

## Wounding of Pacific Salmon in Relation to Spatio-Temporal Variation in Distribution Patterns of Important Predatory Fishes in the Russian Economic Zone

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**Abstract:** Variation in distribution patterns of major predatory fishes in the Russian economic zone was analyzed using Pacific Scientific Research Fisheries Center (TINRO-Centre) archival trawl survey data for 1980–2004. Species analyzed include *Alepisaurus ferox*, *Anotopterus nikparini*, *Lamna ditropis*, *Lampetra tridentata*, *L. camtschatica*, *Prionace glauca*, *Somniosus pacificus* and *Squalus acanthias*. Our data show that there is strong geographic variation in the relative abundance of predatory fishes. Differences in predator abundance were noted among large-scale geographical units (Bering, Okhotsk and Japan seas and adjacent waters of the North Pacific Ocean) and small-scale geographical units (shelf, continental slope, and deep-water basins; the upper epipelagic layer, lower epipelagic layer, upper mesopelagic layer, lower mesopelagic layer). We conclude that the rate of occurrence of Pacific salmon injuries was species-, age- and region-specific. This implies that it is necessary to consider species, age and region when estimating predator-related mortality of Pacific salmon.

**Keywords:** predator-prey interaction, spatial structure, spatial overlap, distribution pattern, vertical distribution, marine mortality, crosscovariance

### INTRODUCTION

Research on the spatio-temporal interaction between Pacific salmon and their predators is important for studying natural mortality of Pacific salmon as indicated by the number of publications on this topic (Beamish et al. 1992; Radchenko 1994; Shuntov 1994; Nakano and Nagasawa 1996; Nagasawa 1998a, among others). In the majority of these studies the influence of only one predator is considered. Estimates of various predators' contribution to Pacific salmon natural mortality are difficult to obtain because it is not known what percentage of Pacific salmon survives attacks by particular predators. Low levels of occurrence of injured individuals in catches may result from either low attack rates or low rates of survival after attacks.

Studies are needed to understand relationships between the occurrence of certain injuries and Pacific salmon mortality. Previous studies suggest that spatial overlap between prey and predators is often a direct measure of predation intensity (Fahrig et al. 1993; Radchenko 1994; Melnikov 1997; Savinykh and Glebov 2003, among others). In our study we focused on the quantifying degree of spatial overlap between Pacific salmon and their predators.

### MATERIALS AND METHODS

Data from the Pacific Scientific Research Fisheries Center (TINRO-Centre) research pelagic trawl surveys for 1980–2004 (2914 stations in the Bering Sea, 6056 in the Sea of Okhotsk, 2164 in the Japan Sea and 7105 in the north-western Pacific Ocean) were used to identify the distribution of Pacific salmon (*Oncorhynchus gorbuscha*, *O. keta*, *O. kisutch*, *O. nerka* and *O. tshawytscha*) and their predators. Species analyzed include North Pacific daggertooth (*Anotopterus nikparini*), longnose lancetfish (*Alepisaurus ferox*), Pacific lamprey (*Lampetra tridentata*), Arctic lamprey (*L. camtschatica*), salmon shark (*Lamna ditropis*), spiny dogfish (*Squalus acanthias*), blue shark (*Prionace glauca*) and Pacific sleeper shark (*Somniosus pacificus*). These species have been identified as the most intensive consumers of Pacific salmon during the marine phase of their life history (Parin 1968; Jones and Geen 1977; Nagasawa and Kaeriyama 1995; Sviridov et al. 2004, among others). Wounding and scarring of Pacific salmon were analyzed based on data from four epipelagic trawl surveys by TINRO-Centre in the western Bering Sea and adjacent Pacific waters (summer surveys - from July 15 to August 24, 2003, and from June 6 to July 17, 2004; autumn surveys - from September 14 to

October 25, 2003, and from September 11 to October 23, 2004). We recorded the presence or absence of each type of injury for every Pacific salmon examined. The analysis was performed separately for every life-history stage: juvenile (age .0), immature (age .1 and older) and maturing (individuals that will spawn in the current season). Subsamples for biological analysis were taken randomly to enable us to extrapolate toward total catch. We calculated the average percentage of individuals with injuries by each predator for each survey. In order to calculate the average percentage of individuals with injuries by each predator for each survey we weighted the percentage of a certain injury at a particular station by CPUE values at that station. This is standard procedure to adjust for the contribution of individual trawl tows to the outcome of an analysis by weighting them in proportion to the values of CPUE. As a result trawl tows with high CPUE have had a greater influence upon calculated average values, as compared to tows with low CPUE. The type of injury was determined based on its external appearance according to published descriptions (Beamish 1980; Welch et al. 1991; Shuntov et al. 1993; Radchenko and Semenchenko 1996; Melnikov 1997; Balanov and Radchenko 1998; Kukuiev 1998; Savinykh and Glebov 2003). Based on these sources, injuries by a particular predator can be summarized as follows: injuries by North Pacific daggertooth are slashes or cuts, which are located only on one side of the body. The other side of the body has a series of very small stab-wounds or hard-to-observe superficial scratches made by the needle-

like teeth on the lower jaw. Slashes are made by large daggers in the North Pacific daggertooth's upper jaw. Injuries by longnose lancetfish are usually located on both sides of the body, unlike North Pacific daggertooth injuries. Lamprey wounds on Pacific salmon vary from circular depressions to longitudinal gouges with a loss of scales at the edges of the wound.

We used a three-dimensional scatterplot to identify predatory fish distributions. During this analysis we considered average values for depth of species occurrence (distance between the sea surface and the middle of the trawl mouth weighted by CPUE), depth at the location of trawling (distance between the sea surface and the sea bottom, weighted by CPUE) and relative biomass. In addition we conducted interspecific cluster analysis on similarities in spatial distribution patterns of Pacific salmon and their predators during the summer in the upper epipelagic layer. For the cluster analysis we used the matrix of Pearson correlation coefficients for relationships between different pairs of species' relative biomass averaged for every 1 x 1 degree cell in Tables 1 and 2 the upper epipelagic layer.

To analyze the adaptive significance of spatio-temporal distributions of major predatory fish species in relation to Pacific salmon we used a traditional geostatistical technique - crosscovariance analysis (Isaaks and Srivastava 1989; Cressie 1993; Goovaerts 1997; Johnston et al. 2003). Cross-covariance is a statistical tendency of variables to vary in ways that are related to each other. Positive crosscovariance

**Table 1.** Average percentage of Pacific salmon with injuries by lamprey, North Pacific daggertooth or longnose lancetfish in the western Bering Sea and North Pacific Ocean during summer 2003 (July 15 to August 24), autumn 2003 (September 14 to October 25), summer 2004 (June 6 to July 17; Northwest Pacific only), and autumn 2004 (September 11 to October 23). J = Juvenile; Imm = Immature; Mat = maturing fish.

Survey	Pink salmon		Chum salmon			Coho salmon		Sockeye salmon			Chinook salmon		
	J	Mat	J	Imm	Mat	J	Imm	J	Imm	Mat	J	Imm	Mat
<b>Lamprey</b>													
2003	summer	0.5	0	0.1	0.2	10.0	0.0	0.4	0			1.2	
	autumn	0	0	0.5	1.0	0	0.3	0.5			0	1.3	
2004	summer	0.4		0	0.3	0	0.0	0			0	100.0	
	autumn	0	0.2	0.4	0.0	0.9	0	0	1.1		0	0	
<b>North Pacific daggertooth</b>													
2003	summer	9.5	0	2.4	6.0	0	0	1.7	16.7			1.3	
	autumn	0.7	0	4.3	2.0	0	1.9	2.7			2.3	1.3	
2004	summer	3.8		6.3	9.7	6.7	5.4	14.3			5.6	0	
	autumn	0.1	0.2	2.9	11.8	0	33.3	0	1.4		0	2.0	
<b>Longnose lancetfish</b>													
2003	summer	0.9	0	0	0	0	0	0.1	0			0.2	
	autumn	0	0	0.2	0	0	0	0.3			0	1.3	
2004	summer	0.1		0	1.3	0	0.0	3.6			0	0	
	autumn	0	0	0.2	0	0	33.3	0	0.0		0	0	

**Table 2.** Average CPUE (number of individuals per km<sup>2</sup>) and total abundance (TA in thousand metric tonnes) of predatory fishes in the western Bering Sea and North Pacific Ocean during summer 2003 (July 15 to August 24), autumn 2003 (September 14 to October 25), summer 2004 (June 6 to July 17; Northwest Pacific only), and autumn 2004 (September 11 to October 23).

Survey	Arctic lamprey		Pacific lamprey		North Pacific daggertooth		Longnose lancetfish	
	CPUE	TA	CPUE	TA	CPUE	TA	CPUE	TA
2003 summer	1.45	0.09	37.11	1.04	1.54	1.73		
autumn	0.72	0.09	6.82	1.04	0.57	0.47	0.10	0.43
2004 summer			0.80	0.23	3.39	2.88	1.11	2.54
autumn			3.49	0.37	0.65	0.40		

occurs when both variables tend to be above their respective means together, and negative crosscovariance occurs if one variable tends to be above its mean when the other variable is below its mean. We restricted our analysis to the following characteristics: relative abundance of maturing pink and chum salmon and North Pacific daggertooth, and percentage of individual salmon with injuries by North Pacific daggertooth.

## RESULTS

The average percentages of individuals with injuries by each predator for each survey are provided in Table 1. Based on their external appearance, the majority of injuries were classified as caused by North Pacific daggertooth. The incidence of injuries by lampreys was lower, and the injuries attributed to longnose lancetfish predation were lowest. The incidence of individuals with lamprey injuries was quite low for Pacific salmon. The highest injury rate was seen in maturing individuals. Due to the lower abundance of Arctic lamprey (compared with Pacific lamprey) in the Bering Sea (Table 1, 2) it can be expected that the latter species is a greater cause of Pacific salmon mortality. Archival trawl survey data analysis has shown that the abundance of Arctic lamprey in the northwestern Pacific was much lower compared to the abundance of Pacific lamprey (Figs. 1 and 2).

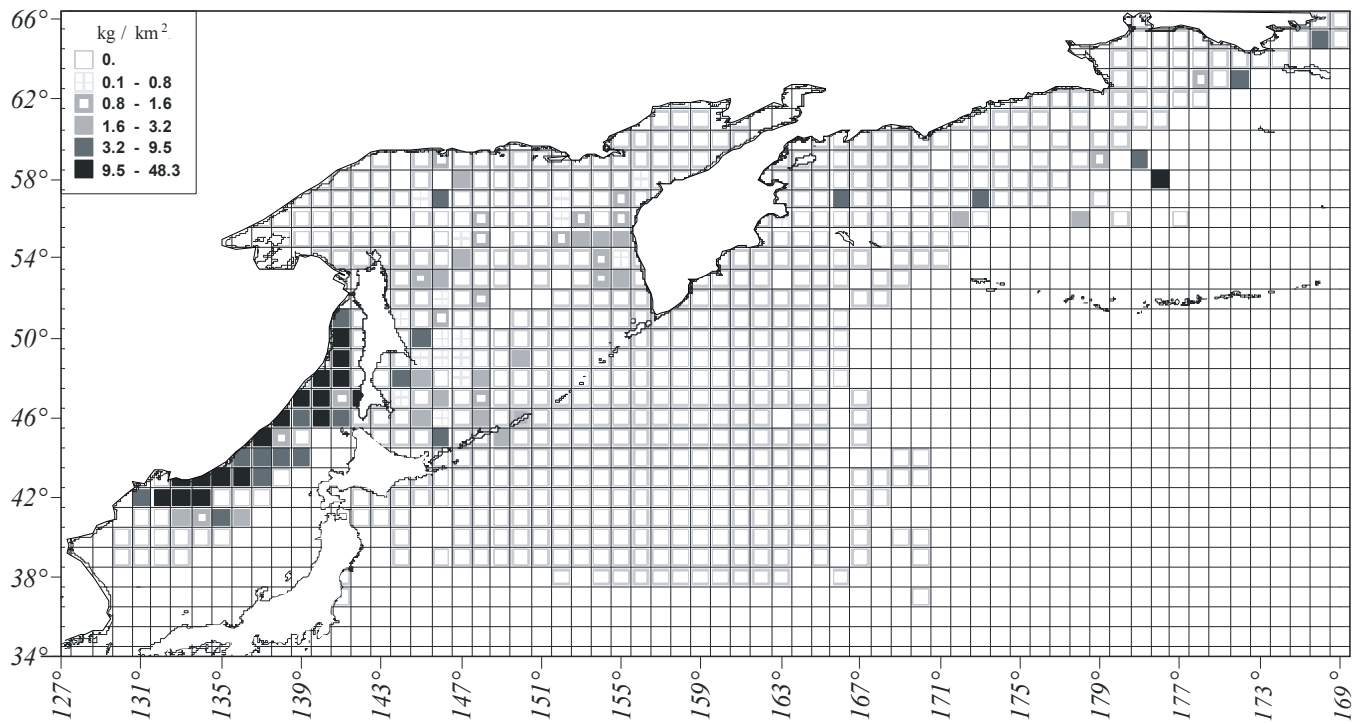
Pacific lamprey abundance in the northwestern Pacific was quite low compared to the levels in the Bering Sea (Fig. 2). This was associated with lower rates of injury by lamprey in the northwestern Pacific (Table 1). The abundance of Arctic lamprey decreased by half from summer to autumn of 2003 but we did not observe a decrease in injury rates. Moreover, in some species we observed an increase in rates of injury by lampreys later in the year. The same situation was noted for Pacific lamprey. The trawl survey data showed that the abundance of North Pacific daggertooth in the Bering Sea was several times lower than in the northwestern Pacific both in summer and autumn (Figs. 3 and 4). This may explain the lower injury rates in the Bering Sea (Table 1). Maturing pink and chum exhibited unexpectedly low injury rates in the northwestern Pacific. The abundance of daggertooth decreased by almost 50% from summer to

autumn (Table 2). However, the rate of injury rose in some species (immature chum, sockeye and chinook) (Table 1). Maturing Pacific salmon were the most intensely wounded by daggertooth (Table 1).

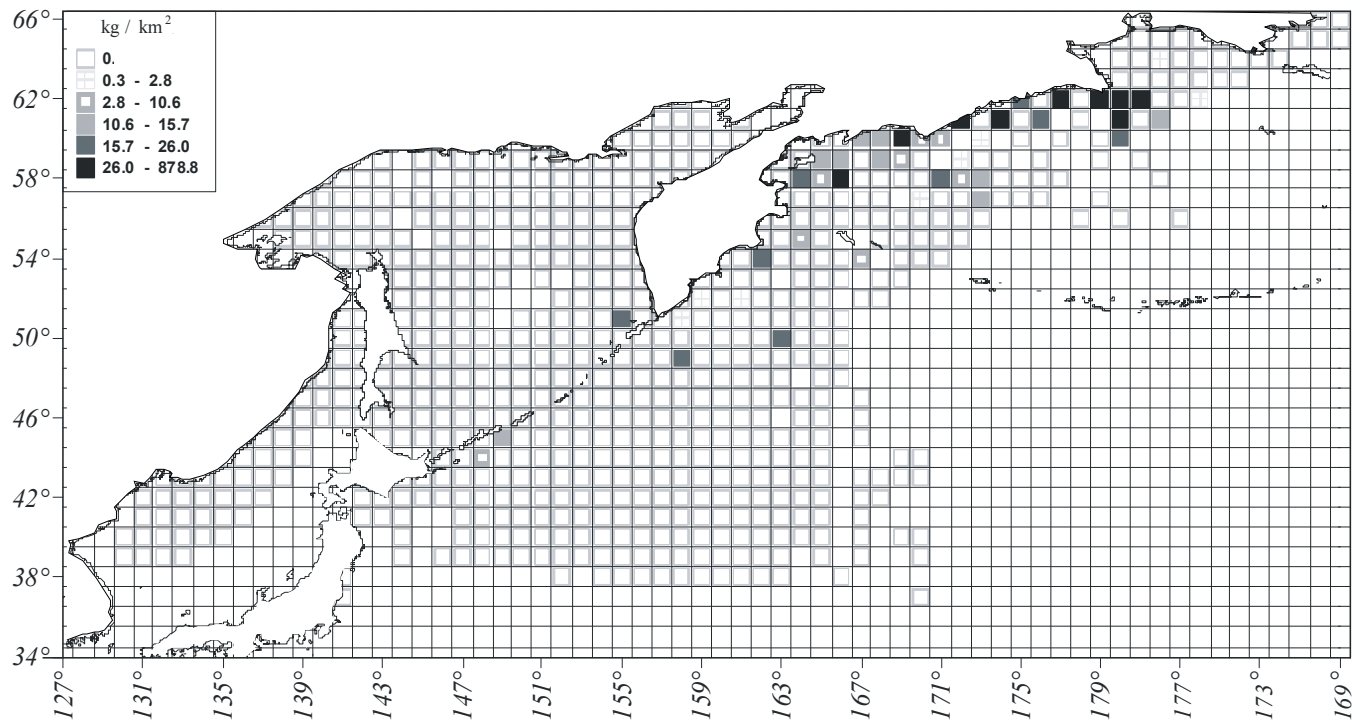
Latitudinal variation in occurrence of individuals injured by North Pacific daggertooth was evident in a statistically significant ( $P < 0.05$ ) negative correlation between the latitude of the trawling location and the percentage of salmon injured by North Pacific daggertooth. This was observed for immature chum and sockeye salmon during two surveys in the northwestern Bering Sea (the summer survey from July 15 to August 24, 2003, and the autumn survey from September 14 to October 25, 2003) (Fig. 5). During summer, North Pacific daggertooth migrate northward to the central Bering Sea, but its main concentrations are located in the Pacific waters off the Kuril Islands (Figs. 3 and 4). The northward decrease in proportion of individuals injured by North Pacific daggertooth, which was observed earlier by Savinykh and Glebov (2003) for chinook and coho salmon in the waters off the Kuril Islands, can also be explained by these migrations.

Juvenile salmon exhibited much lower rates of North Pacific daggertooth injuries compared with immature and maturing fish (Table 1). This may be the result of a lower number of attacks, or lower survival after attacks, or both. There is no doubt that the percentage of individuals that die immediately after North Pacific daggertooth attacks is much higher in juveniles compared with immature and maturing fish. The higher rates of injury in the more abundant salmon species compared with less abundant species are unlikely to be explained by higher survival rates. We hypothesize that daggertooth may forage more intensively on dominant salmon species. Such a concentration of predation on dominant prey species is consistent with the foundations of optimal foraging theory.

The abundance of longnose lancetfish was significantly lower than that of the North Pacific daggertooth (Table 1). Similar to daggertooth, the longnose lancetfish was most abundant in southern regions during summer–autumn (Figs. 6 and 7). The longnose lancetfish injuries were highest on maturing individuals (coho, sockeye, and chum) (Table 1). It is possible that this may be due to the lower survival of smaller individuals compared with larger ones. However, it



**Fig. 1.** Arctic lamprey CPUE (kg/km<sup>2</sup>) in the upper epipelagic layer of the northwest Pacific and adjacent areas during summer. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.



**Fig. 2.** Pacific lamprey CPUE (kg/km<sup>2</sup>) in the upper epipelagic layer of the northwest Pacific and adjacent areas during summer. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.

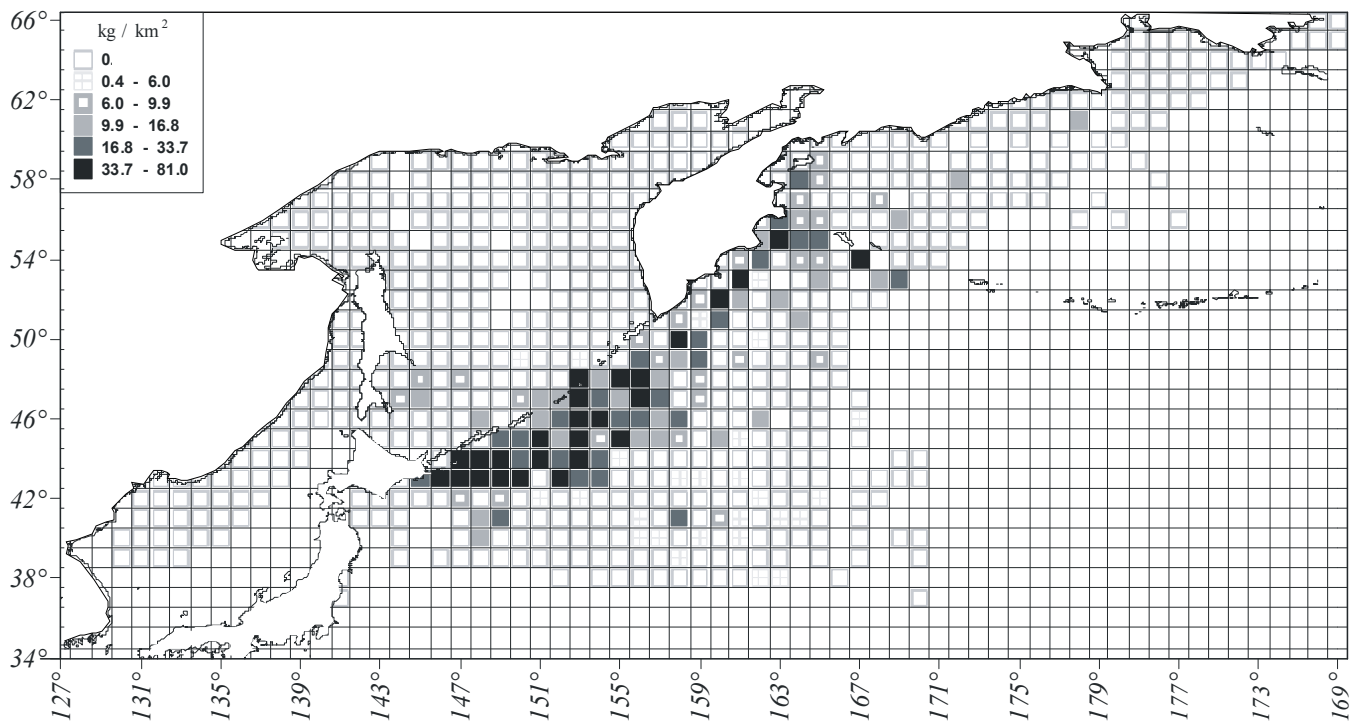


Fig. 3. North Pacific daggertooth CPUE (kg/km<sup>2</sup>) in the upper epipelagic layer of the northwest Pacific and adjacent areas during summer. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.

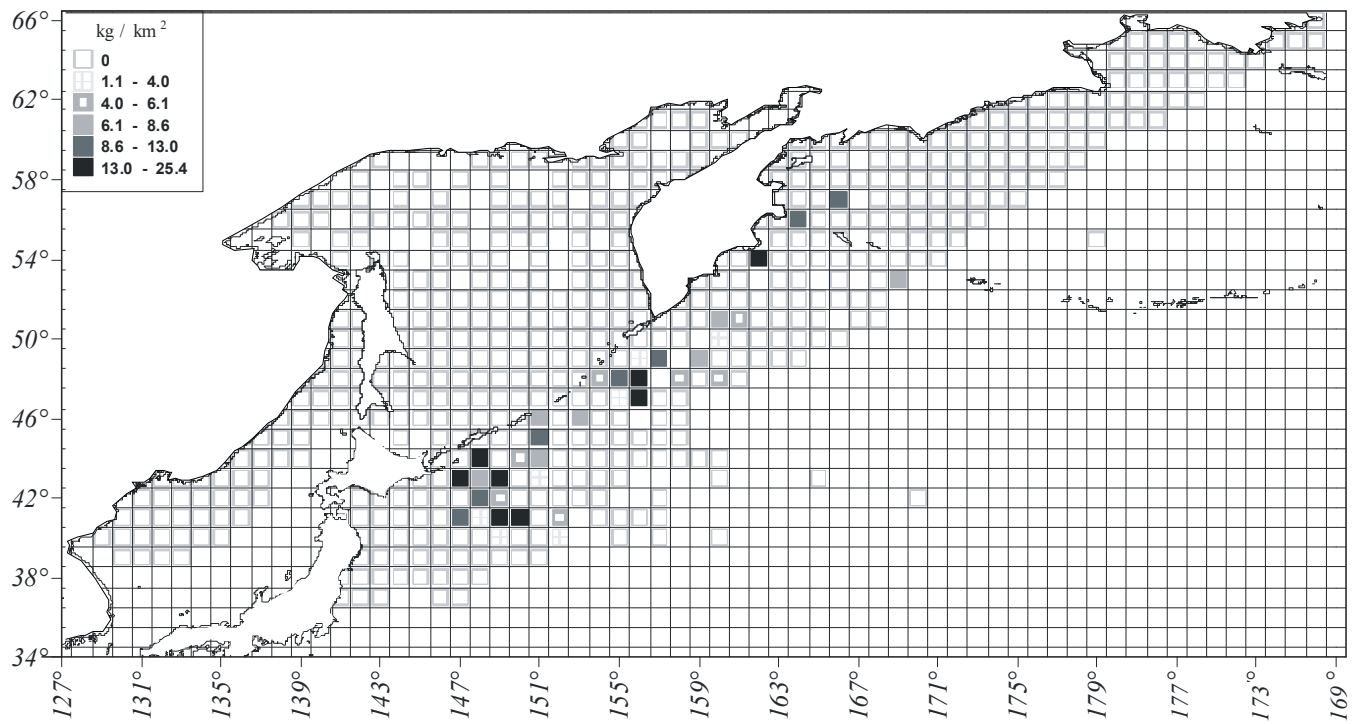
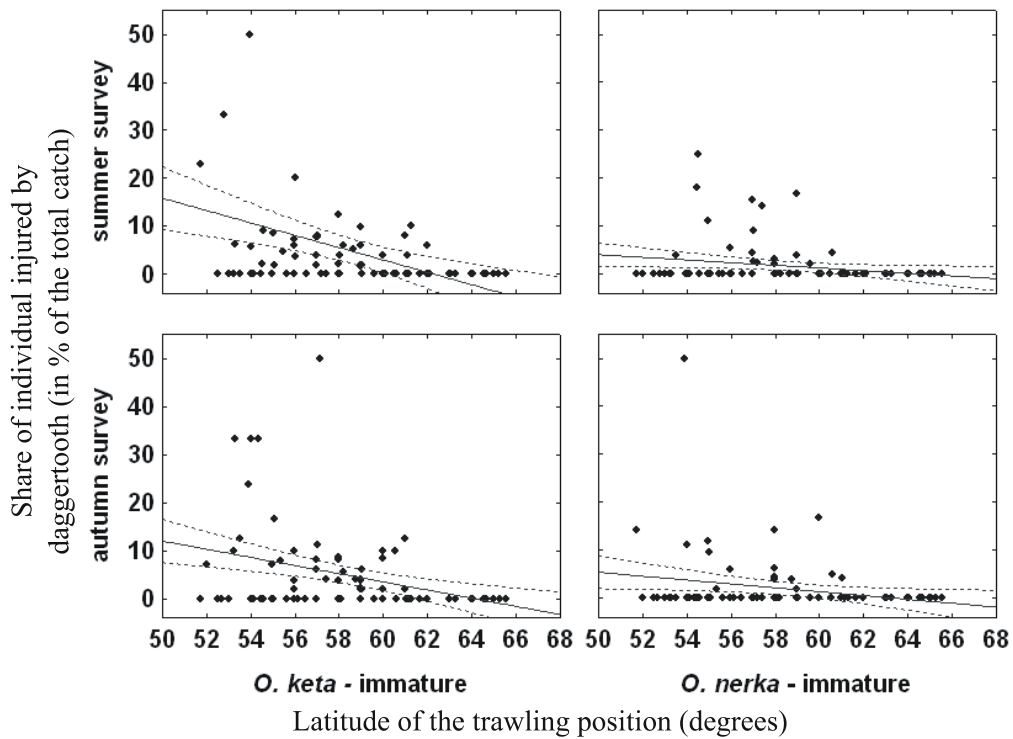
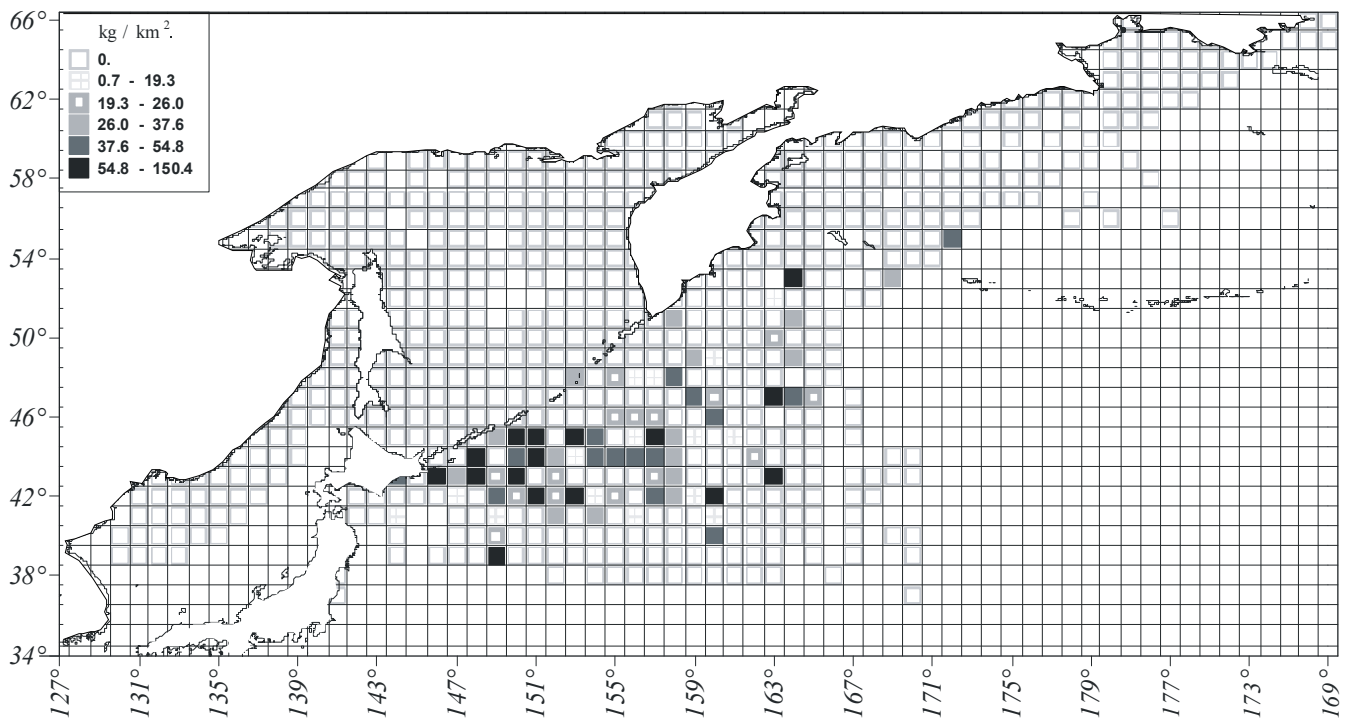


Fig. 4. North Pacific daggertooth CPUE (kg/km<sup>2</sup>) in the upper epipelagic layer of the northwest Pacific and adjacent areas during autumn. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.



**Fig. 5.** The relationship between the latitude of the trawling location and the percentage of individuals injured by North Pacific daggertooth (% of total catch) during two surveys in the northwestern Bering Sea (summer survey from July 15 to August 24, 2003 and autumn survey from September 14 to October 25, 2003). Solid and dotted lines indicate trends and 95% confidence interval of the trend lines, respectively.



**Fig. 6.** Longnose lancetfish CPUE (kg/km<sup>2</sup>) in the upper epipelagic layer of the northwest Pacific and adjacent areas during summer. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.

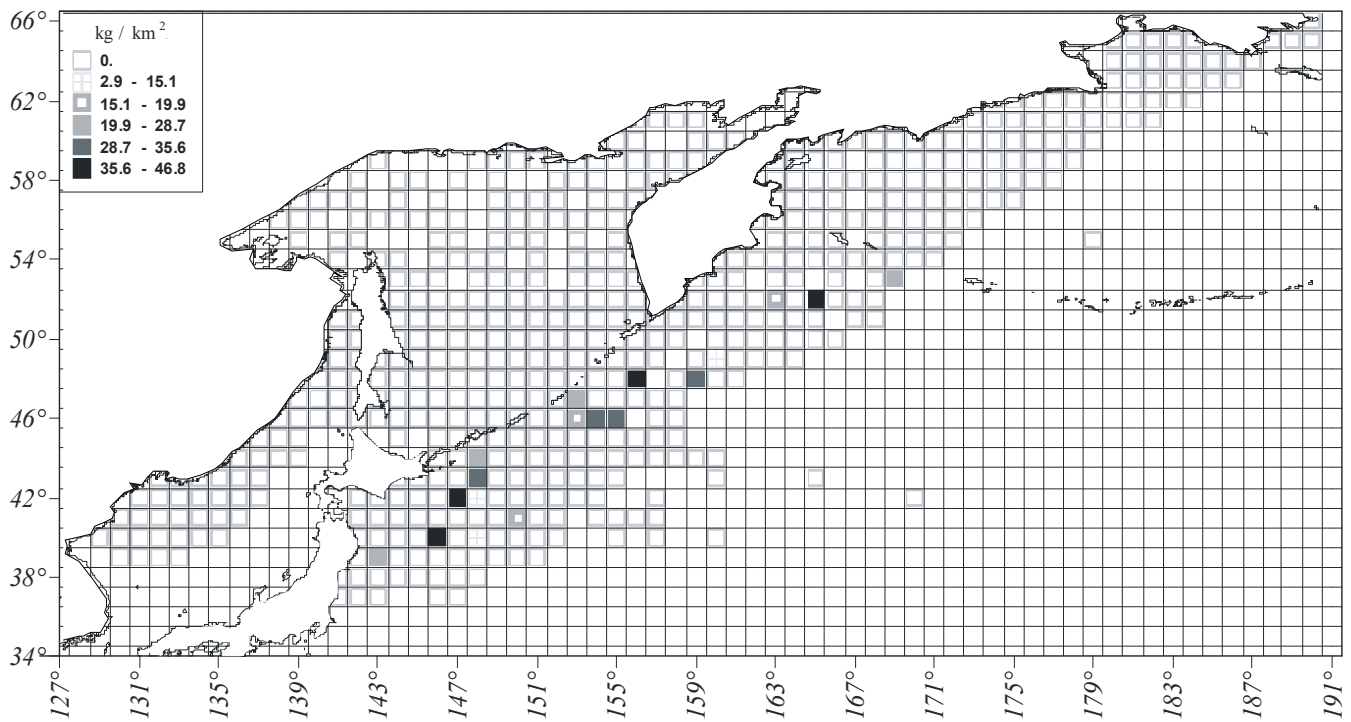


Fig. 7. Longnose lancetfish CPUE (kg/km<sup>2</sup>) in the upper epipelagic layer of the northwest Pacific and adjacent areas during autumn. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.

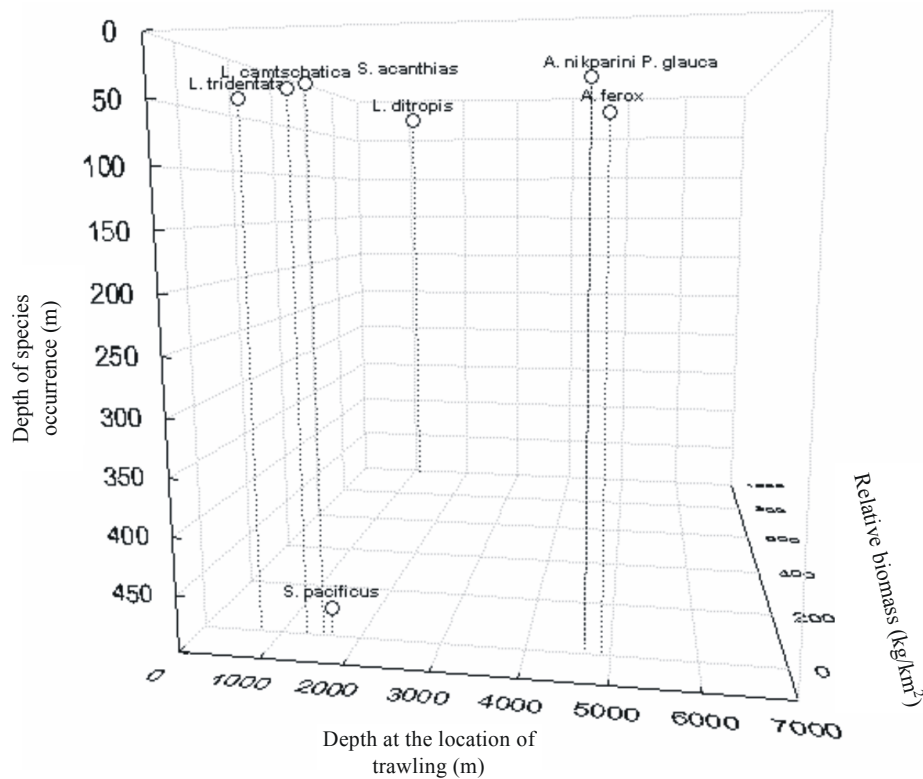


Fig. 8. Interspecific differences in the relationship between average depth at the location of trawling, depth of species occurrence, and relative biomass for different predatory fish during the summer.

could also result from the higher survival of larger fish. A certain accumulation of non-fatal injuries with age may also occur.

The incidence of injuries by longnose lancetfish on salmon were several times lower compared to those caused by daggertooth (Table 1). This may be due either to the lower abundance of longnose lancetfish, or to the higher mortality rate caused by lancetfish attacks.

Injuries by sea mammals were rarely observed during the surveys. It is known that sea mammal attacks, as well as attacks by sharks, are more lethal to salmon than those of the North Pacific daggertooth (Melnikov 1997). This may explain the almost complete absence of salmon with injuries by sea mammals and sharks in our samples. In addition, sea mammals attack Pacific salmon mainly in the coastal zone (Melnikov 1997), which was not included in our surveys.

The three-dimensional scatterplot that we used to identify predatory fish distributions showed that during the summer, which is the period of highest abundance of predatory fish species in the Russian economic zone, three distinct groups of species can be discerned (Fig. 8). The first group includes North Pacific daggertooth, longnose lancetfish and blue shark, living primarily in upper epipelagic layer over deepwater basins. The second group includes Arctic lamprey, Pacific lamprey, spiny dogfish and salmon shark, living primarily in upper epipelagic layer over the continental slope. Salmon sharks had biomass values that significantly exceeded those of other predatory fish. The third group included only Pacific sleeper sharks that live primarily in the mesopelagic layer over the continental slope.

Results of interspecific cluster analysis on similarity in spatial distribution patterns of Pacific salmon and their predators during summer in the upper epipelagic layer are shown in Fig. 9. They are quite different from the results shown in Fig. 8. This is understandable if we keep in mind that during cluster analysis the main emphasis is put not upon environmental preferences, but upon the similarities in small-scale (1 x 1 degree cells) spatial distributions. For instance, the two species of lamprey that lived in similar habitats (Fig. 8) fell into distinct clusters (Fig. 9). This corresponded well with the significant differences in spatial distribution of Pacific and Arctic lampreys (Figs. 3 and 4).

Maps of species spatial distributions revealed that during summer the spatial structure of the North Pacific daggertooth was characterized by relatively higher overlap with maturing pink salmon compared with large chum (Figs. 3, 10 and 11).

Geostatistical analysis of spatio-temporal distributions of major predatory fish species in relation to Pacific salmon revealed the following. The relative abundance of maturing pink salmon exhibited positive crosscovariance with the relative abundance of North Pacific daggertooth at relatively small separation distances, while at relatively large separation distances crosscovariance was negative (Fig. 12). In other words, the locations with relatively high values of

maturing pink salmon abundance were characterized by relatively high North Pacific daggertooth abundance. The crosscovariance between large maturing and immature chum salmon (fork length > 30 cm) and North Pacific daggertooth was opposite to that observed for maturing pink salmon. Large chum salmon exhibited negative crosscovariance with the relative abundance of North Pacific daggertooth at relatively small separation distances, while at relatively large separation distances crosscovariance was positive (Fig. 12). This can be explained if we keep in mind that majority of large chum salmon were located in the Bering Sea (Fig. 11), which is quite distant from the major concentrations of North Pacific daggertooth (Fig. 3). Maturing pink salmon had a distribution similar to that of the North Pacific daggertooth (Fig. 10).

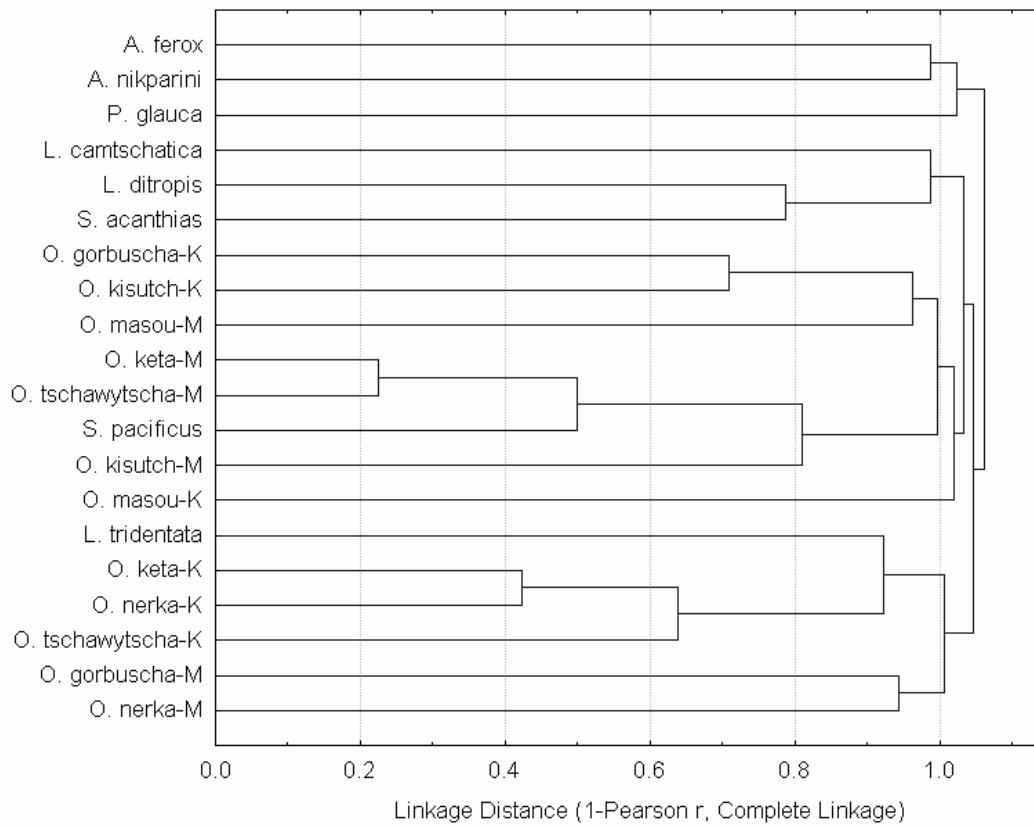
During the prespawning migration of maturing chum salmon in the northwest Pacific in the summer 2004 survey, there was significant spatial overlap with North Pacific daggertooth. This was evident from the positive crosscovariance values at small separation distances between the relative abundance of maturing chum salmon and North Pacific daggertooth. As a result, the relationship between crosscovariance and separation distance was negative ( $r = -0.48$ ,  $p = 0.01$ ).

No statistically significant relationship was observed between separation distance and crosscovariance between the relative abundance of North Pacific daggertooth and the percentage of maturing chum salmon with injuries during the summer 2004 survey. As with maturing chum salmon, no similarity in spatial distribution was observed between North Pacific daggertooth and the percentage of maturing pink salmon with injuries in the catch. This means that the spatial distribution of injured maturing pink and chum salmon was independent of the North Pacific daggertooth distribution in the northwest Pacific during summer 2004. This might be explained by the dispersal of injured individuals away from the places where they were injured.

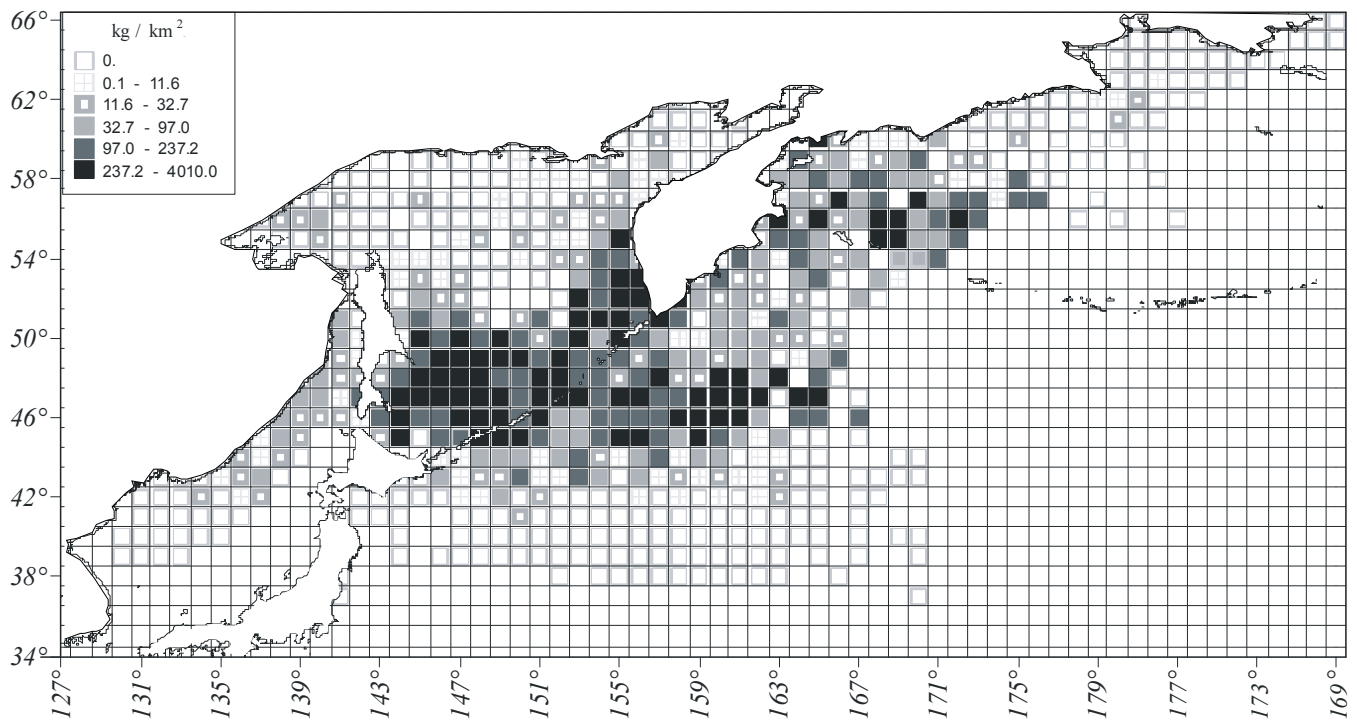
## SUMMARY

Our analysis showed that relative abundance of predatory fishes shows strong geographic variation. Spatial structure of predatory fish species is an indirect but functionally informative indicator of predation intensity. Information on when and where a particular predator is most abundant may reveal locations and time periods when Pacific salmon are most vulnerable.

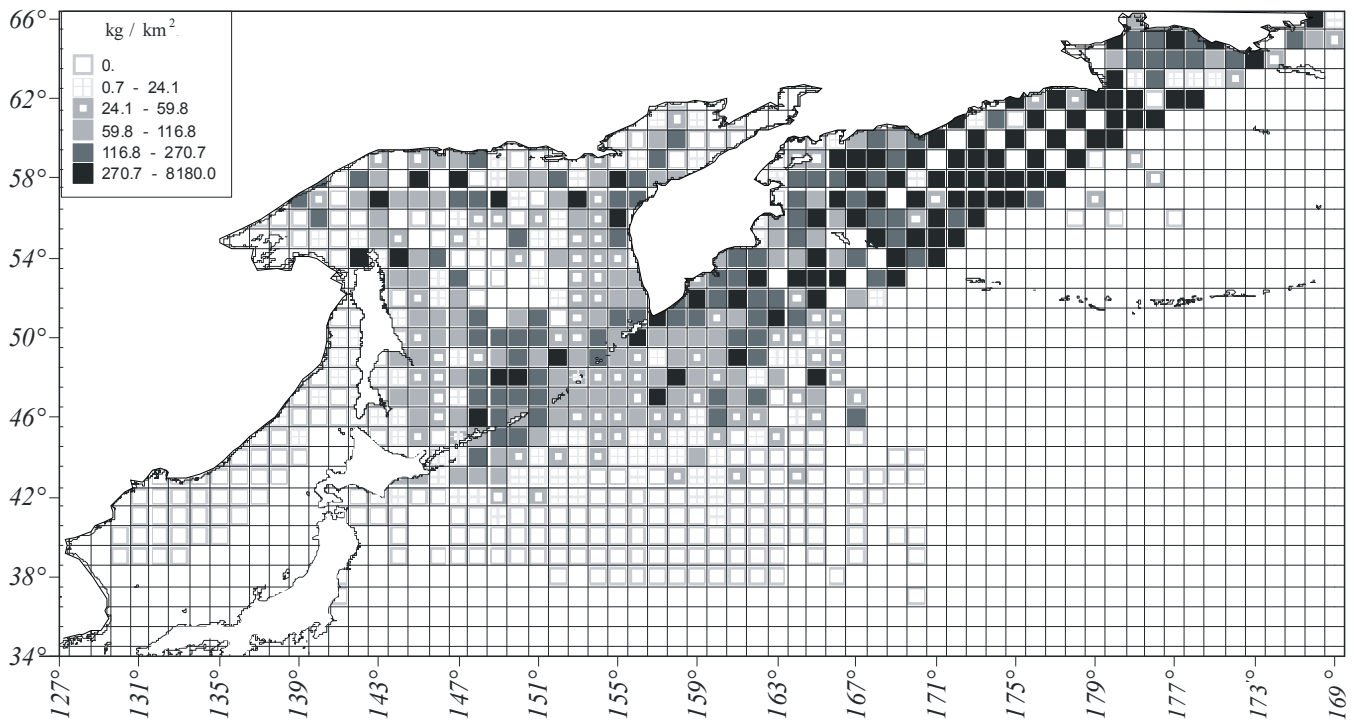
Quite often the abiotic (temperature, depth, e.g.) preferences of Pacific salmon and their predators differ significantly. In this sense the predator's spatial structure is often a tradeoff between an optimal abiotic environment and better feeding conditions. For instance, the spatial distribution of North Pacific daggertooth is mostly restricted to southern, warmer areas of the northwest Pacific, whereas the majority of Pacific salmon are located in more northern, cooler



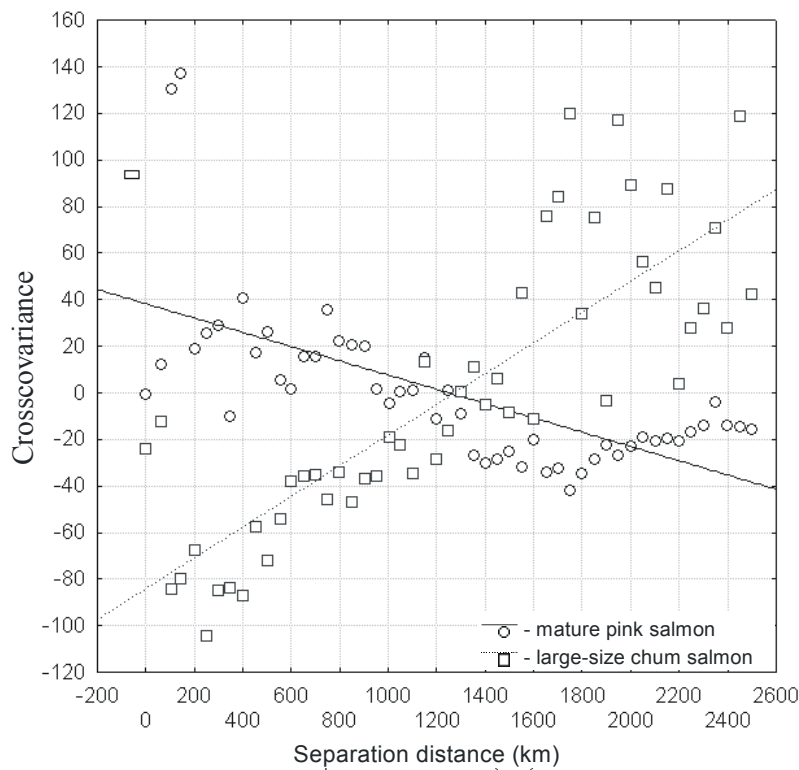
**Fig. 9.** Results of interspecific cluster analysis on similarity in spatial distribution patterns of Pacific salmon and their predators during summer in the upper epipelagic layer. The cluster analysis is based on matrix of Pearson correlation coefficients for relationship between different pairs of species relative biomasses averaged for every 1x1 degree cell sampled in the upper epipelagic layer.



**Fig. 10.** Maturing pink salmon CPUE (kg/km<sup>2</sup>) in the upper epipelagic layer of the northwest Pacific and adjacent areas during summer. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.



**Fig. 11.** Large maturing and immature (fork length > 30 cm) chum salmon CPUE (kg/km) in the upper epipelagic layer of the northwest Pacific and adjacent areas during summer. Long-term (1980–2004) average values are displayed for every 1x1 degree cell sampled.



**Fig. 12.** Relationship between separation distance and crosscovariance between relative abundance of North Pacific daggertooth and relative abundance of: a) maturing pink salmon (circles and solid line;  $r = -0.66, p < 0.001$ ), b) large maturing and immature (fork length > 30 cm) chum salmon (squares and dotted line;  $r = 0.83, p < 0.001$ ). Analysis is based upon relative abundance values in every 1x1 degree cell sampled in the upper epipelagic layer of the northwest Pacific and adjacent areas during summer, 1980–2004.

regions (Melnikov 1997).

Our data testify for species, age, seasonal and geographic specificity in rates of injury of Pacific salmon. This implies the necessity of considering species, age and regional specificity when estimating predator-related mortality of Pacific salmon. The spatio-temporal interaction between Pacific salmon and predatory fishes is complex. It is not simply the product of predator versus prey abundance levels.

Based on datasets of the 2002–2004 surveys in the Bering Sea and northwest Pacific we considered the spatial variability in injuries of Pacific salmon. We observed significant spatial aggregation in the levels of occurrence of Pacific salmon wounding. During both surveys the number of individuals injured by North Pacific daggertooth was greater in the southern, deepwater areas than in the northern, shallower waters. This pattern agrees both with our data on the higher abundance of North Pacific daggertooth in the Pacific waters off the Commander Islands and southwestern regions of the Bering Sea, compared with northern areas of the Bering Sea.

A review of the data on the occurrence of injuries has shown that, probably, maturing Pacific salmon in summer–autumn are somehow more susceptible to daggertooth attacks, compared with fish at other stages of maturity. Another possible explanation for the increased percentage of injured maturing individuals is that a certain accumulation of non-fatal injuries may occur as fish get older.

Previous studies suggest that spatial overlap between prey and predators is often a direct measure of predation intensity (Fahrig et al. 1993; Radchenko 1994; Melnikov 1997; Savinykh and Glebov 2003, among others).

In this study, spatial distribution of injured salmon was not a good indicator of the spatial allocation of predation intensity. This implies that spatial occurrence of injured Pacific salmon should be treated carefully in the context of the predator-prey relationship.

Most mathematical descriptions of predator-prey interactions fail to take into account the spatio-temporal structures of populations, which can lead to errors or misinterpretations (De Angelis and Petersen 2001). For instance, a compact pulse of prey migrating through a field of quasi-stationary predators may not be well described by standard predator-prey models, because the predators and prey are unlikely to be well mixed. The prey may be exposed to only a fraction of the predator population at a time. This underscores the importance of properly accounting for the ‘ecological neighborhood’, or effective feeding range, of predators in models.

If the home ranges of predators are relatively small, the predators could have significantly less effect than they would if they were sufficiently mobile to mix quickly through the entire reservoir and continue their individual contacts with the prey pulse for the entire time of prey passage (De Angelis and Petersen 2001). Thus, modelers dealing with the problem of predation on migrating populations need to take the

feeding range of the predator into account.

Studies characterizing horizontal predator–prey spatial overlap in marine species have documented that at small scales prey distribution is relatively uniform and predator–prey overlap is often poor (Rose and Leggett 1990; O’Driscoll et al. 2000; De Robertis 2002). Spatial overlap between Atlantic cod and capelin has been well studied over a range of scales. At large scales (> 4–20 km) cod exhibit positive overlap with capelin, their primary prey, but the distributions become negatively correlated at smaller scales (< 2–10 km). Planktivorous seabirds overlap poorly with zooplankton at scales < 2.5 km where prey distribution is relatively uniform, but exhibit consistent overlap at larger spatial scales where zooplankton biomass is more variable (Logerwell et al. 1998; De Robertis 2002). Our data on Pacific salmon and the distribution of predatory fish species has a resolution of approximately 30–60 naut mi due to survey grid spacing. Further studies at smaller spatial scales are desirable to explain spatial interactions of Pacific salmon and their predators. As the references cited above imply, it may be that at smaller spatial scales (< 30 naut mi) spatial interaction of Pacific salmon and their predators will differ.

Temporal variation in production processes, density-dependent habitat selection and the resulting changes in spatial structure of Pacific salmon and their predators, can affect Pacific salmon predation through changes in predator-prey spatial overlap. Predation intensity is likely to increase during periods of lower Pacific salmon abundance and increased abundance and geographic range of their predators. To achieve better understanding of Pacific salmon predation-related mortality we need to accumulate long-term data series. However, estimates of various predators’ contributions to Pacific salmon natural mortality are greatly impeded by the fact that at present there are no data on how scarring and wounding relates to mortality. Without this information all estimates of Pacific salmon mortality will be indirect and rough approximations.

## ACKNOWLEDGEMENTS

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