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A Shift in Pink Salmon Dominance in the Okhotsk Sea of Hokkaido in Relation to Coastal Environments during Early Sea Life

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Abstract: Although dominance by the even-year line of pink salmon in the Okhotsk Sea of Hokkaido was maintained from the 1990 to 2000 brood-years, a shift back to odd-numbered year returns occurred. We have monitored the distribution of juvenile pink salmon and the ocean environment in the Abashiri coastal waters of the Okhotsk Sea since 2002 when juveniles from 2001 brood-year pink salmon went to sea. SST measurements were much higher when odd-year juveniles entered coastal waters in 2002 (8.2–9.7ºC) and 2004 (5.5–12.0ºC) than when even-year juveniles entered coastal waters in 2003 (5.3–6.8ºC). Pink salmon juveniles were widely distributed along the coast in May 2002 and 2004, while juveniles in 2003 were densely distributed and restricted to the littoral zone. Mean fork length in 2003 was significantly smaller than those in the other two years. The final number of juveniles captured along the coast from May to July 2003 was 4,700, much lower than the numbers caught in the other two years (19,200 and 21,900, respectively). More interestingly, the abundance of adults in 2003 from pink juveniles (2001 brood year) that experienced the warm temperatures in 2002 was much higher than adults in 2004 that had experienced the cooler temperatures in 2003, resulting in the shift in dominance. These results suggest that shifting between dominance lines might be caused by thermal conditions in coastal waters that result in either long estuary residence times with larger aggregations of fish or rapid dispersal with wider occupation of nursery grounds by pink salmon juveniles after seaward migration.

Keywords: pink salmon, two-year cycle, dominance shift, early sea life, SST, estuary residence

INTRODUCTION

Pink salmon (*Oncorhynchus gorbuscha*) occur mainly in eastern Hokkaido, especially in the Okhotsk Sea. Numbers of pink salmon were low from the 1970s to the 1980s with a two-year cycle of dominance in odd-numbered years. However, in the early 1990s the population size increased sharply, especially in even years, exceeding 10 million. Subsequently, a shift from odd- to even-year dominance occurred (Nagata and Kaeriyama 2004). More interestingly, a shift back to dominance in odd-numbered years has occurred recently.

A great difference in population size between even and odd years is well known in the North Pacific Ocean (Heard 1991). This two-year cycle dominance tends to persist because pink salmon have a two-year life cycle. Although the most probable cause of the initial disparity between two lines is either a disastrous decrease (or a dramatic increase) in the survival rate of one line over the other (Neave 1953; Ricker 1962), little information has been collected to clarify the mechanism that causes the shift in the dominant year. It has been assumed that high mortality of salmonids often occurs soon after juveniles or smolts enter the ocean (Bax 1983; Pearcy 1992; Mueter et al. 2002). The survival rate for pink salmon, especially, may be influenced by mortality during early sea life rather than by environmental factors during downstream migration (Manzer and Shepard 1962; Parker 1965, 1968; Healey 1991; Willette et al. 2001), such as prey availability, feeding condition, zooplankton density and timing of the zooplankton bloom (Healey 1980, 1991; Willette 2001; Willette et al. 2001). Therefore, high mortality or survival during early sea life may cause the shift in pink salmon dominance.

We have monitored the distribution of juvenile pink and chum salmon (*O. keta*) and the ocean environment in the Abashiri coastal waters of the Okhotsk Sea since 2002 when the 2001 brood-year fish entered the sea as juveniles (Nagata et al. 2004, 2005; Ando et al. 2005; Asami et al. 2005). In 2003, a shift back to dominance in odd-numbered years occurred. In this paper we propose a hypothesis that the shift from even- to odd-year dominance in recent years might be caused by differences in growth and habitat conditions in coastal waters during the early sea life of pink salmon.

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MATERIALS AND METHODS

Population Structure of Pink Salmon in Okhotsk Sea of Hokkaido

In order to investigate status of pink salmon and the shift in dominance in the Okhotsk Sea of Hokkaido, data on commercial catches and escapement were analyzed. Annual data on commercial catches in the Okhotsk coastal waters from Cape Soya to the tip of the Shiretoko Peninsula were collected by staff of the Hokkaido Fish Hatchery in collaboration with the local fisheries cooperatives. Escapement data were collected in the 14–26 rivers where salmon enhancement programs and hatcheries operate weirs. We calculated the spawer-to-recruit (SR) index showing survival rates that normalized the data and removed possible within-stock, density-dependent effects (Peterman et al. 1998). This index was the time series of brood-year residuals (i.e., anomalies) from a Ricker (1954) stock-recruitment model. We used available data for odd-year and even-year lines to fit a Ricker model by linear regression of *Ln* (recruit per spawner) on spawner abundance and then calculated SR values as deviations from the line (Peterman et al. 1998).

Sampling Survey and Biological Analysis

Twelve study sites were established in Abashiri coastal waters (Fig. 1). Four sites (A1–D1) were set up 1 km offshore. Four study sites were also established at 4 km (A2–D2) and 7 km (A3–D3) offshore, respectively. The depths at the study sites were 10–15 m at 1 km offshore, 20–30 m at 4 km offshore and 30–40 m at 7 km offshore. Pink juveniles were collected with a surface trawl net (8 m wide x 5 m deep mouth, 18 m long, with wing nets 7 m long and a central bag with 5 mm mesh). The trawl was towed along each transect in the 1 to 2 m surface layer for 1–2 km at 4–6 km/h during the day (5:00–14:00) at 10-d intervals from late April to early July 2004 and mid July 2002 and 2003. Several sites were not sampled because of adverse weather conditions. One study site at the Abashiri fishing port was established in late May 2003. The trawl net was towed there for 0.5 km to capture fish. Another study site was set up in the littoral zone. Pink salmon juveniles were captured using a beach seine (3.5 m wide x 2 m deep mouth, 10 m long, with wing nets 3 m long and a central bag with 3 mm mesh) from 2002 (late May only) to 2004.

Captured fish were sacrificed with an overdose of MS 222 to prevent regurgitation and defecation, and preserved in 5% neutralized freshwater formalin. They were transferred to 70% ethanol after 12 to 24 h. When large numbers of fish were captured, random samples were preserved and the remainder were released soon after weights were obtained to estimate the total number of fish captured. CPUE in surface trawl nets was computed as the number of pink salmon juveniles caught after 2 km towing because of differences in towing distances among study sites. CPUE in beach seines used the actual number of pink salmon juveniles caught because there was little difference in the towing distances between sites. Sea surface temperature (SST) and salinity (SSS) at each study site were measured with STD.

Because chum salmon juveniles were also captured, pink salmon were distinguished from chum by parr marks and pigmentation of the tail against a white background (Phillips 1977; Shirahata 1981). If these characteristics were not evident, gill rakers were counted, because pink salmon have more gill rakers than chum salmon of similar size (Okada and Nishiyama 1970; Shirahata 1981). Pink salmon juveniles at each study site were measured for fork length and wet body weight, to the nearest 1 mm and 0.01 g, respectively. Stomachs in juveniles were dissected and weighed to the nearest 0.0001 g. After the contents were removed, the empty stomachs were re-measured to calculate the weight of stomach contents. A stomach content index (SCI) was calculated by the following formula: SCI (%) = (weight of stomach contents) / (body weight) x 100. Prey items were identified according to taxonomic categories using a binocular microscope.

Statistical Analysis

Differences in fork length and SCI after arcsin square-root transformation of data on juvenile pink salmon captured from the littoral area, and the 1 km, 4 km, and 7 km off-

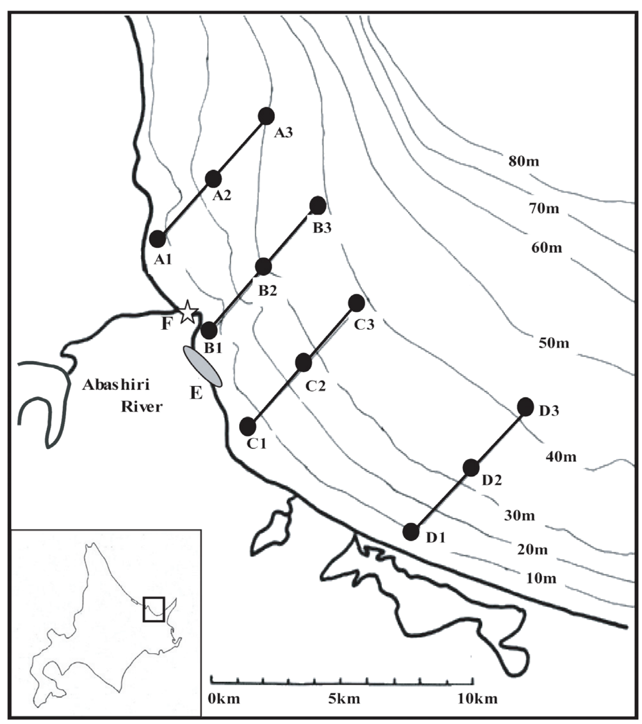

Fig. 1. Map showing the study sites at the fishing port (F), littoral areas (E), and 1 km, 4 km and 7 km off the Abashiri coast (A–D) in the Okhotsk Sea.

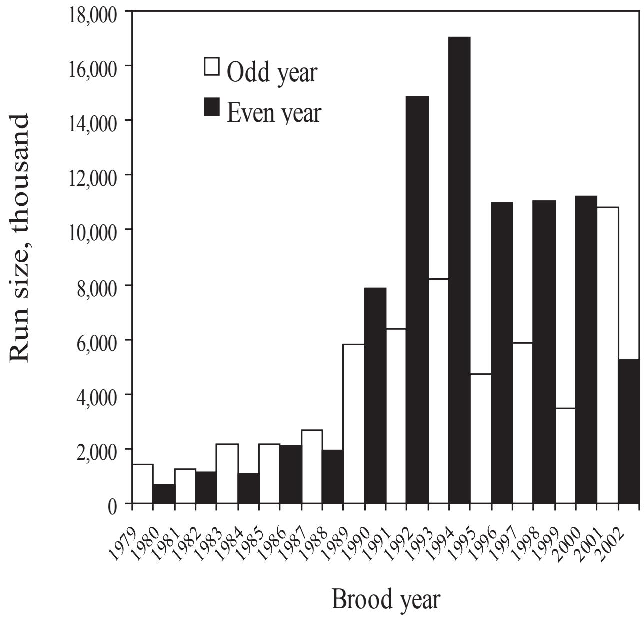

Fig. 2. Population size based on commercial catches and escapement of pink salmon in the Okhotsk Sea of Hokkaido since the 1979 brood year.

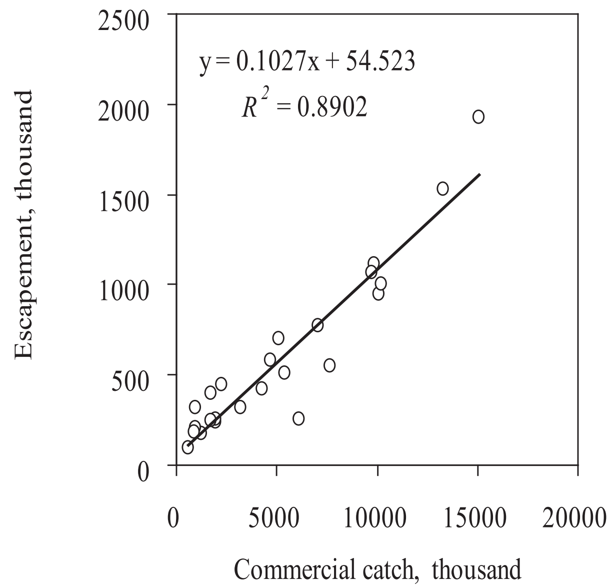

Fig. 3. Relationships between commercial catch and escapement of pink salmon in the Okhotsk Sea of Hokkaido since the 1979 brood year.

shore transects in the same year or among three years were compared with a one-way analysis of variance (ANOVA, p = 0.05). If a significant difference was found, a multiple comparison between them was carried out using Scheffe's test (Zar 1984). Data for each offshore transect consisted of information from all 4 sites (A, B, C and D).

Modes of spatial distribution for juvenile pink salmon in the coastal waters were analyzed using I_δ (Morisita 1959). $I_\delta = (\Sigma^{N}_{i} = 1ni\ (ni - 1))\ N / n\ (n - 1)$ where N is the number of samples, ni is the number of individuals in the ith sample, and n is the total number of individuals in all the samples. If I_δ equals 1, the dispersion of individuals is random; if > 1, the individuals are aggregated; and if < 1, the population has a regular pattern. The significance of the deviation from 1 is tested by the statistic F, where $F = (I_\delta (n - 1) + N - 1)/(N - 1)$ (Poole 1974).

Electivity indices (E) for food preference were calculated from the formula of Jacobs (1974): $E = (ri - pi) / (ri + pi - 2ripi)$ where ri is the proportion of i prey animal consumed by fish and pi is the proportion of the i animal available at the study site. Electivity ranged from -1 to +1; -1 indicates the strongest negative preference and +1 the strongest positive preference. Zooplankton data reported by Asami et al. (2007) were used for analysis.

RESULTS

Pink Salmon Population Structure

Population sizes of pink salmon in the Okhotsk Sea of Hokkaido remained low from 1970s to 1980s (Fig. 2), showing dominance in odd-numbered years. In the early 1990s, population sizes increased sharply (often exceeding 10 million fish), especially in even years. After that a shift from odd- to even-year dominance occurred. While even-year dominance was maintained from the 1990 to 2000 brood year, a shift back to odd-numbered year dominance occurred beginning with the 2001 brood year. The relationship between commercial catch and escapement was positively correlated (Fig. 3), strongly suggesting that pink salmon captured by commercial fishing originated from strains that reproduce in the rivers flowing into the Okhotsk Sea of Hokkaido.

The highest SR index in even-years was recorded in the 1990 brood year when even-numbered year populations dominated. After that, SR values decreased gradually eventually reaching the lowest level in the 2002 brood year (Fig. 4). In contrast the SR indices suddenly skyrocketed in the 2001 brood year when dominance shifted to odd-numbered years, although SR indices in odd years were also relatively high from 1989 to 1993, then decreasing until the 2001 brood year. These results suggest that survival of pink salmon in the 2001 brood year was high and survival in the 2002 brood year was low.

SST and SSS in Coastal Waters

Although the mean SST at each offshore transect in late April in 2002 was < 5°C, it rapidly increased, exceeding 8°C in early May, and then increased further in June, eventually reaching 14–15°C in mid July when our investigation was completed (Fig. 5). On the other hand, mean SST in 2003 was colder than in 2002 until mid June. In 2003 while mean SST at the 1 km offshore transect in late April was 4°C the same as in 2002, the mean SST at the 4 and 7 km offshore

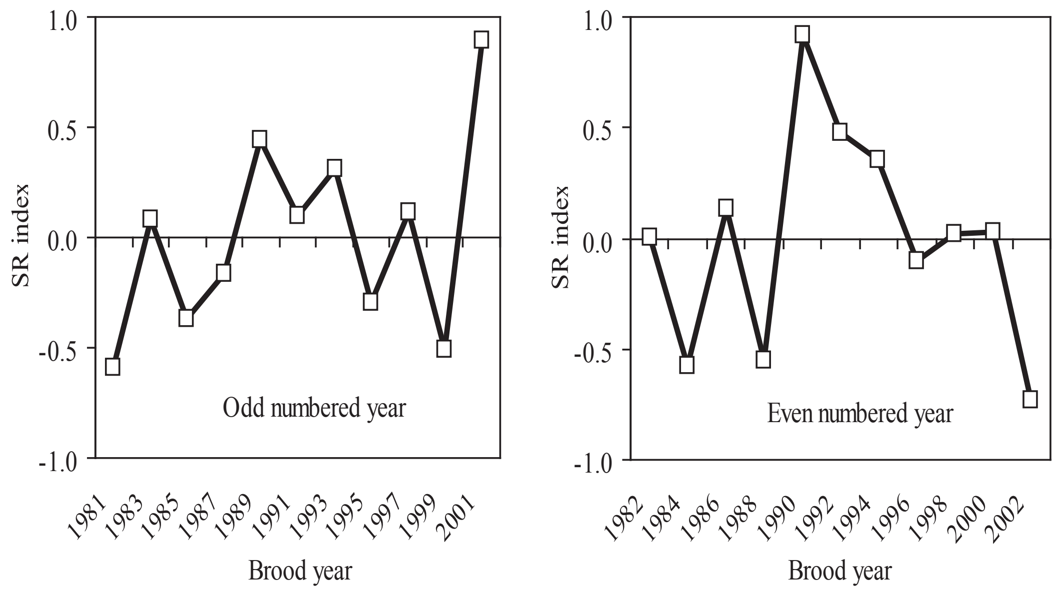

Fig. 4. Time series of spawner-to-recruit (SR) indices for pink salmon in odd- and even-numbered years in the Okhotsk Sea of Hokkaido. SR indices are residuals from the best-fit Ricker (1962) model.

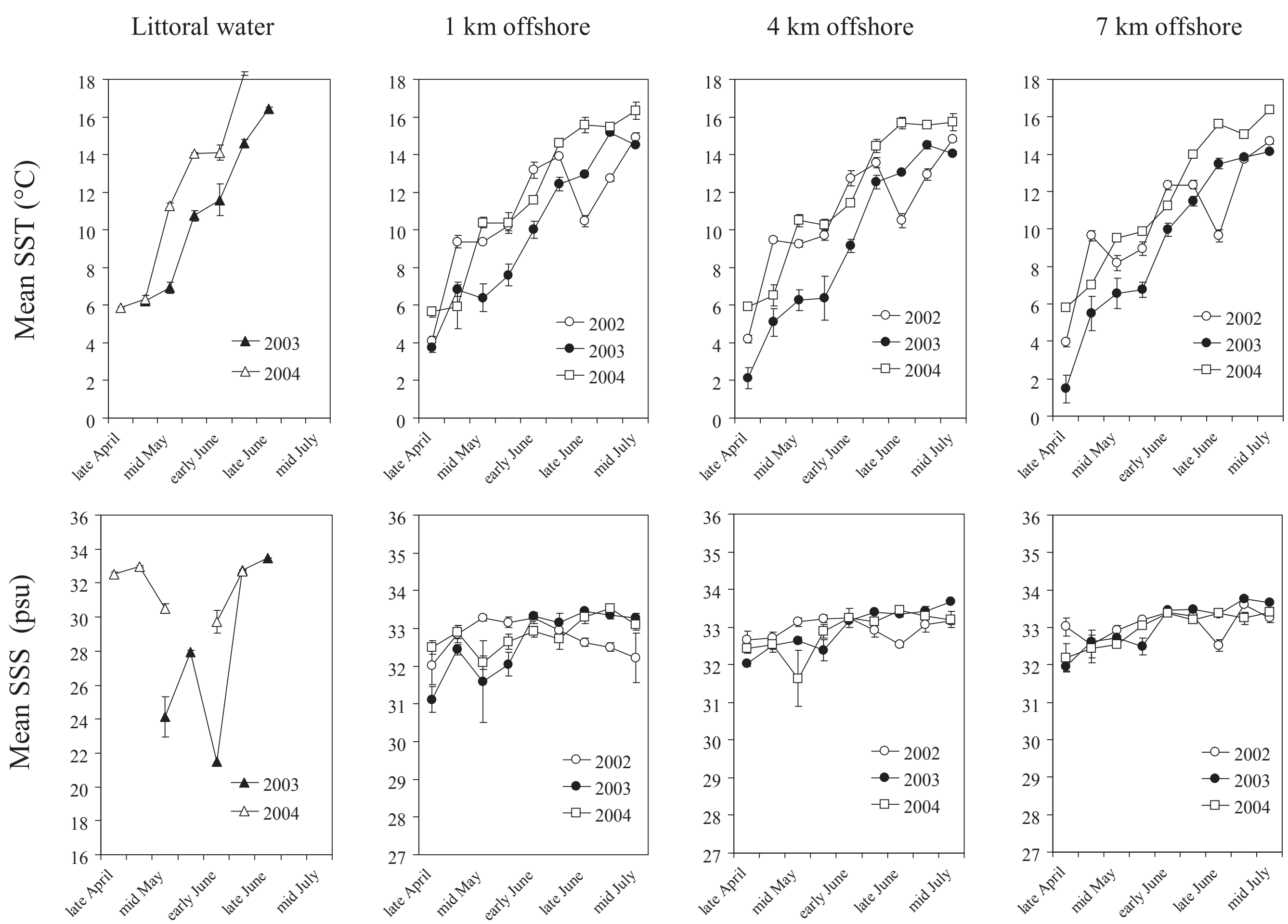

Fig. 5. Changes in mean values (with S.E.) of SST and SSS at the littoral site, and the 1 km, 4 km and 7 km transects off the Abashiri coast in the Okhotsk Sea from 2002 to 2004.

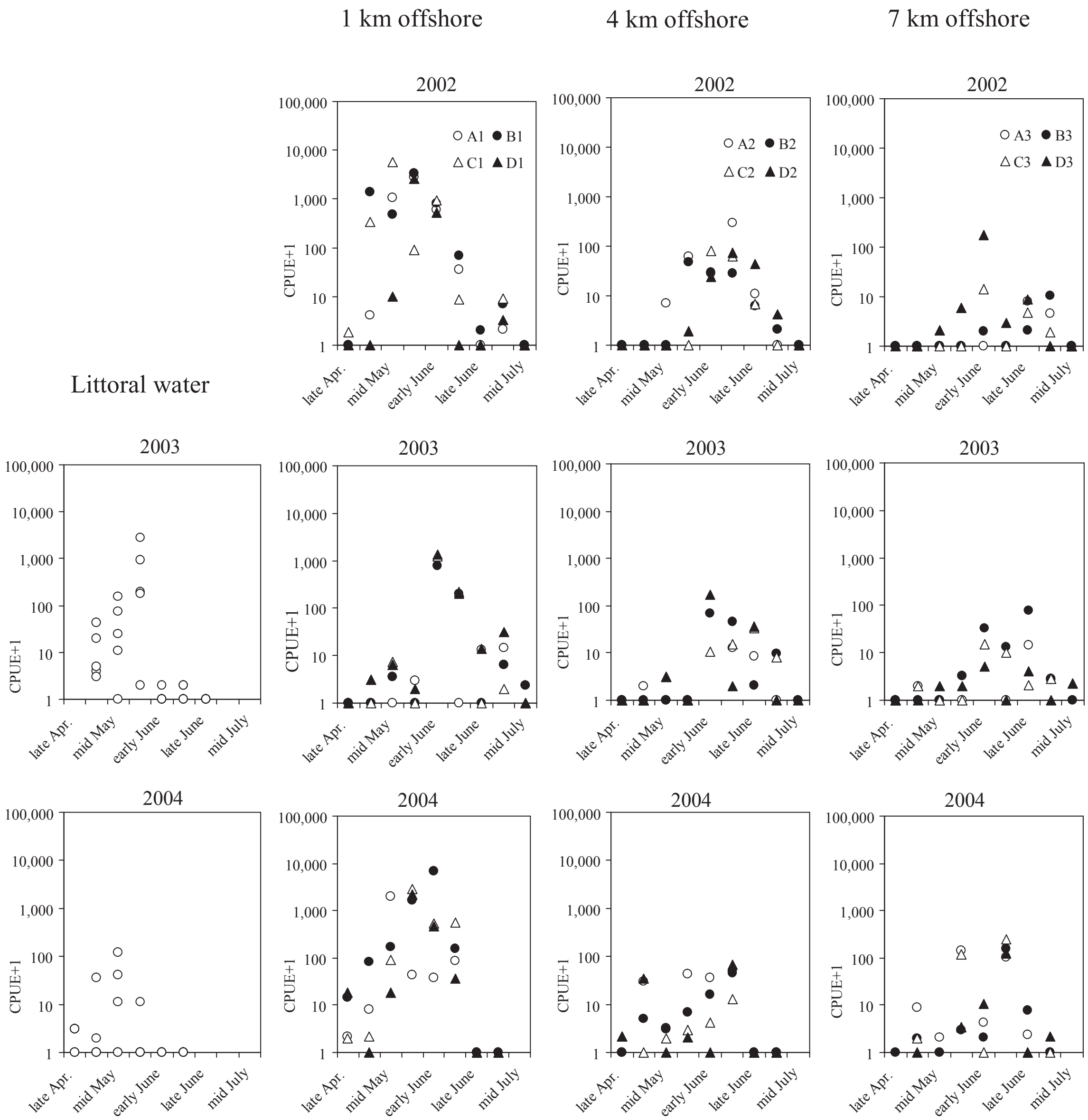

Fig. 6. Changes in CPUE (catch per unit effort, the number of juveniles per 2 km towing or per individual beach seine) of juvenile pink salmon captured at the littoral site (beach seine), and the 1 km, 4 km and 7 km transects (trawl net) off the Abashiri coast in the Okhotsk Sea from 2002 to 2004.

transects was 2°C, much colder than in 2002 and 2004. By early May, mean SST in 2003 increased at every study site, but still remained below 8°C. By early June 2003 mean SST exceeded 8°C at every study site in offshore coastal waters, eventually reaching 14°C in July, similar to 2002. In 2004, the increasing trend in mean SST was almost the same as in 2002 except for colder temperatures in early May and warmer temperatures in mid to late June (Fig. 5).

Although only one set of data on SST was collected in 2002 in the littoral area, by late May, the mean SST there had already reached 14°C, almost the same as in 2004, and warmer than in the coastal waters at the same time in 2002 (Fig. 5). In 2003, mean SST at the littoral site gradually increased from 6 to 7°C from late April to mid May, and exceeded 10°C by late May, differing from coastal waters where temperatures were below 8°C in the same year. Mean SST at the littoral site increased in 2003, reaching 16°C in late June, 3°C warmer than coastal waters. Although mean SST in 2004 was the same as in 2003 until early May, temperatures exceeded 11°C in mid May, 5°C warmer than in 2003, eventually reaching18°C in mid June.

Mean SSS along the 1 km offshore transect from late April to late May 2003 varied between 31 to 32.5 psu and was lower than in the other two years. Mean SSS at the 1 km transect in 2002 gradually decreased from 33 to 32 psu differing from values in 2003 and 2004 which remained over 33 psu (Fig. 5). There were almost no differences in salinity at the 4 and 7 km offshore transects between years, increasing from 32–32.5 to 33–33.5 psu from late April to mid July.

Juvenile Pink Salmon Distribution

The total number of juveniles captured along the coast in 2003 was estimated to be 4,684 fish, much lower than the numbers caught in the other two years (21,867 in 2002 and 19,167 in 2004). In contrast, the total number of juveniles collected in the littoral area in 2003 was estimated to be 4425 fish, much higher than the 222 fish collected in 2004. Moreover, great differences were seen in the spatial distribution of juvenile pink salmon in littoral and coastal waters during the three years of this study.

In 2002 during warm conditions in May, CPUEs at all sites along the 1 km transect were relatively high in early May, and reached a peak in mid to late May (Fig. 6). By mid June, CPUEs decreased rapidly to < 100 fish at each site along the 1 km offshore transect. In contrast, CPUEs at the 4 km and 7 km offshore locations were much lower than those at the 1 km offshore site throughout the survey, with peak CPUEs along both transects occurring 10 days later. Although beach seinings in 2002 were carried out only in late May, no pink salmon juveniles were captured. The Morisita I_δ from early to mid May 2002 was very high (> 7), and then rapidly decreased to 2–3 along with a decrease in CPUE at the 1 km offshore transect and an increase at the 4 and 7 km offshore transects (Table 1). These results indicated that juvenile pink salmon after seaward migration in 2002 were densely aggregated at the 1 km offshore location early in the season, and soon afterward dispersed to the 4 and 7 km offshore sites.

In 2003 under cooler sea water temperatures in May, CPUEs at the 1 km offshore site were relatively low (< 10 fish in May) suggesting that few fish were there. More interestingly, CPUEs at the 1 km offshore sites in 2003 suddenly reached a peak in early June, about one month later than in 2002, but at much lower CPUEs than in 2002. The appearance of pink salmon juveniles at the 4 and 7 km offshore locations was also delayed in 2003. The relatively low I_δ (< 4) was maintained from May to July indicating that pink salmon juveniles were distributed more evenly in coastal waters in 2003 than in 2002. In the littoral waters, pink salmon juveniles in May were more abundant than in the coastal waters, especially in late May when CPUEs were highest. Although surface trawling at the fishing port was carried out only in late May, 302 pink salmon juveniles were captured. By early June, most pink salmon juveniles suddenly disappeared from littoral waters. These results suggest that most of juvenile pink salmon after seaward migration in 2003 remained in the littoral waters and at the fishing port for a long time without moving to the 1 km offshore transect. However, by early June with SST > 8°C they dispersed more evenly into the coastal waters, differing somewhat from the 2002 event. However, the timing of the dispersal of juveniles to coastal waters was almost the same in 2003 as in 2002 (Fig. 6).

Table 1. Changes in Morisita I_δ of pink salmon juveniles captured in coastal waters.

	2002	2003	2004
Late April	10.00^{NS*}	-	3.72
Early May	8.17	1.33^{NS}	3.78
Mid May	7.72	2.20	9.32
Late May	3.87	1.71^{NS}	3.79
Early June	2.55	3.56	8.96
Mid June	3.76	3.09	2.06
Late June	3.47	2.67	8.16
Early July	1.80	2.81	12.00^{NS}
Mid July	-	2.31	-

*NS indicates that the value of the Morishita index was not significantly different from "1", showing random distribution.

In 2004 with warm seawater temperatures in May, similar to the 2002 event, a few pink salmon appeared at the 1 km offshore transect in late April, with numbers increasing gradually thereafter. The peak CPUE at the 1 km offshore transect occurred between late May and early June, 10 days later than in 2002, but 20 days earlier than in 2003. CPUE at the 4 and 7 km offshore transects were low in early May, and then increased from late May to mid June. Pink salmon juveniles in the coastal waters suddenly disappeared in late June. The I_δ was varied in 2004 with alternating high (8) and low (2–3) values, indicating that aggregations at the 1 km offshore transect and dispersion to the 4 and 7 km offshore transect occurred repeatedly. While pink salmon juveniles appeared in littoral waters in early May in 2004, similar to 2003, the peak occurrence was 10 days earlier than in 2003 and maximum CPUEs were much lower. Therefore, while some pink salmon (after downstream migration) in 2004, as well as 2003, spent time in littoral waters, most pink salmon juveniles moved rapidly to the 1 km offshore transect in the warmer year (2004) and remained there until mid June with some dispersal to the 4 and 7 km offshore transects (Fig. 6).

Relationships between CPUE and SST in coastal waters showed almost the same pattern in all three years (Fig. 7). The high CPUEs were observed at seawater temperatures between 9 and 14°C. CPUEs sharply decreased when temperatures were < 9°C and > 14°C. In the littoral waters, relatively high CPUEs occurred at 6 to 14°C with a peak at 10°C.

Pink Salmon Size Structure and Growth

Length-frequency distributions of pink salmon from each time period at the 1 km, 4 km and 7 km offshore transects in the three years and in littoral waters in two years were mostly unimodal except for some data showing skewed distributions. Assuming that mean fork lengths of pink salmon pooled at each offshore transect or in littoral waters were representative of pink salmon juveniles at each location, these mean values were statistically compared among years

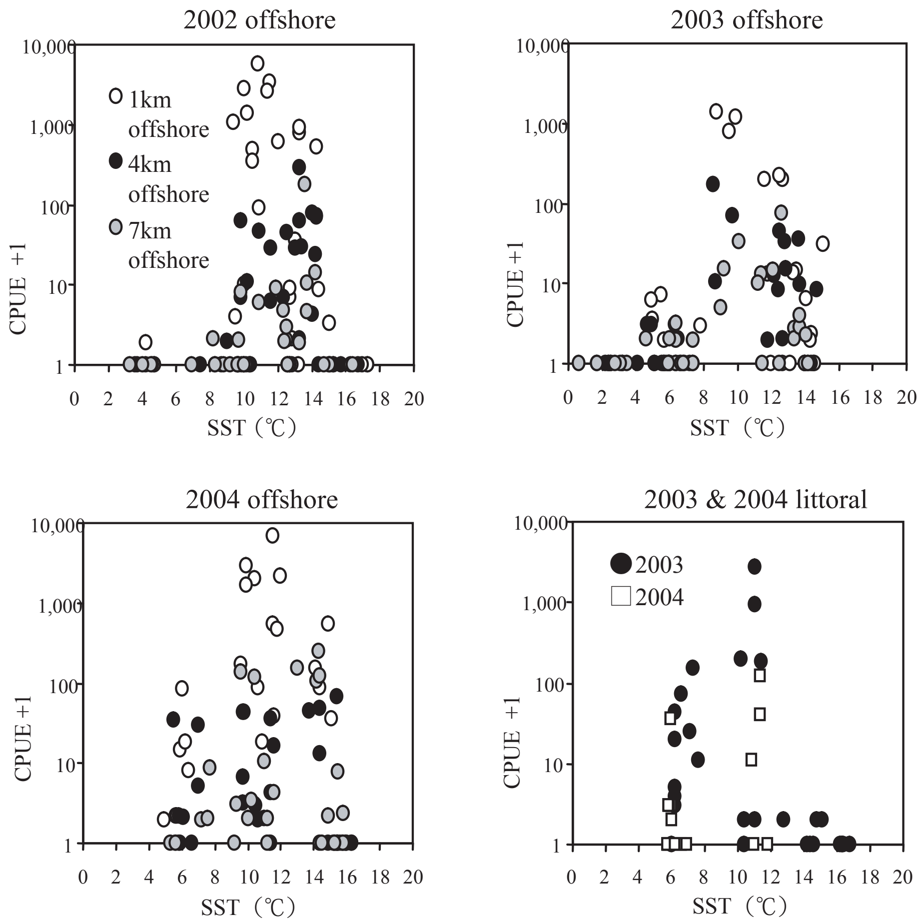

Fig. 7. Relationships between SST and CPUE in pink salmon juveniles captured at the littoral site (beach seine), and the 1 km, 4 km and 7 km transects (trawl net) off the Abashiri coast in the Okhotsk Sea from 2002 to 2004.

and locations.

When comparing mean fork length (MFL) among locations, different trends were found in the same year or among different years (Fig. 8). While MFL at the 1 km offshore transect in 2002 increased linearly from 46.3 mm in early May to 72.9 mm in early July, MFLs from the 4 km and 7 km transects increased more rapidly after mid May, and eventually became significantly larger than juveniles from the 1 km transect, except for early July. In contrast, MFLs at all locations in 2003 did not increase until late May but thereafter increased rapidly, although MFLs of juveniles at the 4 and 7 km transects were significantly larger than those from the 1 km transect from late June to early July. In 2004 while MFLs also showed no increasing trend until mid May, thereafter MFLs at every location increased rapidly, similar to 2003. Although MFLs at the 1 km offshore transect was larger than at the 4 km and 7 km transects in late May 2004, this difference disappeared in early June and eventually MFLs at the 7 km transect became significantly larger than others in mid June.

When comparing MFLs among years at the same location, different trends were observed in the three years (Fig. 8). While MFLs at the 1 km offshore transect from early to mid May 2004 were significantly smaller than those in 2002, MFLs in late May 2004 increased to 54.5 mm as large as in 2002. Eventually MFLs in early and mid June 2004 were significantly the largest. In contrast, while MFL at the 1 km offshore transect in 2003 was 45.5 mm in early May as large as in 2002, MFLs decreased to 36.4 mm in late May, significantly smaller than those in the other two years. MFL in early June 2003, when pink salmon were very abundant at the 1 km transect, was 49.4 mm, significantly smaller than in other years (58.8 mm in 2002 and 64.4 mm in 2004). These MFLs recovered to 61.8 mm by mid June,similar to the other transects. At the 4 km transect, MFLs in 2002 were significantly larger than in 2003 and 2004 from late May to late June. There were no significant differences between 2003 and 2004 except for early June pink salmon were very abundant at the 1 km transect. At the 7 km transect, MFLs in 2002 were always significantly the largest from late May to late June. In contrast, MFLs in 2003 were always the smallest except for early July when few pink salmon were seen. There were no significant differences in MFLs of juveniles in littoral waters between 2003 and 2004. These results suggest that pink salmon juveniles in 2002 and 2004 grew more rapidly than in 2003, and this tendency became more obvi-

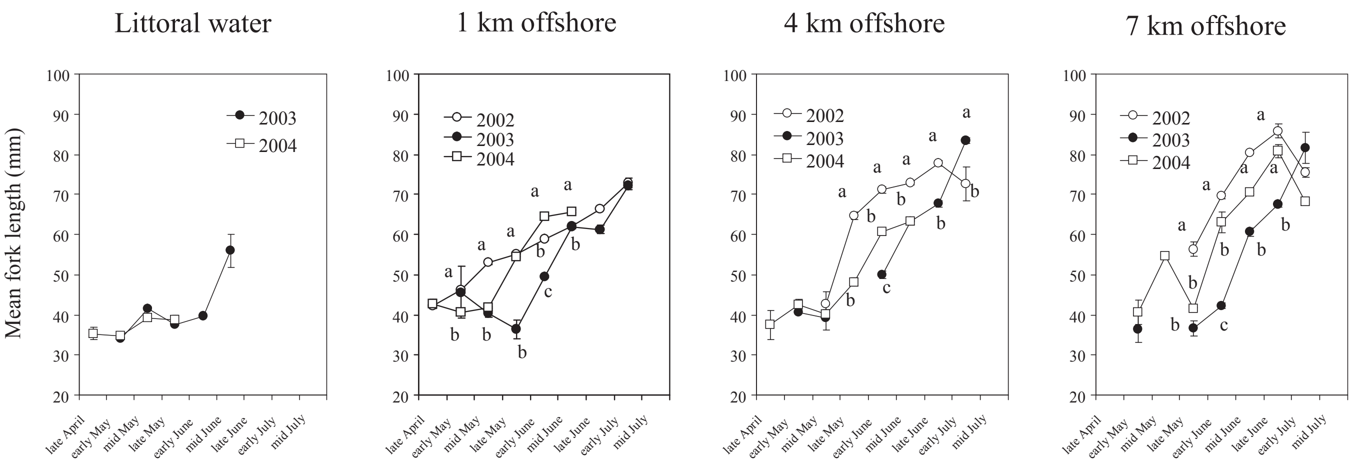

Fig. 8. Changes in mean fork length (with S.E.) of juvenile pink salmon captured at the littoral site, and the 1 km, 4 km and 7 km transects off the Abashiri coast in the Okhotsk Sea from 2002 to 2004. Values not sharing a common small letter among years are significantly different at $p < 0.05$.

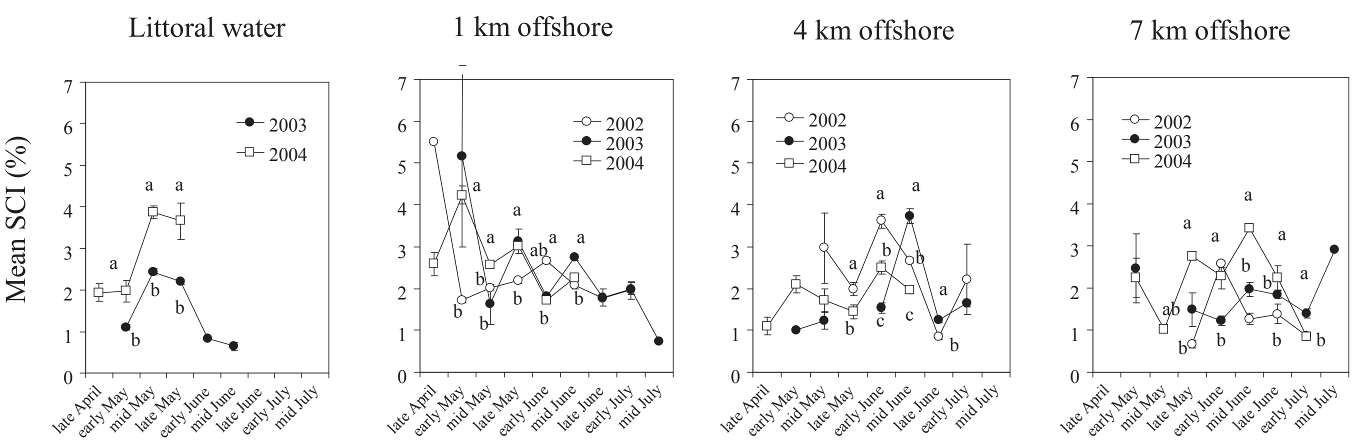

Fig. 9. Changes in mean values (with S.E.) of stomach content indices (SCI: stomach content weight x 100 / body weight) of juvenile pink salmon captured at the littoral site and the 1 km, 4 km and 7 km transects off the Abashiri coast in Okhotsk Sea from 2002 to 2004. The values not sharing a common small letter among years are significantly different at $p < 0.05$.

ous in offshore rather than nearshore waters.

Food Items

When comparing mean stomach contents indices (SCI) of pink salmon juveniles among the three years, different trends were found at different locations. While the fluctuating patterns in SCI in littoral waters in 2003 and 2004 were very similar, with a peak in early and mid May, SCI in 2003, when more fish were present, were significantly lower than those in 2004 (Fig. 9). At the 1 km transect, SCI in three years tended to be higher early in the season when pink salmon were more abundant than later in the season when the number of pink salmon decreased rapidly. In contrast, SCI at the 4 km transect tended to be lower early in the season when fewer fish were present than late in the season when more fish were present. In particular, SCI in 2003 was lower early in the season than in other years. However, when fish dispersed in late June, SCI in 2002 and 2003 decreased markedly. At the 7 km transect there were significant differences in SCI in all three years. From late May to late June when more fish were present, SCI in 2004 were higher than those in 2002 and 2003 except for early June in 2002. In late June when most of pink salmon juveniles had dispersed, SCI at the 4 and 7 km transects decreased.

Diet analysis revealed that juvenile pink salmon at the 1 km and 4 km transects in 2002 consumed primarily cold-water species of copepods (mainly *Pseudocalaunus newmani*, *Neocalanus* spp.) and appendicularians (mainly *Fritillaria borealis* f. *typica*) in May, switching to warm-water species of cladocerans (mainly *Podon leuckarti*, *Evadne nordmanni*), appendicularians (mainly *Oikopleura longicauda*) in June (Fig. 10). In contrast, juvenile pink salmon at the 7 km transect consumed a varied diet including amphipods, insects and fish eggs. Jacobs' (1974) electivity indices showed pink salmon in 2002 favored cladocerans in May and June

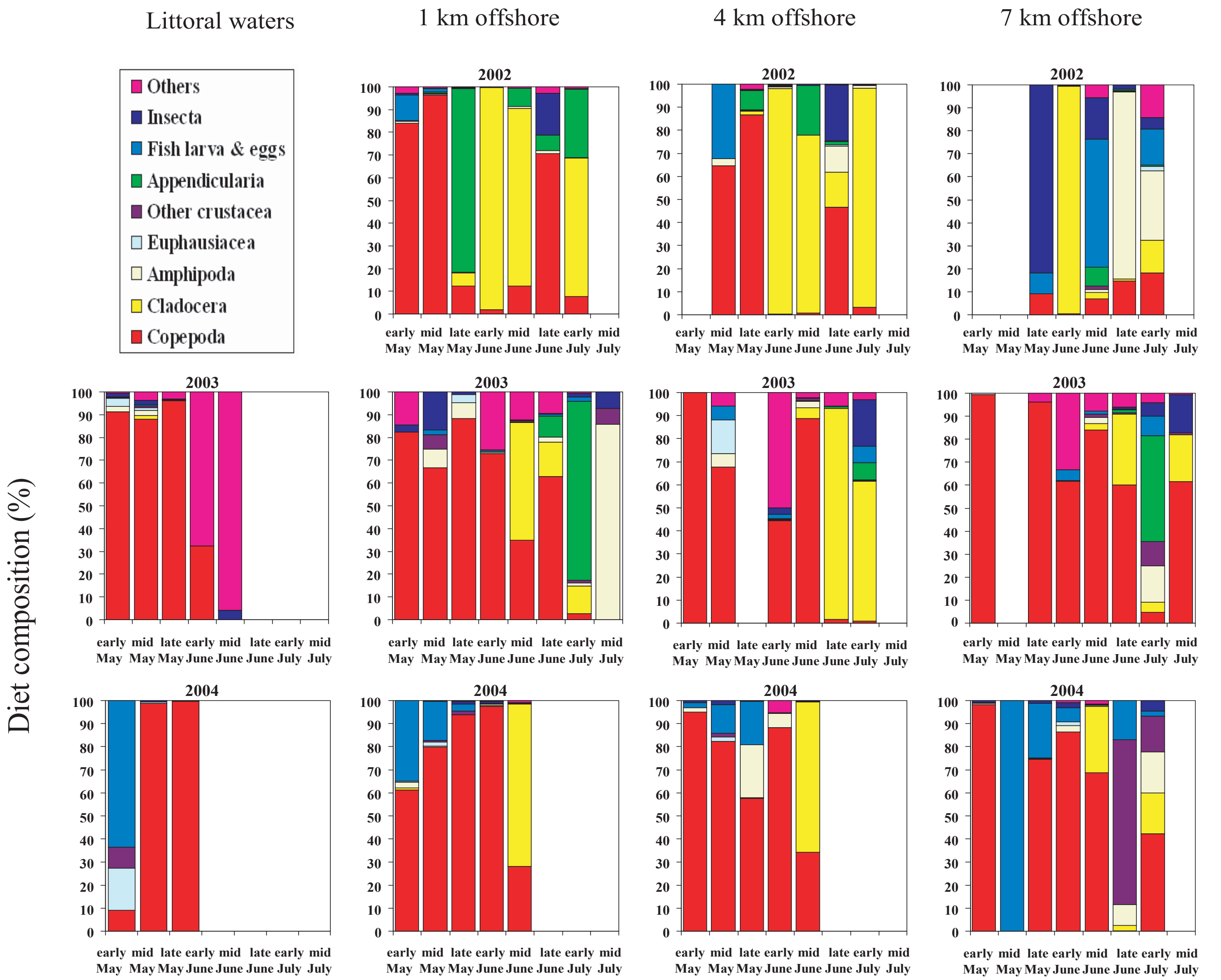

Fig. 10. Changes in diet composition (by number) of pink salmon juveniles at the littoral site and the 1 km, 4 km and 7 km transects off the Abashiri coast in Okhotsk Sea from 2002 to 2004.

when the water was warm, but preferred copepods early in the season (Fig. 11). While juveniles in coastal waters in 2003 consumed predominantly copepods (mainly *Pseudocalaunus newmani*, *Eurytemora herdmani*, *Acartia hudsonica* and *Metridia pacifica*) until mid June, differing from 2002, their diets later became dominated by cladocerans (mainly *Podon leuckarti*), and appendicularians the same as in 2002. Jacobs' electivity indices in coastal waters showed that pink salmon in 2003 favored copepods early, but switched to cladocerans and appendicularians later. Diet composition of pink salmon juveniles in the littoral zone in 2003 was different from that for fish in coastal waters. Juveniles in the littoral zone consumed not only pelagic copepods but also epibenthic crustaceans such as Harpacticoida copepods, indicating that juvenile pink salmon can change their feeding behavior depending on nursery conditions. Although in 2004, diet composition in coastal waters also included copepods early in the season, not only small coastal species such as *Pseudocalanus newmani*, *Tortanus discaudatu*, *Eurytemora herdmani*, but also large oceanic copepods such as *Neocalanus* spp. were comsumed. By mid July, the contribution of copepods to their diet composition decreased as they switched to cladocerans (*Evadne nordmanni*), amphipods and fish eggs. Jacobs' indices also revealed that pink salmon in 2004 preferred copepods early, switching to cladocerans later in the season. Amphipods were favored throughout the season except for sometimes at the 7 km transect. Diet composition in littoral waters in 2004 was clearly different from that in 2003 and was dominated by pelagic copepods such as *Neocalanus* spp, *Sinocalanus tenellus*, *Pseudocalanus newmani*, *Eurytemora herdmani*.

DISCUSSION

Great differences in spatial distribution, abundance and size of juvenile pink salmon were found over three years in

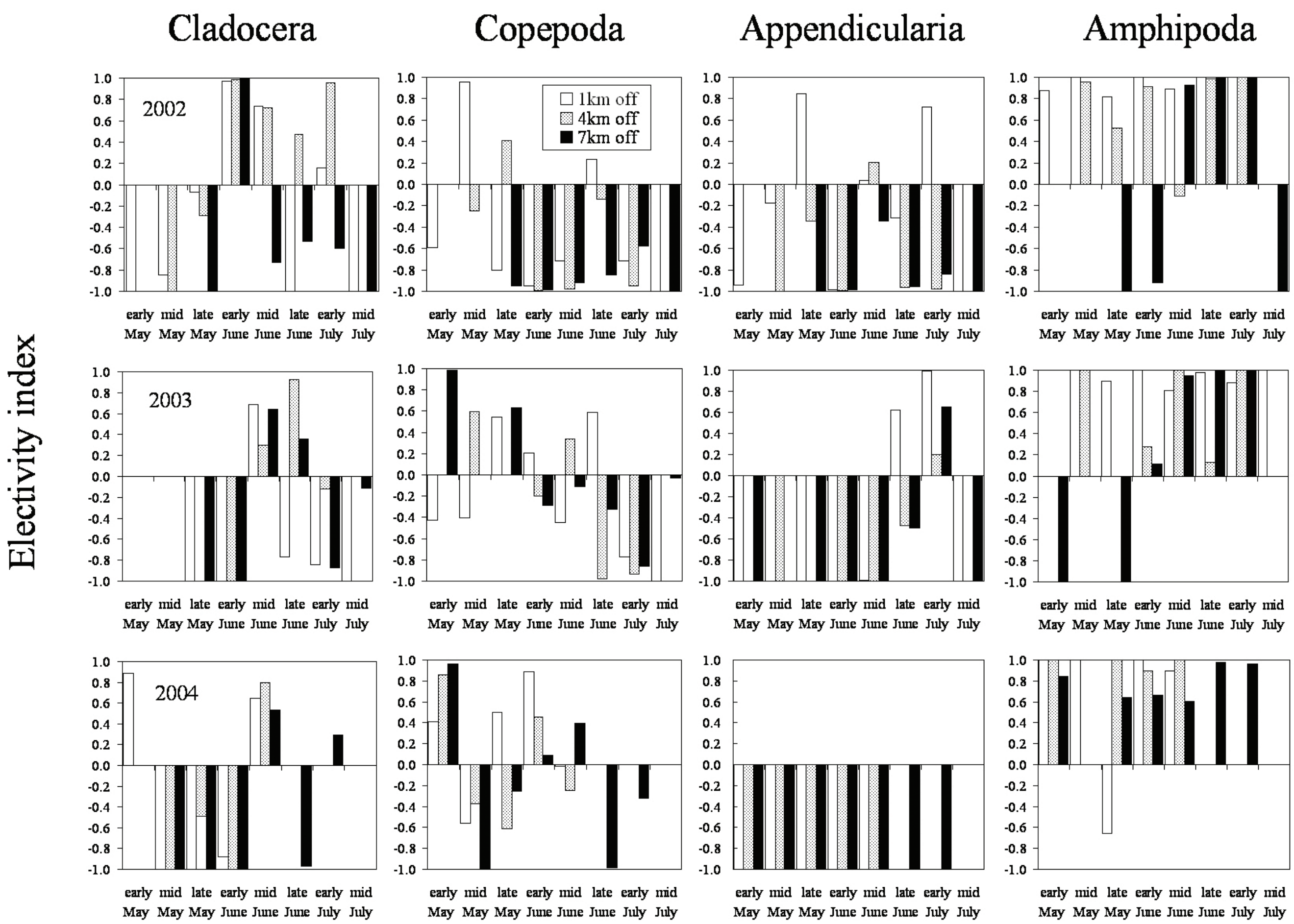

Fig. 11. Changes in electivity indices (by number) of four prey groups. Electivity (Jacobs 1974): E = (ri - Pi) / (ri + Pi - 2ri · Pi), ri: % of i species in stomach contents, Pi: % of i species in coastal waters. +1 = positive preference, -1 = negative preference.

Abashiri coastal waters. In the cool year, 2003, juvenile pink salmon in May were restricted to littoral waters as shown by the CPUE results, while juvenile pink salmon in the warm years, 2002 and 2004, were distributed widely along the 1 km offshore transect with only a short residence time in littoral waters. This pattern was strongly correlated with differences in SST between cool and warm years. Offshore movement of pink salmon is known to be size-dependent, with larger juveniles moving offshore earlier (LeBrasser and Parker 1964; Healey 1980). However, no clear differences in fish size early in the season were found, not only among years until mid May, but also among locations (1 km, 4 km and 7 km offshore transects) in 2003 and 2004, the exception being 2002. Therefore, we hypothesize that cold temperatures < 8°C in coastal waters may restrict the movement of pink salmon juveniles after seaward migration.

However, another hypothesis may also be proposed because the origin(s) of captured pink salmon were unknown. The timing of the downstream migration of pink salmon in 2003 might be different from that in 2002 and 2004 because of differences in spawning times and/or stream water temperatures. For example, while the pink salmon juveniles captured in the littoral waters in May 2003 were composed of early-migrating (or early spawning) fish, other juveniles in 2003 may have been delayed in migrating to sea in June. It is not known whether pink salmon captured in both littoral and coastal waters were of the same origin or cohort because no fish were marked. However, we stocked ALC-marked chum salmon juveniles from 2002 to 2004 during the pink salmon survey. Many marked chum juveniles were captured in littoral waters in May 2003 when no marked chum were caught at the 1 km offshore transect (Nagata et al. 2007). These observations strongly support the first hypothesis that seawater temperatures < 8°C restrict pink salmon movement into coastal waters.

Moreover, differences in areas that pink salmon use as nursery grounds likely affect fish abundance and growth. Pink salmon in the warm years 2002 and 2004 were significantly larger than those in the cool year 2003, in particular in 2002 when pink salmon were always the largest at the 4 km and 7 km transects. Further, 2002 pink salmon were significantly larger at offshore locations than in nearshore areas. This is consistent with previous research showing that offshore movement of pink salmon in North America is size-dependent (LeBrasser and Parker 1964; Healey 1980). In contrast, pink salmon in the cool year, 2003, were always the smallest in coastal waters despite not being significantly different from fish in littoral waters in 2004. Although the zooplankton bloom in spring 2003 was slightly delayed compared with other years (Asami et al. 2007), feeding activity of juveniles in 2003 did not seem to be high, judging from the fact that SCI in the littoral zone and at the 4 km offshore transect were significantly lower in 2003 than in other years. Also, pink salmon juveniles in 2002 and 2004 consumed more large-sized pelagic zooplankton (*Neocalanus* spp.) than in 2003. Stomach evacuation of pink salmon that ranged from 32 to 57 mm in length required 6 and 16 h at temperatures of 12.8°C and 8.5°C, respectively (Bailey et al. 1975), suggesting that pink salmon juveniles consume less food at cooler temperatures. In addition, juvenile chum salmon that were captured in coastal waters (Nagata et al. 2007) were reported to grow rapidly at 10–12°C, and slowly at 5°C (Kaeriyama 1986). Moreover, because pink and chum salmon lived together in dense aggregations and consumed almost same diet in littoral waters in 2003 (Nagata et al. 2007), it is very likely that intra- or inter-specific competition between them became greater than in other warmer years. Therefore, slow growth in 2003 may be the result of depressed feeding activity combined with intensified competition due to low water temperatures and larger aggregations of fish in a limited area. In contrast, rapid growth rates in the warm years, 2002 and 2004, may be related to more active feeding at optimal water temperatures and expanded feeding areas. The abundance of fish captured in coastal waters in the warm years, 2002 and 2004, was much higher than that in 2003 despite the fact that pink salmon in 2003 were more abundant in littoral waters.

Poor survival of pink salmon in 1991 and 1992 was reported in Prince William Sound, Alaska (Willette 1996; Willette et al. 2001). The authors recognized that slow-growing juvenile salmon living at very low ocean temperatures in the spring could have sustained high mortality in 1991 because they are vulnerable to size-selective predators for longer periods of time (Parker 1971; Healey 1982; West and Larkin 1987). Shimizu (2002) reported that the return rate for pink salmon from the 1967 to the 1995 brood years in the Okhotsk coastal region was negatively correlated with the concentration of sea ice, especially because the dramatic increase in the abundance of pink salmon since the 1990 brood year was coincident with a period characterized by much less sea ice. Sea water temperatures in the Abashiri coastal waters in spring are known to be affected by a combination of three influences: the Soya Warm Current with 33.6 psu and high temperatures; the Okhotsk surface water with 32.5 psu and temperatures 2-5°C (related to the distribution and movement of sea ice); and, the coastal waters that are influenced by freshwater inputs (Irie et al. 1981; Takizawa 1982). Moreover, as the Okhotsk Sea is usually covered with sea ice during the winter, the timing of the appearance and disappearance of sea ice also affects oceanic parameters such as seawater temperature and the timing of plankton blooms in the spring (Shimizu 2005). In 2002 and 2004, the sea ice disappeared in early March, one month earlier than in 2003 that had the latest sea ice disappearance in the past 10 years (Shimizu 2005; Asami et al. 2007). Further, in 2003, movement of the front of the Soya Warm Current to the Abashiri coast was also delayed (Asami et al. 2007). As a result of these oceanographic conditions, the cold Okhotsk Surface Water occupied the coastal waters in May 2003 with SST ranging from 5.3–6.8°C, much colder than in the warm years (8.2–9 .7°C in 2002, 5.5–12.0°C in 2004). Therefore, we conclude that temperatures in coastal waters strongly affect the residence time and the offshore movement of pink salmon juveniles after seaward migration and may be controlled by a combination of the amount and timing of sea ice formation and the Soya Warm Current (Asami et al. 2007).

The level of 2004 recruitment (adults) from the 2002 brood-year pink salmon that were juveniles in coastal waters in spring 2003 was much lower than the 2003 recruitment from the 2001 brood year which entered the sea in spring 2002. This reversal of the trend in adult returns between the two years resulted in the shift in dominance. As shown in Fig. 4, the SR index in 2001 brood-year pink salmon was the highest of the past odd-year brood stocks, suggesting that the survival rate in the 2001 brood year was high. Although relatively high mortality is known to occur in both the freshwater and ocean phases of the life cycle, pink salmon mortality during the ocean phase was more variable and higher than that during the freshwater phase (Manzer and Shepard 1962; Parker 1965, 1968; Healey 1991; Willette et al. 2001). In addition, the most probable cause of initial disparity between the two lines is either a disastrous decrease (or a dramatic increase) in the survival rate of one line over the other (Neave 1953; Ricker 1962). If our proposed scenario is true concerning the shift in pink salmon abundance in the Okhotsk Sea of Hokkaido, the shift in dominance lines might be caused by the thermal conditions that result in longer estuary residence times with larger aggregations of fish, or rapid dispersal with wider occupation of nursery grounds after seaward migration.

Unfortunately, we did not separate hatchery-reared pink salmon from wild pink salmon. Morita et al. (2006) estimated that the contribution of hatchery fish to pink salmon catches was 35.4% on average between 1971 and 2003. In 2005 ALC-marked pink salmon were stocked. This mass stocking of marked pink salmon will be continued for three years. Therefore, in the near future we will be able to determine the degree to which hatchery pink salmon contribute to the pink salmon population in the Okhotsk Sea coastal region.

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