Ocean Current Patterns and Aspects of Life History of Some Northwestern Pacific Scorpaenids

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Abstract
The life histories of the most commercially important northwestern Pacific scorpaenids (shortraker rockfish, Sebastes borealis; shortspine thornyhead, Sebastolobus alascanus; and broadbanded thornyhead, Sebastolobus macrochir) and the role of ocean current patterns in transporting pelagic larvae and/or juveniles throughout their range are poorly understood.

Ocean current observations along with biological data on spawning locations, size compositions, and information from captured benthic juveniles from sampling conducted from 1993 to 1999 in the western North Pacific Ocean waters off the northern Kuril Islands, southeastern Kamchatka, and the western Bering Sea were analyzed and compared with published data. From these comparisons, some characteristics of their life histories are considered.

Adult shortraker rockfish are most abundant in waters of eastern Kamchatka, the western Bering Sea, the Gulf of Alaska, and the coastal waters of Washington, Oregon, and British Columbia. Juveniles in significant numbers occur only off the Kuril and Aleutian islands, and in the eastern Bering Sea. Comparison of current data in the subarctic Pacific region suggests that shortraker rockfish complete lengthy migrations. Pelagic larvae and juveniles born off the British Columbia, Oregon, and Washington coasts and in the Gulf of Alaska are transported by currents mostly to the Aleutian Islands. Pelagic larvae and juveniles originating off eastern Kamchatka and to a lesser extent Paramushir Island, are primarily carried by currents to the Kuril Islands. From the western Bering Sea and the Commander Islands, pelagic larvae and juveniles are carried mainly to the northern Aleutians and into the eastern Bering Sea. Settlement of juveniles occurs at a length of approximately 10 cm. Reverse migrations to
reproductive areas peak at lengths over 35 cm. Some juveniles may not perform lengthy reverse migrations but instead form temporary dependent populations by lingering in areas with quasi-stationary anticyclonic eddies.

The main spawning areas of thornyheads and capture sites of their benthic juveniles occur off southeastern Kamchatka, Paramushir Island, and around an underwater plateau southeast of Onekotan Island coinciding with quasi-stationary anticyclonic eddies. Settlement of shortspine thornyhead occurs by a length of about 25 mm while broadbanded thornyheads settle to the sea bottom at a length of approximately 70 mm. After settlement, juvenile broadbanded thornyhead migrate into shallower waters while, conversely, shortspine thornyhead migrate deeper.

Introduction

Shortraker rockfish (Sebastes borealis), shortspine thornyhead (Sebastolobus alascanus), and broadbanded thornyhead (Sebastolobus macrochir) represent an important component of the outer shelf and continental slope fish fauna in temperate and subarctic regions and are common in the North Pacific Ocean. These species are especially prized because their red color and delicious meat make them valuable on the Asian market.

The shortraker rockfish is endemic to the North Pacific Ocean. It is distributed from Japan (39°50′N) and southern California (40°46′N) to the Bering Sea including the Pacific waters off the Kuril and Aleutian islands, the east coast of Kamchatka, the Gulf of Alaska, British Columbia, Oregon, and Washington. This species is considered commercially important off eastern Kamchatka, off the northern Kuril Islands, in the Aleutian Islands region, and in the Bering Sea and Gulf of Alaska.

In the northwestern Pacific, the genus Sebastolobus is represented by two species: broadbanded thornyhead (S. macrochir), and shortspine thornyhead (S. alascanus). The first species is distributed from the Pacific coast of Japan (Sagami Bay) to the central Bering Sea and Aleutian Islands including the continental slope of the Sea of Okhotsk. The other species is distributed more widely, along both American and Asian coasts, from California and northeastern Hokkaido in the south to the central Bering Sea in the north including the southeastern Sea of Okhotsk. Both species are commercially important targets of bottom trawl and gillnet fisheries in the North Pacific (Low 1991, Koya et al. 1995).

All three species have pelagic larvae and juveniles (Moser 1974, Matarese et al. 1989). Their life history is poorly studied and the role of ocean currents in carrying larvae and/or juveniles throughout their geographical range remains unclear. Information important for rational management of the species such as stock structure and the degree of mixing among populations is still missing. Questions such as whether these species perform lengthy migrations or whether discrete populations exist are unanswered. Some recent publications dealing with genetic and parasitologic studies of
rockfishes (Moles et al. 1998, Hawkins et al. 1998) attempted to answer the above questions. In this paper we analyze the spatial distribution and the relative abundance of shortraker rockfish and two species of thornyheads. We provide information on the location of their benthic juveniles, and consider regional changes in size composition of these species. A hypothesis regarding the role of North Pacific current patterns in the life histories of shortraker rockfish and thornyheads is presented.

Material and Methods
Data were analyzed from research cruises conducted from 1995 to 1997 by Japanese trawlers in the western Bering Sea (Kayo Maru No. 28 and Tenyu Maru No. 57) and from cruises conducted from 1993 to 1999 in waters off the northern Kuril Islands and southeastern Kamchatka (Tora Maru No. 58, Tomi Maru No. 82, Tomi Maru No. 53, and Hokuyu No. 88). Data were obtained from more than 1,300 bottom trawl hauls conducted during research surveys and commercial fishing operations. Fishing was conducted 24 hours a day at 75-850 m depths using a 5.0-7.0 m (vertical opening) by 25.0-30.0 m (horizontal opening) bottom trawl constructed from 60 mm (stretched mesh) polyethylene netting. The trawl was outfitted with a steel rubber ball roller gear footrope extending from the forward wings to the mouth of the trawl.

During bottom trawl surveys, the entire catch was weighed and enumerated. During commercial fishing operations, representative samples were obtained from each trawl haul, sorted by species and then counted and weighed. The results were then extrapolated to the total catch.

The total fish length (TL) was measured for each of the three species considered, from the tip of the snout to the end of the center of the caudal fin. To analyze regional geographic variations of shortraker rockfish size composition in the northwestern Pacific, we combined length frequency data within 1° latitudinal sections. To analyze seasonal and interannual changes of shortraker rockfish size composition in the northwestern Pacific, we combined the length frequency data within six areas (central Kuril Islands, north Kuril Islands, southeastern Kamchatka, Olyutorskiy Gulf, and Shirshov Ridge, 171°-177°E, 177°E-180°). During the period of investigation, more than 66,000 specimens of shortraker rockfish, 26,000 specimens of shortspine thornyhead, and 114,000 specimens of broadbanded thornyhead were measured. Data from bottom trawl surveys published by NMFS (Bakkala et al. 1992, Harrison 1993, Ronholt et al. 1994, Martin 1997) were used to derive an analysis of shortraker rockfish size composition in the northeastern Pacific Ocean.

The minimum length of benthic juveniles in bottom trawl hauls was 86 mm for shortraker rockfish, 84 mm for shortspine thornyhead, and 103 mm for broadbanded thornyhead. Broadbanded thornyhead with lengths under 130 mm, and specimens of the other two species with lengths under 150 mm were chosen for an analysis of the spatial distribution of benthic juveniles. Benthic juveniles of both thornyhead species are readily
distinguished each from other by their body form, head spines, and thorns. Larvae and pelagic juveniles of shortraker rockfish have not been described until now. Benthic *Sebastes borealis* juveniles are readily identified by distinctive characteristics. Moreover, there are only two abundant rockfish species in the area considered (Pacific ocean perch [*S. alutus*] and shortraker rockfish), which are easily distinguished from each other by body form, coloration, and size of the symphyseal knob on the tip of the lower jaw. Juvenile shortraker rockfish are also distinguished by their body color from juvenile rougheyse rockfish (*S. aleutianus*), which is rare in the northwestern Pacific.

**Results**

**Shortraker Rockfish**

The analysis of shortraker rockfish size composition data from the northwestern Pacific showed that from the Kuril Islands to the western Bering Sea the mean lengths, modal classes, and abundance of large-size fishes in bottom trawl catches increased, and that the number of juveniles, in contrast, decreased (Fig. 1). The length frequencies of shortraker rockfish in various parts of the northwestern Pacific over a several-year period are presented in Table 1. Shortraker rockfish size composition is characterized also by considerable seasonal variation (Table 2). In the central Kuril Islands area, seasonal and interannual changes in the size composition of shortraker rockfish are low, while in other areas they are rather large.

The map of the multiannual spatial distribution in April-June (Fig. 2) shows that shortraker rockfish are most abundant in the postspawning period within only two areas (CPUE over 500 kg per hour): off southeastern Kamchatka and south of the strait between Paramushir and Onekotan islands. In the same time period, shortraker rockfish juveniles are only abundant (Fig. 3) in the second of the above areas. These juveniles occupied a more narrow depth range in comparison with adults (Table 3). Thus, most adults (64.46 % relative abundance) are distributed within 351-500 m depths while most juveniles (79.08%) inhabit the depth range between 401 and 550 m. From April to June, smaller shortraker rockfish are taken in the southern part of the investigated area and within localized areas off southeastern Kamchatka to the north of 51°N (Fig. 4). Within the same time frame, larger specimens with a mean length over 60 cm are caught off Paramushir Island and southeastern Kamchatka to the north of 52°N, suggesting these areas as potential spawning grounds.

**Thornyheads**

Records of pelagic egg balloons (Pearcy 1962, Fukataki 1963) and the dynamics of gonad maturation of thornyheads (Koya et al. 1995, Koya and Matsubara 1995) showed that mating and spawning occur from February to April. Our observations off the northern Kuril Islands and southeastern
Kamchatka are limited to the period from April to December, therefore information on spawning of thornyheads is derived from indirect data. In April, all mature fishes of both thornyhead species are in postspawning condition. The maps of mean multiannual distribution of thornyheads during April-June, i.e., just after spawning, may allow assessment of their spawning distributions. Catch rates for broadbanded thornyhead of over 50 kg per hour (Fig. 5) were observed along much of the slope with the largest catches (over 500 kg per hour trawling) occurring southeast of Onekotan Island, indicating that spawning may occur continuously within the entire investigated area, but more strongly in the southern part.

This hypothesis is confirmed by the pattern of distribution of broadbanded thornyhead benthic juveniles (Fig. 6), which are also caught more frequently in the above area. Conversely, shortspine thornyhead in postspawning condition are most abundant off Paramushir Island and southeastern Kamchatka (Fig. 7), where mean CPUEs were over 100 kg per hour of trawling. Benthic juveniles were also more frequently observed in the same areas (Fig. 8).

Size composition of broadbanded thornyhead in the Kuril-Kamchatka region is characterized by a high degree of heterogeneity (Fig. 9). The largest fish occurred in three areas: the underwater plateau in the southern

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**Figure 1.** Length frequencies of shorthaker rockfish in various areas of the northwestern Pacific Ocean. N = number of fish sampled, M = mean length, 1 = 47-48°N, 2 = 48-49°N, 3 = 49-50°N, 4 = 50-51°N, 5 = 51-52°N, 6 = 59-60°N, 7 = 60-61°N, 8 = 61-62°N.
### Table 1. Interannual changes in length composition (percent total fish sampled) of shortraker rockfish, *Sebastes borealis*, in various areas of the northwestern Pacific.

<table>
<thead>
<tr>
<th>Area</th>
<th>Years</th>
<th>10-16</th>
<th>16-21</th>
<th>21-26</th>
<th>26-31</th>
<th>31-36</th>
<th>36-41</th>
<th>41-46</th>
<th>46-51</th>
<th>51-56</th>
<th>56-61</th>
<th>61-66</th>
<th>66-71</th>
<th>71-76</th>
<th>76-81</th>
<th>81-86</th>
<th>86-91</th>
<th>91-96</th>
<th>96-101</th>
<th>N</th>
<th>M</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central</td>
<td></td>
<td>0.1</td>
<td>0.2</td>
<td>0.3</td>
<td>0.4</td>
<td>0.5</td>
<td>0.6</td>
<td>0.7</td>
<td>0.8</td>
<td>0.9</td>
<td>1.0</td>
<td>1.1</td>
<td>1.2</td>
<td>1.3</td>
<td>1.4</td>
<td>1.5</td>
<td>1.6</td>
<td>1.7</td>
<td>1.8</td>
<td>95</td>
<td>36.75</td>
</tr>
<tr>
<td>Kuril Islands</td>
<td></td>
<td>0.3</td>
<td>0.5</td>
<td>0.7</td>
<td>0.9</td>
<td>1.1</td>
<td>1.3</td>
<td>1.5</td>
<td>1.7</td>
<td>1.9</td>
<td>2.1</td>
<td>2.3</td>
<td>2.5</td>
<td>2.7</td>
<td>2.9</td>
<td>3.1</td>
<td>3.3</td>
<td>3.5</td>
<td>3.7</td>
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<tr>
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<td>0.9</td>
<td>1.2</td>
<td>1.5</td>
<td>1.8</td>
<td>2.1</td>
<td>2.4</td>
<td>2.7</td>
<td>3.0</td>
<td>3.3</td>
<td>3.6</td>
<td>3.9</td>
<td>4.2</td>
<td>4.5</td>
<td>4.8</td>
<td>5.1</td>
<td>5.4</td>
<td>5.7</td>
<td>6,812</td>
<td>39.28</td>
</tr>
<tr>
<td>Kamchatka</td>
<td></td>
<td>0.9</td>
<td>1.2</td>
<td>1.5</td>
<td>1.8</td>
<td>2.1</td>
<td>2.4</td>
<td>2.7</td>
<td>3.0</td>
<td>3.3</td>
<td>3.6</td>
<td>3.9</td>
<td>4.2</td>
<td>4.5</td>
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<td>5.7</td>
<td>6,812</td>
<td>39.28</td>
<td></td>
</tr>
<tr>
<td>Western</td>
<td></td>
<td>1.2</td>
<td>1.5</td>
<td>1.8</td>
<td>2.1</td>
<td>2.4</td>
<td>2.7</td>
<td>3.0</td>
<td>3.3</td>
<td>3.6</td>
<td>3.9</td>
<td>4.2</td>
<td>4.5</td>
<td>4.8</td>
<td>5.1</td>
<td>5.4</td>
<td>5.7</td>
<td>6,812</td>
<td>39.28</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

N = number of fish measured, M = mean length (cm), + = <0.1.
Table 2. Seasonal changes in length composition (percent total fish sampled) of shortraker rockfish, *Sebastes borealis*, in various areas of the northwestern Pacific.

<table>
<thead>
<tr>
<th>Area</th>
<th>Spring</th>
<th>Summer</th>
<th>Autumn</th>
<th>Winter</th>
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<tbody>
<tr>
<td>Central</td>
<td>0.2</td>
<td>0.4</td>
<td>0.3</td>
<td>0.7</td>
</tr>
<tr>
<td>Kuril Islands</td>
<td>0.2</td>
<td>0.4</td>
<td>0.3</td>
<td>0.7</td>
</tr>
<tr>
<td>Northern</td>
<td>0.2</td>
<td>0.4</td>
<td>0.3</td>
<td>0.7</td>
</tr>
<tr>
<td>Southern</td>
<td>0.2</td>
<td>0.4</td>
<td>0.3</td>
<td>0.7</td>
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<table>
<thead>
<tr>
<th>Season</th>
<th>10-16</th>
<th>17-23</th>
<th>24-30</th>
<th>31-37</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total length (TL), cm</td>
<td>48-55</td>
<td>56-63</td>
<td>64-71</td>
<td>72-79</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Area</th>
<th>Central</th>
<th>Kuril Islands</th>
<th>Northern</th>
<th>Southern</th>
<th>Western</th>
</tr>
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<tbody>
<tr>
<td>Spring 15-20</td>
<td>0.2 (N=4,345)</td>
<td>0.4 (N=38,591)</td>
<td>0.2 (N=34,744)</td>
<td>0.2 (N=1,650)</td>
<td>0.2 (N=47,326)</td>
</tr>
<tr>
<td>Summer 21-26</td>
<td>0.4 (N=21,984)</td>
<td>0.4 (N=55,931)</td>
<td>0.4 (N=57,068)</td>
<td>0.3 (N=58,966)</td>
<td>0.2 (N=58,803)</td>
</tr>
<tr>
<td>Autumn 27-32</td>
<td>0.3 (N=15,144)</td>
<td>0.3 (N=39,518)</td>
<td>0.3 (N=42,484)</td>
<td>0.2 (N=40,464)</td>
<td>0.2 (N=44,067)</td>
</tr>
<tr>
<td>Winter 33-38</td>
<td>0.1 (N=15,727)</td>
<td>0.1 (N=59,048)</td>
<td>0.1 (N=59,048)</td>
<td>0.1 (N=59,048)</td>
<td>0.1 (N=59,048)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Area</th>
<th>Winter 39-45</th>
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<tbody>
<tr>
<td>Northern 46-51</td>
<td>0.1 (N=87)</td>
</tr>
<tr>
<td>Southern 52-57</td>
<td>0.1 (N=61)</td>
</tr>
<tr>
<td>Western 58-63</td>
<td>0.1 (N=90)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Area</th>
<th>Winter 64-69</th>
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<tbody>
<tr>
<td>Northern 70-75</td>
<td>0.1 (N=85)</td>
</tr>
<tr>
<td>Southern 76-81</td>
<td>0.1 (N=90)</td>
</tr>
<tr>
<td>Western 82-87</td>
<td>0.1 (N=105)</td>
</tr>
</tbody>
</table>

N = number of fish measured, M = mean length (cm), + = <0.1.
Figure 2. Distribution and relative abundance of shortraker rockfish categorized by CPUE (kg per hour of trawling) in April-June, 1993-1999 off the northern Kuril Islands and southeastern Kamchatka.
Figure 3. Capture location sites (triangles) of benthic juvenile shortraker rockfish with lengths less than 150 mm off the northern Kuril Islands and southeastern Kamchatka.
Table 3. Relative abundance (%) of shortraker rockfish, shortspine thornyhead, and broadbanded thornyhead in the Pacific waters off the northern Kuril Islands and southeastern Kamchatka in various depth ranges (top number = adults, bottom number = juveniles).

<table>
<thead>
<tr>
<th>Species</th>
<th>Depth, m</th>
<th>&lt;150</th>
<th>151-200</th>
<th>201-250</th>
<th>251-300</th>
<th>301-350</th>
<th>351-400</th>
<th>401-450</th>
<th>451-500</th>
<th>501-550</th>
<th>551-600</th>
<th>601-650</th>
<th>651-700</th>
<th>701-750</th>
<th>751-800</th>
<th>&gt;800</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shortraker rockfish,</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sebastes borealis</em></td>
<td></td>
<td>—</td>
<td>0.15</td>
<td>0.50</td>
<td>1.83</td>
<td>5.71</td>
<td>23.76</td>
<td>23.51</td>
<td>17.19</td>
<td>10.96</td>
<td>5.55</td>
<td>7.88</td>
<td>0.15</td>
<td>1.36</td>
<td>0.30</td>
<td>1.14</td>
</tr>
<tr>
<td>Shortspine thornyhead,</td>
<td></td>
<td>0.03</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.03</td>
<td>5.68</td>
<td>4.52</td>
<td>7.99</td>
<td>8.74</td>
<td>7.83</td>
<td>14.90</td>
<td>18.91</td>
<td>10.37</td>
<td>16.74</td>
<td>4.25</td>
</tr>
<tr>
<td><em>Sebastolobus alascanus</em></td>
<td></td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>8.00</td>
<td>4.00</td>
<td>24.00</td>
<td>36.00</td>
<td>12.00</td>
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<td>—</td>
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<tr>
<td>Broadbanded thornyhead,</td>
<td></td>
<td>—</td>
<td>0.06</td>
<td>0.08</td>
<td>0.71</td>
<td>3.22</td>
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<td>10.63</td>
<td>14.48</td>
<td>18.72</td>
<td>14.64</td>
<td>10.04</td>
<td>5.69</td>
<td>4.31</td>
<td>2.19</td>
<td>7.81</td>
</tr>
<tr>
<td><em>Sebastolobus macrochir</em></td>
<td></td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>12.00</td>
<td>20.00</td>
<td>32.00</td>
<td>12.00</td>
<td>16.00</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>
Figure 4. Mean lengths (cm) of shortraker rockfish off the northern Kuril Islands and southeastern Kamchatka.
part of the region, a localized section southeast of Onekotan Island, and the southeastern Kamchatka coast near 52°N. In each of these areas, mean body length increased from deeper to shallower waters. Shortspine thornyhead exhibited the smallest mean lengths off central Paramushir Island (Fig. 10) with mean lengths increasing to both the north and the south.

During the period of investigation, benthic juvenile shortspine thornyhead were caught at depths ranging from 357 to 615 m (mean depth 505.3 m) while broadbanded thornyhead occupied a somewhat deeper 410-645 m depth range (mean depth 527.9 m). An analysis of the vertical distribution of thornyheads shows juveniles inhabiting a narrower bathymetric range compared with the adults (Table 3) with the juveniles distributed in shallower depths than the adults. This same pattern also appears in the northeastern Pacific (Vetter and Lynn 1997). Thus the relative abundance of juvenile shortspine thornyhead in the investigated area (60.0%) reaches a maximum in 450-550 m depths while most of the adults (65.2% relative abundance) are distributed in depths deeper than 600 m. Juveniles and adult broadbanded thornyhead were most abundant in the same depth ranges.

Discussion

**Shortraker Rockfish**

The large-sized fishes are less abundant off the south and central Kuril Islands, in the eastern Bering Sea, and in Pacific Ocean waters of the Aleutian Islands. Maximum abundance occurs off eastern Kamchatka, the western Bering Sea, the Gulf of Alaska, and in British Columbia waters. Juveniles are most abundant off the Kuril Islands, in the eastern Bering Sea, and in the Pacific waters off the Aleutian Islands. Very few juveniles are caught off eastern Kamchatka, the western Bering Sea, the Gulf of Alaska, and British Columbia waters (Westrheim and Harling 1975, Bakkala et al. 1992, Harrison 1993, Ronholt et al. 1994, Martin 1997). Size composition of shortraker rockfish from the Aleutian Islands is heterogeneous. Smaller fishes are caught in the Pacific waters off the Aleutians where modal classes from various years vary from 35 to 44 cm with mean lengths ranging from 39.1 to 41.2 cm. During the same time periods, larger, 40-63 cm shortraker rockfish with modal lengths ranging from 47.9 to 54.8 cm were observed in the Bering Sea waters off the Aleutian Islands (Harrison 1993, Ronholt et al. 1994). Similar to observations from the northwestern Pacific, shortraker rockfish size composition in the Aleutian Islands varies considerably from year to year.

Geographic variations in size composition between different areas can be attributed to different growth rates. However, recent aging studies of shortraker rockfish show no significant differences in growth rates between fishes from the central Kuril Islands and western Bering Sea (A.A. Abramov,
Figure 5. Distribution and relative abundance of broadbanded thornyhead categorized by CPUE (kg per hour of trawling) during the postspawning period (April-June, 1993-1999) off the northern Kuril Islands and southeastern Kamchatka.
Figure 6. Capture location sites (triangles) of benthic juvenile broadbanded thornyhead with lengths less than 130 mm off the northern Kuril Islands and southeastern Kamchatka.
Figure 7. Distribution and relative abundance of shortspine thornyhead categorized by CPUE (kg per hour of trawling) in April-June, 1993-1999 off the northern Kuril Islands and southeastern Kamchatka.
Figure 8. Capture location sites (triangles) of benthic juvenile shortspine thornyhead less than 150 mm in length off the northern Kuril Islands and south-eastern Kamchatka.
Figure 9. Mean length (cm) of broadbanded thornyhead off the northern Kuril Islands and southeastern Kamchatka.
Figure. 10. Mean length (cm) of shortspine thornyhead off the northern Kuril Islands and southeastern Kamchatka.
unpubl. data) and eastern Kamchatka and the western Bering Sea (A.M. Tokranov, pers. comm.). Shortraker rockfish is a long-lived species (Beamish and McFarlane 1987) with late sexual maturation and low growth rates (McDermott 1994). Large interannual fluctuations in abundance or size-age structure variations are not pronounced. In the northwestern Pacific, seasonal and multiannual variations in size composition, taking into account the low reproductive rate and insignificant harvest rate, cannot be explained by fluctuations in abundance and, according to our hypothesis, should be related to horizontal migrations.

Size composition data, benthic juvenile spatial distribution, and ocean current patterns in the North Pacific Ocean (Favorite et al. 1976, Ohtani 1991) indicate the main habitat of shortraker rockfish is located within the Bering Sea, Gulf of Alaska, and Western Subarctic Gyre (Fig. 11). In the Bering Sea, the main spawning area is probably the continental slope from Cape Navarin and the Commander Islands and along the northwestern and central Aleutian Islands. Main reproductive areas occur along the eastern Kamchatka coast north of 52°N. Another area where spawning may occur is the Paramushir Island slope. Within the Alaska Gyre the main spawning areas are located from British Columbia to the southeastern Gulf of Alaska.

We suggest the following model may explain the pattern of shortraker rockfish migrations. The Alaska Current and Alaskan Stream transport larvae originating in the eastern Gulf of Alaska to the Aleutian Islands with some larvae being transported through several straits into the Bering Sea. In the western North Pacific, the Eastern Kamchatka current carries eastern Kamchatka larvae to the Kuril Islands and through the Kuril straits partly into the Sea of Okhotsk. Most larvae originating in the western Bering Sea are transported eastward. Some larvae are probably transported by the Eastern Kamchatka current to eastern Kamchatka and the Kuril Islands and through straits in the central Aleutian Islands into the Pacific Ocean. Some larvae and/or pelagic juveniles may linger within quasi-stationary anticyclonic eddies around seamounts, near straits, and in areas where currents form a junction. These conditions can result in temporal dependent populations that are regularly replenished by fish migrating to and from feeding areas. Taking into account the prevailing oceanographic conditions, such populations are most likely to be inherent in the Kuril and Aleutian islands areas. The consistent high abundance and small seasonal and interannual variations of shortraker rockfish size compositions off the underwater plateau in the central Kuril Islands area, and the occurrence of a quasi-stationary anticyclonic eddy around that plateau, may indicate the existence of a temporary dependent population.

In recent years, data were obtained which substantiate the hypothesis that ocean currents transport the pelagic young of rougheye rockfish (congeneric species with similar ecology and biology to shortraker rockfish; Hawkins et al. 1998). The minimum length of shortraker rockfish benthic juveniles from bottom trawl catches is about 10 cm, corresponding to an age of about 2 years (Leontiev et al. 1998). It is thought that after shortraker
rockfish larvae settle out, the adults remain relatively stationary and do not engage in lengthy migrations (Barsukov 1981, Parker et al. 2000). This conclusion, however, may only be valid for small-sized specimens. Recent investigations show that increasing size is accompanied by migratory behavior. Thus, small shortraker rockfish consume mainly benthic invertebrates and fishes (Yang 1996), while large specimens feed mostly on squids and mesopelagic fishes (Yang 1993) inhabiting the water column. To feed on squids and mesopelagic fishes, shortraker rockfish need to perform vertical migrations. We suggest that with an increase in size, this species is able to perform not only vertical, but also horizontal, migrations. In the Bering Sea, adult shortraker rockfish have been captured in deep water far from coastal waters (Balanov and Radchenko 1995). Size composition from longline and gillnet catches may also substantiate the assumption that shortraker rockfish are capable of performing horizontal migrations. These passive fishing gears are deployed in stationary locations for relatively long time periods while the spatial distribution of shortraker rockfish is characterized by sporadic movement and considerable distance between individual fish (Krieger 1992). Therefore, high CPUEs obtained in the longline and gillnet fisheries may be explained by fishes actively moving to the fishing gear. Shortraker rockfish begin to occur in longline and gillnet catches at lengths greater than 30 cm but predominantly in the 40-45 cm and larger range (Tokranov and Davydov 1998). Submersible observations (Krieger
and Ito 1999) showed that this species is able to swim at a speed of 1 km per hour, while the average speed of bottom currents in the Gulf of Alaska, Bering Sea, and eastern Kamchatka does not exceed 0.8 km per hour (Stabeno et al. 1999).

Our hypothesis cannot be substantiated by traditional tag-and-release experiments because shortraker rockfish cannot survive the barotrauma of initial capture (Moles et al. 1998). For that reason, the most promising research tools for rockfish stock structure investigations are genetic studies and the use of parasites as naturally occurring biological markers. However, none of the recently completed genetic or parasitologic studies of shortraker and rougheyne rockfishes (Moles et al. 1998, S. Hawkins, NOAA, NMFS, Auke Bay Laboratory, Juneau, Alaska, pers. comm.) corroborated our hypothesis by revealing heterogeneity of these species from specimens collected from the Gulf of Alaska and Aleutian Islands regions.

**Thornyheads**

The ecology of both thornyhead species is similar. However, some characteristics of their spatial distributions, relative abundance, and size compositions exhibit large differences. As it is generally known, thornyheads are egg-layers with internal fertilization (Pearcy 1962) with the eggs being released within gelatinous balloons into the water column. The balloons have a positive buoyancy and float to the surface where the larvae hatch and further development occurs (Pearcy 1962, Moser 1974, Matarese et al. 1989). Anticyclonic eddies exist near the southeastern Kamchatka and Paramushir coasts and within 90-120 miles of the underwater plateau southeast of Onekotan Island. These localized eddies nearly coincide with capture sites of benthic juveniles and the locations of larger catches of postspawners. The co-occurrence of these two groups suggests that early development of the larvae and pelagic juveniles may have occurred within these eddies (primarily broadbanded thornyhead within the southern eddy and shortspine thornyhead within both northern eddies) until settlement. The locations and depths of capture of predominantly small-sized benthic juveniles may indicate that settlement of broadbanded thornyhead occurs within the deeper depths with larger fish migrating into shallower waters. The settlement of shortspine thornyhead probably occurs mostly off central Paramushir Island. From this location, fish disperse along the slope in all directions.

For thornyheads, the transition from a pelagic juvenile form to a benthic life pattern (settlement) is poorly understood. In coastal waters off Oregon, pelagic egg balloons of shortspine thornyhead are found over depths ranging from 364 to 1,820 m (Pearcy 1962) and larvae are captured within a wide depth zone over the shelf and continental slope (Moser 1974). The settlement of shortspine thornyhead juveniles occurs at lengths of 22.5-27.2 mm, mean 25 mm (Moser 1974, Wakefield and Smith 1990). Pelagic egg balloons of broadbanded thornyhead off southern Hokkaido are found in coastal waters outside the 200-m isobath (Fukataki 1963). The length of
settlement of this species is unknown. The only capture data for pelagic juveniles occurred off eastern Kamchatka (depth unknown) where lengths ranged from 21.0 to 29.8 mm, and one instance from a depth of 3,480 m off the southern Kuril Islands with a length of 67 mm (Makushok 1970, Moser 1974). In the same time period, 70-84 mm benthic broadbanded thornyhead juveniles were caught at a depth of 780 m and 107-160 mm individuals from a depth of 445 m (Makushok 1970). So, it may be suggested that settlement of broadbanded thornyhead occurs at a greater length than shortspine thornyhead (probably about 70 mm). The settlement by larger fish is also inherent in juveniles of the congeneric species longspine thornyhead (*Sebastolobus altivelis*), where settlement occurs at lengths of 42-56 mm, mean about 50 mm (Moser 1974, Wakefield and Smith 1990). These data show that broadbanded thornyhead pelagic juveniles inhabit ocean waters over deep depths and with increasing size move toward coastal waters and after settlement begin movement into shallow waters.

Acknowledgments

I express deep gratitude to all the Russian scientists from the Russian Federal (VNIRO), Pacific (TINRO-Center), Sakhalin (SakhNIRO), and Kamchatka (KamchatNIRO) Research Institutes of Fisheries and Oceanography, who participated in the sampling and collection of data on spatial distribution, size composition, and biology of rockfish and thornyheads. I wish to thank the vessel crews and administrators for providing friendly help and support in my study. I especially wish to express the deepest appreciation to Dr. Jonathan Heifetz (NMFS, Auke Bay Lab, 11305 Glacier Highway, Juneau, AK 99801), Dr. Oleg Gritsenko, Dr. Boris Kotenev (both from VNIRO), and an anonymous reviewer who critically read the early manuscript and provided valuable comments and advice. I also wish to thank Dr. Alexei Abramov (VNIRO) and Dr. Alexei Tokranov (KamchatNIRO) for the data on growth rates of shortraker rockfish in the northwestern Pacific. Special thanks go to Dr. Eric Brown (NMFS/NOAA, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115-0070) for improving the manuscript and Mr. Bernard J. Goinen Jr. (NMFS/NOAA, Alaska Fisheries Science Center, Program Support and Publications Distribution, 7600 Sand Point Way NE, Seattle, WA 98115-0070), who helped me obtain several NOAA Technical Memorandum publications.

References


Comparative Spawning Habitats of Anchovy (Engraulis capensis) and Sardine (Sardinops sagax) in the Southern Benguela Upwelling Ecosystem

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Abstract

Data on the abundance and distribution of anchovy (Engraulis capensis) and sardine (Sardinops sagax) eggs in the Southern Benguela upwelling ecosystem were collected during spawner biomass surveys conducted every November from 1984 to 1998. These data were used to characterize anchovy and sardine spawning habitats with respect to sea surface temperature, to compare the spatial distinction of the spawning habitats of these two species, and to provide an egg abundance time-series for each species. Sardine spawn over a wider temperature range than anchovy, and preferentially spawn in cooler water (15.2-20.5°C) than do anchovy (17.4-21.1°C). Anchovy egg distributions have been spatially stable through time, showing consistent spawning east of Cape Point. In contrast, sardine eggs were more patchily distributed through time, with both the west and south coasts being the major spawning grounds during different periods. Despite the more patchy distribution of sardine than anchovy eggs, the two species have shown a broad-scale overlap in spawning habitat during the first two-thirds of the time-series. Since 1994, however, the spawning habitats of sardine and anchovy have become markedly distinct, with sardine spawning principally off the west coast, and anchovy spawning predominantly off the south and east coasts. This spatial distinctiveness reflects changes in the species’ population structure, as well as changes in habitat preference through time, and is likely to impact on egg and larval transport to the nursery grounds and subsequent recruitment strength. Over the time period studied the sardine population has increased 20-fold whereas the anchovy population biomass has shown a steady decline,
albeit with large interannual fluctuations. Biomass trends for anchovy are reflected in their egg data; both spawning area and mean egg density within the spawning area have decreased over time, resulting in a long-term decline in estimated total egg abundance. In contrast to anchovy, the sardine egg data have not shown consistent trends through time, and total egg abundance is not correlated with sardine biomass. These results are of relevance to other upwelling ecosystems where this species pair exists.

**Introduction**

Anchovy (*Engraulis* spp.) and sardine (*Sardinops sagax*) coexist in five of the world’s large marine ecosystems (the southeastern Atlantic, the southeastern Pacific, the northeastern Pacific, the northwestern Pacific, and off southern Australia) where they dominate the landings of local fisheries and together, contribute a substantial portion of the global marine catch. Maximum catches of the two species in any one ecosystem have never occurred simultaneously (Lluch-Belda et al. 1989, 1992b; Schwartzlose et al. 1999). Analysis of fish scales preserved in anaerobic sediments from some of these regions has shown that these two genera have alternated in relative abundance in the absence of fishing over interdecadal and centennial time scales (Soutar and Isaacs 1974, Baumgartner et al. 1992). These large-scale, long-term changes in relative abundance have been termed regime shifts (Lluch-Belda et al. 1989, 1992b), and are currently the subject of much investigation and discussion (Schwartzlose et al. 1999 and references therein).

As in other ecosystems where they coexist, anchovy and sardine in the Southern Benguela have shown long-term changes in relative abundance as indexed by fisheries catch data. Sardine dominated purse-seine catches off South Africa during the 1950s and early 1960s, and landings peaked at 0.41 million tons in 1962 (Crawford et al. 1987). Thereafter, catches of sardine declined and the fishery began to use small-mesh nets to target anchovy, *Engraulis capensis*. Anchovy dominated purse-seine catches from 1965 onward, fluctuating between 41,000 and 596,000 metric tons and with an annual average catch of 254,000 metric tons over the period 1970-1997 (Barange et al. 1999). Over this period, sardine landings have ranged between 16,000 and 176,000 metric tons, and have averaged 66,000 metric tons.

Management procedures for the anchovy and sardine fisheries off South Africa initially used virtual population analysis to provide indices of abundance (Armstrong et al. 1983), but have more recently employed acoustically derived biomass estimates (Cochrane et al. 1998, de Oliveira et al. 1998). Acoustic surveys to estimate anchovy and sardine biomass in the Southern Benguela have been conducted since 1984 (Hampton 1987, 1992; Barange et al. 1999), and these have indicated a steady increase in the biomass of sardine spawners over this period. In contrast, the biomass of anchovy spawners has shown a steady decline, although fluctuations of
more than an order of magnitude have been observed. This contrasting trend in relative biomasses of these two species has led to suggestions that the Southern Benguela is currently undergoing a regime shift, with sardine now becoming more abundant than anchovy (Crawford 1998). Regime switches to sardine dominance occurred during the 1980s in the northeastern (Japan) and southeastern Pacific (Peru), although catches of sardine in these regions have declined since the late 1980s (Schwartzlose et al. 1999).

Hypotheses regarding regime shifts have been divided into two categories (Schwartzlose et al. 1999). The first category proposes that continuous modifications in habitat may benefit one species over the other, and changes in factors such as food composition and temperature have been suggested as likely candidates. For example, since sardine are able to utilize phytoplankton to a greater extent than anchovy (King and Macleod 1976; van der Lingen 1994, 1999), increases in phytoplankton standing stock may promote growth of the sardine population relative to anchovy, as has been suggested by Kawasaki (1993) for the northwestern Pacific sardine. Similarly, the ability of sardine to spawn over a wider temperature range than anchovy (Lluch-Belda et al. 1991) suggests that sardine are better able to take advantage of warm conditions during the spawning season. The second category of hypotheses suggests that episodic environmental events, that trigger changes in populations and/or ecosystems, may lead to altered species dominance. Events leading to the formation of particularly strong year classes could result in rapid population growth (Kondo 1980), whereas mass mortalities, such as that recorded for sardine off Australia in 1995, could severely negatively impact population size (Jones et al. 1997).

The objective of this paper is to compare the spawning habitats of sardine and anchovy in the Southern Benguela through an analysis of egg abundance and distribution data collected over a 15-year period during annual spawner biomass surveys. While both species spawn during spring/summer (September to March), they show a temporal separation in the timing of peak spawning (Shelton 1986, Fowler 1998, Huggett et al. 1998); anchovy have a single spawning peak in October-December, whereas sardine have two spawning peaks (September/October and February/March). Although the spawner biomass surveys are timed so as to survey during peak anchovy spawning, sufficient data concerning the abundance and distribution of sardine eggs have been collected to permit a detailed comparison of spawning habitats. In this paper the spawning habitat of each species is characterized in terms of sea surface temperature, which may permit an evaluation of whether this parameter is likely to be important in initiating or sustaining regime shifts in this region. The spatial distinctiveness of anchovy and sardine spawning habitats in the Southern Benguela is examined, and discussed with reference to management of these resources. Finally, a time-series of egg abundance is presented for each species, and is compared with their respective biomass time-series. Information concern-
ing the spawning habitats of these two clupeoids may increase our understanding of how and why regime shifts occur and is likely to be of relevance to other upwelling systems where sardine and anchovy coexist.

**Materials and Methods**

**General**

Data from 15 pelagic spawner biomass surveys conducted each year during November/December over the period 1984-1998 were used in this analysis. Each survey covered an area from the South African west coast (approximately 30-33°S) to the southeast coast (approximately 24-27°E), and comprised a grid consisting of survey lines extending over the continental shelf (200 m) and positioned perpendicular to the coastline. Survey details are provided by Hampton (1987, 1992) and Barange et. al (1999). Anchovy and sardine eggs were sampled by means of vertical hauls of a CalVET net (Smith et al. 1985) deployed to 100 m or near the sea bottom (depending on bathymetry) and positioned at 5 or 10 nautical mile intervals along survey lines. An electronic temperature/depth sensor suspended below the net recorded sea surface temperature (SST) and vertical temperature profiles. Eggs collected by the CalVET net were identified and counted, and densities were standardized to number per square meter. Survey details are given in Table 1.

**Characterization of Spawning Habitat with Respect to SST**

Egg abundance and SST data were combined for all cruises in order to assess the preferred SST range for spawning for each species. First, the number of eggs found in each 0.1°C SST class was expressed as a percentage of the total number of eggs of that species collected over the study period. This value was then divided by the percentage frequency of occurrence of that particular SST class. The resultant quotient value was taken to reflect the selection of spawning habitat by temperature, or by any other factors associated with such temperature ranges. Assuming that fish do in fact select spawning habitat on the basis of SST, quotient values of >1 indicate positive selection, whereas values of <1 indicate that fish avoid spawning at that SST. Quotient values were plotted against SST and, because of the high interpoint variability, were smoothed using 11-point running means centered on the 6th datum.

**Spatial Distributions of Anchovy and Sardine Eggs**

Distribution maps of anchovy and sardine eggs were generated from data interpolation using standard Kriging routines (Barange and Hampton 1997). To assess the spatial distribution of sardine and anchovy eggs, the survey region was divided into five different predetermined continental shelf strata (Fig. 1): the West Coast, extending north of Cape Columbine; the South-
Table 1. Summary of egg data collected during the spawner biomass surveys, 1984-1998.

<table>
<thead>
<tr>
<th>Year</th>
<th>Survey area (km²)</th>
<th>No. of CalVET hauls</th>
<th>No. of anchovy eggs</th>
<th>No. of sardine eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td>1984</td>
<td>122,240</td>
<td>307</td>
<td>12,746</td>
<td>259</td>
</tr>
<tr>
<td>1985</td>
<td>114,834</td>
<td>294</td>
<td>12,979</td>
<td>216</td>
</tr>
<tr>
<td>1986</td>
<td>103,374</td>
<td>271</td>
<td>14,573</td>
<td>606</td>
</tr>
<tr>
<td>1987</td>
<td>139,714</td>
<td>441</td>
<td>11,818</td>
<td>857</td>
</tr>
<tr>
<td>1988</td>
<td>135,886</td>
<td>480</td>
<td>14,706</td>
<td>2,429</td>
</tr>
<tr>
<td>1989</td>
<td>112,093</td>
<td>361</td>
<td>6,996</td>
<td>1,646</td>
</tr>
<tr>
<td>1990</td>
<td>148,025</td>
<td>338</td>
<td>12,862</td>
<td>1,116</td>
</tr>
<tr>
<td>1991</td>
<td>114,192</td>
<td>418</td>
<td>17,916</td>
<td>1,240</td>
</tr>
<tr>
<td>1992</td>
<td>139,318</td>
<td>425</td>
<td>10,591</td>
<td>604</td>
</tr>
<tr>
<td>1993</td>
<td>110,660</td>
<td>357</td>
<td>9,664</td>
<td>631</td>
</tr>
<tr>
<td>1994</td>
<td>110,823</td>
<td>305</td>
<td>6,829</td>
<td>1,292</td>
</tr>
<tr>
<td>1995</td>
<td>113,065</td>
<td>322</td>
<td>6,540</td>
<td>1,394</td>
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<tr>
<td>1996</td>
<td>135,390</td>
<td>472</td>
<td>1,835</td>
<td>1,679</td>
</tr>
<tr>
<td>1997</td>
<td>124,828</td>
<td>286</td>
<td>3,649</td>
<td>727</td>
</tr>
<tr>
<td>1998</td>
<td>150,280</td>
<td>369</td>
<td>3,708</td>
<td>856</td>
</tr>
</tbody>
</table>

Figure 1. Site map, bathymetry, and locations of the five strata used for the egg data analysis.
West Coast, extending from Cape Point to Cape Columbine; the Western Agulhas Bank, extending from Cape Agulhas to Cape Point; the Central Agulhas Bank, extending from Cape St. Blaize to Cape Agulhas; and the Eastern Agulhas Bank, extending eastwards from Cape St. Blaize. The following parameters were calculated for each species in each stratum:

1. $A =$ the area surveyed (expressed in m$^2$);
2. $P =$ the percentage of CalVET stations at which eggs were collected (percentage positive stations);
3. $G =$ the geometric mean density (expressed per m$^2$) of eggs at positive stations; and
4. $T =$ the estimated total number of eggs, calculated from $A(P/100)G$.

Average egg density at positive stations was calculated using geometric rather than arithmetic means because the egg data were log-normally distributed. The relative importance ($R$) of each stratum to spawning in any one year was assessed by expressing $T$ as a percentage of the estimated total number of eggs for that survey, i.e.

$$R = \frac{T \times 100}{\sum T}$$

Values of $P$, $G$, and $R$ for each stratum were then plotted by year for each species.

**Egg Abundance Time Series**

An estimate of the total number of anchovy and sardine eggs was derived for each survey by summing the values of $T$ for each year, and was plotted by year for each species. This egg abundance time-series was then compared with a biomass time-series derived from hydroacoustic data collected during the spawner biomass surveys.

**Results**

**Characterization of Spawning Habitat with Respect to SST**

SSTs at CalVET stations sampled during November surveys ranged from 8.8 to 23.8°C, with the majority of samples collected from waters where the SST was between 15 and 20°C (Fig. 2a). Although eggs of anchovy and sardine were collected over a similar SST range, the egg percentage/SST percentage quotient transformation (Fig. 2b) shows that a substantial difference exists between the preferred spawning temperatures of these two species. The preferred spawning range of anchovy lies between 17.4 and 21.1°C, is unimodal, and peaks between 19.5 and 20.5°C. The preferred
spawning range of sardine is somewhat larger, ranging from 15.2 to 20.5°C. The quotient curve for sardine is essentially bimodal, with a major peak from 15.5 to 17.5°C and a secondary peak between 18.7 and 20.5°C. Anchovy therefore preferentially spawn in warmer waters than do sardine.

**Spatial Distributions of Sardine and Anchovy Eggs**

Examples of anchovy egg distributions are provided in Fig. 3 and those for sardine are shown in Fig. 4. An obvious feature of these distribution maps is that anchovy eggs were much more abundant during November surveys than were sardine eggs. In addition to their low abundance, sardine eggs were much more patchily distributed than were anchovy eggs. For most of the time-series, areas of high (>1,001 eggs per m²) anchovy egg abundance were located over much of the Agulhas Bank, although high egg abundances were on occasion located off the West Coast (e.g., 1987; Fig. 3). Anchovy eggs found over the Agulhas Bank were generally restricted to shelf waters (<200 m), whereas those off the West and South-West Coasts were found offshore of the shelf edge. Anchovy eggs over the Central and Eastern Agulhas Banks were frequently located offshore of the cool ridge, a quasi-permanent, large-scale, subsurface thermal feature of this region (Swart and Largier 1987). High abundances of sardine eggs were limited to isolated
Figure 3. Surface distribution of anchovy egg density (eggs per m²) during the spawning biomass surveys conducted in 1984, 1987, 1990, 1993, 1996, and 1998. The 200-m depth contour is shown.
Figure 4. Surface distribution of sardine egg density (eggs per m²) during the spawner biomass surveys conducted in 1984, 1987, 1990, 1993, 1996, and 1998. The 200-m depth contour is shown.
patches primarily off the West and South-West Coasts, and were located offshore of the continental shelf (Fig. 4).

The spawning area of anchovy, as indexed by the percentage positive stations ($P$), showed significant ($P < 0.05$) or weakly significant ($P < 0.1$) declines during the time period studied in all five strata (Fig. 5). Although a high percentage of stations sampled off the West and South-West Coasts contained anchovy eggs during the early years of the time-series (particularly 1986-1988), less than 20% of stations off the West Coast contained eggs during the 1990s, while for the South-West Coast this value was seldom above 50% and was also less than 20% in recent years. Values of $P$ for anchovy eggs over the strata comprising the Agulhas Bank showed less interannual variability than data for the West and South-West Coasts, with $P$ declining over time from about 80% to 40% for the Western and Central Agulhas Banks, and from about 60% to 30% for the Eastern Agulhas Bank. In contrast to the significant decline in spawning area shown by anchovy, percentage positive stations for sardine eggs showed weakly significant ($P < 0.1$) increases for the South-West Coast and the western Agulhas Bank, but a significant ($P < 0.05$) decline off the West Coast. The declines in $P$ for both anchovy and sardine off the West Coast may well be an artefact of the low numbers of CalVET stations (<15) that were sampled there during the early years of the time-series. Values of $P$ for sardine eggs off the Central and Eastern Agulhas Banks showed no trends over time, with consistent values of about 20% common for the Central Agulhas Bank, and the Eastern Agulhas Bank showing a dome-shaped pattern in $P$, increasing to a peak value of 60% in 1990 and declining thereafter (Fig. 5).

In addition to showing significant declines in spawning area in all five strata, the reproductive output of anchovy within its spawning area also declined through time (Fig. 6). The South-West Coast, and the Western and Central Agulhas Banks all showed a significant ($P < 0.05$) decline in geometric mean anchovy egg density, the most marked being over the Western Agulhas Bank, where densities of about 1,000 eggs per m$^2$ at the beginning of the time-series dropped to about 200 eggs per m$^2$ at the end. A weakly ($P < 0.1$) significant decline in $G$ was observed for anchovy eggs off the West Coast. As could be seen from a comparison of Figs. 3 and 4, sardine eggs were present at much lower densities than anchovy eggs (Fig. 6), with values >200 eggs per m$^2$ uncommon. Although the only significant relationship observed for geometric mean sardine egg density was a declining trend for the Central Agulhas Bank, values of $G$ were generally higher at the end of the time-series than at the beginning for the West and South-West Coasts.

Anchovy and sardine showed contrasting patterns in trends through time of the relative importance to spawning of the various strata (Fig. 7). The West and South-West Coasts were relatively unimportant to anchovy spawning, contributing a maximum of 30% to total egg abundance during 1986-1988, but <10% thereafter. The Western Agulhas Bank showed a significant ($P < 0.05$) decline in $R$ over time for anchovy, decreasing from
Figure 5. Scatterplots of percentage positive stations (P) against time for anchovy (circles) and sardine (black dots) in each of the five strata used in this analysis. Significant regressions are shown; solid line, $P < 0.05$; dashed line, $P < 0.1$. 

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Figure 6. Scatterplots of geometric mean egg density (G) at positive stations against time for anchovy (circles) and sardine (black dots) in each of the five strata used in this analysis. Significant regressions are shown; solid line, $P < 0.05$; dashed line, $P < 0.1$. Note that the y-axes are differently scaled for anchovy and sardine.
Figure 7. Scatterplots of the relative importance to spawning (R, expressed as the percentage contribution to total egg abundance during the survey) against time for anchovy (circles) and sardine (black dots) in each of the five strata used in this analysis. Significant regressions are shown; solid line, $P < 0.05$; dashed line, $P < 0.1$. 
about 40% to 20% of estimated total egg production, whereas the Central Agulhas Bank showed a weakly significant \( P < 0.1 \) increase in \( R \) over time. In 1998, 72% of the estimated total number of anchovy eggs were found over the Central Agulhas Bank (Fig. 7). The Eastern Agulhas Bank also showed an increasing trend in \( R \) over time, although the very low value for 1998 rendered this relationship insignificant. For sardine, the relative contribution to total egg abundance made by the West and South-West Coasts showed a high degree of variability, but a weakly significant \( P < 0.1 \) trend was evident for the South-West Coast (Fig. 7). The Western and Eastern Agulhas Banks also showed high variability in \( R \) for sardine, whereas a significant \( P < 0.05 \) decreasing trend for this parameter was observed for the Central Agulhas Bank.

Contouring the relative contribution to spawning by stratum through time permits temporal patterns in the abundance and distribution of the eggs of anchovy and sardine to be visualized in a single figure (Fig. 8). This figure indicates that anchovy egg distributions were most spatially stable through time, showing consistent spawning east of Cape Point. Although 30-40% of anchovy eggs were found west of Cape Point during the period 1986-1988, the Agulhas Bank was the principal anchovy spawning habitat during the rest of the time-series, with areas of intense spawning on the Agulhas Bank differing along the coast from year to year. In contrast, sardine eggs were more patchily distributed through time, with the regions to both the west and to the east of Cape Point being major sardine spawning habitat during different periods. Despite the patchier distribution of sardine than anchovy eggs, both have shown a broad-scale overlap during the first two-thirds of the time-series. Since 1994, however, the spawning habitats of these two species have become markedly distinct, with anchovy spawning principally east of Cape Point, and sardine spawning principally west of Cape Point. More than 80% of anchovy eggs have been found east of Cape Point during each survey since 1994, with most eggs being found over the Central and Eastern Agulhas Banks. In contrast to anchovy, at least 65% of sardine eggs have been found west of Cape Point during surveys since 1994.

The eastward shift in sardine egg distributions observed between 1989 and 1993, when sardine spawning was concentrated primarily on the Central and Eastern Agulhas Banks (Fig. 8), appears to have been linked to SST. A time-series of SST per stratum shows that average SSTs off the West and South-West Coasts were markedly lower than those over the Agulhas Banks during the period 1989-1993 (Fig. 9). Despite the fact that sardine are able to spawn in cooler waters than anchovy, this correspondence between sardine egg distributions and average SSTs suggests that the West and South-West Coasts may have been too cold for extensive sardine spawning during those years. This hypothesis requires better data and further testing however, with, for example, satellite data being used to estimate stratum-specific SSTs.
Figure 8. Changes in the patterns of abundance and distribution of eggs through time for anchovy and sardine. The x-axis represents the coastline, which has been “straightened” and divided into the five strata used in this analysis, and the y-axis represents time. The percentage contribution to total egg abundance during the survey is shown for each of five strata by year, and contouring is used to interpolate between years and strata. The vertical white line indicates the approximate position of Cape Point.
Egg Abundance Time Series

The egg abundance time-series for anchovy and sardine, together with acoustically derived estimates of their respective spawner biomass over this time period, are shown in Fig. 10. Anchovy egg abundance showed a significant linear decline over the time-series ($r^2 = 0.88; F = 92.5; \text{d.f.} = 1,14; P < 0.001$), and was significantly correlated with anchovy spawner biomass ($r^2 = 0.35; F = 7.02; \text{d.f.} = 1,14; P < 0.03$). Although sardine spawner biomass increased 20-fold over the time-series, sardine egg abundance did not show a significant trend through time, nor was it correlated with sardine spawner biomass.

Discussion

Data on the abundance and distribution of the eggs of anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) were collected using a CalVET net during annual spawner biomass surveys in the Southern Benguela upwelling ecosystem over the period 1984-1998. These data were used to characterize spawning habitat with respect to sea surface temperature, compare the...
spatial distinctiveness of anchovy and sardine spawning habitats, and provide an egg abundance time-series for each species. Results obtained indicate that anchovy prefer to spawn in warmer water than do sardine; that anchovy and sardine spawning distributions no longer overlap, although this was the case prior to 1994; that anchovy spawning distribution has shifted eastward and sardine westward since 1994; and that biomass trends are reflected in the egg abundance time-series for anchovy, but not for sardine.

The egg percentage/SST percentage quotient transformation indicates that anchovy and sardine differ in their preferred spawning temperatures; anchovy prefer to spawn in warmer waters than do sardine. Although the sardine quotient curve is bimodal, the major sardine peak and the anchovy peak are well separated. A study conducted by Lluch-Belda et al. (1991), who used the egg/SST quotient transformation to examine anchovy and sardine spawning in the California Current, found similar results to those reported above; California sardine spawned over a wider SST range than

Figure 10. Time-series of estimated total egg abundance for anchovy and sardine, 1984-1998. Also shown are the time-series of relative acoustic estimates of the two species (Barange et al. 1999; Marine and Coastal Management, unpublished).
did anchovy, and the sardine quotient curve was bimodal whereas that for anchovy was unimodal. However, unlike anchovy and sardine in the Southern Benguela, the major California sardine quotient peak (at 15°C) was similar to the California anchovy quotient peak (14°C). Lluch-Belda et al. (1991) concluded that sardine were eurythermic and anchovy stenothermic, and that anchovy seemed better adapted to spawning in cooler water than sardine. While the data presented above for these clupeoids in the Southern Benguela also suggest that sardine are eurythermic compared to anchovy, they suggest that in this system, sardine should be better adapted to spawning in cooler waters than anchovy. This dissimilarity between the anchovy/sardine species pair in the Benguela and California Current systems, with sardine preferentially spawning in cooler waters in the former and anchovy preferentially spawning in cooler waters in the latter, may be partially responsible for the phase difference in cycles of abundance observed between anchovy and sardine populations in these two ecosystems. Shifts in the relative dominance of anchovy and sardine in the Southern Benguela are out-of-phase compared to this species pair in the California Current (and the other major upwelling systems), with the sardine population off southern Africa increasing and the anchovy decreasing over periods during which anchovy increased and sardine decreased off California (Schwartzlose et al. 1999). If the mechanism responsible for regime shifts between clupeoid species pairs is one of global teleconnections (Schwartzlose et al. 1999 and references therein), then the phase difference between regime shifts in the southeastern Atlantic and the other regions could plausibly be attributed to the observed differences in preferred spawning temperature between anchovy and sardine in the various systems. For example, whereas sustained warm periods have been associated with greater abundance and extended spawning of sardine in the California and Humboldt Current systems (Lluch-Belda et al. 1992a), warm periods are likely to favor anchovy rather than sardine spawning in the Southern Benguela Current system.

Anchovy egg distributions during the spawner biomass surveys have been extensively described by Armstrong et al. (1988), Shelton et al. (1993) and Roel et al. (1994). These authors considered the Western Agulhas Bank to be the major anchovy spawning area, selected by the fish because of the efficiency of transport of eggs and larvae to the West Coast nursery grounds by the shelf-edge jet current (Shelton and Hutchings 1982, Boyd et al. 1992). The data presented here suggest that the Western Agulhas Bank is no longer the major anchovy spawning area: the Central and Eastern Agulhas Banks now appear to be the most important anchovy spawning grounds. Sardine egg distributions during spawner biomass surveys were mentioned by Roel et al. (1994), but have not yet been described in any detail for this region. After conducting a geostatistical analysis on egg data from the spawner biomass survey of 1994, Barange and Hampton (1997) noted that sardine eggs were more patchily distributed than anchovy eggs, and inferred that sardine spawning was sporadic and possibly driven by local conditions.
Conversely, anchovy appeared to display a consistent spawning strategy at the population level.

The apparent eastward shift in anchovy spawning habitat over the Agulhas Bank is linked to changes in the anchovy population structure observed recently: poor recruitment over the past few years has resulted in older fish constituting a larger proportion of the population (Roel et al. 1994, Barange et al. 1999). In addition to moving eastward with age (Barange et al. 1999), older, and therefore larger, anchovy make a disproportionately large contribution to spawning. Eggs spawned over the Central and Eastern Agulhas Banks tend to be located offshore of the cool ridge where they are more susceptible to offshore advection. Boyd et al. (1992) documented regular, strong offshore flow from the southern tip of the Agulhas Bank that was likely to contribute to offshore loss of eggs; hence, they speculated that eggs spawned east of Cape Agulhas were unlikely to contribute significantly to recruitment. However, a transport model derived from Acoustic Doppler Current Profiler–derived current data has indicated that eggs spawned offshore of the cool ridge could be successfully transported to the West Coast nursery grounds (Shannon et al. 1996, Boyd et al. 1998). Concurrent with the eastward shift in anchovy spawning habitat is an apparent offshore shift of anchovy eggs on the Western Agulhas Bank, possibly due to anchovy being excluded from the inner Western Agulhas Bank by the high densities of sardine observed there in recent years (Barange et al. 1999). This eastward and offshore shift in anchovy spawning habitat is likely to increase the potential for advective loss, and therefore could have significant impacts on recruitment variability of this species.

Anchovy and sardine showed a broad-scale overlap in their egg distributions, and hence spawning habitats, for the first two-thirds of the time-series. Since 1994, however, the spawning habitats of these two species have become spatially distinct; anchovy now spawn primarily east of Cape Point while sardine spawn west of Cape Point. It is worth pointing out that 1994 was the first year of the acoustically estimated biomass time-series when the relative biomass of sardine was higher than that of anchovy (Barange et al. 1999). Recent work has shown that pelagic fish school composition reflects the relative species abundance within the pelagic community in upwelling systems (Cury et al. 2000): when sardine, sardinellas, or anchovy are abundant they tend to form pure schools, whereas when their relative abundance diminishes they mix with other species. These findings have led to the school trap hypothesis (Bakun and Cury 1999) which postulates that “a fish species driven to school together with a more abundant species must effectively subordinate its specific needs and preferences to the ‘corporate volition’ of a school largely driven by a different set of needs and preferences.” The similarity in sardine and anchovy spawning habitat prior to 1994, and dissimilarity thereafter, may provide some evidence for the school trap hypothesis. Spatially distinct spawning habitat between anchovy and sardine has also been observed in the California Current ecosystem (Hernandez-Vazquez 1994).
Anchovy have shown consistent decreases in spawning area and spawning output within the spawning area over the time-series, a period during which the population biomass of this species has declined. These decreases have resulted in declining total egg abundance estimates from 1984 to 1998. By contrast, sardine showed no clear patterns in either spawning area or reproductive output, and no long-term increase in total egg abundance, despite substantial increases in population biomass. These results show partial correspondence with those of Barange et al. (1999), who found that while the area occupied by adult anchovy was related to stock size, no such relationship was observed for sardine. Barange et al. (1999) speculated that increases in sardine stock size were reflected in actual school densities, without a corresponding increase in the area occupied by sardine. Assuming this to be the case would explain the lack of a consistent increase in sardine spawning area. If this were true however, it could be assumed that egg density and hence reproductive output within an unchanged spawning area would increase; the data presented above do not show this.

The egg data used in this analysis were collected during spawner biomass surveys conducted in November/December, the peak anchovy spawning period. Although sardine also spawn over spring/summer, the spawning peaks of this species occur on either side of the November/December surveys (September/October and February/March). In a study examining within-season variability in the abundance and distribution of clupeoid eggs and larvae, Fowler (1998) showed evidence to suggest that sardine egg abundance was highest over the Western Agulhas Bank during August-October and January/February, while abundance was highest on the South-West Coast during November/December. Fowler's (1988) study therefore suggests that sardine do shift their spatial patterns in spawning over the spawning period, and implies that the results of this study may be biased by the timing of the surveys during which the data were collected.

An additional assumption of this analysis is that the spawner biomass surveys cover most, if not all, of the spawning habitat of anchovy and sardine. Both of these species are known to spawn in waters off the east coast (east of 28°E), with sardine eggs often being dominant in ichthyoplankton surveys in this region (Beckley and Hewitson 1994, Connell 1996) and sardine larvae being collected in light traps off Durban through most of the year (Naidoo 1998). However, because of the narrow continental shelf along the east coast, this region is considered too small to contribute appreciably to the adult stock of these species (Armstrong et al. 1991). A third factor confining interpretation of the sardine egg data is the low numbers of eggs collected for this species; whereas about 150,000 anchovy eggs were collected over the time-series, only about 15,500 sardine eggs were collected (Table 1). The data from this study are therefore likely to provide a more accurate reflection of anchovy spawning habitat than they are for sardine; consequently, less confidence can be placed in interpretations derived from the sardine egg data. Despite these reservations con-
cerning the data for sardine eggs, it was felt that the large-scale coverage and relatively long time-series of data collected permitted a meaningful comparison between the spawning habitats of these two clupeoid species.

The results discussed above have implications for the management of anchovy and sardine in the Southern Benguela. First, they suggest that our current understanding of the life history of these two species requires revision, particularly for anchovy which is considered to be relatively well understood (Hutchings 1992, 1998). For example, the assumption that the Western Agulhas Bank is the major spawning habitat for both species no longer appears correct, requiring an expansion and/or shift in the spatial focus of monitoring programs used to provide information for various models that attempt to predict anchovy recruitment strength (Cochrane and Hutchings 1995, Korrubel et al. 1998, Painting and Korrubel 1998, Richardson et al. 1998). The offshore shift in anchovy eggs, particularly over the Eastern Agulhas Bank, is likely to increase the probability of advective loss, and hence impact negatively on recruitment success. Second, apart from the potential for increased advective loss on the exposed West Coast, the implications of a westward shift in sardine egg distributions are not well understood. Third, the recent spatial separation in anchovy and sardine spawning habitats may well be linked to the regime shift between these two species currently under way in the Southern Benguela: anchovy and sardine spawning habitats became spatially distinct in 1994, the first year when the relative biomass of sardine was higher than that of anchovy. Finally, a better understanding of such shifts in relative dominance, and the mechanisms by which these shifts are initiated and sustained, can only enhance management strategies of these commercially important clupeoid species.

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References


Spatially Specific Growth Rates for Sea Scallops (*Placopecten magellanicus*)

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Abstract
Past analyses have shown that sea scallops (*Placopecten magellanicus*) in the Bay of Fundy exhibit differing growth rates according to area and depth of capture. Area-specific shell height-at-age estimates from the resultant growth models are routinely used in stock assessments for a number of the management areas in the Bay of Fundy. These models have been based on fitting von Bertalanffy curves to cross-sectional data and it has been assumed that this annual snapshot of growth characteristics is applicable over time for different cohorts. Data on shell height-at-age for each annular ring are also available for scallop shells for a number of years, thus providing growth information for cohorts and over time. These data are used to evaluate how consistent spatially specific growth characteristics are over time. Given that these measurements of shell height-at-age are longitudinal and hence correlated over time, nonlinear mixed effects models are used to incorporate the serial correlation into the model.

Introduction
Spatial variation in the growth of scallops, particularly for the sea scallop (*Placopecten magellanicus*) has been reported in a number of studies (e.g., Caddy et al. 1970, MacDonald and Thompson 1985, Schick et al. 1988, Robert et al. 1990, Kenchington et al. 1997). For the most part, these studies have concentrated on examining differences in growth characteristics between scallops caught at different depths because depth has been recognized as having a strong influence on almost all aspects of sea scallop growth and biology (Naidu 1991). Depth is assumed to be a proxy for differences in either temperature or food availability or both but many
authors favor food availability as being more influential on growth rate and maximum size (e.g., MacDonald and Thompson 1985, Shumway et al. 1987).

On 1 January 1997, an area-based management plan was implemented for the sea scallop fishery in the Bay of Fundy, dividing the bay into seven scallop production areas (Fig. 1). While these areas were intended to reflect historical fishing patterns, the new management boundaries have grouped together areas where scallops were known to exhibit very different growth characteristics. However, to date management measures such as setting limits on meat count (number of adductor muscles per 500 g in the catch) and the minimum shell size which should reflect growth characteristics, are applied to an area as a whole.

Prior to the establishment of the scallop production areas, analyses of yield-per-recruit and optimum size and age of capture for scallops in the Bay of Fundy were based on growth estimates for areas where the scallops exhibited very similar growth rates (e.g., Roddick et al. 1994). Given the

Figure 1. Scallop production areas in the Bay of Fundy as of 1 January 1997. Latitude and longitude are given in decimal degrees. Latitude 43.66 (43°40' N) corresponds to the outer boundary of the inshore scallop fishing area.
change to the new areas, these analyses need to be revised to take into account spatial patterns of growth characteristics within the management areas.

In this paper we analyzed scallop growth data from one of the scallop production areas in the Bay of Fundy to investigate spatial patterns in growth. Traditionally, the most recent age and associated shell height-at-age data are used from each scallop to estimate growth parameters. However, the scallop shell contains the animal's complete growth history that can also be used to examine spatial patterns in growth that may have occurred over the lifetime of the animal.

Growth was modeled here using the von Bertalanffy growth curve, as it has been in many of the previous studies on scallop growth. One difference between our study and the other studies on the growth of scallops is that we also applied the von Bertalanffy model to the complete growth history from each scallop shell. This application of the model was done by using nonlinear mixed effects models which were developed for these kinds of repeated measures data (Lindstrom and Bates 1990). Linear forms and nonlinear forms of the mixed effects models have been used to model repeated measures of growth in grey seal pups (*Halichoerus grypus*) (linear, Bowen et al. 1992) and snapper (*Pagrus auratus*) (nonlinear, Millar et al. 1999).

Management measures such as limits on meat count and minimum shell height of scallops in the catch were based upon yield-per-recruit analyses, which in turn require a growth model. The current limits set for many of the new scallop production areas in the Bay of Fundy may not reflect the spatial variation in growth in these areas.

**Materials and Methods**

**Data**

The major source of data on abundance, growth, and shell height-at-age for scallops in the Bay of Fundy is the research surveys conducted by the Department of Fisheries and Oceans. Annual surveys have been conducted every June by the department since the late 1970s in what is now known as scallop production area 4 (Fig. 1). The survey design has varied over time but has been a consistent stratified random design since 1991. No matter what design was used, survey tows were made at randomly located stations using a gang of four Digby drags (scallop dredges) with steel rings (75-78 mm inside diameter) knitted together with rubber washers. The drags were towed for 8 minutes on the bottom. Two of the four drags were lined with 38 mm polypropylene stretch mesh to retain the smaller scallops.

From each tow, all or a sample of scallop shells were measured for height (tangential dorso-ventral measurement, Naidu 1991), the adductor muscles (meat) were removed and weighed. The shells were read for annual growth rings which are formed each winter when water temperatures
decline and the shell growth slows down causing the deposition of a dark band on the shell. Age determination can be subjective, as growth rings can be very difficult to distinguish at times. All ages in this data set were determined by one person (M.J. Lundy) in an attempt to ensure consistency. Shell height at each age for each shell was determined by measuring the height of each growth ring from the shell umbo.

For our study we chose the data collected during the June 1990 survey because these data consisted of a fairly large number of animals from which we had measurements of shell heights and ages over the whole life-span of the animal. In addition, these data had come from survey tows located in four of the strata used in the current stratified survey of this area known to have different growth characteristics. The strata labeled Centreville and Gullivers Head on Fig. 2 are generally considered to be areas of low growth rate, whereas the strata labeled Digby Gut and Delaps Cove are known to be areas where scallops exhibit high growth rates. The data used in this study are from only one survey in one year and therefore the results are intended to be illustrative and not definitive with respect to Bay of Fundy scallop populations.

In general, growth curves are estimated from the oldest ring and associated shell height from each shell. These kinds of data are referred to as cross-sectional here in that they represent size-at-age across a number of cohorts at one period in time. There were 706 animals in our data set and hence we had 706 cross-sectional measurements over the different survey strata (Table 1). Each of the 706 shells also had measurements on shell height to each annual growth ring for a total of 2,562 measurements. The literature on modeling these kinds of data where there is within-subject (scallop) and between-subject variation refers to these as repeated measurements or if measurement over time is involved, as longitudinal data.

In addition to measuring the scallops caught at each tow the depth of the tow was also recorded. Survey work was conducted during daylight hours and at least one tidal cycle was experienced. Water depths varied by 0.2-9.0 m at any one spot in the study area during June 1990 due to the strong tides in the Bay of Fundy. Therefore, all of the depths used in this study were corrected to their chart datum value using tidal height predictions supplied by the Canadian Hydrographic Service. Comparisons of the predictions for 1990 with measurements recorded during June 1990 from tidal gauges at the Parkers Cove measurement station (Fig. 2) indicated differences of less than 1 m.

**Growth Models**

**Cross-Sectional Data**

The standard three-parameter von Bertalanffy model was used here to model the growth from cross-sectional data on age and shell height (e.g., Quinn and Deriso 1999).
Table 1. Numbers of scallops measured for shell height and age by sampling stratum and measurement type. Longitudinal measurements ranged from 5 to 13 years per animal.

<table>
<thead>
<tr>
<th>Stratum</th>
<th>Cross-sectional</th>
<th>Longitudinal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Centreville</td>
<td>120</td>
<td>530</td>
</tr>
<tr>
<td>Gullivers Head</td>
<td>80</td>
<td>353</td>
</tr>
<tr>
<td>Digby Gut</td>
<td>264</td>
<td>860</td>
</tr>
<tr>
<td>Delaps Cove</td>
<td>242</td>
<td>819</td>
</tr>
<tr>
<td>Total</td>
<td>706</td>
<td>2,562</td>
</tr>
</tbody>
</table>

Figure 2. Scallop production area 4 in the Bay of Fundy as of 1 January 1997. Rectangles indicate strata used in resource surveys. Samples in this study are from the four strata identified by name on the map. Latitude and longitude are given in decimal degrees. Depths are measured in fathoms (1 fathom = 1.8 m). Depth contours are approximate.
where
\[ L_{ia} = L_\infty \{1 - \exp[-K(a - T_0)]\} + \varepsilon_i \]  

\( L_{ia} \) is shell height (mm) for scallop \( i \) at age \( a \) in years;
\( L_\infty \) is asymptotic shell height;
\( K \) is Brody growth parameter \( (y^{-1}) \);
\( T_0 \) is age at which \( L_a = 0 \); and
\( \varepsilon_i \) is random error.

This model was fit to the data using the \texttt{nls()} function in S-PLUS (Mathsoft 1999) which uses the Gauss-Newton algorithm to estimate the parameters. The random error was assumed to be normally distributed with zero mean and constant variance.

**Longitudinal Data**

At the level of individual scallop shell \( i \), the shell height at age \( a \), \( L_{ia} \) was modeled using a von Bertalanffy curve with individual parameters.

\[ L_{ia} = L_\infty, i [1 - \exp[-K_i(a - T_{0i})]] \]

The nonlinear mixed effects model approach expresses each individual parameter as being a function of a population parameter or fixed effect and an individual deviation from that fixed effect is referred to as a random effect (Lindstrom and Bates 1990). That is,

\[ L_{ia} = (L_\infty, i - L_\infty)[1 - \exp[-(K - k_i)(a_i - (T_0 - t_{0i}))]] + \xi_{ia} \]  

\( L_\infty, K, \) and \( T_0 \) represent fixed effects and \( L_\infty, i, k_i, \) and \( t_{0i} \) are the random effects. The random effects are all assumed to follow a Normal distribution with zero mean and variance-covariance matrix \( \sigma^2 D_i \).

For the von Bertalanffy model the variance-covariance matrix is of dimension 3 \( \times 3 \) with diagonal elements \( \sigma^2 L_\infty, \sigma^2 K, \) and \( \sigma^2 T_0 \). The general procedure of fitting the nonlinear mixed effects model assumes that the variance-covariance matrix is a general positive definite matrix allowing the fitting algorithm to estimate covariances between the random effects.

For the longitudinal measurements made for each scallop, the random error associated with shell height at each age, \( \xi_{ia} \) is also assumed to have a normal distribution with zero mean and variance-covariance matrix \( s^2 A_i \).

The matrix \( A_i \) was initially set to the identity matrix when fitting the model and hence repeated measurements made on the same animal are assumed to be independent over age once the random effects have been accounted for. Serial correlation using a wide range of models can be incorporated into this matrix once the initial model has been fit to the data.
The S-PLUS (Mathsoft 1999) function `nlme()` was used to fit the nonlinear fixed effects models in this study. From our experience with using the von Bertalanffy model in the nonlinear mixed effects approach we found that the fitting algorithm was most stable when $K$ was reparameterized as $\exp(K')$. This reparameterization ensures that the estimated growth parameter, $K = \exp(K')$ in the model was always positive.

**Results**

Initial analysis of the cross-sectional and longitudinal growth data indicated that ages with shell heights less than 40 mm were poorly modeled by the von Bertalanffy model, suggesting that growth at these young ages did not follow the same pattern observed at older ages. Therefore the growth analysis was restricted to scallops greater than or equal to 40 mm which resulted in an age range of 3-13 for the cross-sectional data and 2-13 for the longitudinal data.

**Cross-Sectional Growth Data**

A comparison of the residuals from each area from fitting one von Bertalanffy model to the data from all areas illustrates a commonly made observation for scallop growth data from this area (Fig. 3). The resultant growth model tends to overestimate shell height-at-age in the Centreville and Gullivers Head area and underestimate in the Digby Gut and Delaps Cove area. One approach proposed by Kenchington et al. (1997) for dealing with this pattern was to fit separate growth curves for each area and based on previous studies, separate curves were used for depths shallower and deeper than 88 m (observed depth not corrected to chart datum). While such a model consisting of separate curves for areas and depth zones provides a significant improvement over using just one curve for the whole area, a total of 21 parameters are required to describe the model (model I vs. II in Table 2a).

As discussed earlier, depth has been identified as an influential variable and the residuals from the fit of the von Bertalanffy model to the data from all areas indicate a very strong linear trend with respect to depth (corrected to chart datum) (Fig. 4). This trend was characterized here by fitting a loess curve to the residuals (Cleveland and Devlin 1988). The asymptotic shell height parameter ($L_\infty$) is the only linear parameter in this growth model and the residual pattern in Fig. 4 suggests that a model with $L_\infty$ modeled as a linear function of depth might be appropriate here.

The first model used here for $L_\infty$ was a quadratic relationship with depth,

$$L_\infty = \beta_0 + \beta_1 \text{Depth} + \beta_2 \text{Depth}^2 \quad (3)$$

While the quadratic model may capture the curvature indicated by the loess line, there also appears to be evidence of a change in the relationship at around 80-96 m. To capture this feature a model with a bilinear relationship with depth was also used for $L_\infty$. 
Figure 3. Scatter plot of residuals from each area based on a fit of one von Bertalanffy growth model to age and shell height measurements from 706 scallops from all areas. Data collected from the research dredge survey of the Bay of Fundy, June 1990. Panels illustrate residuals by sampling strata. Note: CV = Centreville, GH = Gullivers Head, DG = Digby Gut, DC = Delaps Cove. A loess line has been fitted to the residuals in each panel to investigate for trend.

$$L_\infty = \begin{cases} \beta_{0,1} + \beta_{1,1} \text{Depth, if Depth < } D_c \\ \beta_{0,2} + \beta_{1,2} \text{Depth, otherwise} \end{cases}$$

where $D_c$ needs to be estimated but appears to be between 80 and 96 m.

The quadratic model (model III in Table 2a) explained significantly more of the variation in the data than model II. However, the additional amount of variation explained by the bilinear form of the model (model IV) over that explained by the quadratic model was significant as well. The estimate of $D_c = 90$ m was obtained by the bilinear models for a range of depths and choosing the depth which resulted in the largest model sum of squares. Comparison of parameter estimates from the von Bertalanffy model for all of the data with those for the bilinear model exhibits a greater $L_\infty$ when depths are less than 101 m and lower values for $K$ and $T_0$ over all depths for the latter model (Table 2b). The residuals from the bilinear model do not exhibit any apparent trend with depth (Fig. 5).
Table 2. Results from fitting the von Bertalanffy growth model to the cross-sectional scallop shell height and age data using the nonlinear least-squares method.

<table>
<thead>
<tr>
<th>Model</th>
<th>Test</th>
<th>DF</th>
<th>SS</th>
<th>DF</th>
<th>SS</th>
<th>F-statistic</th>
<th>P-value</th>
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<td>I</td>
<td></td>
<td>703</td>
<td>26992.07</td>
<td></td>
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<tr>
<td>II</td>
<td>I vs. II</td>
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<td>21932.30</td>
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<td>&lt; 0.0001</td>
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<tr>
<td>III</td>
<td>I vs. III</td>
<td>701</td>
<td>21392.08</td>
<td>2</td>
<td>5599.99</td>
<td>91.75</td>
<td>&lt; 0.0001</td>
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<tr>
<td>IV</td>
<td>III vs. IV</td>
<td>700</td>
<td>20772.41</td>
<td>1</td>
<td>619.67</td>
<td>20.88</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>

b. Parameter estimates.

<table>
<thead>
<tr>
<th>Model</th>
<th>$L_\infty$</th>
<th>$K$</th>
<th>$T_0$</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>113.98</td>
<td>0.65</td>
<td>1.09</td>
</tr>
<tr>
<td>IV</td>
<td>$131.75 - 0.12 \times \text{depth} (&lt;90 \text{ m})$</td>
<td>0.47</td>
<td>1.09</td>
</tr>
<tr>
<td></td>
<td>$144.41 - 0.30 \times \text{depth} (\geq 90 \text{ m})$</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Models are: I, one growth curve for whole area; II, one growth curve for each subarea; III, one growth curve and a quadratic relationship between depth and $L_\infty$; IV, one growth curve and a bilinear relationship between depth and $L_\infty$.

The curve for the predicted shell heights-at-age from the model for all of the data was not parallel with those from the bilinear model for particular depths (Fig. 6). The general shape of the all-data curve may reflect the fact that most of the data for the older ages came from the deepwater samples while the greater proportion of data on the younger ages tended to come from the samples from shallower water.

**Longitudinal Growth Data**

The growth trajectories for individual scallops indicate that there is strong evidence for individual variation in their respective von Bertalanffy parameters (Fig. 7). Animals that are larger (or smaller) than average at a younger age remain so as they grow older.

A nonlinear mixed effects version of the von Bertalanffy model was fit to the data portrayed in Fig. 7 both for the whole data set and within area/depth subareas as was done for the cross-sectional data. In both models, $L_\infty$, $K$ and $T_0$ were all defined as having fixed and random effects.

Similar to the results for the cross-sectional data, the model for area/depth subareas provided a significant improvement over the model for all areas (Table 3a). Residuals from these models were obtained for each scallop at each age by subtracting the fitted values at that level from the observations and dividing by the estimated within-scallop standard error if
standardized residuals are required. However, given the added flexibility of allowing the von Bertalanffy parameters to vary for each individual, these residuals are probably not very informative about lack-of-fit. Instead, lack-of-fit could be ascertained from looking at the estimated random effects \( l_{\infty,i} \), \( k'_i \) and \( t_{0,i} \) from each scallop.

Scatter plots for each of the parameter random effects are presented in Fig. 8. Again, loess lines were used to determine if trends with depth existed in these graphs. While the panels for \( k'_i \) and \( t_{0,i} \) indicate little or no trend, the very strong pattern for \( l_{\infty,i} \) is striking (Fig. 8). The trend in \( l_{\infty,i} \) appears to be quadratic or bilinear with an inflection point in the same depth range as noted for the cross-sectional data.

The pattern in this figure suggests that the mean of the random effects \( l_{\infty,i} \), that is the fixed effect \( L_{\infty} \), is not stationary with increasing depth. Therefore, the fixed effect \( L_{\infty} \) was modeled as having either a quadratic or a bilinear relationship with depth. The results from fitting these two forms of the growth model were similar to those obtained for the cross-sectional data (Table 3a). Both models provided better fits to the data with fewer parameters than either the growth model fit to all of the data or fitting individual
growth curves to each area/depth combination. Also, the bilinear model was a significant improvement over the quadratic model. The scatter plot for the random effects for $L_\infty$ from the bilinear model shows little trend with increasing depth (Fig. 9).

Comparison of the parameter estimates from the original nonlinear mixed effects model fit to all of the data with the bilinear model shows little change in the fixed effects estimates for $K^*$ (and $K$) and $T_0$ between the two models (Table 3b). The fixed effect estimate for $L_\infty$ from the bilinear model was less than that from the model for all of the data for depths greater than 90 m. The slopes for the depth terms were assumed to be fixed effects only; however, the intercept term did have a random effect. The addition of the bilinear term for $L$ reduced the standard error, $s_{L_\infty}$ (intercept of bilinear relationship) of the associated random effects but did not affect any of the standard errors of the other random effects.

The hypothesis of independence between random effects was tested by setting $D_i$ to the identity matrix and refitting the bilinear model. The

![Figure 5. Pearson residuals from fit of modified von Bertalanffy growth model to age and shell height measurements from 706 scallops measured on a research dredge survey of the Bay of Fundy, June 1990. Growth model has depth incorporated as a bilinear relationship between depth and $L_\infty$. Residuals plotted against observed depths (corrected to chart data, see text) at dredge sites. A loess line has been fitted to the residuals to investigate for trend.](image-url)
Figure 6. Predictions from modified von Bertalanffy growth model. Growth model has depth (corrected to chart data, see text) incorporated as a bilinear relationship with $L_\infty$ term.

Figure 7. Scatter plot of longitudinal age and shell height measurements from 706 scallops measured on a research dredge survey of the Bay of Fundy, June 1990. Measurements from same animal are connected with lines.
Table 3. Results from fitting the von Bertalanffy growth model to the longitudinal scallop shell height and age data using a nonlinear mixed effects model.

a. Model fitting results.

<table>
<thead>
<tr>
<th>Model</th>
<th>Test</th>
<th>DF</th>
<th>Log likelihood</th>
<th>Likelihood ratio</th>
<th>P-level</th>
</tr>
</thead>
<tbody>
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<td></td>
<td>-7062.72</td>
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<tr>
<td>II</td>
<td>I vs. II</td>
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<td>227.53</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>III</td>
<td>I vs. III</td>
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</tr>
<tr>
<td>IV</td>
<td>III vs. IV</td>
<td>13</td>
<td>-6919.90</td>
<td>23.57</td>
<td>&lt;0.0001</td>
</tr>
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</table>

b. Parameter estimates for nlme model.

<table>
<thead>
<tr>
<th>Model</th>
<th>( L_\infty )</th>
<th>( K )</th>
<th>( K' )</th>
<th>( T_0 )</th>
<th>( \sigma_{L_\infty} )</th>
<th>( \sigma_K )</th>
<th>( \sigma_{T_0} )</th>
<th>( s )</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>129.04</td>
<td>-0.94</td>
<td>0.39</td>
<td>0.57</td>
<td>12.56</td>
<td>0.24</td>
<td>0.25</td>
<td>1.64</td>
</tr>
<tr>
<td>IV</td>
<td>147.25 (-0.18 \times \text{depth (&lt;90 m)})</td>
<td>-0.97</td>
<td>0.38</td>
<td>0.55</td>
<td>10.01</td>
<td>0.23</td>
<td>0.25</td>
<td>1.62</td>
</tr>
<tr>
<td></td>
<td>155.48 (-0.30 \times \text{depth (\geq 90 m)})</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Models are: I, one growth curve for whole area; II, one growth curve for each subarea; III, one growth curve and a quadratic relationship between depth and \( L_\infty \); IV, one growth curve and a bilinear relationship between depth and \( L_\infty \).

The likelihood-ratio test rejected the null hypothesis of independence (P-value < 0.0001).

Examples of predicted growth curves for selected depths appear to be parallel with the curve from the model fit to all of the data (Fig. 10). Recall that in the cross-sectional case, the predicted curve from the model fit to all of the data tended to resemble the curves for the shallower depths at the younger ages and the deeper depths for the older ages. In the case of the longitudinal data, the smaller number of older animals from the shallower depths contributes more information than was the case for the cross-sectional data. That is, all animals of age \( a \) also contribute shell heights at ages \( a-1, a-2 \), etc.

A comparison of observed and predicted shell heights by sampling strata from the bilinear form of the model does not show any area specific deviations once depth has been incorporated into the model (Fig. 11).

**Yield-Per-Recruit**

One of the major uses of growth data in fisheries management is to calculate yield-per-recruit and estimate reference points such as \( F_{0.1} \) and \( F_{\text{max}} \). Unfortunately, no meat weights or weights of any kind were taken during the 1990 survey. At present the only survey for which we have both shell height with meat weight data and depth corrected to chart data is the June
Figure 8. Scatter plot of standardized random effects for each of the parameters of the nonlinear mixed effects version of von Bertalanffy growth model fitted to longitudinal age and shell height measurements from 706 scallops measured on research dredge survey of the Bay of Fundy, June 1990. Random effects are plotted against observed depths (corrected to chart data, see text) at dredge sites. A loess line has been fitted to the data to see if any trend exists in the random effects.

1996 survey of the same area. Given that our analyses are intended to be illustrative we used the 1996 meat weight data to calculate yield-per-recruit. Preliminary analysis of a regression of the natural logarithm of meat weight on the natural logarithm of shell height indicates that a depth effect similar to those observed in the growth data analyzed here was also apparent in the meat weight data (S.J. Smith, unpubl. data). The study of these data is ongoing but indications are that modeling the intercept of the regression as a bilinear function of depth with a break point at 90 m provides the best fit. A full analysis of these will not be presented here but predicted meat weights at shell heights by depth were used to estimate mean weight-at-age for the growth models analyzed in this report.

The Thompson-Bell model for yield-per-recruit (Ricker 1975) was chosen here with the selectivity curve used in Roddick et al. (1994). Estimates of $F_{0.1}$ for cross-sectional growth curves are higher than those from the longitudinal growth curves for comparable depths (Table 4). The cross-sectional models also indicate that this optimal level of fishing mortality will result in the average age of scallops in the catch being 1 year younger.
than expected from the longitudinal model. As a result meat counts and mean meat weights were also less for the cross-sectional models compared to the longitudinal models. Within model type, mean age in the catch was the same for each $F_{0.1}$ but the expected mean weight was smaller for the deeper depths.

Note that neither the counts nor the meat weights presented here take into account the substantial meat growth that occurs from June to the fall. In recent years the fishery has opened in October and closed when the total allowable catch has been taken, usually in November.

**Discussion**

The finding that depth appears to have a significant effect on growth in scallops is not a new one as indicated by the literature cited in the introduction to this paper. Scallops appear to grow slower or have a smaller asymptotic size, or both, the deeper they are found (Caddy et al. 1970,
MacDonald and Thompson 1985, Schick et al. 1988, Robert et al. 1990, Kenchington et al. 1997). Barber et al. (1988) also noted that scallops had lower fecundities in deeper water than scallops in shallower waters with respect to the number of eggs spawned.

Most of these studies on depth and growth suggested that lower availability of food at the deeper depths may be the controlling factor. A comparison of gut contents from scallops caught at 20 m and 180 m showed that there were differences in the species composition of algae consumed by the scallops at the two depths (Shumway et al. 1987). Pelagic species and benthic species were equally abundant in the gut contents of scallops from 20 m but the pelagic species were outnumbered by benthic species in the 180 m sample. While the authors did not report on possible nutritional differences between pelagic and benthic species of algae, they suggested that the seasonal availability of algae during blooms was probably more beneficial for animals in shallow water than in deep water.

Food availability may also be a function of the water currents in the area. The Bay of Fundy has a highly complex system of currents given the large tides in the area but unfortunately there has been little detailed work on the currents in this area (J. Loder, Bedford Institute of Oceanography, Ocean Sciences Division, Dartmouth, Nova Scotia, pers. comm.). Predic-
Figure 11. Scatter plot of observed shell heights versus fitted values for nonlinear mixed effects version of von Bertalanffy growth model modified to include depth. Model was fitted to longitudinal age and shell height measurements from 706 scallops measured on a research dredge survey of the Bay of Fundy, June 1990. Panels refer to sampling strata. Note: CV = Centreville, GH = Gullivers Head, DG = Digby Gut, DC = Delaps Cove.

Sections from oceanographic models show that the velocity of tidal currents decrease with distance and depth from the Nova Scotia shore into the Bay (J. Loder, unpubl. data). Lacking direct observation we can only speculate that lower velocity currents may transport lower amounts of food to the deeper depths.

The fact that the 90 m depth is important for both the cross-sectional and longitudinal data and the preliminary finding that it is also important for the 1996 cross-sectional meat weight and shell height relationship suggests that it is probably a constant feature for this area. As such this depth may be a point where there is a dramatic decrease in current velocity due to boundary layers or some other feature. The 90 m depth appears to be specific to this area of the Bay of Fundy. Lundy and Smith (1999) analyzed the residuals from the von Bertalanffy model for cross-sectional data from the Brier Island/Lurcher Shoal area at the mouth of the Bay of Fundy and found that the breakpoint for the residuals corresponded to a combination of depth and westward location. In this case, there appears to be a relationship between the residuals and the location of a frontal zone.
If food availability is the underlying cause for the differences in growth with depth then it may be quite natural to model these differences as a function of the maximum size $L_\infty$. Beverton and Holt (1957) suggested that in the von Bertalanffy model, when applied to weights-at-age, the parameter for maximum size $W_\infty$ is proportional to the cube of the ratio of the coefficients of anabolism and catabolism, while $K$ is proportional only to catabolism. Changes in food supply would solely affect the rate of anabolism and such a change would then only be reflected by changes in $W_\infty$.

Originally the von Bertalanffy model had been defined to describe the growth of a single animal (see Southward and Chapman 1965). In the application of this model to measurements from a group of animals, individual variability was assumed to be characterized by the $\epsilon_i$ term in equation 1. As such, this term acts as a catchall for the cumulative effects of individual genetic variability and environmental effects. Individual variability in growth might be more appropriately characterized as having individual growth parameters (Sainsbury 1980). Sainsbury predicted that if this situation exists then the estimate of $K$ from equation 1 would be greater than the actual mean $K$ over the population. Therefore the estimated size at age from equation 1 would underestimate the true size at age. However, this latter prediction was based on assuming that there was no individual variability in $T_0$ and that $L_\infty$ and $K$ were independent. Our analysis indicates that neither of these assumptions was true. While the growth parameter from equation 1 is higher than from equation 2 as predicted by Sainsbury (1980), the estimated size at age from the latter is not greater than the former over all ages due to the differences in all of the parameters for both models and the correlation between the parameters.

Although Sainsbury (1980) suggested that the amount of bias in the estimated size-at-age might not be large enough for concern given the typical

<table>
<thead>
<tr>
<th>Method</th>
<th>Depth (m)</th>
<th>$F_{0.1}$</th>
<th>Mean meat weight (g)</th>
<th>Mean meat count/500 g</th>
<th>Age</th>
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</thead>
<tbody>
<tr>
<td>Cross-sectional</td>
<td>All</td>
<td>0.22</td>
<td>11.24</td>
<td>44</td>
<td>4+</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>0.20</td>
<td>14.09</td>
<td>35</td>
<td>4+</td>
</tr>
<tr>
<td></td>
<td>80</td>
<td>0.20</td>
<td>13.67</td>
<td>37</td>
<td>4+</td>
</tr>
<tr>
<td></td>
<td>110</td>
<td>0.22</td>
<td>6.91</td>
<td>72</td>
<td>4+</td>
</tr>
<tr>
<td>Longitudinal</td>
<td>All</td>
<td>0.19</td>
<td>12.89</td>
<td>39</td>
<td>5+</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>0.18</td>
<td>16.45</td>
<td>30</td>
<td>5+</td>
</tr>
<tr>
<td></td>
<td>80</td>
<td>0.19</td>
<td>15.40</td>
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<tr>
<td></td>
<td>110</td>
<td>0.21</td>
<td>7.35</td>
<td>68</td>
<td>5+</td>
</tr>
</tbody>
</table>
range of variation in individuals of most fish populations, the results of Table 4 appear to warrant concern here. The results of the yield-per-recruit for the longitudinal data are more optimistic than those from the cross-sectional data by suggesting that meat yields will be higher and that the mean age of the scallops in the catch will be one year older at $F_{0.1}$.

The difficulty we encountered in fitting shell height-at-age for animals less than 40 mm in both types of data may be due to the fact that many of those animals were not or had just become sexually mature. While scallops may become sexually mature as early as 1 year old (23-35 mm) their fecundity is low relative to their mass (Young-Lai and Aiken 1986). Day and Taylor (1997) recommended that the von Bertalanffy model not be used for growth up to and including age-at-maturity because the model does not acknowledge the change in resource allocation at maturity. In addition, because the curve is asymptotic the model does not accurately represent the growth trajectory of an animal during its prereproductive stage of life when all of its energy is dedicated to growth. Our situation was further complicated by the use of the 38 mm liner in the survey drags which precluded the representative sampling of small scallops and probably resulted in the catch of the faster-growing individuals at the younger ages.

Scallops are largely sedentary creatures and therefore the fishery can be spatially selective targeting areas with higher growth rates until densities are reduced to below commercially viable levels. The strong relationship between growth and depth presented here means that spatial targeting can be facilitated by simply knowing the depth you are fishing at within the scallop production area. The imposition of any or all of meat count limits, minimum meat weights, or minimum shell size would only increase the degree of targeting.

Under the current management system for scallop production area 4, the only enforceable control on the size composition in the catch is the monitoring of meat counts. In practice, a range of meat sizes is allowed in the catch as long as the average meat count from two monitoring samples meets the regulated count. Under this regime, fishing in the lower-growth areas will occur and catches from high- and low-growth areas are “blended” to meet the regulated count.

The practices of targeting and blending result in differential fishing mortality with depth. Depending upon the degree of these practices, the population of scallops in the whole management unit may not correspond to the fished population. Initial expectations of productivity based on the whole population may greatly overestimate the actual productivity as higher growth areas are targeted and fished down. In recent years, the major recruitment to scallop production area 4 has been in the deeper areas and we have realized that we probably underestimate fishing mortality when using survey indices calculated from the whole management area (Smith and Lundy 1998). Accurate estimates of fishing mortality and productivity will require more specific knowledge on the spatial behavior of the fishing fleet.
Acknowledgments
The authors thank Glenn King (Bedford Institute of Oceanography, Canadian Hydrographic Service) for providing tidal information for the Bay of Fundy to correct the observed depths for each of the survey tows. We also thank John Loder (Bedford Institute of Oceanography, Ocean Sciences Division) for discussions on the system of currents in the Bay of Fundy and adjoining areas. Comments from two anonymous referees were helpful to us in preparing the final draft.

References


Spatial Distribution and Recruitment Patterns of Snow Crabs in the Eastern Bering Sea

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David R. Ackley
National Marine Fisheries Service, Juneau, Alaska

Abstract
Data from summer trawl surveys and spring commercial fisheries from 1978 to 1999 were analyzed to understand the spatial dynamics of snow crabs (*Chionoecetes opilio*) in the eastern Bering Sea. Males were generally more dispersed than females. Mean sizes at maturity for females increased from north to south and slightly from shallow to deep water. Some crabs appeared to move gradually from shallow water in the northeast to deeper water in the southwest during ontogeny. Centers of distribution of mature females and large males have gradually moved to the northwest over time since the late 1970s. Newshell mature females were broadly distributed during years of high abundance but were concentrated in the north during years of low abundance. Recruits (newshell male and immature female crabs <45 mm carapace width) to the middle, eastern, or southern areas may have better opportunities to grow to commercial sizes than those to the north. During the past 22 years, recruitment has been periodic: strong recruitment occurred every 4-7 years. However, extremely low recruitment in recent years may interrupt this pattern. Questions remain about the degree of stock separation, the total geographic range of the stock, and the loss of oldshell males from the survey stock due to emigration or high natural mortality.

Introduction
Snow crabs (*Chionoecetes opilio*) are widely distributed in the Bering Sea, extending as far north as the Chukchi Sea and Arctic Ocean (Wolotira et al.)
Within the eastern Bering Sea, mean sizes of mature males and females increase with decreasing latitude or increasing depth (Otto 1998). Large males are found in high abundance primarily in the southern part of the eastern Bering Sea and in a band along the outer margin of the continental shelf (Somerton 1981) where the snow crab fishery in the eastern Bering Sea occurs.

Snow crabs in the eastern Bering Sea currently support one of the largest and most valuable fisheries in the United States. The Japanese fleet first harvested snow crabs as bycatch in the 1960s until 1973 when a directed fishery was initiated. The catch gradually increased through the 1970s (Otto 1990). Total catch was relatively small until the directed domestic fishery was developed in the late 1970s. The Magnuson Fisheries Conservation and Management Act prohibited fishing for snow crabs in 1980. The domestic fishery expanded quickly in the late 1980s, and catch peaked in 1991 at 0.15 million t (Morrison 1999). Annual ex-vessel value peaked in 1994 at US$192 million (Morrison 1999). Catches have fluctuated widely during recent years, tracking the abundance of large male crabs estimated by the National Marine Fisheries Service (NMFS) trawl surveys (Stevens et al. 1998). Because of the low abundance estimated in the 1999 summer survey, the catch quota (12,900 t) for 2000 was the lowest in the last two decades.

The objectives of this study were to conduct an exploratory analysis on the spatial distribution of snow crabs in the eastern Bering Sea and to examine spatial recruitment patterns. Annual spatial data by size and sex were mapped to identify spatial distribution patterns. Annual centers of abundance of different size groups of males and females were computed, and relationships between crab carapace size, depth, and latitude examined. Finally, size frequencies of male and female crabs were followed over time to identify strong and weak year classes.

**Methods**

Summer trawl survey data for snow crabs in the eastern Bering Sea from 1978 to 1999 were obtained from NMFS. Before 1978, the survey covered a limited area that does not fully represent the snow crab stock. The survey employs a systematic design where a 20 × 20 nautical mile grid was overlaid on the eastern Bering Sea. One 0.5-hour trawl tow was usually made per 400 square nautical miles. Multiple tows (usually two tows) have been conducted for a single station for small areas around the Pribilof Islands and St. Matthew Island. Occasionally, multiple tows were conducted at stations with an extremely high catch of red king crabs (*Paralithodes camtschaticus*) or blue king crabs (*P. platypus*). Surveys occurred from May 20 to September 3, primarily during June-July (Table 1). After 1978 over 300 stations were surveyed, with the total number of tows ranging from 349 to 522 each year dependent on the number of stations with multiple tows and the number of stations surveyed north of St. Matthew Island.
More than 16,000 snow crabs were caught and measured each year. For the purpose of estimating total population abundance, we stratified the surveyed stations based on number of tows commonly conducted for a station. Specifically, 18 multiple-tow stations around the Pribilof Islands were regarded as one stratum, and 9 multiple-tow stations west of 173°W near St. Matthew Island were grouped together as another stratum. All other stations were treated as one station per stratum. An abundance index for each station was computed as crabs per square nautical mile, and total population abundances by size group, sex, and shell condition were estimated for the whole eastern Bering Sea using the “area-swept” method (Alverson and Pereyra 1969).

Annual station abundance indices (by size and sex) were mapped to identify spatial distribution patterns and to reveal spatial recruitment patterns. Abundance indices for periods with similar spatial patterns were averaged and contrasted with abundance indices during periods with different patterns. Spatial patterns during periods with strong recruitment were contrasted with those during periods with poor recruitment. For the purpose of this study, we defined recruitment as newshell male and immature female crabs <45 mm carapace width (CW). This definition is arbitrary but approximately reflects an index of cohort strength sampled up by the survey gear. Annual centers of distribution for three size groups of males and for immature, newshell mature, and oldshell mature females were computed by averaging locations (in longitude and latitude) weighted by abundance to illustrate the change in distribution and recruitment over time. Annual crab indices from all surveyed stations were used to compute centers of distribution. Mean carapace sizes and crab densities for males and mature females for each station were plotted over depth and latitude to examine their relationships, which were revealed by the LOWESS (locally weighted regression scatter plot smoothing) procedure with the fraction parameter \( f \) equal to \( \frac{2}{3} \). Size frequencies of males and females were plotted over time to identify strong and weak year classes.

Commercial catch data by fishery statistical area from 1985 to 1999 were obtained from the Alaska Department of Fish and Game. Mean catches by statistical area from January to June from 1985 to 1999 were mapped to show spatial distributions. The fishery was typically opened from January to June throughout 1991 and from January to March thereafter.

**Results and Discussion**

**General Spatial Distribution**

Spatial distribution of snow crabs is both size- and depth-dependent (Figs. 1-3). Small males and immature females generally occur in the northeastern part of the eastern Bering Sea in relatively shallow water. Mean crab body size increases toward the southwest or with depth. Mean female size at maturity increases from north to south, and slightly from shallow to deep water. These findings are consistent with those derived by Somerton...
Table 1. Catch sampling of eastern Bering Sea snow crabs in NMFS trawl surveys from 1978 to 1999. Numbers of males caught are classified by three carapace width intervals, and numbers of females caught are classified by immatures, newshell matures (NS-M), and oldshell matures (OS-M).

<table>
<thead>
<tr>
<th>Year</th>
<th>Sampling dates</th>
<th>No. of stations</th>
<th>No. of tows</th>
<th>Empty tows</th>
<th>Total measured</th>
<th>Number of males</th>
<th></th>
<th>Number of females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>&lt;50 mm 50-90 mm &gt;90 mm</td>
<td>Total measured</td>
<td>Immature</td>
<td>NS-M</td>
</tr>
<tr>
<td>1978</td>
<td>5/20-8/18</td>
<td>254</td>
<td>314</td>
<td>76</td>
<td>16,843</td>
<td>24,853 24,932 10,631</td>
<td>8,616</td>
<td>28,149</td>
</tr>
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Figure 1. Distributions of male (upper panel) and female (lower panel) snow crabs in the eastern Bering Sea derived from NMFS summer trawl survey data from 1978 to 1999. Crab density is expressed as the number of crabs per square nautical mile. The three depth contour lines represent 50, 100, and 200 m.
(1981) using only trawl survey data in 1979 and Otto (1998) using trawl survey data from 1989 to 1994. Both Somerton (1981) and Otto (1998) conducted a limited study on spatial distributions of eastern Bering Sea snow crabs by plotting general distribution of different size groups of crabs and computing mean sizes of mature crabs as a function of longitude, latitude, or depth. Our study not only used a much longer time series of data but also examined spatial distribution patterns by shell condition, and the mean sizes of males and mature females as a function of a combination of abundance, location, and depth. For females, the molt to maturity is the final, or terminal, molt. Oldshell mature females, which generally have been mature for at least 1 year, mostly occur in deep water and concentrate within a smaller area than other groups of crabs. Males were more abundant than females in Bristol Bay (southeastern Bering Sea). The paucity of small crabs in Bristol Bay indicates that a substantial number of snow crabs in Bristol Bay probably immigrate from the north. It appears that, during ontogeny, crabs gradually move from shallow water in the northeast to deep water in the southwest.
Commercial catches occurred primarily between 100 m and 200 m and within the survey area (Fig. 4). Some catches, however, were made in deep water outside the survey area. Most catches were taken during January-March, and the fishery shifted to the northwest during May and June (Fig. 4). The low catch in the southeast during May and June was partially due to area closures and partially due to prospects for higher catch rates to the northwest as the ice edge retreats in spring.

Body size is related to depth and latitude in snow crabs and other crab species in the Bering Sea. During the 1985 trawl survey, mean carapace widths of snow crabs were 34.4 mm for males and 33.2 mm for females in Norton Sound versus 47.2 mm for males and 38.8 mm for females in the northeast Bering Sea (Stevens and MacIntosh 1986). On average, the Norton Sound survey area is about 1.5° north of the survey area in the northeast Bering Sea. Within a similar depth range, Chukchi Sea snow crabs were generally larger for the southern stations (within 68-70°N) than for the northern stations (within 70-72°N) in 1990-1991 (Paul et al. 1997). Female snow crabs in the Chukchi Sea are about 50 mm CW at 50% maturity (Jewett
Figure 4. Distributions of commercial catch (in a unit of 1,000 crabs) by statistical area during January, February, and March from 1985 to 1999 (upper panel) and during April, May, and June from 1985 to 1991 (lower panel) for eastern Bering Sea snow crabs. Most areas in the southern part of the eastern Bering Sea were closed to fishing during May and June.
similar to the mean CW of 46 mm for mature females (Paul et al. 1997). This size range (46-50 mm CW) was similar to the mean size of mature females in the northeast Bering Sea (Stevens and MacIntosh 1986) and the northern part of the eastern Bering Sea (Fig. 3) and smaller than those in the southern part of the eastern Bering Sea (Fig. 3). In the southwestern Gulf of St. Lawrence, snow crab size increased with increasing depth (Desrosiers et al. 1982). In the eastern Bering Sea, mature blue king crabs are generally larger at the Pribilof Islands than at St. Matthew Island (Stevens et al. 1998), and mature female red king crabs from the Pribilof Islands are larger than those in Bristol Bay. Norton Sound red king crabs are the smallest of these three red king crab stocks (Otto et al. 1990).

Smaller crab body sizes in the northern area may be attributed to lower molting probabilities for a given size and/or smaller growth increments per molt. For two blue king crab stocks in the eastern Bering Sea, the molting probability for a given size is much lower for the St. Matthew Island stock than for the Pribilof Islands stock (Otto and Cummiskey 1990). Both growth increment and molting probability are lower for red king crabs in Norton Sound than in Bristol Bay (Weber and Miyahara 1962, Brannian 1987). For juvenile red king crabs, growth is positively related to temperature (Stevens 1990); therefore, crabs in warmer southern areas have higher growth rates than those in colder northern areas. Temperature may, therefore, influence size differentiation of mature snow crabs in different parts of the eastern Bering Sea.

The broad, continuous distribution of snow crabs over the eastern Bering Sea makes it difficult to identify separate stocks. Using survey data from 1975 to 1979, Somerton (1981) concluded that management subareas, defined by either longitude or latitude based on size differences, are ineffective because there is no clear-cut separation line to divide the subareas. Within the eastern Bering Sea, there is little genetic difference among snow crabs at St. Matthew Island, the Pribilof Islands, and in Bristol Bay, and little genetic differentiation was found even between snow crabs in the eastern Bering Sea and North Atlantic (Merkouris et al. 1997). Current fisheries regulations divide the eastern Bering Sea (Bering Sea District) into two management subareas: the Eastern Subdistrict (north of 54.6°N and east of 173.0°W) and the Western Subdistrict (north of 54.6°N and west of 173.0°W) (ADF&G 1998). Area-swept estimates of abundance from all surveyed areas are used to set the catch quota and to determine reference points for overfishing (NPFMC 1998). Questions remain whether size differentiation of mature snow crabs within the eastern Bering Sea is large enough to separate the stock into multiple substocks, and whether smaller-sized mature crabs in the northern part of the eastern Bering Sea, which may not recruit into the exploitable stock, should be included for estimating harvestable biomass and overfishing levels.
Changes in Distribution Over Time

Change in crab distribution can be simply illustrated by plotting annual distribution centers from the survey data. Centers of small crab (males <50 mm CW and immature females) abundance were generally located in the northwest portion of the standard survey area during the mid- and late 1990s and in the middle or east during 1985 and 1986 (Fig. 5). It appears that centers of distribution of mature females and large males have moved gradually to the northwest since the late 1970s (Fig. 5). During the mid-1970s, snow crabs were abundant in the southern part of the eastern Bering Sea, but we cannot compute the overall centers of distribution because the surveys did not extend sufficiently to the north. Comparing distributions of mature females in the late 1970s and late 1990s illustrates this dramatic change (Fig. 6). During 1978-1979, newshell mature females were widely distributed and centered in the middle of the standard survey area at 50-100 m, and oldshell mature females were generally found in the south (Fig. 6). During 1998-1999, newshell mature females generally were in the northeast and oldshell mature females in the northwest (Fig. 6). Generally, males were more dispersed than females. Oldshell males, which can be used to approximate relatively old crabs, were concentrated in the middle and south during 1978-1979 and extended to the north considerably during 1981-1999, especially crabs ≥90 mm CW (Fig. 7).

One possible cause of the northward movement since the late 1970s is the regime shift in climate and physical oceanography that occurred in 1976-1977. A measure of the regime shift is the intensity of the Aleutian Low, which generally intensified from 1977 to 1988 (Beamish and Bouillon 1993; Adams and Bond 1999; Zheng and Kruse 2000). During this period of intensification, seawater temperatures were generally warmer, which could cause snow crabs to concentrate in the colder northern area. Distributions of red king crabs in Bristol Bay also showed a northward movement from the 1970s to the 1980s (Hsu 1987). Small male and immature female snow crabs generally concentrate in the northeast and do not show dramatic changes in spatial distribution over time.

Fishing can also affect the spatial distribution of crabs. Because the most valuable and accessible resources were depleted first, Orensanz et al. (1998) speculated that overfishing might have caused serial depletion of crustacean stocks in the Gulf of Alaska. However, we do not believe that fishing pressure has played an important role on the changes in spatial distribution of eastern Bering Sea snow crabs for several reasons. First, harvest rates were relatively low during the late 1970s and early 1980s when the change in distribution occurred. Second, large snow crabs were not depleted in the early 1980s in the southeastern area, which was most easily accessible to the fleet. Large crabs continued to move into the southeastern area during the summer and expanded their range into the northwestern area. Finally, because of their smaller size and incomplete spatial overlap with commercial-size males, mature females were subject
Figure 5. Centers of distribution of eastern Bering Sea snow crabs derived from NMFS summer trawl survey data from 1978 to 1999. Years are plotted as data points.
Figure 6. Distributions of mature female snow crabs in 1978 and 1979 (upper panel) and in 1998 and 1999 (lower panel) in the eastern Bering Sea derived from NMFS summer trawl survey data. Crab density is expressed as the number of crabs per square nautical mile. The three depth contour lines represent 50, 100, and 200 m.
Figure 7. Distributions of oldshell male snow crabs from 1978 to 1980 (upper panel) and from 1981 to 1999 (lower panel) in the eastern Bering Sea derived from NMFS summer trawl survey data. Crab density is expressed as the number of crabs per square nautical mile. The three depth contour lines represent 50, 100, and 200 m.
Recruitment Patterns

Recruitment to the eastern Bering Sea snow crab stock was periodic. High abundances of juvenile crabs (<45 mm CW for males and immature females) recruited to the survey gear during 1978-1979, 1986-1987, and 1991-1994, but there was little recruitment during 1981-1982, 1989-1990, and 1995-1998 (Fig. 8). Therefore, strong recruitment tends to occur every 4-7 years. The last 5 years was the longest period with low recruitment. In 1999, the biomass of mature crabs fell below the overfished level defined in the fishery management plan (NPFMC 1998; Bob Otto, NMFS, Kodiak, pers. comm.). Stock rebuilding depends on strong recruitment events. If no strong recruitment occurs in the next 2 years, this recruitment pattern will have been broken, and it will be difficult to use historical patterns to project the future recruitment.

There are approximately 20 survey stations north of 61.2°N, but only a few of these were surveyed each year since 1978 (Stevens et al. 1998). Except in 1979, few crabs were caught in these northern stations before 1988 (Fig. 8). The high abundance of small crabs in these northern stations in the 1990s is due to more stations being surveyed and a concentration of small crabs in the northern part of the standard survey area during this period. How many small crabs move to the north or west beyond the survey area is unknown, as few crabs north of 61.2°N reach harvestable size (Fig. 8). The current size limit is 78 mm CW (ADF&G 1998), but processors prefer a minimum size of 102 mm CW for economic reasons. Therefore, the annual catch quota is based on the abundance of male crabs ≥102 mm CW (Stevens et al. 1998).

The estimated highest abundance of crabs ≥102 mm CW occurred in 1991, the year of record catches (Stevens et al. 1998). These crabs most likely recruited to the <45 mm CW size group during 1985-1987. The recruitment during 1991-1994 was also the strongest since the stock has been surveyed (Fig. 8); however, the proportion of these crabs that grew to 102 mm CW in the survey area by 1997-1999 was much smaller than the proportion of recruits from the 1985-1987 period. The locations of small crabs were generally centered more in the southeastern areas during 1985-1987 than during 1991-1994; this suggests that recruits in the middle, eastern, or southern areas may have a better chance to grow to a large size than those in the north. It may be that the increased probability of attaining large commercial sizes in the middle and southern areas is attributable to temperature-dependent growth of juvenile crabs.

Similar to small males, high abundance of immature females occurred during 1978-1979, 1986-1987, and 1991-1994, and high abundance of newshell mature females generally occurred a year later (Fig. 9). Because females do not molt after maturity, the abundance of oldshell mature
Figure 8. Size frequency distribution of area-swept estimates of male snow crab abundance in the eastern Bering Sea. Solid lines represent abundances south of 61.2°N, dotted lines represent abundances north of 61.2°N, and the two vertical dashed lines indicate 45-mm carapace width.
females can be used as an index of survival after maturity. Based on abundances of oldshell mature females during 1981-1983, 1989-1991, and 1996-1998, high natural mortality rates did not occur within the first 3 years of maturity (Fig. 9). The large decline in oldshell female abundance from 1983 to 1984, 1991 to 1992, and 1998 to 1999 may be due to senescence. With extremely low abundance of immature females from 1996 to 1999, the population will continue to be depressed until a strong cohort occurs.

Comparison of spatial distributions of crabs during periods with high and low abundances helps us understand the recruitment patterns. As expected, immature females and small males were more dispersed during periods of high abundance than during periods of low abundance (Fig. 10). These crabs were generally concentrated at 50-100 m and did not occur in high abundance in Bristol Bay (Fig. 11). Newshell mature females were broadly distributed during years of high abundance but concentrated in the north during years of low abundance (Fig. 11). Contraction of spatial distribution during periods of low crab abundance was much greater for mature females than for large males. According to MacCall's (1990) "basin model," the range of a stock expands or contracts around its center as a function of overall abundance and large-scale changes in density-independent factors. Although snow crab distributions in the eastern Bering Sea expand and contract as a function of overall abundance, their population centers change over time. The closest fit to the "basin model" is mature females since the early 1980s with its center around the northwestern part of the standard survey area. Male snow crabs, regardless of abundance, gradually move to deeper water toward the southwest as they grow.

Although the causes are not well understood, periodic or quasiperiodic recruitment patterns are common in many crab and fish stocks. For Bristol Bay red king crabs, strong recruitment occurred in the mid- and late 1970s, and weak year classes occurred in the late 1980s and early and mid-1990s (Zheng et al. 1995). Recruitment in red king crab stocks in the northern Gulf of Alaska and along the Aleutian Islands was strong during the late 1970s and has been weak since the mid-1980s (Zheng and Kruse 2000). Recruitment to eastern Bering Sea blue king crab stocks was strong in the mid- and late 1970s, weak in the mid-1980s, and relatively strong in the early and mid-1990s (Zheng and Kruse 2000). Year classes for Bristol Bay Tanner crabs (Chionoecetes bairdi) from 1968 to 1989 showed a strong cyclic behavior with 13- or 14-year periodicity (Zheng and Kruse 1998). Recruitment in Tanner crab stocks in the northern Gulf of Alaska was strong in the mid-1970s but has been weak since the early 1990s (Zheng and Kruse 2000). The recruitment periodicity of snow crabs in the northwest Gulf of Saint Lawrence is 8 years (Sainte-Marie et al. 1996), whereas periodicity for Dungeness crabs (Cancer magister) off northern California is about 10 years (Higgins et al. 1997). Recruitment of many fish stocks has periodicities ranging from 10 to 26 years (Koslow 1989). Therefore, the apparent recruitment period for the eastern Bering Sea snow crab stock is
Figure 9. Size frequency distribution of area-swept estimates of female snow crab abundance south of 61.2°N in the eastern Bering Sea. Dashed lines represent immature crabs, solid lines represent newshell mature crabs, dotted lines represent oldshell mature crabs, the two vertical dashed lines indicate 45-mm carapace width.
Figure 10. Distributions of immature female and newshell male (<50 mm carapace width) snow crabs during years of high abundance (1978-1979, 1987, and 1991-1993; upper panel) and low abundance (1981-1983 and 1997-1999; lower panel) in the eastern Bering Sea derived from NMFS summer trawl survey data. Crab density is expressed as the number of crabs per square nautical mile. The three depth contour lines represent 50, 100, and 200 m.
Figure 11. Distributions of newshell mature female snow crabs during years of high abundance (1979-1980, 1987-1988, and 1992-1994; upper panel) and low abundance (1984-1985, and 1997-1999; lower panel) in the eastern Bering Sea derived from NMFS summer trawl survey data. Crab density is expressed as the number of crabs per square nautical mile. The three depth contour lines represent 50, 100, and 200 m.
among the shortest observed for crab and fish stocks. The sharp contrast
between strong cohorts and recruitment failures is another feature of snow
krabs in the eastern Bering Sea. Because of very high natural mortality
(Otto 1998), eastern Bering Sea snow krbs cannot sustain long periods of
very weak recruitment without sharp declines in abundance. If strong co-
horts do not occur during the next 2 years, this stock may fall to abun-
dance levels that are much lower than the lowest level previously observed.

Although the summer trawl survey and spring commercial catch data
provide important information about abundance and dynamics of snow
krbs in the eastern Bering Sea, our study raises some important questions
about the krab distribution with respect to the standard survey area. One
line of questioning is concerned with snow krbs in the northernmost (north
of ~61°N) survey stations with respect to exploitation. Is this a juvenile
rearing area? Do these krbs move south during ontogeny or do they re-
main in the north as a separate stock? Based on the general pattern of
southwesterly movement with ontogeny, some of these krbs, if they move
at all, may move to deep water west of the survey area because southward
movement is blocked by the shallow water surrounding St. Matthew Island.
If krbs from these stations move out of the standard survey area, or if
they do not grow to commercial size owing to cold temperatures, they
should be excluded from yield calculations. A second line of questioning
concerns the distribution of snow krbs on and off the shelf with respect to
the areas routinely surveyed. What proportion of the stock exists in waters
deeper than those routinely surveyed? How deep do snow krbs occur?
Older mature males seem to disappear from the surveyed area at high
rates. Do they migrate off the shelf or do they suffer higher mortality?
What is the contribution of deepwater snow krbs to the reproductive stock?
Extending the trawl survey to additional stations to the northwest and to
deep waters off the shelf, augmented with pot surveys if necessary, may
help answer these questions. Answers to these questions will not only lead
to better estimates of stock abundance, but they will also facilitate the
development of optimal harvest strategies.

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References


Yelloweye Rockfish (Sebastes ruberrimus) Life History Parameters Assessed from Areas with Contrasting Fishing Histories

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Abstract
Experimental manipulation of rockfish (Sebastes) stocks has been proposed to accelerate the learning process for fishery stock assessments. In this study, fishers’ anecdotal knowledge of fishing history is used retrospectively as a surrogate for experimental manipulation, to examine the spatial impacts of fishing on yelloweye rockfish (S. ruberrimus). This project was undertaken jointly with the hook and line industry in British Columbia, Canada, as a first attempt at a research collaboration to assess yelloweye rockfish status in a northern and southern area of the coast and at specific sites that fishers identified as heavily and lightly fished. Chartered longline fishing vessels conducted research surveys at the study sites in September 1997 and May 1998. Samples of yelloweye rockfish from the sites were examined for differences in age composition, growth, and size and age at maturity. In addition, commercial logbook data corresponding to the sites were analyzed to determine whether catch rate information was consistent with the research surveys.

Yelloweye rockfish populations showed symptoms consistent with their respective fishing histories. Age distributions were remarkably truncated at one of the heavily fished sites relative to the lightly fished sites. Northern sites, with the shorter exploitation history, yielded larger commercial catch rate observations than the southern sites. This result illustrated that past harvest activities could be detected in sedentary, long-lived rockfish populations and that biological data are capable of assessing the effects. However, the possible ambiguity of results was also demonstrated when alternative explanations for the results could not be discounted.
Introduction

In British Columbia (B.C.), Canada, a hook and line fishery targeting rockfish (*Sebastes*) catches up to 22 species with quillback (*S. maliger*), copper (*S. caurinus*), and yelloweye (*S. ruberrimus*) rockfish traditionally dominating the landings. In recent years, nontraditional deepwater species such as redbanded (*S. babcocki*), rougheye (*S. aleutianus*), and silvergray (*S. brevispinis*) rockfishes have been increasing in proportion. This fishery shares features with many recreational and artisanal fisheries in that fishing vessels operate close to shore and the catch is diverse, with small individual landings marketed to local live or fresh fish retailers.

The fishery has progressed northward along the coast of B.C. over the last 20 years, moving from areas close to local markets to more distant fishing grounds. Declines in rockfish populations in the more accessible southern grounds likely occurred through the serial depletion of local reef areas. Fishers typically maintain high catch rates by continually moving to new fishing reefs. This fishing tactic can have two effects. First, from an assessment perspective, the apparent stability (hyperstability) of catch rates can mask population declines when data are aggregated over large management areas (Hilborn and Walters 1992). Second, from a fisher perspective, the effect of local depletion on overall abundance may appear to be minimal because they can maintain catch rates by moving and hence have the impression of a large population size. In addition, a high participant turnover within the B.C. hook and line rockfish fleet has eroded the historical frame of reference required for the appropriate evaluation of spatial trends in fishing success. New participants find it difficult to accept harvest restrictions as they have been able to find fish and achieve monthly limits in the last few years and have had no comparable experience over the last 20 years.

Assessment and management of nearshore rockfishes (*Sebastes* spp.) is complicated by the constraints imposed by their life history (Leaman 1991) and a lack of information on biological parameters such as maximum age, natural mortality, and size and age at maturity (Love et al. 1990). Catch and effort data from the B.C. fishery required for stock assessment are temporally limited and are reported for areas defined on a large spatial scale (Haigh and Richards 1997). A logbook program was initiated in 1986 but biologists and managers have not used logbook data extensively largely due to the uncertainty in whether catch rate measures abundance (Fox and Starr 1996). Population data such as age distributions and maturity schedules are sparse in B.C., with only a few species and locations sampled in any year.

In general, rockfish abundance cannot be assessed using conventional tagging studies because rockfishes possess a closed swim bladder that is susceptible to barotrauma. Acoustic methods or swept-area trawl surveys are of limited use for nearshore species because of their close association with rocky bottom, although some progress has been made on semipelagic rockfishes (Stanley et al. 2000). These restrictions have led to new approaches using submersibles and video cameras for in situ estimation of
abundance combined with habitat quantification (Richards 1986, O’Connell and Carlile 1993, Palsson 1998, Wakefield et al. 1998). These new methodologies remain expensive relative to traditional sources of fishery-dependent catch and effort data.

Passive collection of fishery-dependent data for long-lived rockfishes is unlikely to provide timely information on stock status (Walters 1998). Fishing experiments over space and time have been proposed to accelerate learning about fish population response to harvest (Walters 1986, 1998; Walters and Collie 1989; Leaman and Stanley 1993); however, few experiments have been implemented for rockfishes. Prospects for experimentation are poor since the managing agency and industry stakeholders must commit to a long-term proposition (Leaman and Stanley 1993) given that the lag between the experimental intervention and the detection of a response can be at least 10-20 years (Francis 1986, Leaman 1991). Thus, consideration should be given to retrospective studies that use fishing history as a surrogate for experimental manipulation. For the data-limited nearshore rockfishes in B.C., traditional fishery-dependent data sources have not provided a time series of spatial contrast in harvest because of an absence of data and poor spatial resolution of the data.

In this paper, we describe a project undertaken in collaboration with the rockfish hook and line industry to use experienced fishers’ knowledge on specific fishing areas and their fishing histories retrospectively to enhance the data collection for stock assessment and evaluate yelloweye rockfish population response to harvests. Yelloweye rockfish have been a target species in the hook and line fishery since its inception. Given that these fish are long-lived and sedentary, past fishing harvests in spatially discrete areas could be evident in the remaining population.

Experienced fishers from the hook and line fleet were asked to identify a “heavily” fished site and a relatively “lightly” fished site in both the southern and northern portions of B.C. Commercial vessels were chartered to conduct research fishing for yelloweye rockfish at the selected sites. Biological samples were obtained to allow comparison of population parameters. Based on the site classification provided by fishers, we expected to find a truncated age spectrum and a reduced size or age at maturity at the heavily fished sites relative to the lightly fished ones. Catch rates were also expected to be lower at the heavily fished sites. The northern sites were expected to show less fishing impacts than the southern sites due to their relatively short fishing history.

Logbook data corresponding to the study sites were then examined to evaluate whether commercial catch rate data were consistent with the results of the research fishing charter. If consistency could be demonstrated among logbook data, research charter data, and industry opinion on fishing history, then fishers may be more willing to provide detailed information in their logbooks. Collected over the long term, this information might reveal differential impacts of fishing at a spatial scale commensurate with localized depletion of yelloweye rockfish populations.
Methods

Data Collection

Experienced fishers were consulted and they identified sites off the west coast of Vancouver Island and the west coast of the Queen Charlotte Islands (Fig. 1). West coast Vancouver Island sites included waters adjacent to Triangle Island (area bounded by $50^\circ42'$ to $50^\circ51'N$ and $129^\circ00'$ to $129^\circ20'W$) and Top Knot (area bounded by $50^\circ28'$ to $50^\circ32'N$ and $128^\circ12'$ to $128^\circ19'W$). The Top Knot site was considered by industry to be the most heavily fished site over the last 20-30 years primarily because of its proximity to home ports and shelter from foul weather. The Triangle site is farther offshore and is frequently subject to inclement weather conditions without many safe anchorages. Sites in the Queen Charlotte Islands included Tasu (area bounded by $52^\circ40'$ to $52^\circ47'N$ and $132^\circ00'$ to $132^\circ16'W$) and Flamingo (area bounded by $52^\circ03'$ to $52^\circ12'N$ and $132^\circ13'$ to $132^\circ27'W$). Fishers reported that the Flamingo site was sheltered, easily accessible, and one of the first areas heavily fished in the Queen Charlotte Islands as the fleet moved northward along the B.C. coast during the late 1980s. The Tasu site was designated as lightly fished due to its isolation and exposure to the weather.

Commercial longline vessels were chartered to conduct targeted fishing for yelloweye rockfish in September 1997 and also in May 1998. Longline gear was standardized to a 500-hook string with a hook spacing of approximately 2.4 m. Size 14/0 circle hooks with a swivel and perlon were clipped onto the groundline (snap gear). Hooks were baited with whole California squid ($Loligo opalescens$). Gear was set and soaked for a 2-hour period delimited by the time that the first anchor was deployed and the time that the last anchor was retrieved. The number of sets ranged from 20 at the Top Knot site to 34 at the Triangle site.

The date, time, duration, position, and minimum and maximum depths fished were recorded for each set. The catch was identified to species for all sets and the number of each species was recorded. For sets where biological sampling was required, all yelloweye rockfish were sampled at sea for fork length (millimeters), sex, and maturity stage. The sagittal otoliths were excised for later age determination using the burnt otolith section method (MacLellan 1997). Maturity state was determined macroscopically and fish were partitioned into one of seven maturity stages (Westrheim 1975). Weights of individual fish could not be determined at sea because conditions aboard the charter vessels precluded accurate weighing.

Maturity Analyses

Maturity ogives were fit to age and size data using logistic regression (Hosmer and Lemeshow 1989). For these analyses, fish at maturity stages 1 and 2 were treated as immature and fish at stages 3-7 were treated as mature. Maturity was therefore a binary response with the probability of a mature fish given by the logistic function.
Figure 1. Coastal British Columbia with the locations of the Flamingo, Tasu, Top Knot, and Triangle study sites identified (insets).
\[ \pi(x_i) = \frac{\exp\left(\sum_{j=0}^{p} \beta_j x_{ij}\right)}{1 + \exp\left(\sum_{j=0}^{p} \beta_j x_{ij}\right)}, \]  
\[ (1) \]

where \( x = (x_{i0}, x_{i1}, \ldots, x_{ip}) \) is a list of \( p \) explanatory variables, \( i = 1, \ldots, n \), and \( x_{i0} = 1 \). The logit transformation (Hosmer and Lemeshow 1989) yields the logistic linear regression

\[ \log\left(\frac{\pi(x_i)}{1 - \pi(x_i)}\right) = \sum_{j=0}^{p} \beta_j x_{ij}. \]  
\[ (2) \]

Nominal scaled variables, or factors, with \( k = 1, \ldots, K \) levels can be represented by \( K-1 \) design variables. Age and length were treated as continuous explanatory variables, while the study site was considered a factor variable with four levels. The probability of maturity was modeled as a function of age, or length, and site. Allowing interaction between age (length) and site permitted a model with essentially a separate linear regression for each site

\[ \log\left(\frac{\pi(x_i)}{1 - \pi(x_i)}\right) = \beta_0 + \tau_k + \beta_k x_{ik}, \]  
\[ (3) \]

where \( \tau_k \) is a factor variable representing the sites. The hypotheses of interaction between age (length) and sites were tested to determine equality of regression slopes using likelihood ratio statistics (Hosmer and Lemeshow 1989). Age (length) at 50% maturity was computed by inverting a simple logistic regression of maturity on age (length) with \( \pi(x_i) = 0.5 \) and solving for the value of the explanatory variable.

**Growth Analysis**

Growth curves were estimated using a model proposed by Schnute (1981) that incorporated a variety of growth forms, including von Bertalanffy (1938) growth. Subsequent description of the growth model (Appendix 1) follows the notation of Schnute (1981). The model involves six parameters, two of which are fixed at arbitrary ages \( \tau_1 \) and \( \tau_2 \), with the restriction that \( \tau_2 > \tau_1 \). If \( Y(t) \) is the size of a fish at time \( t \), then \( y_1 \) is the size of a fish at time \( \tau_1 \) and \( y_2 \) is the size of a fish at time \( \tau_2 \) with \( y_2 > y_1 > 0 \). Two additional parameters, \( a \) and \( b \), determine the shape of the growth curve by controlling the acceleration (deceleration) in growth from times \( \tau_1 \) to \( \tau_2 \). Specialized growth forms are obtained by applying constraints to the parameters \( a \) and \( b \). For example, specialized von Bertalanffy growth is obtained by the constraints
(a > b, b = 1). Schnute (1981) provided the necessary equations to compute classical parameters for the age at time 0, $\tau_0$, and the expected asymptotic size, $y_\infty$, where they exist. Growth curves among areas were compared using likelihood ratio methods as reviewed recently by Quinn and Deriso (1999).

**Logbook Data**

Although commercial logbooks have been collected since 1986, compliance with recording exact location and depth fished was poor until about 1994 (Haigh and Richards 1997). Beginning in 1994 about 75% of the recorded fishing sets included geo-referencing and depth information. Data were included in the analysis if the fishing position was within the boundaries of one of the four study sites, and the reported depth was less than 250 m, to coincide with the fishing conducted by the charter vessels. Some records might be erroneously included or excluded from the analysis due to the limits of the spatial resolution of the data recorded. This filtering effectively limited valid logbook records to 1994 through 1998 data where a total of 79, 172, 136, and 302 sets qualified at the Flamingo, Tasu, Top Knot, and Triangle sites, respectively. Because of the short time span covered by the qualified data and the small sample size in some site-by-year combinations, the data were pooled over time for subsequent analysis.

**Results**

**Age and Maturity Analyses**

Aging data are summarized in Table 1. The youngest yelloweye rockfish caught at the survey sites ranged in age from 7 to 14 years and the oldest fish ranged in age from 35 to 115 years. Very young fish may not be vulnerable to the gear or were not available at the survey sites. The median age was less than the mean age for all sites and both sexes indicated positive skewness. The fall 1997 samples included a greater component of older fish than spring 1998 samples for all sites except Top Knot. Inspection of the quartiles suggested that the age distribution at the Top Knot site was most severely skewed in comparison to the other sites, with the majority of Top Knot fish less than about 20 years of age. Data were pooled by sex and sampling time to produce the age-frequency histograms shown in Fig. 2. A nonparametric kernel density estimate (Silverman 1986) is shown as a solid line overlaid on each histogram. The Top Knot age distribution was sharply truncated at about age 30 relative to the other sites where, in contrast, fish were distributed to at least 80 years of age. At each site there was a large mode of fish centered on age 20 as fish become fully vulnerable to the gear.

The sex ratio varied considerably among sites during each sampling period (numbers by sex in Table 1). Females were dominant at all four sites in the fall 1997 survey, while males were dominant in the spring 1998 survey with the exception of the Tasu site. Inspection of the median, mean,
Table 1. Summary of yelloweye rockfish age and maturity by year, sex, and study site.

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>Sex</th>
<th>n</th>
<th>Min</th>
<th>1st quartile</th>
<th>Median</th>
<th>Mean</th>
<th>3rd quartile</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flamingo</td>
<td>1997</td>
<td>F</td>
<td>239</td>
<td>9</td>
<td>17.0</td>
<td>24</td>
<td>30.57</td>
<td>40.00</td>
<td>93</td>
</tr>
<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td></td>
<td>M</td>
<td>144</td>
<td>9</td>
<td>18.0</td>
<td>25</td>
<td>30.76</td>
<td>39.00</td>
<td>81</td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>F</td>
<td>107</td>
<td>11</td>
<td>18.0</td>
<td>20</td>
<td>26.92</td>
<td>36.50</td>
<td>82</td>
</tr>
<tr>
<td></td>
<td></td>
<td>M</td>
<td>140</td>
<td>9</td>
<td>18.0</td>
<td>21</td>
<td>26.61</td>
<td>28.00</td>
<td>67</td>
</tr>
<tr>
<td>Tasu</td>
<td>1997</td>
<td>F</td>
<td>238</td>
<td>9</td>
<td>16.0</td>
<td>23</td>
<td>30.99</td>
<td>41.00</td>
<td>115</td>
</tr>
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<td></td>
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</tr>
<tr>
<td></td>
<td></td>
<td>M</td>
<td>123</td>
<td>9</td>
<td>18.0</td>
<td>24</td>
<td>29.63</td>
<td>39.00</td>
<td>87</td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>F</td>
<td>123</td>
<td>8</td>
<td>9.7</td>
<td>19</td>
<td>23.50</td>
<td>25.00</td>
<td>83</td>
</tr>
<tr>
<td></td>
<td></td>
<td>M</td>
<td>110</td>
<td>10</td>
<td>17.0</td>
<td>19</td>
<td>23.83</td>
<td>25.75</td>
<td>67</td>
</tr>
<tr>
<td>Top Knot</td>
<td>1997</td>
<td>F</td>
<td>93</td>
<td>7</td>
<td>15.0</td>
<td>17</td>
<td>19.98</td>
<td>19.00</td>
<td>60</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>M</td>
<td>84</td>
<td>8</td>
<td>16.0</td>
<td>17</td>
<td>19.95</td>
<td>18.00</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>F</td>
<td>88</td>
<td>9</td>
<td>17.0</td>
<td>19</td>
<td>19.59</td>
<td>21.00</td>
<td>49</td>
</tr>
<tr>
<td></td>
<td></td>
<td>M</td>
<td>127</td>
<td>9</td>
<td>17.5</td>
<td>19</td>
<td>19.20</td>
<td>21.00</td>
<td>35</td>
</tr>
<tr>
<td>Triangle</td>
<td>1997</td>
<td>F</td>
<td>275</td>
<td>8</td>
<td>21.0</td>
<td>35</td>
<td>36.57</td>
<td>44.50</td>
<td>98</td>
</tr>
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</tr>
<tr>
<td></td>
<td></td>
<td>M</td>
<td>133</td>
<td>13</td>
<td>19.0</td>
<td>24</td>
<td>30.27</td>
<td>39.00</td>
<td>84</td>
</tr>
<tr>
<td></td>
<td>1998</td>
<td>F</td>
<td>204</td>
<td>10</td>
<td>18.0</td>
<td>22</td>
<td>28.42</td>
<td>35.00</td>
<td>88</td>
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<tr>
<td></td>
<td></td>
<td>M</td>
<td>288</td>
<td>9</td>
<td>18.0</td>
<td>21</td>
<td>23.80</td>
<td>26.00</td>
<td>84</td>
</tr>
</tbody>
</table>

The sample size (n) and minimum (Min), maximum (Max), median and mean ages are listed along with the quartiles of the age distribution. The number of 500-hook longline sets fished is indicated in parentheses below each year.
Figure 2. Age-frequency distributions for yelloweye rockfish at the four study sites. Each panel shows an age-frequency histogram with a kernel density estimate overlaid as a solid line.
and 3rd quartile in Table 1 suggests a lower relative abundance of old females in spring at the Flamingo, Tasu, and Triangle sites. These differences in sex ratio may be related to the seasonal behavior patterns of rockfish since the bias in the sex ratios is consistent among sites for both the fall and spring sampling periods. Rockfish copulate in the fall, delay fertilization, then release live larvae in the spring. Sex-specific patterns of movement on a seasonal basis have not been documented for yelloweye rockfish; however, seasonal depth-related movement on a small spatial scale is known for other rockfish species (Matthews 1990).

Due to the prevailing bathymetry, fishing at the Top Knot site was restricted to a range of about 35-100 m. The depth restriction introduced possible confounding of the age differences with depth, since deeper fishing was possible at the other sites. However, plots of depth of fishing against age for each site (Fig. 3) showed that the first 100 m sampled at the Flamingo and Triangle sites included fish up to 80 years of age. Thus, it seems that shallow depths fished at Top Knot do not preclude the occurrence of fish older than 60 years. Sample size could also have affected the results at Top Knot, where about half the specimens were obtained relative to the other sites due to the lower catch rate.

The oldest fish observed at Top Knot was 60 years of age (Table 1). An ad hoc investigation of the effect of sample size on the upper tail of the age-frequency distribution was conducted by drawing 1,000 random samples from the age-frequency distribution observed at Triangle (Fig. 2). Samples of size 400 and 200 were selected to simulate the sample sizes obtained in a single year at Triangle and Top Knot, respectively. Of the 1,000 simulated age distributions of sample size 400, 1,000 included fish older than 60 years of age and 995 included fish older than 70 years of age. The 1,000 simulated age distributions of sample size 200 contained fish older than 60 years in 996 cases, and fish older than 70 years in 913 cases. Thus, a sample of 200 fish, similar to the sample size obtained at Top Knot, should include fish older than 70 years if they are present in the population. We concluded that the absence of fish older than 60 years at Top Knot was unlikely to be an artifact of the lower sample size.

Independent simple logistic regressions of maturity on age (length) were computed for each site to produce the estimates of age ($A_{50}$) and length ($L_{50}$) at 50% maturity listed in Table 2. Only data from female yelloweye rockfish sampled in May 1998 were used in these calculations. The maturity stage of the female gonad is less ambiguous in spring since larvae are either still present or have recently been extruded. A multiple logistic regression of maturity against age and site was fit to determine whether differences existed among the sites. A model that included an age-by-site interaction was compared to one with only the main effects of age and site. The interaction term was not significant ($\chi^2_{0.053} = 2.617, P = 0.454$), which suggested a model with a common slope coefficient for age but different intercepts for each site. The intercepts differed since the main effect of site was significant ($\chi^2_{0.053} = 8.476, P = 0.037$). Inspection of the estimates
Table 2. Age (years) and length (cm) at 50% maturity for yelloweye rockfish sampled at the study sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>$A_{50}$</th>
<th>$L_{50}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flamingo</td>
<td>20.3 (17.6, 23.0)</td>
<td>49.1 (47.4, 50.8)</td>
</tr>
<tr>
<td>Tasu</td>
<td>18.9 (17.5, 20.5)</td>
<td>48.5 (47.0, 49.9)</td>
</tr>
<tr>
<td>Top Knot</td>
<td>16.5 (13.1, 18.4)</td>
<td>42.1 (40.0, 43.7)</td>
</tr>
<tr>
<td>Triangle</td>
<td>17.2 (14.3, 18.9)</td>
<td>42.4 (40.1, 44.0)</td>
</tr>
</tbody>
</table>

95% Confidence intervals are indicated in parentheses.

Figure 3. Depth caught as a function of age for fish sampled in 1997 and 1998 at the four study sites. The horizontal dashed lines in each panel correspond to the depth interval sampled at the Top Knot site. The observations have been randomly offset along the depth axis to expose the density of the observations.
of $A_0$ and associated confidence intervals suggested that Flamingo and Tasu estimates were older than Top Knot and Triangle estimates. To test for a difference, the main effect of site was replaced by a factor that compared Flamingo and Tasu against Top Knot and Triangle, i.e., Queen Charlotte Island sites against Vancouver Island sites. A significant difference was found between the two groupings ($\chi^2 = 7.036, P = 0.008$).

Similar results were found for the analysis of maturity against size and sites. The interaction between size and site effects was not significant ($\chi^2 = 4.939, P = 0.176$), while the main effect of site was significant ($\chi^2 = 50.4, P < 0.001$). As before, a model with a common slope coefficient for size but different intercepts for each site was adequate. Inspection of $L_{50}$ estimates and associated confidence intervals in Table 2, once again, suggest that the Flamingo and Tasu data be compared to the Top Knot and Triangle data. The difference between the two groups was significant ($\chi^2 = 49.2, P < 0.001$), with fish from the Queen Charlotte Islands sites larger at 50% maturity than fish from the Vancouver Island sites.

**Growth**

Exploratory plots of the length-at-age relationship by sex and year (not shown) suggested little difference in the growth pattern between fish sampled in 1997 and 1998. Consequently, data were pooled from each sampling period to produce the length-at-age plots shown in Fig. 4. Growth curves were fit to the data for each site and sex using Schnute’s (1981) model, assuming additive normal errors and with $\tau_1 = 10$ and $\tau_2 = 60$. The values of $a$ and $b$ were not subject to constraints for these fits; i.e., the full model was fit (Appendix 1). The growth curves are shown as solid lines in each panel of Fig. 4 with the corresponding parameter estimates and their standard errors listed in Table 3. At the Flamingo, Tasu, and Triangle sites, the strong tendency for rockfish growth to asymptote early in the life span is evident. For the Top Knot site, the relative absence of fish over about 20 years of age, and the complete absence of fish older than 60 years of age, distorts the growth curves to the point where there is no growth asymptote for males.

Inspection of the standard errors for $b$ indicated that it is the least precisely known parameter in the model. Residual plots (not shown) showed no obvious lack of fit or patterns that would suggest a multiplicative error structure. Estimates of size at age 10 ($y_1$) and age 60 ($y_2$) were similar among the sites. To determine whether the growth form could be simplified, the model was applied to the data with the constraints ($a > 0, b = 1$), which corresponds to von Bertalanffy growth. The hypothesis that $b = 1$ was tested for each site and sex independently by comparing the observed likelihood ratio statistic to $\chi^2 = 3.84$ for significance (Table 3). Growth of female yelloweye rockfish at the Flamingo site, and of males at the Top Knot and Triangle sites, was best explained using the full model rather than the specialized von Bertalanffy model. Regardless of the model used, the standard errors of parameter estimates were relatively large for the Top Knot fits,
Figure 4. Length at age for yelloweye rockfish males and females from the four study sites. The solid line in each panel indicates the growth curve obtained using Schnute’s (1981) model.
Table 3. Summary of parameter estimates and standard errors (SE) from growth model fits.

<table>
<thead>
<tr>
<th>Site</th>
<th>$y_1$ S.E.($y_1$)</th>
<th>$y_2$ S.E.($y_2$)</th>
<th>$a$ S.E.($a$)</th>
<th>$b$ S.E.($b$)</th>
<th>$\tau_0$</th>
<th>$y_\infty$</th>
<th>$\sigma^2$</th>
<th>$n$</th>
<th>ln $L$</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Females</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flamingo</td>
<td>37.3 1.00</td>
<td>63.9 0.53</td>
<td>0.114 0.027</td>
<td>-2.742 1.848</td>
<td>—</td>
<td>64.20</td>
<td>16.28</td>
<td>353</td>
<td>993.29</td>
<td>6.81*</td>
</tr>
<tr>
<td>Tasu</td>
<td>37.5 0.79</td>
<td>65.0 0.49</td>
<td>0.066 0.015</td>
<td>0.055 1.161</td>
<td>-42.83</td>
<td>63.38</td>
<td>14.41</td>
<td>338</td>
<td>930.53</td>
<td>0.760</td>
</tr>
<tr>
<td>Top Knot</td>
<td>36.5 1.17</td>
<td>62.8 2.87</td>
<td>0.103 0.109</td>
<td>-3.093 6.428</td>
<td>—</td>
<td>63.30</td>
<td>23.88</td>
<td>181</td>
<td>544.00</td>
<td>0.578</td>
</tr>
<tr>
<td>Triangle</td>
<td>36.7 1.01</td>
<td>61.6 0.36</td>
<td>0.063 0.013</td>
<td>-0.451 1.246</td>
<td>—</td>
<td>63.25</td>
<td>13.78</td>
<td>512</td>
<td>1398.09</td>
<td>1.67</td>
</tr>
<tr>
<td>POOLED</td>
<td>36.6 0.92</td>
<td>66.2 0.46</td>
<td>0.049 0.012</td>
<td>1.239 0.898</td>
<td>-2.54</td>
<td>68.89</td>
<td>22.21</td>
<td>1176</td>
<td>3485.02</td>
<td>761.8*</td>
</tr>
<tr>
<td><strong>Males</strong></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Flamingo</td>
<td>35.2 0.84</td>
<td>64.3 0.47</td>
<td>0.062 0.005</td>
<td>1</td>
<td>-2.29</td>
<td>65.69</td>
<td>16.59</td>
<td>353</td>
<td>996.69</td>
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</tr>
<tr>
<td>Tasu</td>
<td>37.0 0.64</td>
<td>65.0 0.47</td>
<td>0.054 0.004</td>
<td>1</td>
<td>-4.84</td>
<td>67.05</td>
<td>14.45</td>
<td>338</td>
<td>930.91</td>
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<tr>
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Pooled label indicates the fit with common parameters by sex. Significant likelihood ratio test statistics ($\chi^2$) are denoted by asterisks.
and for $y_2$ in particular due to the absence of older fish. Differences in growth among areas were examined independently for each sex by comparing the sum of the likelihood values over sites to the likelihood value obtained by pooling the data over sites and fitting a model with a common parameter set $\Theta = (\tau_1, \tau_2, y_1, y_2, a, b)$ and unequal variances, $\sigma^2_i$, $i = 1, \ldots, 4$. For both the full and constrained model there were significant differences in the parameter sets $\Theta_i = (\tau_1, \tau_2, y_1, y_2, a, b)$ among the sites (Table 3, row labeled “Pooled”).

**Catch Rates**

The number of yelloweye rockfish caught on each set by the charter vessels was plotted against depth (Fig. 5). Catch rates at Top Knot were lower and less variable than catch rates at other sites. The largest catch rates were observed at about 150 m depth with the exception of the Top Knot site where all fishing occurred at depths less than 100 m. Given the typically skewed distribution of catch rate data, and the unequal variance among sites, a nonparametric Kruskal-Wallis test (Conover 1980) was used to test the hypothesis that the catch rate distribution functions were identical among sites. The test was significant ($\chi^2_{30.05} = 11.34, P < 0.01$), indicating that at least one site tended to yield larger catch rates than at least one of the other sites. A multiple comparison procedure described by Conover (1980) was used to conduct pairwise comparisons of the sites and confirmed that no differences among distributions could be detected for the Flamingo, Tasu, and Triangle sites and the Top Knot catch rate distribution differed from the other sites.

Plots of catch rates against depth for the 1994-1998 commercial logbook data (Fig. 6) showed patterns similar to those observed for the survey data (Fig. 5). Depths of up to 150 meters fished at Top Knot failed to yield catch rates as large as those observed from similar depths at the Triangle and Flamingo sites. The test of identical catch rate distribution functions among sites was rejected (Kruskal-Wallis $\chi^2_{30.05} = 32.25, P < 0.01$). Pairwise multiple comparisons showed that a difference in distribution functions existed between the Top Knot and Triangle sites, and that both differed from the Flamingo and Tasu sites. No difference in catch rate distributions was detected between the Flamingo and Tasu sites.

**Discussion**

We are entering a period where greater collaboration with the B.C. hook and line industry on rockfish assessment problems is possible, provided mutual confidence in the experimental process is maintained. The lack of an abundance-based assessment for nearshore rockfishes in B.C. has resulted in low industry confidence in recommended catch limits. At the same time, industry is eager for a larger role in the collection and analysis of data for stock assessment. For fisheries where little historical fishing information is available, using firsthand knowledge about the development
Figure 5. Research catch rates (number of yelloweye rockfish per set) as a function of depth at the four sites in 1997 (open circles) and 1998 (closed circles). The trend line (solid line) in each panel was computed using loess regression. Vertical dashed lines delimit the depth range sampled at the Top Knot site.
Figure 6. Commercial catch rates (number of yelloweye rockfish per 500-hook set) as a function of depth at the four study sites. The trend line (solid line) in each panel was computed using loess regression. Vertical dashed lines delimit the depth range sampled at the Top Knot site.
of the fishery from experienced fishers can be a valuable source of information on rockfish distribution, their preferred habitats, and historical population levels. This anecdotal information can be utilized in retrospective analyses where harvest-related processes can be investigated. Fishers also express their own scientific skepticism that inevitably enriches the experimental design (Stanley et al. 2000). Their involvement may also bring them a full appreciation of the investment in project design and the data collection required to show clear results. Furthermore, they make it possible to carry out projects by contributing to the costs of research and data collection either directly or through the provision of vessel time and technical support.

Although the results obtained at the Top Knot site were consistent with expectations, the truncated age structure is difficult to interpret in the absence of data to support a sequential population analysis or an absolute abundance estimate. The difficulty lies in distinguishing whether the observed age structure is a result of juvenation of the population due to excessive fishing or a result of increased recruitment to a particular site. Alternatively, age-dependent emigration of fishes either spatially, or by depth, could explain a truncated age distribution sampled from a discrete locality.

Like the interpretation of the age distributions, it is hard to attribute biological significance to statistical differences in maturity and growth estimates without a modeling framework to evaluate long-term population implications. The more recent exploitation of Queen Charlotte Island sites relative to the Vancouver Island sites may contribute to the differences observed in the maturity estimates. Growth comparisons among the four sites detected differences in the growth parameters. However, much of the difference can be attributed to the lack of older fish at the Top Knot site where there were insufficient data to define a growth asymptote for old male fish and estimates of size at age 60 were poorly determined.

Although logbook data have been collected since 1986, the completeness of the data was poor until the early 1990s. However, patterns in survey and logbook catch rates between Top Knot and the other sites were consistent. This project demonstrated to the industry participants that harvest activities could leave symptoms of fishing on yelloweye rockfish populations. Explanations for the truncated age distribution and lower catch rates at the Top Knot site that do not require fishing pressure illustrated the possible ambiguity of results. These alternative explanations may provide impetus for future work. Indeed, fishery managers and industry agreed to close the three southernmost study sites to rockfish harvest in 1999. This intervention affords an opportunity to examine whether the signal created by the age truncation at Top Knot is a result of local recruitment or age-dependent movement of fish. If on subsequent sampling the age mode at 20 years is shifted forward an appropriate interval, one conclusion would be that the closure was effective at protecting a resident population of yelloweye rockfish. If the mode does not propagate into older ages, then
alternative explanations such as differential migration of fish by age or depth, strong incoming recruitment, or undocumented harvests are plausible. Industry collaboration in future investigations is a key to eliminating the latter explanation.

Recent support in the fisheries literature to manage rockfishes using area closures (Yoklavich 1998, Walters and Bonfil 1999, Parker et al. 2000) raises questions about the extent and distribution of closures required to ensure conservation. The requirement to monitor the effectiveness of closed areas means that performance diagnostics, including changes in age structure, growth, and maturity characteristics, are required for nearshore rockfishes since estimates of abundance are generally not available. Retrospective studies for sedentary, long-lived fishes, which contrast areas with different exploitation histories, may be a means of identifying the requisite measures. Furthermore, the involvement of industry in this type of data collection and interpretation may assist in building support for spatial management measures such as closed areas.

Acknowledgments

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References


Love, M.S., P. Morris, M. McCrae, and R. Collins. 1990. Life history aspects of 19 rockfish species (Scorpaenidae: Sebastes) from the southern California Bight. NOAA-TR-NMFS-87, La Jolla, California.


Appendix 1

This appendix describes the growth model (Schnute 1981) used to compare growth curves among areas. The model involves six parameters \( \Theta = (\tau_1, \tau_2, y_1, y_2, a, b) \), where \( \tau_1 \) and \( \tau_2 \) are two arbitrary ages in the life a fish, such that \( \tau_2 > \tau_1 \). The parameter \( y_1 \) is the size of a fish at time \( \tau_1 \) and \( y_2 \) is the size of a fish at time \( \tau_2 \) with \( y_2 > y_1 > 0 \). Parameters \( a \) and \( b \), determine the shape of the growth curve by controlling the acceleration (deceleration) in growth from times \( \tau_1 \) to \( \tau_2 \). The parameter \( a \) has units \((\text{time}^{-1})\), while \( b \) is dimensionless. Although mathematical expression of the model has four cases, these four cases actually represent the limiting forms of a single equation as \( a \) and/or \( b \) approach 0. Let \( Y(t) \) be the size at time \( t \), then:

**Case 1:** \( a \neq 0, b \neq 0 \)

\[
Y(t) = y_1^b + \left(y_2^b - y_1^b\right) \frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \, ^{\gamma/b},
\]

(1)

**Case 2:** \( a \neq 0, b = 0 \)

\[
Y(t) = y_1 \exp \left[ \ln(y_2/y_1) \frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right],
\]

(2)

**Case 3:** \( a = 0, b \neq 0 \)

\[
Y(t) = y_1^b + \left(y_2^b - y_1^b\right) \frac{t-\tau_1}{\tau_2-\tau_1} \, ^{\gamma/b},
\]

(3)

**Case 4:** \( a = 0, b = 0 \)

\[
Y(t) = y_1 \exp \left[ \ln(y_2/y_1) \frac{t-\tau_1}{\tau_2-\tau_1} \right].
\]

(4)

Suppose that the age and size of a sample of fish are measured to give \( n \) data points \((t_j, Y_j), j = 1,2,...,n\). If the ages are determined exactly, then additive or multiplicative errors may be specified

\[
\hat{Y}_j = Y_j + \sigma e_j; \quad j = 1,...,n,
\]

(5)
\( \hat{Y}_j = Y_j e^{\alpha j}; \quad j = 1, \ldots, n, \)  \hspace{1cm} (6)

where the random variables \( \varepsilon_j (j = 1, \ldots, n) \) are assumed to be normally distributed with mean 0 and variance \( \sigma^2 \).

There are compelling reasons to adopt this formulation of growth. The parameters \( \Phi = (\tau_1, \tau_2, \gamma_1, \gamma_2, a, b) \) always exist even in cases where, for example, the most appropriate model does not include a maximum growth asymptote. Model parameters are expressed as quantities that have direct biological interpretation, and the parameterization has superior statistical properties (Ratkowsky 1986). In any case, Schnute (1981) provided transition equations to convert the parameter set \( \Phi \) to those used in the various specialized growth forms.

We used likelihood ratio tests to compare growth among groups. Suppose size-at-age data are collected for \( i = 1, \ldots, m \) groups of data. Given that an appropriate growth formulation has been selected, there are four possible situations defined by equal or unequal variances \( \sigma^2 \) and independent or common parameter sets \( \Phi \) (Quinn and Deriso 1999). The full model is defined by independent parameter sets and unequal variances; all other situations are obtained by reduction in the number of parameters. For example, a reduced model can be specified by assuming a common parameter set and equal variances among groups, i.e., fitting the growth model to the pooled data. Under the assumption of independent, additive normal errors, the likelihood of the data given the parameters for group \( i \) is specified by

\[
L_i(\Phi_i, \sigma_i | \{Y_{ij}\}) = (2\pi \sigma_i^2)^{-n_{ij}/2} \exp \left[-\frac{1}{2\sigma_i^2} \sum_{j=1}^{n_{ij}} (Y_{ij} - \hat{Y}_{ij})^2 \right].
\]  \hspace{1cm} (7)

In practice, parameter estimates \( \hat{\Phi}_i, \hat{\sigma}_i^2 \) are determined by minimizing the (negative) of the logarithm of the likelihood function, calculated by summation of the log-likelihood components over the \( m \) groups:

\[
\ln L = \sum_{i=1}^{m} \ln L_i(\hat{\Phi}_i, \hat{\sigma}_i | \{Y_{ij}\}) = \sum_{i=1}^{m} \left[ -\frac{n_i}{2} \log(2\pi \hat{\sigma}_i^2) - \frac{1}{2\hat{\sigma}_i^2} \sum_{j=1}^{n_i} (Y_{ij} - \hat{Y}_{ij})^2 \right],
\]  \hspace{1cm} (8)

where

\[
\hat{\sigma}_i^2 = \frac{1}{n_i} \sum_{j=1}^{n_i} (Y_{ij} - \hat{Y}_{ij})^2.
\]  \hspace{1cm} (9)

The likelihood ratio statistic
\[ X^2 = 2 \ln L_R - 2 \ln L_F \] (10)

can be used to test a hypothesis between a full (F) and reduced (R) model by comparing \( X^2 \) to a chi-square critical value \( \chi^2 \) with degrees of freedom equal to the difference in the number of parameters between full and reduced models.