suggested that total mortality of quahogs 7-10 years of age was high with estimates of $Z$ ranging from 1.00 to 1.42, implying annual survival rates of only 24 to 37%. The modified catch curve analysis of survey numbers indicated no significant difference ($P < 0.05$) in year-class abundance for the 1992-1995 cohorts, quahogs aged 7-10 years in 2001-2003. The steepness of the common slope also suggested a high rate of mortality ($Z = 1.32$). As a result, a catch curve analysis was conducted using the pooled data which gave an estimate of $Z = 1.40$ equivalent to a survival rate of about 25% (Fig. 6).

While total mortality was estimated to be high, mortality attributed to commercial harvest of the lease appears to be low. The exploitation rate for 2003 was calculated to be 3.0% for quahogs $\geq 45$ mm. For all three years, the estimated proportion of the fishable biomass taken in the fishery ranged from about 5 to 10%.

Discussion

Quahog densities in St. Mary’s Bay were 3-10 times higher than commercially harvested populations in the Gulf of St. Lawrence (Landry et al. 1993). In North America, Fegley (2001) reported that 80% of density studies found relatively low population densities of 1-15 individuals per m$^2$ for quahogs $\geq 30$ mm. The other studies documented densities of $>500$ individuals per m$^2$. Because the high densities described by Fegley (2001) were reflective of intensive shellfish aquaculture and rarely occur in nature, the densities observed in St. Mary’s Bay (Table 1) were higher than other natural quahog populations in North America (Castagna 1984, Fegley 2001).
Table 2. Length frequency, shell length in mm, of northern quahogs from population surveys (n = 45 traditional stations) conducted in June 2001 and 2002 and in May 2003 in the lease area in St. Mary’s Bay, Nova Scotia, Canada.

<table>
<thead>
<tr>
<th>Shell length (mm)</th>
<th>2001</th>
<th>2002</th>
<th>2003</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-5</td>
<td>66</td>
<td>447</td>
<td>71</td>
</tr>
<tr>
<td>6-10</td>
<td>4</td>
<td>21</td>
<td>34</td>
</tr>
<tr>
<td>11-15</td>
<td>1</td>
<td>3</td>
<td>9</td>
</tr>
<tr>
<td>16-20</td>
<td>0</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>21-25</td>
<td>4</td>
<td>11</td>
<td>8</td>
</tr>
<tr>
<td>26-30</td>
<td>25</td>
<td>25</td>
<td>5</td>
</tr>
<tr>
<td>31-35</td>
<td>67</td>
<td>61</td>
<td>29</td>
</tr>
<tr>
<td>36-40</td>
<td>103</td>
<td>115</td>
<td>74</td>
</tr>
<tr>
<td>41-45</td>
<td>124</td>
<td>129</td>
<td>110</td>
</tr>
<tr>
<td>46-50</td>
<td>107</td>
<td>92</td>
<td>113</td>
</tr>
<tr>
<td>51-55</td>
<td>55</td>
<td>44</td>
<td>90</td>
</tr>
<tr>
<td>56-60</td>
<td>34</td>
<td>23</td>
<td>42</td>
</tr>
<tr>
<td>61-65</td>
<td>8</td>
<td>6</td>
<td>15</td>
</tr>
<tr>
<td>66-70</td>
<td>6</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>71-75</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>76-80</td>
<td>3</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>81-85</td>
<td>4</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>86-90</td>
<td>0</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>91-95</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>96-100</td>
<td>2</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>101-105</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>106-110</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>111-115</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>617</td>
<td>995</td>
<td>618</td>
</tr>
</tbody>
</table>
Table 3. Age composition of quahogs of 25 mm and larger from population surveys (numbers expanded to the survey area) conducted in June 2001 and 2002 and May 2003 and from the 2003 commercial landings in the lease area in St. Mary’s Bay, Nova Scotia, Canada.

<table>
<thead>
<tr>
<th>Age</th>
<th>Population surveys (thousands)</th>
<th>Landings (thousands)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2001</td>
<td>2002</td>
</tr>
<tr>
<td>3</td>
<td>2,425</td>
<td>2,039</td>
</tr>
<tr>
<td>4</td>
<td>4,369</td>
<td>3,949</td>
</tr>
<tr>
<td>5</td>
<td>22,119</td>
<td>24,061</td>
</tr>
<tr>
<td>6</td>
<td>59,755</td>
<td>56,786</td>
</tr>
<tr>
<td>7</td>
<td>107,617</td>
<td>101,312</td>
</tr>
<tr>
<td>8</td>
<td>46,912</td>
<td>44,341</td>
</tr>
<tr>
<td>9</td>
<td>4,523</td>
<td>3,256</td>
</tr>
<tr>
<td>10</td>
<td>2,061</td>
<td>3,178</td>
</tr>
<tr>
<td>11</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>12</td>
<td>472</td>
<td>1,417</td>
</tr>
<tr>
<td>13</td>
<td>472</td>
<td>472</td>
</tr>
<tr>
<td>14</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>15</td>
<td>0</td>
<td>472</td>
</tr>
<tr>
<td>Unspecified</td>
<td>6,138</td>
<td>472</td>
</tr>
<tr>
<td>Total</td>
<td>256,865</td>
<td>241,755</td>
</tr>
</tbody>
</table>

The unspecified group is composed of large individuals, >70 mm and equal to 11 years, for which no age assignment could be made.

The fishery appears to be exploiting quahogs of 6 years and older. Mean age to market for these quahogs was 7 years and ranged from 5 to 8 years. Populations in the Gulf of St. Lawrence reach commercial market size, shell length 50 mm, between 9 and 13 years (Landry et al. 1993) while southern populations reach market size in 2-5 years (Grizzle et al. 2001). In St. Mary's Bay, age to market appears to be faster than for populations of the Gulf of St. Lawrence. Differences in growth could be attributed to many factors including temperature, food quality and quantity, and salinity.

It is important to note that the age-length key for 2002 was used to calculate the age composition of the 2001-2003 surveys, as well as the commercial harvest in 2003 (Tables 2 and 3). This assumes that during this short period there have not been large changes in growth. The survey age-length key used for the calculations contained few large individuals,
which might have affected the estimation of the age composition of commercial harvest in 2003. However, for age groups used in the analyses (7-10 years) the age composition was based on 232 readings. There is usually little difficulty in identifying annuli for these age classes (Jones et al. 1990).

The increasing number of age 3-7 quahogs in the spring surveys for the three years of observations suggested that younger quahogs have a distribution that is larger than the survey area and that quahogs progressively “recruit” to the survey area. For St. Mary’s Bay, passive transport may significantly affect the distribution of this population, particularly...
Figure 4. Catch curves for quahogs in St. Mary’s Bay from the 2001-2003 spring survey age compositions. Closed circles are data points used in the analysis; open circles were not.
Figure 5. Catch curves for quahogs in St. Mary’s Bay from 2003 age composition of commercial harvest. Closed circles are data points used in the analysis; open circles were not.

Figure 6. Combined catch curve analysis of survey numbers along cohorts. Ages 7–10 were used in the analysis. Symbols indicate year classes.
the younger and smaller animals. The movement of smaller quahogs may be caused by storm surges in the 7 m tidal range, which are characteristic to the area. Geospatial differences in distribution between spat, juveniles, and adults may have ecological implications to overall population fitness (Rice et al. 1989). Large concentrations of adult quahogs may also affect the recruitment of juvenile quahogs (Rice et al. 1989). Fegley (2001) has also documented that when there are large numbers of widely dispersed spawning quahogs, this can lead to lower fertilization rates.

All of the catch curve analyses of mortality rates suggested that total mortality for ages 7-10 was high. This would include both natural mortality, such as predation and disease, and the commercial harvest.

These estimates assume that the adult portion of the population is closed and thus not subject to emigration or immigration. Because there are no other known adult populations nearby, passive transport such as that hypothesized for small quahogs is considered less likely for the larger adult animals. The analyses conducted on the age-structured data from the surveys for individual years, or the 2003 harvest, also assumed constant recruitment. Survey data from 2001 to 2003 indicated that there was significant variation in recruitment in the area for year classes produced in the early 2000s. However, the analysis of covariance, which used all three years of survey data, showed that there was no significant difference in year-class strength for year classes produced in the early to mid-1990s (ages 7-10 in 2001-2003). This analysis, which took into account potential differences in year-class strength, also produced a similarly high estimate of total mortality. In summary, all estimates of $Z$, either from the survey or the harvest data and using various methods, were relatively high. We could not identify specific reasons to discount these estimates.

Given the apparent high total mortality, the low estimates of exploitation rate for 2003 and of the fraction of the fishable biomass taken by the fishery in 2001-2003 would imply that natural mortality on these age groups was unusually high.

Mortality rates for adult quahog populations from New England states are usually low and uniform throughout the year and rarely exceed 50% for age classes between 6 and 10 years (Kennish 1978). Predation may partly explain high mortality rates. Predation by seagulls is common over the lease area. Annual predation rates of seagulls on adult quahogs in the intertidal mudflat at Hamble Spit in Southampton, England, were estimated at 5-10 individuals per m$^2$ (Hibbert 1977). Large losses of adult quahogs may also be attributed to winterkill caused by ice scouring on the lease. Photographs taken of the lease area in December 2002 showed the presence of large ice cakes of $1.5 \times 2 \times 2$ m (height $\times$ length $\times$ width). Ice cakes covered the intertidal region from January to April 2002-2004. Winterkill has been suggested for losses of large amounts of oysters (*Crassostrea virginica*) and quahogs throughout much of the
Gulf of St. Lawrence region in 2002-2003 (T. Landry, DFO, pers. comm. 2003). This phenomenon has not been quantified in Atlantic Canada but may be an important factor in the population dynamics of quahogs in St. Mary’s Bay.

Low survival rates can have serious implications for the sustainability of a population. Size structure is important for the reproductive fitness of a population and in terms of fishery management. *M. mercenaria* is described as a protandrous consecutive hermaphrodite, meaning that males typically dominate the younger size classes, the sex ratio changes with age distribution, and the sex ratio of adults is not 1:1 with growth whereby males may still outnumber the females (Eversole 2001). Though separate sexes do exist, fully functional hermaphrodites are common to quahogs (Eversole 2001). In the Gulf of St. Lawrence, sexual maturity can be attained at 25 mm and 30 mm shell lengths for males and females respectively with one major spawning event usually occurring in mid-June (Landry et al. 1999). In this case, the fishery mainly harvests animals that are 45 mm and larger and the bulk of the mortality for quahogs 7 years and older appears to be largely due to causes other than exploitation. If further analyses confirm these results, this could be a natural characteristic of this population.

In conclusion, while the simple methods used are subject to a number of assumptions that need to be verified, these analyses provide a description of population structure and initial estimates of mortality for this understudied population. In our study, the limited data precluded the use of more complex models but the results underline the usefulness of basic methods to generate hypotheses about population dynamics, in this case high natural mortality. We hope that this information combined with continued sampling of the population and the fishery will lead to the use of age-structured population models, such as virtual population and statistical catch-at-age analyses, to gain a better understanding of population dynamics of quahogs in St. Mary’s Bay.

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**References**


Timing of Parturition and Management of Spiny Dogfish in Washington

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Abstract
Management of the spiny dogfish (*Squalus acanthias*) fishery in the eastern North Pacific Ocean has historically been limited, and not focused on conservation of the species. Washington State Department of Fish and Wildlife (WDFW) recently adopted a new management strategy aimed specifically at protecting the spiny dogfish during the critical reproductive period. There is currently little information on the reproductive biology of the Puget Sound stocks of spiny dogfish, and much of it is anecdotal. The aim of this project is to improve the data poor nature of spiny dogfish fishery management. This paper reports some of the findings of an extensive investigation into the reproductive biology of Puget Sound spiny dogfish. The pupping season appears to be from May through November, longer than the anecdotal data indicate and much longer than current regulations were written to cover.

Introduction
The spiny dogfish (*Squalus acanthias*) fishery in the Puget Sound and Pacific Northwest waters has received little management and has been
characterized by fluctuations in catch and effort. Management of this species in Puget Sound is based on poor data, managers have little local information about the species, and much of that information is anecdotal and from fishery stakeholders. Prior to 2003, spiny dogfish management goals were reduction of interactions with other fisheries, reduction of bycatch, or to conform to market practices (WDFW 2003).

In 2003, Washington Department of Fish and Wildlife (WDFW) amended the fishing regulations for setnet and set-line spiny dogfish fisheries. The 2003 amendments effectively closed the fishery in most of the Puget Sound areas during the summer months (June 16–September 15). This time frame was suggested by industry as the period when females were pupping and was adopted into the regulation. The impetus to put regulations in place was justified by the generally accepted need to practice precautionary management (FAO 1995) to conserve the species and maintain the fishery.

Recent stock assessments in the western North Atlantic have shown that the stocks are not stable, fishable biomass has greatly decreased, there is low recruitment of females, and the stocks may be fully exploited (Rago et al. 1998). Managers took dramatic steps to reduce the impact on the stocks as a whole and on large females in particular. While stocks have not had the same trend in Washington state waters, there is cause for concern. Catch rates have shown dramatic declines over the last two decades (Fig. 1) and recent stock assessments also suggest a decline (WDFW 2003). In neighboring British Columbia, stock assessments show their stocks to be stable. Given the geographic range of the stocks in the eastern North Pacific (WDFW 2003, McFarlane and King 2003), the populations are transboundary and require cooperative management between the two countries. This begins with creating accurate methods for assessing the status of these stocks, and managing accordingly.

*Squalus acanthias* is common, small, and easy to maintain in laboratory conditions. Literature on this species comes from many areas: North Atlantic (Rago et al 1998, Soldat 2002), North Sea (Stenberg 2002, Jones and Ugland 2001), Black Sea (Polat and Guemes 1995), and the North Pacific (Bonham 1954; Holland 1957; Ketchen 1972, 1975, 1986; Wood et al. 1979; McFarlane and Beamish 1987; Saunders and McFarlane 1993; McFarlane and King 2003). Laboratory studies with detailed examinations of the anatomy, physiology, and reproductive cycles, including endocrinology have been conducted (Tsang and Callard 1987, Koob and Callard 1999).

In 1948, Bigelow and Schroeder determined that the populations in the North Pacific were the same species as those in the North Atlantic. However, research indicates that the animals in these two areas do differ in some aspects. In the North Pacific, the spiny dogfish are longer lived, mature later and at a larger size, and they grow much larger than those
in the North Atlantic (Ketchen 1972, 1975; McFarlane and Beamish 1987; Saunders and McFarlane 1993).

In the eastern Pacific Ocean, spiny dogfish research has focused on aging, migrations, and population dynamics (Bonham 1954, Holland 1957, Wood et al. 1979, McFarlane and Beamish 1987, Saunders and McFarlane 1993, McFarlane and King 2003) with less emphasis on life history. McFarlane and King (2003) show some animals move between Strait of Georgia and Puget Sound waters, and that the animals from the coastal tagging area (west coast Vancouver Island) are more prone to migration. Three separate stocks have been identified by McFarlane and King (2003) and WDFW (2003): coastal stocks (including Washington coast, and west coast Vancouver Island), northern (including the Strait of Georgia and the San Juan archipelago) and southern (waters from Port Townsend to the south).

Around the world, pupping and mating seasons vary by area. An in-depth analysis of reproductive biology for spiny dogfish found in British Columbia waters suggested that mating occurs from December through February and that parturition occurs October through November (Ketchen 1972). Soldat (2002) reported that pupping in the western North Atlantic
occurs year-round with most activity between November and April. In waters near Sweden and Norway, pupping is reported to occur from November to December and mating from December to February (Stenberg 2002), while Jones and Ugland (2001) report pupping from September to December and fertilization (and onset of pregnancy) from October to February. It is important to note that the time of mating and the onset of pregnancy may not be closely linked if the female stores the sperm for a period of time prior to fertilization. The objective of this paper is to present results from an ongoing and in-depth study into the reproductive biology of spiny dogfish in Puget Sound. We propose that the timing of the critical reproductive events may differ from that previously reported, which has a direct impact on current management strategies.

Our investigation of the reproductive biology of the spiny dogfish is an effort to refine parameters for more accurate stock assessment and management strategies. Although this study focuses on the spiny dogfish in north Puget Sound (NPS), we also sampled spiny dogfish from the south Puget Sound (SPS), east Puget Sound (EPS), and coastal (C) areas, in an effort to compare reproductive timing and animal sizes (Fig. 2). The results presented in this paper will quantify the reproductive season for NPS spiny dogfish, contribute to a comparison of the timing of reproductive seasons with spiny dogfish from other areas, and suggest the role of this information in defining fishing seasons and harvest regulations. Information from this study will contribute to management of the spiny dogfish fishery in Puget Sound, and possibly to British Columbia management.

**Materials and methods**

This study has three parts: sample collection, lab analysis, and hormone analysis. Sample collections involved demographic information, size and sex distributions, and catch effort. The laboratory section included examination and measurement of reproductive tracts. The hormone component is not presented here but will appear in a future paper (M.S. thesis draft, Cindy A. Tribuzio).

Spiny dogfish samples were collected from November 2002 to October 2003. Fish were sampled from the catch of a commercial bottom trawl fisherman in the southern Strait of Georgia, Washington (48°N, 123°W) between 73 and 128 meters (40-70 fathoms) depth (Fig. 2). Up to 25 spiny dogfish were taken from the trawl catch on each sampling date and maintained in an onboard live tank with flowing seawater until brought to the dock. This was not considered a random subsample, as the vagaries of the collection effort did not allow for guarantee of randomization. Non-random samples may induce size bias, and while the captain was instructed to randomly sub-sample animals, it is the nature of the fishery to take the largest, and it is possible that our samples are upwardly biased. Given the nature of the project objectives, the non-random sampling and possible
bias are inconsequential. Fish were processed at the Sea-K Warehouse in Blaine, Washington. Dockside processing allowed WDFW samplers to collect the data from fresh fish without requiring samplers to be onboard the vessel and without requiring samples to be frozen.

Each animal was weighed whole and data recorded for pre-caudal length (PCL), fork length (FL), and total length-natural (TLnat) (Fig. 3). To compare length distributions to previous studies 146 spiny dogfish were randomly sampled from the same fishing ground and measured for TLnat and TLext (Fig. 3). Male clasper inner length (CIL) was also measured. Blood
was collected (~5ml), in a 15 ml centrifuge tube, from the caudal vein by removing the caudal fin and catching the blood flowing from vein. These tubes were kept cold overnight to allow the blood to clot and the serum to separate out. The serum was drawn from each blood sample and divided into 3 separate 1.5 ml micro-centrifuge tubes, prior to shipping. Samples were kept on ice, not frozen, and shipped overnight to the University of Washington for further analysis.

The second dorsal spine was removed, from tip to vertebrae, for age determination. Maturity stages of the reproductive tracts (based on Stehmann 2002) were recorded, and the entire female reproductive tract or testes (males) were removed and kept on ice.

Female reproductive tracts were measured for length, width (both to the nearest millimeter) and weight (to the nearest tenth of a gram) of ovaries, oviducts, oviducal glands, and uteri. In adult females (Stehmann 2002, stages D-G), the diameters of the developing ova within the ovary were measured to the nearest millimeter. In pregnant females with

Figure 3. Length measurements for whole animal. Lower left, tail in natural position for measuring $T_{LN_{nat}}$. Lower right, tail extended to line up with body, for measuring $T_{L_{ext}}$. 

was collected (~5ml), in a 15 ml centrifuge tube, from the caudal vein by removing the caudal fin and catching the blood flowing from vein. These tubes were kept cold overnight to allow the blood to clot and the serum to separate out. The serum was drawn from each blood sample and divided into 3 separate 1.5 ml micro-centrifuge tubes, prior to shipping. Samples were kept on ice, not frozen, and shipped overnight to the University of Washington for further analysis.

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candles, the candles were weighed and the number of eggs counted. For those females with pups, each pup was weighed with and without the yolk sac, sexed, and measured for PCL, FL, and TL\textsubscript{ext}. For male spiny dogfish, the testes were weighed and measured for length and width.

Maturity classifications in the field were based on Stehmann (2003). However, the reproductive analysis in this project required a fine scale. We initially used a scale proposed by Tsang and Callard (1987), with 4 reproductive stages and did not account for post-natal females (Table 1). Table 1 shows the stages used for this study. The stages of pregnancy were based on the presence of candles with embryos too small to measure with the naked eye, those with embryos in candles that were measurable, and those females with embryos free of the candle in the uterus based on size. Given the extended gestation in this species and the short period between pregnancies we classified all mature females with empty uteri as spent/post-natal or pre-fertilization (stage I).

Samples from outside the above sample area were also collected for comparison during the summer of 2003 (Fig. 2). For comparison, spiny dogfish from Willapa Bay, Washington (C) and south Puget Sound (SPS) were collected as bycatch in ongoing research by WDFW. Targeted hook and line fishing for spiny dogfish was conducted near Orcas Island, Washington (EPS). For most of these samples the only measurements taken

<table>
<thead>
<tr>
<th>Stage</th>
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<tr>
<td>A</td>
<td>Candles, embryos up to 3.5 cm, follicles 3-10 mm</td>
<td>A</td>
<td>Candle present, embryo not measurable</td>
</tr>
<tr>
<td>B</td>
<td>Embryos 3-10 cm, follicles 17-20 mm</td>
<td>B</td>
<td>Candle present, embryo measurable</td>
</tr>
<tr>
<td>C</td>
<td>Embryos 17-25 cm, follicles 28-34 mm</td>
<td>C</td>
<td>No candle, embryo TL &lt; 10 cm</td>
</tr>
<tr>
<td>D</td>
<td>Embryos &gt;25 cm, follicles 32-38 mm</td>
<td>D</td>
<td>Embryo TL 10.1-15 cm</td>
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<tr>
<td>E</td>
<td>Embryo TL 15.1-17.5 cm</td>
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<td>Embryo TL 15.1-17.5 cm</td>
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<tr>
<td>F</td>
<td>Embryo TL 17.6-20.5 cm</td>
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<td>Embryo TL 17.6-20.5 cm</td>
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<tr>
<td>G1</td>
<td>Embryo TL 20.6-23 cm</td>
<td>G1</td>
<td>Embryo TL 20.6-23 cm</td>
</tr>
<tr>
<td>G2</td>
<td>Embryo TL 22.5-24.5 cm</td>
<td>G2</td>
<td>Embryo TL 22.5-24.5 cm</td>
</tr>
<tr>
<td>H</td>
<td>No external yolk sac embryo TL 10.1-15 cm</td>
<td>H</td>
<td>No external yolk sac embryo TL 10.1-15 cm</td>
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<tr>
<td>I</td>
<td>Post-partum</td>
<td>I</td>
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TL = total length.
were sex, lengths, weight, maturity, and blood, while a few were sent to the lab for further measurements.

**Results**

This paper reports on results from the first 11 months of a 12-month sampling program. Sampling catch rates were relatively constant throughout the sampling period, with the exception of early spring and early summer (Fig. 4). The sampling plan was for two trips each month, approximately every other week, with a targeted sample number of 25 fish for each trip. Due to weather (wind and tides) fishing did not always occur regularly. Inclement windy weather was the primary factor contributing to the low fishing effort during the period 26 February 2003 and 14 April 2003, resulting in no samples in March. Fishing was not affected by weather during the period from 14 May 2003 to 11 June 2003, but catches of spiny dogfish were lower during that period.

Numbers and maturities of males and females varied between sampling dates. Mature males were caught consistently from 7 November 2002 to 27 February 2003 (Fig. 5). Between 27 February 2003 and 29

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**Figure 4. Total catch for each sampling date. Star (*) represents when no sampling occurred. N = 471.**
April 2003, the maturity of the males sampled changed significantly, with immature animals becoming prominent (t-test, alpha = 0.05, P-value = 0.002). In the early summer months (May and June) mature males become more prominent in the catch and peaked at 26 Aug 2003. The composition of the female catch varied more than the males throughout the sampling period (Fig. 6). Immature females made up most of the female catch 7 November 2002 to 5 December 2002, 26 February 2003 to 14 May 2003, 11 June 2003, and 29 July 2003 to 9 September 2003. At no point was the female catch composed entirely of mature animals, but between 26 February 2003 and 14 May 2003, and between 29 July 2003 and 9 September 2003, there was a significant increase in the proportion of immature females sampled (t-test, alpha = 0.05, P-value < 0.001).

**Reproductive seasonality**

The relative frequency of mature females in each stage for each month sampled shows that post-natal females (stage I, Fig. 7) were present much of the year, but were absent most of February (after 10 February 2003,
only two mature females were sampled) and April (one mature female was sampled during the last sampling event in April; no samples were collected in March). However, this was also the time of least intensive sampling. Stage I females were caught with the greatest frequency (the entire mature female catch) in June and September, and made up a large portion of the mature female catch in July and August. Late stage pregnancy females (stages G and H) were also present in July and August. The least frequent catches of stages, G-H, were in January through May, where the earlier stages of pregnancy were seen most often (stages A-B). Females may begin pupping in June and continue through November, while ovulation and fertilization occur November through February.

With the gestation occurring over about 22 months, in the population there are two groups of pregnant females: those in the first year of pregnancy and those in the second year. The graph of embryo size against sampling date shows this trend (Fig. 8). There were no females caught that were in the first year of pregnancy, in the months of August and September (in September, all females were stage I). In November and December 2002 and October 2003, embryos of three stages are seen
simultaneously, indicating some temporal overlap between pupping and fertilization.

**Comparisons to other areas**

Three areas sampled around Puget Sound and coastal Washington state waters were compared for differences in size and stage of maturity. For females all three areas were sampled in July and August, and just the north Puget Sound (NPS) and coastal (C) areas in September. In July, the sizes of the females caught were significantly different in the three areas ($t$-test, alpha = 0.05, all $P$-values < 0.004), but in August and September, the sizes were not significantly different from one another ($t$-test, alpha = 0.05, all $P$-values > 0.166). Males were encountered only in NPS and C and only in July and August. As with females, the sizes were significantly different between the two areas in July ($t$-test, alpha = 0.05, $P$-value = 0.01) but not in August ($t$-test, alpha = 0.05, $P$-value = 0.105). Also, tests between months within the same area showed that in NPS and C, different sized females were caught in July than in August ($t$-test, alpha = 0.05, $P$-values < 0.001), and between August and September in NPS ($t$-test, alpha
The relative frequencies of females in each stage of the reproductive cycle were compared for the females in all three areas in the month of July (Fig. 9). A Mann-Whitney U test for ordinal data was used to test the null hypothesis that the regions have the same reproductive stage frequencies and thus the same timing of reproductive events. The null hypothesis was rejected for all three tests conducted (alpha = 0.05, all P-values < 0.001), and the three regions were all significantly different from each other in the frequencies of females in reproductive stages.

**Discussion**

The principal consideration in the WDFW 2003 management plan was timing of parturition. The NPS samples indicate that there may be a prolonged pupping season, which contrasts with earlier studies in nearby areas. Ketchen (1972) reported that pupping in British Columbia occurs in October and November and breeding December through February. At
public aquariums in the Pacific Northwest, spiny dogfish show different reproductive timing. Pups have been found in December and January at the Seattle Aquarium, and records at the Point Defiance Zoo and Aquarium show pupping roughly March through June (Jeff Christiansen, Seattle Aquarium, pers. comm., September 2003; John Rupp, Point Defiance Zoo and Aquarium, Tacoma, pers. comm., September 2003). The animals on display at both aquariums were from stocks in Puget Sound. The Oregon Coast Aquarium, with spiny dogfish from coastal stocks near Newport, Oregon, reports pupping for all months except March, July, August, and November with peaks in May and October. Evidence of mating (damage to caudal and pectoral fins from biting males) has been recorded in March, June, July, and September (Colleen Green, Oregon Coast Aquarium, Newport, pers. comm., September 2003). Evidence of mating, however, is not necessarily indicative of fertilization and pregnancy; there may be a time lag due to the possibility of storage of sperm in the oviducal gland for a significant period of time. This phenomenon has not been studied in spiny dogfish.

**Figure 9. Comparison of uterine (pregnancy) stages in three different sampling areas.** D = early pregnancy, E = mid pregnancy, F = late, and G = post partum (Stehmann 2002). NPS = north Puget Sound, SPS = south Puget Sound, C = coastal.
Our study suggests that pupping occurs from May to November for the NPS stocks and ovulation and fertilization from October to January. It is also possible that the spiny dogfish exhibit a year-round reproductive seasonality with peaks in activity. Data on reproductive females were lacking between much of February through late April, and more intense sampling during that period may provide more insight into the seasonal pattern. Most reports for spiny dogfish are that they have either a specific seasonality or a prolonged seasonality to their reproductive cycle.

Females in the earliest stages of pregnancy (stage A: eggs are still contained within the candles in utero and the embryos are too small to be measured with the naked eye) were encountered from November through February. Jones and Ugland (2001) estimated the candle stage to last 13 months and Ketchen (1972) estimated length of embryos at the end of the first year to be about 14-15 cm. In this study, we consider the candle stage in two parts (Table 1): one where the embryo cannot be measured and the other where it can be measured by the naked eye. We estimate that the candle stage lasts less than one year and that stage A lasts about 1 month. The average monthly growth rate estimate for the first year is 11.67-12.50 mm (assuming that growth is constant during that year), based on Ketchen (1972). The smallest embryo we found not contained in a candle was 71 mm TLe and the largest within a candle was 49 mm TLe. Based on these observations and the proposed growth rate, the entire candle stage lasts somewhere between 3.9 months and 6.1 months. The smallest measurable embryos still in the candle were about 12.5 mm, which takes an estimated 1-1.07 months to achieve. We can assume that females in stage A of pregnancy have been pregnant for only about 1 month, thus those females encountered in stage A during November may have ovulated and fertilized in October, and those encountered in February became pregnant in January. Since samples were not taken in March, we were unable to determine if this period extends through February. No stage A females were encountered in April, indicating ovulation and fertilization were completed by March.

With the gestation being about 22 months long, the ovaries must continuously develop the next cohort of eggs instead of having a resting period between pregnancies. The next crop of eggs is then developing for the subsequent pregnancy while the current pregnancy is ongoing. After the female has pupped, the eggs finish development, ovulate, are fertilized, and move to the uteri. Maximum ova diameters are seen in September and November (prior to the final sampling event in October), and again in February. Given the broad temporal span of the pupping season, the measurements of ova diameter from spent females would be expected to vary over the time period. However, the variation in the size through time appears to fall into two groups of development, suggesting two broad and overlapping pupping seasons; the first being in the early summer and the next in the fall.
As with the developing ova, the developing embryos can be used to support the timing of reproductive events. Data for embryonic growth show two distinct groups of development, which are explained by the almost two-year gestation. Pregnant, mature females are either in their first or second year of gestation. Currently there is no evidence to suggest that females segregate by year of gestation. However, within these two-year classes of gestation, there does appear to be variation in the degree of embryo development, suggesting more broad timing of fertilization (Fig. 8).

Spiny dogfish harvest encompasses areas outside the NPS, so management strategies will need to be flexible enough to encompass the timing of reproductive events in the various areas. Comparisons between fishing areas in south Puget Sound (SPS) and coastal (C) waters were made. These comparisons did suggest differences in the timing of reproductive events in the three areas during the month of July. This relationship will be examined further in future reports.

This study was undertaken to investigate the timing of critical reproductive events to assist with development of management. The current management plan closes the fishery during the time period perceived to be when the females are most vulnerable. This paper is the first in a series that examines these events as well as reproductive physiology, endocrinology, and embryonic development. This paper specifically reports on the timing of pupping and fertilization, which is more broad than expected. The pupping season appears to extend well past the time frame over which WDFW enacted fishing closures, and is different from published data on nearby British Columbia populations. The data presented are for a one-year period. We have no evidence that year-to-year variability is minimal, so that the 2002-2003 data may not be representative. We suggest extending this study and refining the methods based on what was learned during this first year if more precise dates are needed.

**Acknowledgments**

We thank Washington State Department of Fish and Wildlife for supporting this project with funding and valuable staff hours. Sue Hoffmann and Debbie Farrer at WDFW worked countless hours and late nights dissecting out reproductive tracts, for which we are very grateful. Heather Weindenhoft and Danny Badger helped with sample collection and lab analysis. Shawn Waters, skipper of the F/V *Tulip*, supplied time and effort in catching and maintaining the spiny dogfish onboard his boat. Sea-K Fisheries allowed us to use warehouse space and accommodated our sampling needs. We also thank the students in the University of Washington School of Aquatic and Fishery Sciences shark group, who helped with advice, ideas, input, and sampling.
References


Developing Assessments and Performance Indicators for a Small-Scale Temperate Reef Fish Fishery

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Abstract

In Australia, the development of live fish markets in the early 1990s created strong demand for temperate reef fish species, particularly banded morwong (Cheilodactylus spectabilis). The fishery expanded rapidly over a very short period but has subsequently undergone a marked decline. Several management controls have been progressively introduced, including size limits, seasonal closures, and limited entry. Only simple performance indicators based on catch and catch rate trends have been utilized to monitor stocks.

Banded morwong are sedentary and appear to have a depth-structured sex and size distribution. They are long-lived (>80 years), and growth rates and maximum sizes are distinctly different for males and females. These life-history characteristics and the likely population structuring at small spatial scales have marked consequences for stock assessment.

A variety of simple assessment approaches, including catch rate standardization, yield-per-recruit and spawning biomass-per-recruit analyses, catch curve analysis, and biological indicators (median size and age, sex ratio) have been examined. These methods proved inconclusive in indicating whether current fishing levels are sustainable, or based on continued reduction of accumulated biomass and/or serial depletion of spatially structured populations. General uncertainty regarding data quality from the commercial fishery and spatial representation of biological data within the populations are of concern.
Because data intensive assessment techniques cannot be justified for this small-scale fishery, we propose the development of an operating model that can be used to evaluate whether simple biological and/or fishery indicators can assist performance monitoring and address issues of sustainability.

Introduction

The development of live-fish fisheries in Australia during the 1990s has placed increased pressure on tropical and temperate reef fish populations, with fisheries expanding rapidly during the mid to late 1990s (Rimmer and Franklin 1997). Recent annual production from the tropical fisheries has exceeded 1,500 metric tons (QDPI 2002), much of which is exported to Asian markets. By contrast, catches from the temperate fisheries, principally banded morwong (Cheilodactylus spectabilis) and wrasse (Notolabrus spp.), are low, in the order of 200 t, and service domestic live-fish markets.

Typically reef fish populations are spatially structured and reef fish fisheries tend to be small in size. This combination makes the application of data intensive assessment techniques difficult to justify both practically and economically. Using banded morwong as a case study, we examine the current stock assessment approaches applied in Tasmania, Australia. First, we evaluate catch and effort data and then investigate alternative assessments and reference points based on available biological information. Industry perceptions about resource status, fish behavior, and fishery developments have also been canvassed to supplement biological and fishery information. Our data, however, are patchy in space and time and present significant challenges when applied to assessing stock status.

Banded morwong fishery

The live-fish fishery for banded morwong is a coastal gillnet fishery off eastern Tasmania, with catches concentrated off the central and south-east coasts (Fig. 1). The fishery expanded rapidly in the early 1990s and reported catches peaked at almost 150 t in 1993-1994 (November-October fishing year, Fig. 2). Between 1994-1995 and 1999-2000, annual production declined steadily to below 40 t but has since stabilized at around 50 t, with catches generally tracking changes in effort.

Fishers generally operate out of dinghies or small vessels and target banded morwong using a fleet of large mesh gillnets (130-140 mm) over exposed rocky reefs. To minimize effects of barotrauma and thus maximize fish survival, fishing is largely restricted to maximum depths of about 25 m even though the species occurs to greater depths.

Despite low production and value, currently less than AU$ 0.7 million per year, the fishery is highly regulated. Minimum and maximum size lim-
its (330 and 430 mm fork length, FL) were introduced in 1994 to protect large adults and permit spawning prior to recruitment to the fishery, in addition to matching market size requirements. In 1998 both limits were increased by 30 mm after it became apparent that they offered minimal protection to mature females and the lower limit was set close to the size at maturity (Murphy and Lyle 1999). A two-month closed season during the peak spawning period (March and April) was introduced in 1995 and has remained in place since that time. Interim licensing arrangements were implemented in 1996, with around 90 live-fish endorsements issued,
and replaced by a specific banded morwong license in 1998. There are currently 29 license holders.

Management of the fishery falls under the Tasmanian Scalefish Fishery Management Plan (DPIF 1998). The plan contains a series of performance indicators and reference points that are applied generically to all species. For routine assessments, annual summaries of catch, effort, and catch rates are evaluated against a set of reference points (Lyle et al. 2004). While target reference points are not part of this strategy, limit reference points or trigger points have been defined as levels or rates of change that are considered to be outside the normal variation of the stocks and the fishery. Limit reference points are reached when one or more of the following criteria are met:

- Total catch, fishing effort, or catch rates are outside levels of reference years;
- Total catch declines or increases in a year by more than 30% from the previous year;

Figure 2. Annually reported catch (filled circles, in metric tons) and total effort (open circles, in days fished) for banded morwong in Tasmania from 1990-1991 to 2002-2003. Daily effort data have been reported only since 1995-1996. Dotted line represents minimum catch reference point level.
• A significant change occurs in biological characteristics, e.g., size or age composition; and

• Any other indications of stock stress.

These reference points provide a framework against which the performance of the fishery is assessed and, if necessary, flag the need for management action. However, while the catch and effort reference points are clearly defined, the other definitions remain vague and leave much room for interpretation. In addition, apart from the implementation of a review process, management responses are not formally defined if reference points are reached.

**Banded morwong life-history characteristics**

Banded morwong is a large temperate reef fish that occurs around southeastern Australia and New Zealand to depths of at least 50 m (Gomon et al. 1994). Tagging studies have indicated that movement of juvenile and adult fish is very limited, implying that individuals remain largely site-attached (Murphy and Lyle 1999). Size- and sex-based population structuring by depth has also been observed in banded morwong, with females and juveniles more prevalent in the shallow sections of the reef and males tending to dominate deeper reef regions (McCormick 1989a). Adults display a complex spawning behavior, with males exhibiting territorial behavior and occupying the same area of reef over periods of several years (McCormick 1989b).

The species demonstrates an unusual combination of very fast initial growth, early age at maturity, and long life expectancy, with maximum ages for males and females of over 80 years (Murphy and Lyle 1999). In addition, growth rates and maximum sizes are distinctly different for the two sexes (Fig. 3). Growth in females is relatively rapid for the first 5-6 years to a size of about 350 mm, after which it slows dramatically. By contrast, males grow relatively rapidly for the first 10-12 years, up to about 450 mm, before growth slows. These growth characteristics in conjunction with spatial structuring have marked consequences for the assessment of this species.

**Catch and effort assessment**

Previous routine assessments have only been based on analysis of catch and effort information derived from compulsory logbook returns. Catch returns provide daily summaries of fishing operations, including method, location (based on 30×30 nautical mile fishing blocks), fishing depth, effort, catch weights, and whether seal interference had occurred. Catch returns are unverified and accuracy is uncertain.

Since 1995-1996 catches have, to a large degree, tracked changes in effort (Fig. 2). After apparent high fishing pressure early in the fishery,
reported catches declined steadily to 1999-2000, but stabilized and even recovered slightly thereafter. Limit reference points based on catch have been breached every year since the management plan was implemented in 1998 (Fig. 2). Unstandardized catch rates based on geometric mean have generally declined since 1995-1996 and remained below reference levels each year since 1999-2000 (Fig. 4). Initial declines in catch and catch rates occurred at a time when there was ample capacity to take larger catches and markets were strong. This led resource managers and researchers to express concern about the status of the stocks, and biological and catch sampling was implemented. Recent stability is difficult to interpret in

Figure 3. Size-at-age and von Bertalanffy growth functions for (a) male (N = 333), and (b) female banded morwong (N = 614) in 1996-1997 (after Murphy and Lyle 1999).
terms of stock condition, but may be linked to market demand which has become increasingly important in determining harvest levels, with fish buyers often placing fishers on catch limits.

Catch rate standardization using generalized linear models (GLM) has also been attempted to reduce the impact of obscuring effects such as region, depth, season, or skipper (Kimura 1981, 1988). The standardization was conducted on an annual base statewide and for all reports by fishers that had been in the fishery for at least two years and caught a median annual catch of at least one metric ton. The optimal model, fitted by assuming a lognormal distribution with an identity link, was based on Akaike’s and the Bayesian information criterion (AIC and BIC; Burnham and Anderson 1998) and provided by:

\[ \ln \text{CPUE} = \text{Constant} + \text{year} + \text{season} + \text{vessel} + \text{skipper} + \text{fishing block} + \text{depth} + \text{seal interference} + \text{fishing block} \times \text{seal interference} \]

Standardization suggested a greater degree of stability by comparison with unstandardized catch rates, with catch rates remaining above reference levels (Fig. 4). The catch rate analyses generally support industry perceptions that fishing has had negative effects on the stocks, but that in recent years catch rates have stabilized or even improved.

Catch rates, however, offer limited insights into the sustainability of current harvest levels and stock status. There are several reasons for this. First, catch rates ignore the unique biological characteristics of the species. Second, we are dealing with spatially structured populations and the spatial scale for reporting may be too large to detect localized and/or serial depletions. In addition, fishers operate over relatively wide areas of coast to maintain catches and this behavior may mask localized depletion effects and result in apparent hyper-stability in catch rates. Third, data reliability is questionable.

In relation to data reliability, discussions with industry have identified a number of issues. For instance, catches are believed to have been substantially overstated before the introduction of live-fish endorsements in 1996, and data quality is considered variable at least up until approximately 2000. Furthermore, the “meaning” of catch and effort data has changed as a result of an increasing incidence of seal interference, resulting in loss of catch and damage to gear. Fishing practices have been altered as fishers have attempted to minimize these impacts, mainly by dispersing gear over large areas. In any case, fishing activity is not always reported for days when seal interactions are severe partly out of concern it could indicate poor catch rates and elicit a management response. Data quality and reporting consistency, along with the impacts of seal interactions, are therefore important factors affecting any interpretation of fishery-dependent information in this fishery.
Alternative assessments

Biological and catch sampling were undertaken between 1996 and 1997 by Murphy and Lyle (1999) and resumed in 2001 because of concerns about the stock status. These data provide the basis for assessments such as yield-per-recruit, spawning biomass-per-recruit, catch curve analysis, and examination of simple biological indicators.

Yield-per-recruit and spawning biomass-per-recruit analyses

The yield-per-recruit and spawning biomass-per-recruit have been calculated using the current size limits (360-460 mm) and a natural mortality of $M = 0.05$, derived by using the Sparre et al. (1989) approximation. These analyses highlight the dilemma faced when determining fishing reference levels for species with strong sex-based differences in growth parameters (Fig. 5). For instance, the reference level $F_{0.1}$ (Gulland and Boerema 1973) from the yield-per-recruit analysis was estimated as 0.25 for males but just 0.11 for females. Females recruit to the fishery at around six years of age and typically remain vulnerable for the remainder of their lives. On the other hand, males remain vulnerable to the fishery
on average between four and ten years of age and can thus sustain much higher levels of fishing mortality. In practice, reference levels are probably conservative because the effect of lower selectivity by the fishing gear toward the upper end of the keyhole size limit has not been taken into account.

While $F_{0.1}$ often has been used as a target to minimize growth overfishing, it does account for recruitment (e.g., Clark 1991, 1993; Mace and Sissenwine 1993). To address recruitment overfishing for stocks where little is known about the stock-recruitment relationships and resilience, the fishing mortality rate $F_{30\%}$, which reduces spawning biomass-per-recruit to 30% of the unfished level, has been applied as a recruitment overfishing limit, and $F_{40\%}$ as a target limit (Clark 1993, 2002; Mace and Sissenwine 1993; Mace 1994). Using ovary weight-at-size as a proxy for fecundity, the spawning biomass-per-recruit curve drops fast with increasing fishing mortality, and hence fishing mortalities are low for both reference levels, with $F_{40\%} = 0.07$ and $F_{30\%} = 0.12$ (Fig. 5). This analysis suggests that only low fishing mortalities, close to $F_{0.1}$ for females, are sustainable. At mortality rates $F > 0.2$, relative spawning biomass falls below 20%.

A precautionary approach would favor reference mortality rates for recruitment overfishing of females as the basis for management advice. However, since it is impractical to manage the fishery differently based on sex, this level of fishing mortality would provide only about 50% of the theoretical maximum yield for males.

Increased minimum size limits would of course provide more effective protection to the female spawning biomass. The increase in the minimum size limit from 330 to 360 mm in 1998 represented a compromise between biological results from yield- and spawning biomass-per-recruit analyses and economic considerations (Murphy and Lyle 1999). Due to a market preference for small fish, any higher minimum size limits would have had a severe negative effect on access to the live-fish markets.

Yield-per-recruit and egg-per-recruit analyses are useful tools in setting management controls such as size limits and can provide target and limit reference levels for fishing mortality. But independent estimates or indicators of biomass and/or fishing mortality are still required to provide information about stock status.

**Catch curve analyses**

Research sampling conducted during the spawning closures in 1996 and 1997 and again in 2001, 2002, and 2003 has yielded a range of biological information for legal-sized as well as under- and over-sized individuals.

Age-frequency information is available from over 2,500 individuals, but because of longevity and spatial structuring, sample sizes at individual collection sites are low and thus may not be representative of the associated populations. Recognizing this uncertainty but attempting to
Figure 5. Yield-per-recruit curves for (a) male and (b) female banded morwong, and (c) spawning biomass-per-recruit curves. Results shown for size limits of 360-460 mm and natural mortality $M = 0.05$. 
reduce noise in the data, we have pooled information across sites for each year. Age-frequency samples have been corrected for gillnet mesh selectivity (determined empirically and modeled using gamma distribution, after Millar and Holst 1997), and total mortality $Z$ was estimated based on catch curve analysis (Beverton and Holt 1957, Ricker 1975).

This analysis revealed a considerable range of estimates of $Z$ based on recruited ages up to 14 years, namely 0.16 for males and 0.22 and 0.12 for females in 1996 and 1997, respectively, and a range of 0.15-0.43 for males and 0.07-0.32 for females in the 2001-2003 samples (examples of 1996 and 2003 shown in Fig. 6). As over half of the reported catches had already been taken by 1996 (refer Fig. 3), even the earliest samples would have been impacted by the fishery. By comparison with many other fisheries, total mortality rates are low, but they do suggest that the reference points $F_{0.1}$, $F_{30\%}$, and $F_{40\%}$ for females derived from yield-per-recruit and spawning biomass-per-recruit analyses have been exceeded. Higher levels of noise in the data due to pooling of sites and low sample sizes, however, limits the utility of this analysis as an estimator for fishing mortality.

Age-frequency plots reveal an apparent dichotomy between trends for younger (to 14 years) and older age classes for both sexes. For males this is not unexpected, since most individuals over about 14 years are larger than the maximum size limit and are thus subject to much reduced fishing mortality. By contrast, females effectively remain vulnerable once recruited to the fishery, and thus the relatively high proportion of old females still present in the catches suggests that either catchability changes with age and/or fish down of accumulated biomass is still occurring.

If, as suggested by McCormick (1989a), large males concentrate at greater depths they may receive further protection from fishing through a “depth refuge,” since fishing rarely occurs at depths over 25 m. Any females found in deeper water will also be less vulnerable to capture. Anecdotal reports suggest that fish in the deeper waters are in fact large specimens and fishers contend that there is replenishment of fishing grounds throughout the year and associated with spawning, possibly due to movement of fish from deeper water. This gives rise to the suggestion that a portion of the population may be protected from fishing by depth. Unfortunately we have no information about the structure or relative abundance of populations in the deeper reef areas or potential mixing rates with the shallower areas. Fishing surveys of such areas and an understanding of the size and distribution of suitable deep reef habitat relative to the shallow fished reef areas may prove informative in evaluating the potential importance of depth refuges.

**Biological parameters**

Trends in the biological characteristics of exploited stocks have the potential to provide indications of more general changes in stock status (e.g., Caddy and Mahon 1995, Caddy 1998). Biological parameters, de-
Figure 6. Catch curves for male and female banded morwong in Tasmania for 1996 and 2003. The log-transformed and selectivity-corrected age-frequencies are based on direct age estimates of $N = 205$ (1996) and $N = 216$ males (2003), and $N = 280$ (1996) and $N = 164$ females (2003). Data between 4 years (fish fully selected to fishing gear) and 14 years (first zero catches) have been used for mortality estimation (filled circles).

Since 1996, the median size and age of the samples has declined for both sexes and, not surprisingly, these changes have been far more pronounced for females. For instance, median ages have fallen from around 20 to 7 years for females compared to 7 down to 5 years for males over the sampling period. Such variability between the sexes is clearly linked to growth rate differences and the effects of the legal size limits. Sex ratios also seem to have shifted from females dominating until 2001 to
roughly equal numbers of males and females in the more recent samples. This biological response would at least be partly due to the greater selective fishing pressure on females.

Changes in the biological characteristics of populations are to be expected with exploitation (e.g., Buxton 1993, Harris and McGovern 1997, Helser and Almeida 1997). But without reliable and meaningful reference points, it is difficult to determine whether changes are indicative of stock stress and thus whether fishing pressure exceeds sustainable levels.

**Discussion**

Fished species, which are known or suspected to be spatially structured, often violate many of the assumptions typically used in stock assessment models (e.g., Parma et al. 2003). They can have heterogeneous stock structure, spatial gradients in life-history characteristics such as growth or size at maturity, and diverse stock-recruitment relationships. If the fishery is also small-scale and low in value, then extensive data collection and assessments at the appropriate spatial scales are difficult to justify.

Reliable but simple estimators of stock status together with management reference points that take into account the sedentary character and the specific life-history characteristics of the species are therefore needed. These can be based on simple biological indicators, singly or as a suite of indicators (Caddy and Mahon 1995; Caddy 1998, 1999). For example, Die and Caddy (1997) proposed a single reference point for total or fishing mortality which considers the size at first capture in relation to mean size at maturity to allow spawning before capture. Multiple reference points are generally considered “safer” than applying a single option especially when information sources are highly uncertain and insufficient. Caddy (1999) proposed a semi-quantitative approach where the fisheries management cycle incorporates a resource “traffic light” system indicating the state of the fishery on a multiple reference point board.

In our analyses for banded morwong, a range of basic assessment tools have been examined, but none have provided clear indications about stock status. Catch and effort analyses indicate recent stability but such stability could be based in part on the serial depletion of spatially structured populations and/or fish down of accumulated biomass of a large number of age classes. In effect, the catch and effort data suggest stability in the fishery but are generally uninformative about stock condition. Per-recruit and catch curve analyses suggest that sustainable fishing mortality levels are low and that current fishing pressure may be too high, though there is considerable variability in the data. Changes in biological indicators such as median age and size and sex ratio are consistent with the stocks having been impacted by fishing. Age structure information, particularly for females, indicates that the representation of old fish is still relatively high, supporting the notion that there is residual biomass
Figure 7. Biological indicators for banded morwong in Tasmania based on spawning season research surveys conducted between 1996 and 2003. (a) Median fork length and; (b) median ages (pooled samples) of males (filled circles) and females (open circles); and (c) proportion of females (mean of daily catches ± 95% confidence intervals).
still available to be fished. These observations are set against general uncertainties regarding data quality from the commercial fishery and representation of biological indicators in regard to the effects of spatial structuring within the populations.

Modeling offers a way forward to investigate the potential utility of various indicators and, in particular, to assist in determining which of these may or may not be informative about stock status. To progress, we propose to develop an operating model that incorporates spatial structuring and is tuned to the combined biological and commercial fishery data available for banded morwong (Haddon et al. 2005). Progressively, the model will be extended to simulate fishing activity, data sampling, stock assessment, and management responses. Model outputs will also be used to guide the development of cost-effective options for the monitoring and assessment of this fishery and may provide a template for the development of assessments for other spatially structured and data limited species.

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References


