

**Diet Overlap and Potential Feeding Competition Between  
Yukon River Chum Salmon and Hatchery Salmon in the  
Gulf of Alaska in Summer**

by

**Katherine W. Myers, Robert V. Walker,  
Nancy D. Davis, and Janet L. Armstrong**

**High Seas Salmon Research Program  
Fisheries Research Institute  
School of Aquatic and Fishery Sciences  
University of Washington  
Box 355020  
Seattle, Washington 98195-5020**

**November 2004**

**Final Report to the Yukon River Drainage Fisheries Association, Contract Number:  
04-001; Financial Coding: #4 NRDA, Obj. 1; Project Name: Stock Origins,  
Migration Patterns, and Marine Productivity of Yukon River Salmon**

A publication of the Yukon River Drainage Fisheries Association pursuant to National Oceanic and Atmospheric Administration (NOAA) Award No. NA06FM0316. The views expressed do not necessarily reflect the views of NOAA or any of its sub-agencies.

**Diet Overlap and Potential Feeding Competition Between  
Yukon River Chum Salmon and Hatchery Salmon in the  
Gulf of Alaska in Summer**

by

**Katherine W. Myers, Robert V. Walker,  
Nancy D. Davis, and Janet L. Armstrong**

**High Seas Salmon Research Program  
Fisheries Research Institute  
School of Aquatic and Fishery Sciences  
University of Washington  
Box 355020  
Seattle, Washington 98195-5020**

**November 2004**

**Final Report to the Yukon River Drainage Fisheries Association, Contract Number:  
04-001; Financial Coding: #4 NRDA, Obj. 1; Project Name: Stock Origins,  
Migration Patterns, and Marine Productivity of Yukon River Salmon**

# **Diet Overlap and Potential Feeding Competition Between Yukon River Chum Salmon and Hatchery Salmon in the Gulf of Alaska in Summer**

## **Study History**

The Yukon River Drainage Fisheries Association (YRDFA) funded this study in late November 2003 to begin to address concerns about the effects that competition with hatchery salmon may have on the ocean growth and survival of Yukon River chum salmon. Data compilation and analyses were completed in September 2004. A final report of research results was submitted to YRDFA in November 2004.

## **Abstract**

Diet overlap and potential feeding competition between Yukon River chum salmon and Asian and Alaskan hatchery chum, pink, and sockeye salmon in the Gulf of Alaska in summer (1993-2003) were investigated. Our results indicate that overlap in the diets and geographic distribution of Yukon River chum salmon and hatchery salmon in the Gulf of Alaska in summer varies by species, body size group, and geographic region. We identified regions of our Gulf of Alaska study area with the highest potential for feeding competition between Yukon River chum salmon and Japanese and Alaska hatchery salmon in summer. Overlap in diets among different body size groups of chum salmon in these regions was high, indicating a high potential for intra-specific feeding competition between Yukon River chum salmon and Japanese and Alaska hatchery chum salmon. Although inter-specific overlap in salmon diets was low to moderate, the quality of chum salmon diets (mean calories per fish) was low compared to diets of all size groups of pink salmon and large-size sockeye salmon in all geographical regions where these species co-occurred. When the amount or quality of prey available to chum salmon is reduced by locally abundant stocks of hatchery salmon, adverse climatic and oceanographic changes are more likely to result in a decrease the ocean growth and survival of Yukon River chum salmon.

## **Key Words**

Gulf of Alaska, chum, diet overlap, food habits, competition, hatchery, wild.

## **Project Data**

Project data result from the analysis of salmon stomach content samples collected during the Gulf of Alaska survey of the R/V *Kaiyo maru* (August 2003) and historical data collected during research vessel surveys of the T/S *Oshoro maru* (July 1993-2002). These data include environmental (sample location and date, sea surface temperature), salmon biological (species, size, sex, age), and salmon food habits data. Data are formatted as Microsoft Excel spreadsheets.

Project data are archived by the High Seas Salmon Research Program, School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA, USA 98195-5020 (contact: K.W. Myers, [kwmyers@u.washington.edu](mailto:kwmyers@u.washington.edu), tel. 206-543-1101). There are no access limitations to the project data, but costs associated with filling sample and data requests (staff salaries, data storage media, shipping costs) must be paid by the person(s) or agency requesting the data.

**This report should be cited as follows:**

K.W. Myers, R.V. Walker, N.D. Davis, and J.L. Armstrong. 2004. Diet Overlap and Potential Feeding Competition Between Yukon River Chum Salmon and Hatchery Salmon in the Gulf of Alaska in Summer. Final Report to the Yukon River Drainage Fisheries Association. SAFS-UW-0407. School of Aquatic and Fisheries Sciences, University of Washington, Seattle. 63 p.

## Table of Contents

List of Tables.....	iv
List of Figures.....	v
List of Appendix Tables.....	viii
Executive Summary.....	1
Introduction.....	4
Objectives.....	6
Methods.....	6
Results.....	8
Discussion.....	10
Conclusions.....	15
Acknowledgments.....	15
Literature Cited.....	16

## List of Tables

Table 1. Preliminary 2003 hatchery releases of juvenile salmon in Canada, Japan, Korea, Russia, and the United States in millions of fish. Data source: North Pacific Anadromous Fish Commission (2004).....	21
Table 2. Percentage prey composition by prey wet weight (W, grams) in the stomach contents of three size groups of chum, sockeye, and pink salmon caught in six regions of the Gulf of Alaska in summer 1993-2003. Mean calories consumed per fish is an index of diet quality (Q, see methods section).....	22
Table 3. Mean caloric values (cal/g wet weight) of prey categories used to calculate an index of salmon diet quality (Q, mean calories per fish, Table 2).....	25
Table 4. Maturity composition of three size groups of chum and sockeye salmon in six regions of the Gulf of Alaska in summer 1993-2003, collected for stomach content analysis.....	30
Table 5. Number of otolith-marked salmon released from Pacific Rim hatcheries in 2003 (A), and preliminary number of otolith-marked salmon released from Pacific Rim hatcheries in 2004 (B).....	31

## List of Figures

Figure 1. Commercial salmon harvests, by species, in Canada, Japan, Russia, and the United States from 1972 to 2003 (round weight in metric tons).....	32
Figure 2. Map of the study area in the Gulf of Alaska and adjacent North Pacific waters .....	33
Figure 3. Mean caloric content (cal/g wet weight) of prey categories used in analysis of salmon diet similarity (see Table 3 for data sources).....	34
Figure 4. Mean number of calories per fish in the diets of large (top panel), medium (middle panel), and small (bottom panel) body weight categories of chum, pink, and sockeye salmon in the Gulf of Alaska food habits study area by region (Fig. 2).....	35
Figure 5. Percent Similarity Index (PSI; values shown in figure legend) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon in the Northwest region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 157°-165°W longitude, Fig. 2).....	36
Figure 6. Percent Similarity Index (PSI; values shown in figure legend) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon in the Southwest region of the Gulf of Alaska (GOA; south of the sea surface temperature minimum and between 157°-165°W longitude, Fig. 2).....	37
Figure 7. Percent Similarity Index (PSI; values shown in figure legend) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon in the North Mid region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 149°-156°W longitude, Fig. 2).....	38
Figure 8. Percent Similarity Index (PSI; values shown in figure legend) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon in the South Mid region of the Gulf of Alaska (GOA; south of the sea surface temperature minimum and between 149°-156°W longitude, Fig. 2).....	39
Figure 9. Percent Similarity Index (PSI; values shown in figure legend) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon in the Northeast region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 139°-148°W longitude, Fig. 2).....	40
Figure 10. Percent Similarity Index (PSI; values shown in figure legend) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon in the Southeast region of the Gulf of Alaska (GOA; south of the sea surface temperature minimum and between 139°-148°W longitude, Fig. 2).....	41
Figure 11. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum and pink salmon in the Northwest region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 157°-165°W longitude, Fig. 2).....	42
Figure 12. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon and two size groups of pink salmon in the Southwest region of the Gulf of Alaska	

(GOA; south of the sea surface temperature minimum and between 157°-165°W longitude, Fig. 2).....	43
Figure 13. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum and pink salmon in the North Mid region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 149°-156°W longitude, Fig. 2).....	44
Figure 14. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon and two size groups of pink salmon in the Northeast region of the Gulf of Alaska (GOA; north of the sea surface temperature minimum and between 139°-148°W longitude, Fig. 2).....	45
Figure 15. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon and two size groups of pink salmon in the Southeast region of the Gulf of Alaska (GOA; north of the sea surface temperature minimum and between 139°-148°W longitude, Fig. 2).....	46
Figure 16. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum and sockeye salmon in the Northwest region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 157°-165°W longitude, Fig. 2).....	47
Figure 17. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum and sockeye salmon in the Southwest region of the Gulf of Alaska (GOA; south of the sea surface temperature minimum and between 157°-165°W longitude, Fig. 2).....	48
Figure 18. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum and sockeye salmon in the North Mid region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 149°-156°W longitude, Fig. 2).....	49
Figure 19. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon and two size groups of sockeye salmon in the South Mid region of the Gulf of Alaska (GOA; south of the sea surface temperature minimum and between 149°-156°W longitude, Fig. 2).....	50
Figure 20. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum and sockeye salmon in the Northeast region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 139°-148°W longitude, Fig. 2).....	51

Figure 21. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum and sockeye salmon in the Southeast region of the Gulf of Alaska (GOA; south of the sea surface temperature minimum and between 139°-148°W longitude, Fig. 2) .....	52
Figure 22. The high seas distribution of seasonal races (summer and fall) of immature Yukon River chum salmon by month, as shown by tagging experiments (1956-2003).....	53
Figure 23. The high seas distribution of seasonal races (summer and fall) of maturing Yukon River chum salmon by month, as shown by tagging experiments (1956-2003) .....	54
Figure 24. The high seas distribution of immature Japanese chum salmon by month, as shown by tagging experiments (1956-2003) and otolith mark recovery experiments (2002) .....	55
Figure 25. The high seas distribution of maturing Japanese chum salmon by month, as shown by tagging experiments (1956-2003) .....	56
Figure 26. The high seas distribution of immature and maturing Prince William Sound, Alaska, chum salmon by month, as shown by tagging experiments (1956-2003) and otolith mark recovery experiments (1997-2002) .....	57
Figure 27. The high seas distribution of immature and maturing southeastern Alaska chum salmon by month, as shown by tagging experiments (1956-2003) and otolith mark recovery experiments (1997-2000) .....	58
Figure 28. The high seas distribution of maturing Kodiak Island, Alaska, pink salmon by month, as shown by tagging experiments (1956-2003) .....	59
Figure 29. The high seas distribution of maturing Prince William Sound, Alaska, pink salmon by month, as shown by tagging experiments (1956-2003) and otolith mark recovery experiments (1998-2002) .....	60
Figure 30. The high seas distribution of Cook Inlet, Alaska, sockeye salmon by month, as shown by tagging experiments (1956-2003) .....	61
Figure 31. The high seas distribution of Prince William Sound, Alaska, sockeye salmon by month, as shown by tagging experiments (1956-2003) .....	62

## **List of Appendix Tables**

Appendix Table 1. List of prey animals and food items of Pacific salmon in the Gulf of Alaska in 1994-2000. Source: Kaeriyama et al. (2004) .....	63
---	----

## Executive Summary

With funding from the Yukon River Drainage Fisheries Association (YRDFA; contract no. 2004-001), we investigated diet overlap and potential feeding competition between Yukon River chum salmon and hatchery chum, pink, and sockeye salmon in offshore waters (primarily, international waters beyond the U.S. 200-mile zone) of the Gulf of Alaska in summer. The specific objectives of this study were: (1) to estimate salmon diet overlap by species, body size group, and region, (2) to provide information on the times and areas where intermingling of hatchery salmon and Yukon River chum salmon in the Gulf of Alaska are likely to occur, and (3) to evaluate these results with respect to the potential effects of large-scale releases of hatchery salmon on the marine growth and survival of Yukon River chum salmon in the Gulf of Alaska.

We collected salmon stomach contents data aboard Japanese research vessels during NOAA-funded international cooperative high seas salmon research cruises in the Gulf of Alaska in summer 1993-2003. The pooled (summer 1993-2003) stomach contents data were stratified into six geographic regions, including two (North and South) latitudinal regions and three (West, Mid, East) longitudinal regions in the Gulf of Alaska. The boundary of the two latitudinal regions was defined by the position of the annual summer (July) sea surface temperature minimum, which is associated with two distinct summer feeding zones for salmon in our Gulf of Alaska study area. The three longitude regions (West, 157°-165°W; Mid, 149°W-156°W; and East, 139°W-148°W) included transect lines with the most similar oceanographic conditions.

We assumed that similarity in diets is likely to be highest among salmon of similar body sizes. The results of a previous study indicated that in the Gulf of Alaska, pink and sockeye salmon between the body weights of 600 and 1200g switch from feeding on zooplankton to squid. We stratified our stomach contents data into three body size groups (small= $\leq$ 600 g, medium = 600-1200 g, and large =  $>$ 1200 g) of chum, sockeye, and pink salmon in each of the six geographic regions.

Diet overlaps of the three species (chum, pink, and sockeye salmon) and body-size groups in the six regions of our Gulf of Alaska study area were estimated using a modified Schoener's index, called the Percent Similarity Index (PSI). For each species and body-size group, we also calculated an index of diet quality (Q) or the mean number of calories consumed per fish in each of the six regional strata.

The North Pacific Anadromous Fish Commission (NPAFC) high seas salmon tag recovery database (1956-2003), the high seas coded-wire tag recovery database (1980-2004), and the otolith mark recovery database (1997-2002) were used to plot maps of the ocean distribution of Yukon River chum salmon and salmon from geographic regions that produce the majority of hatchery chum (Japan, Prince William Sound, and Southeast Alaska), pink (Prince William Sound and Kodiak Island), and sockeye salmon (Cook Inlet and Prince William Sound) by month with respect to the Gulf of Alaska food habits study area. We also reviewed information from the literature on the genetic stock composition of immature and maturing chum salmon in the Gulf of Alaska. These data were used to infer spatial and temporal overlap in distribution and potential feeding

competition between Yukon River chum salmon and hatchery chum, pink, and sockeye salmon in the Gulf of Alaska in summer.

Food habits data from 4,996 salmon stomachs collected in 1993-2003 were analyzed, including 1,719 chum, 1,499 pink, and 1,778 sockeye salmon. The samples included a mixture of immature and maturing chum and sockeye salmon and maturing pink salmon. For all body weight groups of chum salmon the percentages of fish with empty stomachs, which may indicate poor feeding conditions, were highest in the eastern regions of our Gulf of Alaska study area. The quality of chum salmon diets was low compared to the diets of all size groups of pink salmon and large-size sockeye salmon in all geographical regions where the species co-occurred. The diets of medium- and small-size chum and sockeye salmon were often similar in quality, except in the eastern regions of the study area, where chum salmon had lower quality diets than sockeye salmon. Overlap in the diets of chum, pink, and sockeye salmon in the Gulf of Alaska varied by species, body size group, and geographic region.

The PSI values for pairwise comparisons between different size groups of chum salmon in regions north of the SST minimum were usually high, and tended to be higher in northern regions than in southern regions. In northern regions, the prey category with the highest PSI values for all size groups of chum salmon was usually pteropods, which are a low-calorie food. In the three southern regions, PSI values were highest for small- and medium-size chum salmon that fed on amphipods, which are also a relatively low-calorie food (although they have a higher caloric content than pteropods). The PSI values were moderate to low in the Southwest region, and were high in the Southeast region.

The PSI values for pairwise comparisons between different size groups of chum and pink salmon were usually low to moderate. The PSI values for pairwise comparisons between different size groups of chum and sockeye salmon were often higher in northern regions than in southern regions. Interspecific overlap in diets tended to be highest when all species were feeding on amphipods or pteropods or both.

Limited data from high seas tagging experiments indicate that immature Yukon River chum salmon are distributed in the Gulf of Alaska throughout the summer, although their distribution shifts to the north and west as the season progresses. Older age groups of immature Yukon River chum salmon tend to be distributed farther to the north and west than younger age groups. Maturing Yukon River chum salmon are distributed primarily in the northern regions of our study area. Maturing Yukon River chum migrate from the Gulf of Alaska to the Bering Sea in June and July. By July maturing Yukon River summer chum salmon have left the Gulf of Alaska, and maturing Yukon River fall chum salmon may occur only in the Northwest region of our study area.

High seas salmon tag, otolith-mark, and genetic data indicate that in our study area in summer overlaps in the distributions and diets of Yukon River chum salmon and Japanese hatchery chum salmon are most likely to occur in the West regions, and overlaps with Alaskan hatchery chum, pink, and sockeye salmon are most likely to occur in the Mid and East regions.

In our Gulf of Alaska study area in summer, the highest potential for feeding competition between maturing Yukon River chum salmon and hatchery chum salmon is

probably in the Northwest region. Tag recovery data indicate that by late June and early July, many maturing Yukon River and Japanese hatchery chum salmon have already migrated to the Bering Sea. Previously published genetic stock composition estimates indicate that approximately 30% of maturing chum salmon in the western regions of our study area in summer are Japanese hatchery fish, and only 10% are western Alaska fish. Even though similarity in the diets of different size groups of chum salmon in the Northwest region was high, the quality of large- and medium-size chum salmon diets was also high relative to other regions of our study area, and percentages of fish with empty stomachs were low. These results suggest that the potential for intra-specific feeding competition between maturing Yukon River chum salmon and Japanese hatchery salmon in our Gulf of Alaska study area in summer may be relatively low.

Our results indicate that the highest potential for feeding competition between immature Yukon River chum salmon and Alaska hatchery salmon is in the eastern regions of our study area. Chum salmon in the Northeast and Southeast regions had relatively high percentages of empty stomachs and low calorie prey (e.g., gelatinous zooplankton) in their diets compared to fish in other regions. Although chum salmon have a diverse diet, it is likely that competition for food within and between stocks of chum salmon could occur, particularly when chum salmon are locally abundant. The potential for intra-specific feeding competition between immature Yukon River chum salmon and Alaska hatchery chum salmon may be particularly high in the Northeast region, where all size groups of chum salmon had lower diet quality and higher diet similarity than in the Southeast region. The potential for inter-specific competition with Alaska hatchery pink and sockeye salmon also seems to be higher in the Northeast region than in the Southeast region. In the Northeast region, the diets of large- and medium-size pink salmon and large-size sockeye salmon contained higher percentages of high-calorie zooplankton and squid and the diets of large-size chum salmon contained a higher percentage of low-calorie gelatinous zooplankton than in the Southeast region. Previous studies have indicated that when pink salmon abundance is high, chum salmon may switch their diets to alternative low-calorie prey, e.g., gelatinous zooplankton, which decreases feeding competition with other zooplanktivorous salmon.

We hypothesize that inter- and intra-specific competition with hatchery salmon in the Gulf of Alaska may reduce the growth of immature Yukon River chum salmon, particularly when adverse oceanographic and climatic conditions limit prey availability. We also hypothesize that reductions in growth due to competition with hatchery fish may reduce the survival of immature Yukon River chum salmon by several possible mechanisms, e.g., an increase in predation, a decrease in storage of lipids, and an increase in parasites and diseases.

In conclusion, our results indicate that overlap in the diets and geographic distribution of Yukon River chum salmon and hatchery salmon in the Gulf of Alaska in summer varies by species, body size group, and geographic region. Regions of the Gulf of Alaska with the highest potential for feeding competition between Yukon River chum salmon and hatchery chum, pink, and sockeye salmon in summer were identified. Overlap in diets among different size groups of chum salmon in these regions was high, indicating a strong potential for intra-specific feeding competition between Yukon River and hatchery chum salmon. Although inter-specific overlap in salmon diets was low to moderate, the

quality of chum salmon diets in the Gulf of Alaska was low compared to the diets of pink and sockeye salmon. Consumption of low quality prey (e.g., gelatinous zooplankton) by chum salmon may decrease intra-specific competition between different size or maturity groups of chum salmon and inter-specific competition with pink and sockeye salmon. When the amount or quality of prey available to chum salmon is reduced by abundant stocks of hatchery salmon, adverse climatic and oceanographic changes are more likely to result in a decrease the ocean growth and survival of chum salmon.

A better understanding of the spatial and temporal patterns of ocean distribution, abundance, food habits and feeding behavior, growth, and bioenergetics of hatchery and wild salmon and their prey is needed. Future investigations of potential feeding competition between Yukon River chum salmon and hatchery salmon should be expanded to include other oceanic regions where they are distributed, particularly the central North Pacific Ocean, Aleutian Islands, and eastern Bering Sea. Little is known about interactions between immature and maturing Yukon River chum salmon and hatchery salmon in coastal and offshore waters within the U.S. 200-mile zone. In the international waters of the Gulf of Alaska, new field research should focus on interactions between maturing Yukon River chum salmon and Japanese hatchery chum salmon in the western regions of our study area, and immature Yukon River chum salmon and Alaska hatchery chum, pink, and sockeye salmon in the Mid and East regions of our study area. Historical salmon food habits data collected in the Gulf of Alaska and other oceanic regions during the winter, spring, and fall seasons should be incorporated into the existing summer database. Further analyses of these data would expand our knowledge of other critical locations and seasons when inter- and intra-specific competition between Yukon River chum salmon and hatchery salmon are most likely to occur. Finally, new research should emphasize the development and application of methods to identify the stock origins of individual fish in mixed-stock ocean fishery and research vessel samples, including the tagging or marking of all hatchery salmon released into the North Pacific Ocean and Bering Sea.

## **Introduction**

Approximately 5 billion juvenile Pacific salmon (*Oncorhynchus* spp.) are released annually into the North Pacific Ocean by hatcheries in Asia and North America (Table 1). Limited information from high seas tagging studies indicates that in summer Yukon River chum salmon (*O. keta*) are distributed in both the Bering Sea and Gulf of Alaska (Myers et al. 1996), where they intermingle with Asian and North American hatchery salmon. There is increasing evidence that western Alaska stocks of salmon are food limited during their offshore migrations in the North Pacific Ocean and Bering Sea (e.g., Rogers 1980; Rogers and Ruggerone 1993; Aydin 2000; Aydin et al. 2000; Kaeriyama et al. 2000, 2004; Ruggerone et al. 2003). Since the mid 1970s, there has been a large increase in the commercial catches of Asian and North American salmon (Fig. 1). This increase in commercial catches is correlated with climate change (e.g., Beamish and Bouillion 1993), as well as an increase in the production of hatchery salmon and a decrease in the body size of adult salmon returning to both continents, indicating a limit to the carrying capacity of salmon in the ocean (e.g., Kaeriyama 1989, Ishida et al. 1993,

Helle and Hoffman 1995, Bigler et al. 1996). U.S. marine research on salmon carrying capacity in the ocean has focused largely on the early (juvenile) life-history phase, when salmon are migrating in waters over the continental shelf during their first summer at sea (Brodeur et al. 2003). Results of international cooperative high seas salmon research, however, suggest that inter- and intra-specific competition for food and density-dependent growth effects occur primarily among older age groups of salmon, when stocks originating from all geographic regions around the Pacific Rim mix and feed in offshore waters (e.g., Ishida et al. 1993, Ishida et al. 1995, Myers et al. 2000; Tadokoro et al. 1996, Walker et al. 1998, Azumaya and Ishida 2000, Bugaev et al. 2001, Davis 2003). In addition, time-series analysis of scale pattern and abundance data indicates a substantial decrease in marine survival of western Alaska salmon during years of peak abundance of Asian salmon (Ruggerone et al. 2003). The period of overlap when marine survival was affected seems to be from winter of the first year at sea, when western Alaska salmon move off the continental shelf, through at least summer of the second year at sea, when they are distributed across broad regions of the North Pacific Ocean and Bering Sea (Ruggerone et al. 2003).

In a previous study funded by the Yukon River Drainage Fisheries Association (YRDFA), food habits data from salmon collected in fall 2002 from the Bering Sea and in summer 1991-2002 were analyzed for seasonal (summer-fall 2002) and long-term comparisons of salmon diets (Davis et al. 2003). Samples were grouped into three major habitats, representative of the distribution of Yukon River salmon: (1) eastern Bering Sea shelf (<200-m depth contour), (2) central Bering Sea basin (>200-m depth contour), and (3) Aleutian Islands. In fall diet overlap values (modified Schoener's index) were low to moderate for sockeye (*O. nerka*) and chum salmon (49%, basin) and chum and chinook (*O. tshawytscha*) salmon (28% basin, 30% shelf). Diet overlap between sockeye and chum salmon was very high (80%) in the Aleutian Islands, where both species consumed macro-zooplankton (crustaceans and pteropods), and was reduced when chum salmon consumed gelatinous zooplankton (medusae and ctenophores). Shifts in prey composition of sockeye, chum, and chinook salmon between seasons, habitats, and salmon age groups were likely due to changes in prey availability. Davis et al. (2003) concluded that if prey availability is reduced by poor ocean conditions, then increased food competition could decrease growth and survival of Yukon River salmon in the Bering Sea and Aleutian Islands.

In the current study we extend our work on trophic interactions to salmon in the offshore waters of the Gulf of Alaska, primarily in international waters beyond the U.S. 200-mile zone. Limited information from high seas tagging studies indicates that in summer immature Yukon River chum salmon are distributed in both the Bering Sea and Gulf of Alaska (Myers et al. 1996), where they intermingle with salmon released from hatcheries in Asia and North America. Poor offshore rearing conditions (low zooplankton abundance, warm water temperatures) in the Gulf of Alaska in summer may increase food competition between hatchery salmon and Yukon River chum salmon (Kaeriyama et al. 2004). We examine this problem by analyzing time-series data on salmon food habits (1993-2003) and stock distribution (1956-2003) in the Gulf of Alaska in summer. We assume that these stomach contents data are representative of the food

habits of all hatchery and wild salmon stocks (including Yukon River chum salmon) migrating in the study area.

## Objectives

The specific objectives of this study were: (1) to estimate salmon diet overlap by species, body size group, and region, (2) to provide information on the times and areas where intermingling of hatchery salmon and Yukon River chum salmon in the Gulf of Alaska are most likely to occur, and (3) to evaluate these results with respect to the potential effects of large-scale releases of hatchery salmon on the marine growth and survival of Yukon River chum salmon in the Gulf of Alaska.

## Methods

The methods used to collect high seas salmon food habits data in the Gulf of Alaska are described by Kaeriyama et al. (2000; 2004). In August 2003, the Japanese research vessel *Kaiyo maru* conducted an extensive (approximately 1-month) survey of salmon in the Gulf of Alaska. Scientists from the School of Aquatic and Fishery Sciences (SAFS), University of Washington participated in this survey (Myers et al. 2004a). The YRDLA funding was used to analyze salmon food habits data from the 2003 survey. The results were combined with our existing time-series of summer (late June-July 1993-2002) Gulf of Alaska salmon food habits data. Diet overlap by species, size group, and geographic region were estimated. Stock identification information from tags, thermal otolith marks, and genetics was used to infer spatial and temporal overlap in distribution and to evaluate the potential for feeding competition between Yukon River chum salmon and hatchery chum, pink (*O. gorbuscha*), and sockeye salmon in the Gulf of Alaska in summer.

### Study Area and Fishing Methods

Our Gulf of Alaska study area was located primarily in international waters beyond the U.S. 200-mile zone (Fig. 2). In 1993-2002, SAFS scientists collected salmon stomach contents data during cooperative Japan-U.S. salmon gillnet surveys aboard the Japanese research vessel *Oshoro maru* in the Gulf of Alaska, primarily along two north-south transects (145°W and 165°W) in June and July. Salmon were caught using a research gillnet. The net, designed to eliminate fishing (salmon body size) selectivity, was constructed of web panels with 10 different mesh sizes (48, 55, 63, 72, 82, 93, 106, 121, 138, and 157 mm stretched mesh). The net hung from the surface to a depth of approximately 6 m below the surface, and was soaked overnight.

In 2003, SAFS scientists collected salmon stomach contents data during a cooperative Japan-U.S. salmon trawl survey aboard the R/V *Kaiyo maru* in the Gulf of Alaska in August (research funded by NOAA Contract 50ABNF1-0002; Myers et al. 2004a). Salmon were caught using a NICHIMO model NST-60-K1 surface rope trawl (manufactured by NICHIMO CO. LTD., Japan; 202.2 m total length, 63 m headrope length, hexagonal mouth opening, 13-mm liner in the codend, and a typical vertical and horizontal spread of 60 m). Floats were attached to the headrope to keep it at the surface, and weights were attached to the front of the trawl to sink the footrope. The trawl was

towed for 1 hour at the surface at 5 knots with 250 m of warp. Four north-south transects were fished (160°W, 155°W, 150°W, and 145°W).

### **Analysis of Salmon Stomach Contents**

Scientists on board the research vessels sorted the salmon catch by species, and biological data, including fork length (mm), body weight (g), sex, gonad weight (g), and a scale sample for age determination, were collected. The stomachs of salmon representing a range of body sizes and maturity groups from each species were collected for food habits analysis. Aboard the research vessels, the stomach of each fish was weighed to the nearest gram (full weight, FW), and then opened. The stomach fullness was examined, and the number of fish with empty stomachs was recorded. If the stomach contained food, the fresh contents were removed, and the empty stomach was weighed (empty weight, EW). The total weight of stomach contents or prey weight (PW) of each fish  $i$  was calculated as:

$$PW_i = FW_i - EW_i \quad (1)$$

The fresh stomach contents were sorted into taxonomic groups, using a binocular dissecting microscope in most years. The major taxonomic groups of prey included euphausiids (EU), copepods (CO), amphipods (AM), larval crabs (CR), squid (SQ), pteropods (PT), fish (FI), polychaetes (PO), chaetognaths (CH), and gelatinous zooplankton (medusae and ctenophores, GE). The percent volume of each prey category was estimated visually.

### **Data Analysis**

For each fish  $i$  in the summer 1993-2003 Gulf of Alaska stomach contents samples, the weight ( $W$ , in grams wet weight) of each prey category  $j$  was calculated as:

$$W_{ij} = V_j \times PW_i \quad (2)$$

where  $V$  is the percent volume of each prey category  $j$  (estimated visually).

The pooled summer 1993-2003 stomach contents data were stratified into six geographic regions, including two (North and South) latitudinal regions and three (West, Mid, East) longitudinal regions (Fig. 2). Aydin et al. (2000) found two distinct summer feeding zones for salmon associated with the July latitudinal sea surface temperature minimum. The diets of salmon in the southern zone are often high in micronektonic squid (primarily 60-120 mm mantle length, *Berryteuthis anonychus*), while the diets of salmon in the northern zone are often higher in mesozooplankton (e.g., euphausiids, copepods, amphipods, pteropods). The boundary between the North and South latitudinal regions in summer varied from year to year and between longitude regions, depending on the location of the sea surface temperature (SST) minimum. The annual summer position of the North-South boundary was determined from satellite data or from CTD data collected at the fishing stations in the study area, according to methods described by Aydin (2000) and Aydin et al. (2000). In general, the three longitude regions (West, 157°-165°W; Mid, 149°W-156°W; and East, 139°W-148°W) include transect lines having the most similar oceanographic conditions (Fig. 2; Aydin 2000).

We assumed that similarity in diets is likely to be highest among salmon of similar body sizes. In the Gulf of Alaska, pink and sockeye salmon between the body weights of 600 and 1200g switch from feeding on zooplankton to squid (Aydin 2000). We calculated the percentage prey composition by total prey weight in the stomach contents of three body size groups (small= $\leq 600$  g, medium = 600-1200 g, and large =  $>1200$  g) of chum, sockeye, and pink salmon in each of the six geographic regions (Fig. 2).

A modified Schoener's index, called the Percent Similarity Index (PSI), was used to calculate diet overlap between pairwise combinations of the three size groups of chum, pink, and sockeye salmon in the six geographic regions. The PSI is the sum of the proportional weights of individual prey categories in common between two predators, and is calculated according to the formula (Buckley et al. 1999):

$$PSI = \sum [\min (p_{xj}, p_{yj})] \quad (3)$$

where  $p$  is the proportion of prey category  $j$  in predators  $x$  and  $y$ .

The PSI ranges from 0 to 100%, where 0% indicates no overlap and 100% indicates complete overlap in diet of the two predators (low similarity = 0-24%, moderate = 25-40%; high = 50-74%, very high = 75-100%; Buckley et al. 1999). Because stomach contents were identified to general taxa, the PSI may overestimate diet similarity. Prey identified to the lowest possible taxa, however, included the same major species in the stomach contents of all species of salmon in our Gulf of Alaska data time series (Kaeriyama et al. 2004; Appendix Table 1).

An index of diet quality ( $Q$ ) or the mean number of calories consumed per fish  $i$  by each predator  $x$  in each region and body weight stratum, was calculated as:

$$Q = \sum [(p_{xj} \times \sum W_{ij} \times C_j)/n] \quad (4)$$

where  $C_j$  is the mean caloric content (cal/g wet weight) of prey category  $j$ , and  $n$  is the number of fish in each strata, including fish with empty stomachs. Caloric values used to calculate the mean for each prey category were derived from previously published studies.

The North Pacific Anadromous Fish Commission (NPAFC) high seas salmon tag recovery database (1956-2003), the high seas coded-wire tag recovery database (1980-2004), and the high seas otolith mark recovery database (1997-2002), archived at SAFS, were used to plot maps of the ocean distribution of Yukon River chum salmon and salmon from geographic regions that produce the majority of hatchery chum (Japan, Prince William Sound, and Southeast Alaska), pink (Prince William Sound and Kodiak), and sockeye salmon (Cook Inlet and Prince William Sound) by month with respect to the Gulf of Alaska food habits study area. We also reviewed information from the literature on the genetic stock composition of immature and maturing chum salmon in the Gulf of Alaska. We are not aware of any published genetic stock composition estimates for pink and sockeye salmon migrating in the international waters of the Gulf of Alaska in summer. Data from ongoing studies by the Fisheries Agency of Japan on the genetic stock composition of chum salmon and the recovery of otolith-marked hatchery salmon in the August 2003 *Kaiyo maru* catches were not available at the time of completion of this report.

## Results

Food habits data from 4,996 salmon stomachs collected in 1993-2003 were analyzed, including 1,719 chum, 1,499 pink, and 1,778 sockeye salmon (Table 2). For all body weight groups of chum salmon, the percentages of fish with empty stomachs were highest in the eastern regions of the study area (Table 2). The estimated mean caloric density of salmon prey categories used in the analysis ranged from 92 cal/g wet weight (gelatinous zooplankton) to 1,561 cal/g wet weight (squid; Fig. 3, Table 3). The maturity composition of chum and sockeye salmon in the stomach contents samples by body weight group and study area region is shown in Table 4. All pink salmon in the 1993-2003 food habits samples were maturing fish. For all body weight groups, the quality of chum salmon diets (mean calories consumed per fish) was always lower than that of pink salmon in all regions where the two species co-occurred (Table 2, Fig. 4). The quality of large sockeye salmon diets was higher than that of large chum salmon in all regions (Table 2, Fig. 4). The diets of medium and small size chum and sockeye salmon were often similar in quality. In the Northeast region, however, the diets of medium-size sockeye salmon were higher in quality than those of medium-size chum salmon (Table 2, Fig. 4). In the Southeast region, the diets of small sockeye salmon were higher in caloric content than those of small size chum salmon (Table 2, Fig. 4).

The PSI values for pairwise comparisons between different size groups of chum salmon in regions north of the SST minimum were usually high, and tended to be higher in northern regions than in southern regions (Figs. 5-10). In northern regions, the prey category with the highest PSI values for all size groups of chum salmon was usually pteropods (Figs. 5, 7, and 9), although in the Northeast region similarities between small- and medium-size chum salmon were highest for euphausiids (Fig. 9). In the three regions south of the SST minimum, diet overlaps were highest for small- and medium-size chum salmon feeding on amphipods (Figs. 6, 8, and 10). The PSI values were moderate to low in the Southwest region (Fig. 6), and were high in the Southeast region (Fig. 10). Samples of chum salmon were insufficient to adequately characterize diet overlaps in the South Mid region (Fig. 8).

The PSI values for pairwise comparisons between different size groups of chum and pink salmon were usually low to moderate (Figs. 11-15). The PSI values were high between medium-size chum salmon and large-size pink salmon in the North Mid region (61.6%, Fig. 12), between small-size chum salmon and medium-size pink salmon in the Southwest region (56.0%, Fig. 12), and between small- and medium-size chum salmon and medium-size pink salmon in the Southeast region (53.8% and 62.0%, respectively; Fig. 15).

The PSI values for pairwise comparisons between different size groups of chum and sockeye salmon were often higher in northern regions than in southern regions (Figs. 16-21). Overlap in diets was highest when both species were feeding on amphipods or pteropods or both.

The results of high seas tagging experiments indicate that immature Yukon River chum salmon likely occur in the Gulf of Alaska throughout the summer, although their

distribution shifts to the north and west as the season progresses (Fig. 22). Older age groups of immature Yukon River chum salmon tend to be distributed farther to the north and west than younger age groups (Fig. 22). Maturing Yukon River chum salmon are distributed primarily in the northern (Mid and West) regions of our study area in summer (Fig. 23). Maturing Yukon River chum migrate from the Gulf of Alaska to the Bering Sea in June and July. By July maturing Yukon River summer-run chum salmon have left the Gulf of Alaska, and maturing Yukon River fall-run chum salmon may occur only in the Northwest region of our study area.

There have been few recoveries from tagged and otolith-marked Japanese chum salmon in the Gulf of Alaska in summer (June-July; Figs. 24 and 25). The majority of tag recoveries in Japan were from fish released farther to the west (west of 165°W) in the North Pacific Ocean, Aleutian Islands, and Bering Sea (Figs. 24 and 25). With respect to our study area, overlaps in the summer distribution of Yukon River chum salmon and Japanese hatchery salmon are most likely to occur in the western regions (Figs. 22-25).

The high seas tag and otolith mark recovery data indicate that maturing Prince William Sound (PWS) and Southeast Alaska (SE) chum salmon are distributed primarily in the North Mid and Northeast regions of our study area in June and July (Figs. 26 and 27). The distributions of immature PWS/SE chum salmon in international waters in June and August are not well known, but in July they seem to be distributed primarily in the eastern region of the study area. Overlaps in the summer distribution of PWS/SE hatchery chum salmon and Yukon River chum salmon are most likely to occur between maturing fish in the North Mid region, between maturing PWS/SE fish and immature Yukon fish in the North Mid, Northeast, and Southeast regions, and between immature fish in the Northeast and Southeast regions of the study area (Figs. 22, 23, 26, and 27).

In June and July, maturing Kodiak Island (KI) and PWS pink salmon are distributed throughout the mid- and east-regions of the study area (Figs. 28 and 29). In addition, limited otolith-mark recovery data show that PWS hatchery pink salmon also occur in the western regions of the study area in summer. By August, KI/PWS pink salmon stocks may remain only in the North Mid region of the study area. Overlaps in the summer distribution of maturing KI/PWS pink salmon and maturing Yukon River chum salmon are most likely to occur in the Northwest and North Mid regions, and overlaps with immature Yukon fish may occur throughout the entire Gulf of Alaska study area (Figs. 22, 23, 28, and 29).

In June and July, maturing Cook Inlet (CI) and PWS sockeye salmon are distributed across the northern regions of our study area, with major concentrations in the North Mid and Northeast regions (Figs. 30 and 31). Immature CI/PWS sockeye salmon are distributed to the south and west of maturing CI/PWS fish. Overlaps in summer distribution of maturing CI/PWS sockeye salmon and immature and maturing Yukon River chum salmon in our study area are most likely to occur in the North Mid and Northeast regions (Figs. 23, 30, and 31). Overlaps in summer distribution of immature CI/PWS sockeye salmon and immature Yukon River chum salmon are most likely to occur across the southern regions of our study area (Figs. 22, 30, and 31).

## Discussion

The results of high seas tag and otolith-mark recovery experiments and genetic stock identification studies show that chum, pink, and sockeye salmon originating from most major salmon producing regions in Asia and North America are distributed for at least part of their ocean life in the Gulf of Alaska (e.g., Myers et al. 1996, Kawana et al. 1999, Urawa et al. 2000, Seeb et al. 2004). We assumed that the 1993-2003 Gulf of Alaska salmon food habits data used in our study are representative of hatchery and wild salmon originating from all Asian and North American regions, including Yukon River chum salmon. Maturing chum salmon were present in our summer samples from the Gulf of Alaska (Table 4). Because of the sample period (late June-August) and the long distance of our Gulf of Alaska study area from the Yukon River, however, it is unlikely that many of these were maturing summer-run Yukon River chum salmon, which by convention are defined as those fish returning to the mouth of the Yukon River by July 15. We consider stomach content data from immature chum salmon in our study to be representative of both summer- and fall-run Yukon River fish.

Our results do not account for any species, size-related, or seasonal differences in diel behavior of salmon or their prey. Davis et al. (2000) found inter-specific differences in diel gillnet catches and feeding behavior of chum, pink, and sockeye salmon in the central Bering Sea, as well as shifts in their prey between daytime and nighttime feeding periods. Pearcy et al. (1984) found that the consumption of diel migrating prey (e.g., euphausiids, fish, squid) by salmon in the Gulf of Alaska varies throughout the day. We may have under- or over-estimated diet overlaps for salmon consuming diel migrating prey because our 1993-2002 samples were collected by driftnets soaked overnight and hauled in the early morning, and our 2003 samples were collected only during daylight hours by a surface research trawl. In addition, diel vertical distribution of salmon varies among species, as well as by season and maturity stage. For example, chum salmon migrate vertically throughout the day, and their maximum swimming depths can exceed 300 m below the surface, whereas sockeye salmon usually remain within 30 m of the surface (Walker et al., in press).

To our knowledge, the only published estimates of the genetic stock composition of immature and maturing chum salmon our Gulf of Alaska study area in summer (June and July 1998) are by Urawa et al. (2000). These estimates indicate that most chum salmon in the eastern region of our study area are of North American origin (15% western Alaska, 25% Alaska Peninsula/KI, 28% SE/PWS, and 18% British Columbia), and most chum salmon in the western region are of Asian origin (25% Japan, 53% Russia, and 13% western Alaska). Percentages of immature SE/PWS stocks are higher in the Southeast region than in the Northeast region, and are highest among age 0.1 fish. Percentages of western Alaska stocks are low (<1%) in age 0.1 fish, and are higher in older age 0.2 (21%) and age 0.3 (17%) fish. A high percentage (58%) of maturing fish in the Northeastern region of our study area in July is from southern North American stocks (British Columbia and Washington). Genetic analyses of chum salmon tissue samples collected by Japanese researchers in our Gulf of Alaska study area after 1998 are ongoing or postponed until funding is available.

Direct information on the distribution of Alaska hatchery salmon in our Gulf of Alaska study area in summer was limited to a few published studies of high seas recoveries of otolith-marked fish. At present, approximately 1.4 billion otolith-marked hatchery salmon are released by hatcheries in Asia and North America (Table 5). Alaska hatchery releases of otolith-marked sockeye salmon, however, are relatively low (31.2 million fish in 2004) compared to pink (695 million fish) and chum (448 million fish) salmon (Table 5). To date, there have been no attempts to recover otolith-marked sockeye salmon in our Gulf of Alaska study area.

One of the largest salmon hatchery programs in the world is located in PWS, where over 600 million pink salmon fry are released each year (e.g., McNair 2002). All otolith-marked hatchery pink salmon recovered in our Gulf of Alaska study area in summer 1998 (27 June-10 July) were from four hatcheries in PWS (Kawana et al. 1999), where about 295 million otolith-marked pink fry were released in 1997 (Geiger and Munk 1998). The catch per unit effort (CPUE) of the marked PWS hatchery pink salmon was higher in the eastern regions of our study area than in the western regions, and in the eastern region the CPUE was higher in the Northeast region (55-56°N) than in the Southeast region (49-52°N) (Kawana et al. 1999). There were no otolith-marked hatchery pink salmon among samples collected from our Gulf of Alaska study area in late July 2002 (Myers et al. 2004b).

Recoveries of otolith-marked hatchery chum salmon in our study area in July 1998 (9.7% of fish examined) were mostly immature fish from four hatcheries in SE/PWS, where about 200 million marked chum fry were released annually (Urawa et al. 2000). Percentages of otolith-marked hatchery chum salmon were higher in the eastern region of our study area (14.5% of the total number of fish examined) than in the western region (1.1%; Urawa et al. 2000). The percentages of otolith-marked chum salmon were higher in the Southeast region (21.5%) than in the Northeast region (8.9%). Urawa et al. (2000) concluded that most of the SE/PWS chum salmon in the eastern regions of the study area in summer may be hatchery fish, if the survival rate is similar among otolith-marked and unmarked hatchery fish. Mass otolith marking of Japanese hatchery chum salmon began with 1998 brood year stocks. Analyses of chum salmon otolith samples collected by Japanese researchers in our Gulf of Alaska study area after 1998 are ongoing or postponed until funding is available. The first reported recovery of an otolith-marked Japanese hatchery chum salmon in the Gulf of Alaska in summer was in the Northeast region of our study area in July 2002 (Fig. 24; Myers et al. 2004b).

For maturing Yukon River chum salmon in our Gulf of Alaska study area in summer, the highest potential for feeding competition with hatchery salmon is probably in the Northwest region (Fig. 2). Tag recovery data and published genetic stock composition estimates indicate that by late June and early July, most maturing Yukon River and Japanese hatchery chum salmon have migrated to the Bering Sea (Figs. 23 and 25; Seeb et al. 2004). Genetic stock composition estimates indicate that approximately 30% of maturing chum salmon in the western regions of our study area in summer are Japanese hatchery fish, and only 10% are western Alaska fish (Urawa et al. 2000). Even though similarity in the diets of different size groups of chum salmon in the Northwest region was high (Fig. 5), the quality of large- and medium-size chum salmon diets was also high relative to other regions of our study area (Fig. 4), and percentages of fish with empty

stomachs were low (Table 2). These results suggest that the potential for intra-specific feeding competition between maturing Yukon River chum salmon and Japanese hatchery chum salmon in our Gulf of Alaska study area in summer may be relatively low. Overlap in distribution and feeding competition between maturing Yukon River chum salmon and Japanese hatchery chum salmon in the Gulf of Alaska are more likely to occur in winter and spring.

Although chum salmon have a diverse diet (Table 2), our results indicate that intra-specific competition for food between different size groups of immature chum salmon is likely (Figs. 5-10). In locations where large numbers of Asian and North American chum salmon intermingle, growth reductions of immature Yukon River chum salmon may result. Significant negative relationships have been observed between the abundance of chum salmon and mean fish size (e.g., Ishida et al. 1993, Kaeriyama 1996), and density-dependent factors explained 35% of the decrease in average size of chum salmon in the central North Pacific Ocean (Ishida et al. 1993). Analyses of scale patterns indicate that density-dependent interactions may reduce body size of immature chum salmon in the third year of ocean life (Kaeriyama 1989; Ishida et al. 1993; Walker et al. 1998; Azumaya and Ishida 2000). Migration routes estimated from fish abundance and genetics data show that after their second summer at sea immature Japanese hatchery chum salmon migrate between summer feeding grounds in the Bering Sea and winter habitat in the Gulf of Alaska (Urawa 2004).

For immature Yukon River chum salmon in the Gulf of Alaska in summer, the highest potential for feeding competition with hatchery salmon is in the eastern regions of our study area. Chum salmon in the Northeast and Southeast regions had relatively high percentages of empty stomachs and low calorie prey (e.g., gelatinous zooplankton) in their diets (Table 2). The potential for intra-specific feeding competition between immature Yukon River chum salmon and immature and maturing hatchery chum salmon may be particularly high in the Northeast region, where all size groups of chum salmon had lower diet quality and higher diet similarity than in the Southeast region (Table 2, Figs. 8 and 9).

Our results substantiate earlier food habits studies in the Gulf of Alaska in summer, which have shown that chum salmon feed primarily on zooplankton, whereas pink and sockeye salmon may feed alternatively on zooplankton or gonatid squid (*B. anonychus*; LeBrasseur 1966, 1972; Percy et al. 1988; Aydin 2000; Aydin et al. 2000; Kaeriyama et al. 2000, 2004; Table 2). Carbon and nitrogen stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) analyses indicate that all species of Pacific salmon in the Gulf of Alaska occupy the same branch of the food web, and that sockeye salmon occupy a slightly higher trophic level than chum and pink salmon (Satterfield and Finney 2002; Kaeriyama et al. 2004). The potential for inter-specific competition between immature Yukon River chum salmon, maturing Alaska hatchery pink salmon, and immature and maturing Alaska hatchery sockeye salmon seems to be higher in the Northeast region than in the Southeast region. In the Northeast region, the diets of large- and medium-size pink salmon and large-size sockeye salmon contained higher percentages of high-calorie zooplankton and squid, and the diets of large-size chum salmon contained a higher percentage of low-calorie gelatinous zooplankton than in the Southeast region (Table 2). When pink salmon abundance is high, chum salmon may switch their diets to alternative prey, e.g.,

gelatinous zooplankton, to decrease feeding competition with other zooplanktivorous salmon (Andrievskaya 1966, Tadokoro et al. 1996, Davis 2003). Although gelatinous zooplankton are a low-calorie food, they may provide some dietary advantages because chum salmon guts are anatomically specialized to quickly digest prey (Welch 1997), and gelatinous zooplankton are more easily and quickly digested than prey with higher lipid content (Arai et al. 2003; Dulepova and Dulepov 2003). In future studies, inter-specific differences in digestion and consumption rates should be considered when assessing diet quality.

Inter-specific competition for food among Asian and North American chum, pink, and sockeye salmon is a likely mechanism for density-dependent reduction in their ocean growth (e.g., Takagi et al. 1981, Heard 1991, Bugaev et al. 2001). Length and weight of Ozernaya River (western Kamchatka) sockeye salmon were substantially reduced in years when marine abundance of Kamchatka pink salmon was high (Bugaev et al. 2001). Edge-of-scale growth in high-seas chum salmon was negatively correlated with Asian pink salmon abundance (Walker et al. 1998). Davis (2003) observed increases (13% in sockeye, 19% in chum, 72% in pink salmon) in the weight of low calorie prey (pteropods, amphipods, or gelatinous zooplankton) in salmon stomach contents collected in the central Bering Sea in odd-numbered years, when maturing pink salmon were abundant. Bioenergetic models indicate that salmon in summer are feeding at rates close to their physiological maximum, and that small, short-term decreases in daily ration caused by competition could significantly decrease growth (Davis et al. 1998). Under these conditions, small- and medium-size pink and sockeye salmon in the Gulf of Alaska may not attain a size large enough to feed on squid, and would continue to compete with chum salmon for zooplankton prey (Aydin 2000).

Our results showed that there were differences in diet overlap among species and size groups in different regions in the Gulf of Alaska. Regional differences in diet overlap could result from the effects of physical oceanographic conditions (water temperatures, salinity, currents, mixed-layer depth, etc.) on the distribution, abundance, or progression of life-history stages of salmon and their prey (Davis et al. 2003). We hypothesize that intra- and inter-specific competition with hatchery salmon in the Gulf of Alaska may reduce the growth of immature Yukon River chum salmon, particularly when adverse oceanographic and climatic conditions limit prey availability. Kruse (1998) discussed the potential link between salmon run failures in western Alaska in 1997-1998 and anomalous ocean conditions. Kaeriyama et al. (2004) reported an increase in food-niche overlap among chum, sockeye, and pink salmon in our Gulf of Alaska study area in summer 1997-2000, i.e., a shift in diets from micronekton (in pink and sockeye salmon diets) or gelatinous zooplankton (in chum salmon diets) to a more diverse array of zooplankton prey in all species, which corresponded to changes in ocean conditions caused by climate events (El Niño, La Niña).

Competition for food may also be a direct cause of shifts in ocean distribution of salmon. For example, Azumaya and Ishida (2000) observed a southeastward shift in the summer distribution of Japanese hatchery chum salmon in years when Asian pink salmon are abundant, which could increase competition between Japanese hatchery chum and less abundant North American stocks distributed in the southeastern Bering Sea and Gulf of Alaska. Shifts in salmon diets or geographic distribution and reductions in growth due

to competition with hatchery fish may also reduce the survival of Yukon River chum salmon by several possible mechanisms, including increased predation (Ruggerone et al. 2003), decreased storage of lipids needed to sustain salmon through winter (Nomura et al. 2002), and increased susceptibility to parasites and disease.

## **Conclusions**

Our results indicate considerable overlap in the diets and distribution of Yukon River chum salmon and hatchery salmon in the Gulf of Alaska in summer. Our study does not address the potential for feeding competition between Yukon River chum salmon and major wild populations of salmon that are distributed in the Gulf of Alaska, e.g., Bristol Bay and Fraser River sockeye salmon. Regions of the Gulf of Alaska with the highest potential for feeding competition between Yukon River chum salmon and hatchery chum, pink, and sockeye salmon in summer were identified. Overlap in diets among different size groups of chum salmon in these regions was high, indicating a strong potential for intra-specific feeding competition between Yukon River and hatchery chum salmon. The quality of chum salmon diets in the Gulf of Alaska was low, compared to the diets of pink and sockeye salmon. Consumption of low quality prey (e.g., gelatinous zooplankton) by chum salmon may decrease intra-specific competition between different size or maturity groups of chum salmon and inter-specific competition with pink and sockeye salmon. When the quantity or quality of prey available to chum salmon is reduced by abundant stocks of hatchery pink, chum, and sockeye salmon, adverse climatic and oceanographic changes are more likely to result in a decrease of the ocean growth and survival of chum salmon.

A better understanding of the mechanisms that cause variation in the spatial and temporal patterns of ocean distribution, abundance, food habits and feeding behavior, growth, and bioenergetics of hatchery and wild salmon and their prey is needed. Future investigations of potential feeding competition between Yukon River chum salmon and hatchery salmon should be expanded to include other oceanic regions where they are distributed, particularly the central North Pacific Ocean, Aleutian Islands, and eastern Bering Sea. Little is known about interactions between immature and maturing Yukon River chum salmon and hatchery salmon in coastal and offshore waters within the U.S. 200-mile zone. In the international waters of the Gulf of Alaska, new field research should focus on interactions between maturing Yukon River chum salmon and Japanese hatchery chum salmon in the western regions of our study area, and immature Yukon River chum salmon and Alaska hatchery chum, pink, and sockeye salmon in the Mid and East regions of our study area. Our salmon food habits data were limited to summer, but feeding competition may be more intense in winter, spring, or fall. Historical salmon food habits data collected in the Gulf of Alaska and other oceanic regions during the winter, spring, and fall seasons should be incorporated into the existing summer database. Further analyses of these data would expand our knowledge of other critical locations and seasons when inter- and intra-specific competition between Yukon River chum salmon and hatchery salmon are most likely to occur. Finally, new research should emphasize the development and application of methods to identify the stock origins of individual fish in mixed-stock ocean fishery and research vessel samples, including the tagging or marking of all hatchery salmon released into the North Pacific Ocean and Bering Sea.

## Acknowledgments

We thank the Fisheries Agency of Japan, Tokyo, and Hokkaido University, Faculty of Fisheries, Hakodate, Japan, for inviting us to participate in Gulf of Alaska research cruises aboard the *Oshoro maru* (1993-2002) and *Kaiyo maru* (2003), and for providing cruise data, biological data, and samples. We thank Professor M. Kaeriyama and his students at Hokkaido Tokai University, Sapporo, Japan, for providing some of the food habits data used in this report. We thank E. Farley, Auke Bay Laboratory, and S. Urawa and M. Kawana, National Salmon Resources Center, Sapporo, for providing otolith mark recovery data. We thank the Auke Bay Laboratory, Nat. Mar. Fish. Serv. (NOAA Contract 50-ABNF-1-00002) for funding our salmon food habits fieldwork aboard the *Oshoro maru* and *Kaiyo maru*, as well as our work on the high seas salmon tag, coded-wire tag, and otolith-mark databases. Funding for this study was provided by the Yukon River Drainage Fisheries Association through a grant from NOAA (Award No. NA06FM0316).

## Literature Cited

- Andrievskaya, L.D. 1966. Food relationships of the Pacific salmon in the sea. *Voprosy Ikhtologii* 6:84-90. (In Russian, translated by U.S. Bureau of Comm. Fish., 1966.)
- Arai, M.N., D.W. Welch, A. L. Dunsmuir, M.C. Jacobs, and A. R. Ladouceur. 2003. Digestion of pelagic Ctenophora and Cnidaria by fish. *Can. J. Fish. Aquat. Sci.* 60: 825-829.
- Aydin, K.Y. 2000. Trophic feedback and variation in carrying capacity of Pacific salmon (*Oncorhynchus* spp.) on the high seas of the Gulf of Alaska. Ph.D. Dissertation, University of Washington, Seattle. 383 p.
- Aydin, K.Y., K.W. Myers, and R.V. Walker. 2000. Variation in summer distribution of the prey of Pacific salmon (*Oncorhynchus* spp.) in the offshore Gulf of Alaska in relation to oceanographic conditions, 1994-98. *N. Pac. Anadr. Fish Comm. Bull.* 2:43-54.
- Azumaya, T., and Y. Ishida. 2000. Density interactions between pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) and their possible effects on distribution and growth in the North Pacific Ocean and Bering Sea. *N. Pac. Anadr. Fish Comm. Bull.* 2:165-174.
- Beamish, R.J., and D.R. Bouillion. 1993. Pacific salmon production trends in relation to climate. *Can. J. Fish. Aquat. Sci.* 50:1002-1016.
- Bigler, B.S., D.W. Welch, and J.H. Helle. 1996. A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). *Can. J. Fish. Aquat. Sci.* 53:455-465.
- Boldt, J.L. 1997. Condition and distribution of forage fish in Prince William Sound, Alaska. M.Sc. Thesis. University of Alaska, Fairbanks. 155 p.

- Brodeur, R.D., K.W. Myers, and J.H. Helle. 2003. Research conducted by the United States on the early ocean life history of Pacific salmon. N. Pac. Anadr. Fish Comm. Bull. 3:89-131.
- Buckley, T.W., G.E. Tyler, D.M. Smith, and P.A. Livingston. 1999. Food habits of some commercially important groundfish off the coasts of California, Oregon, Washington, and British Columbia. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-102. 173 p.
- Bugaev, V.F., D.W. Welch, M.M. Selifonov, L.E. Grachev, and J.P. Eveson. 2001. Influence of the marine abundance of pink salmon (*Oncorhynchus gorbuscha*) and sockeye salmon (*O. nerka*) on growth of Ozernaya River sockeye. Fish. Oceanogr. 10:26-32.
- Davis, N.D. 2003. Feeding ecology of Pacific salmon (*Oncorhynchus* spp.) in the central North Pacific Ocean and central Bering Sea, 1991-2000. Ph.D. Dissertation, Hokkaido University, Hakodate. 190 p.
- Davis, N.D., J.L. Armstrong, and K.W. Myers. 2003. Bering Sea salmon food habits: Diet overlap in fall and potential for interactions among salmon. Final Report to the Yukon River Drainage Fisheries Association. SAFS-UW-0311. Fisheries Research Institute, School of Aquatic and Fisheries Sciences, University of Washington, Seattle. 34 p.
- Davis, N.D., K.Y. Aydin, and Y. Ishida. 2000. Diel catches and food habits of sockeye, pink, and chum salmon in the central Bering Sea in summer. N. Pac. Anadr. Fish Comm. Bull. 2:99-109.
- Davis, N.D., K.W. Myers, and Y. Ishida. 1998. Caloric value of high-seas salmon prey organisms and simulated salmon ocean growth and prey consumption. N. Pac. Anadr. Fish Comm. Bull. 1:146-162.
- Dulepova, E.P., and V.I. Dulepov. 2003. Interannual and interregional analysis of chum salmon feeding features in the Bering Sea and adjacent Pacific waters of eastern Kamchatka. N. Pac. Anadr. Fish Comm. Doc. 728. Pac. Sci. Res. Fish. Ctr. (TINRO-Centre), Vladivostok. 8 p.
- Geiger, H.J., and K.M. Munk. 1998. Otolith thermal mark release and mass-processing history in Alaska (USA), 1988-1998. N. Pac. Anadr. Fish Comm. Doc. 368. Alaska Department of Fish and Game, CWT & Otolith Processing Lab, Juneau, Alaska. 9 p.
- Heard, W.R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). Pages 119-230 in C. Groot and L. Margolis (eds.). Pacific salmon life histories. UBC Press, Vancouver.
- Helle, J.H., and M.S. Hoffman. 1995. Size decline and older age at maturity of two chum salmon (*Oncorhynchus keta*) stocks in western North America, 1972-1992. Pages 245-260 in R.J. Beamish (ed.). Climate change and northern fish populations. Can. Spec. Publ. Fish. Aquat. Sci. No. 121.

- Ishida, Y., S. Ito, M. Kaeriyama, S. McKinnell, and K. Nagasawa. 1993. Recent changes in age and size of chum salmon (*Oncorhynchus keta*) in the North Pacific and possible causes. *Can. J. Fish. Aquat. Sci.* 50:290-295.
- Ishida, Y., S. Ito, and K. Murai. 1995. Density dependent growth of pink salmon (*Oncorhynchus gorbuscha*) in the Bering Sea and western North Pacific. *N. Pac. Anadr. Fish Comm. Doc.* 140. Nat. Res. Inst. Far Seas Fish., Shimizu. 17 p.
- Kaeriyama, M. 1989. Aspects of salmon ranching in Japan. *Physiol. Ecol. Japan. Spec.* 1:625-638.
- Kaeriyama, M. 1996. Population dynamics and stock management of hatchery-reared salmon in Japan. *Bull. Nat. Res. Inst. Aquat. Suppl.* 2:11-15.
- Kaeriyama, M., M. Nakamura, M. Yamaguchi, H. Ueda, G. Anma, S. Takagi, K. Aydin, R.V. Walker, and K.W. Myers. 2000. Feeding ecology of sockeye and pink salmon in the Gulf of Alaska. *N. Pac. Anadr. Fish Comm. Bull.* 2:55-63.
- Kaeriyama, M., M. Nakamura, R. Edpalina, J.R. Bower, H. Yamaguchi, R.V. Walker, and K.W. Myers. 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. *Fish. Oceanogr.* 123:197-207.
- Kawana, M., S. Urawa, G. Anma, Y. Kamei, T. Shoji, M. Fukuwaka, K. Munk, K.W. Myers, and E.V. Farley, Jr. 1999. Recoveries of thermally marked maturing pink salmon in the Gulf of Alaska in the summer of 1998. *Bull. Nat. Salmon Res. Center* 2:1-8.
- Kruse, G.H. 1998. Salmon run failures in 1997-1998: A link to anomalous ocean conditions? *Alaska Fishery Res. Bull.* 5:55-63.
- LeBrasseur, R.J. 1966. Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. *J. Fish. Res. Bd. Can.* 23:85-100.
- LeBrasseur, R.J. 1972. Utilization of herbivore zooplankton by maturing salmon. Pages 581-588 *in* A.Y. Takenouti (ed.). *Biological oceanography of the northern North Pacific Ocean*. Idemitsu Shoten, Tokyo.
- McNair, M. 2002. Alaska Salmon Enhancement Program 2001 annual report. Alaska Department of Fish and Game, Division of Commercial Fisheries, Juneau, Alaska. 45 p.
- Myers, K.W., R.V. Walker, N.D. Davis, and J.L. Armstrong. 2004a. High seas salmon research program, 2003. SAFS-UW-0402, School of Aquatic and Fishery Sciences, University of Washington, Seattle. 93 p.
- Myers, K.W., R.V. Walker, K.F. Van Kirk, and M. Kaeriyama. 2004b. Thermal otolith mark recoveries from salmon in international waters of the Gulf of Alaska in 2003. *N. Pac. Anadr. Fish Comm. Doc.* 805. SAFS-UW-0405, School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington. 10 p.
- Myers, K.W., K.Y. Aydin, R.V. Walker, S. Fowler, and M.L. Dahlberg. 1996. Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging

- experiments, 1956-1995. N. Pac. Anadr. Fish Comm. Doc. 192. FRI-UW-9614. Fish. Res. Inst., Univ. Washington, Seattle. 232 p.
- Myers, K.W., R.V. Walker, H. R. Carlson, and J. H. Helle. 2000. Synthesis and review of US Research on the physical and biological factors affecting ocean production of salmon. N. Pac. Anadr. Fish Comm. Bull. 2:1-9.
- Nishiyama, T. 1977. Food-energy requirements of Bristol Bay sockeye salmon *Oncorhynchus nerka* (Walbaum) during the last marine life stage. Res. Inst. N. Pac. Fish. Spec. Vol. pp. 289-320. (In Japanese with English summary.)
- Nomura, T., M. Fukuwaka, N. Davis, and M. Kawana. 2002. Total lipid contents in the white muscle, liver, and gonad of chum salmon caught in the Bering Sea and the Gulf of Alaska in summer 2001. N. Pac. Anadr. Fish Comm. Doc. 615. Nat. Salmon Res. Ctr., Sapporo. 12 p.
- North Pacific Anadromous Fish Commission. 2004. Report of the Committee on Scientific Research and Statistics (CSRS). N. Pac. Anadr. Fish Comm. Doc. 835. Vancouver, B.C., Canada. 45 p.
- Pearcy, W., T. Nishiyama, T. Fuji, and K. Masuda. 1984. Diel variations in the feeding habits of Pacific salmon caught in gillnets during a 24-hour period in the Gulf of Alaska. Fish. Bull. 82:391-399.
- Pearcy, W.G., R.D. Brodeur, J. Shenker, W. Smoker, and Y. Endo. 1988. Food habits of Pacific salmon and steelhead trout, midwater trawl catches, and oceanographic conditions in the Gulf of Alaska, 1980-1985. Bull. Ocean. Res. Inst. 26:29-78.
- Perez, M.A. 1994. Calorimetry measurements of energy value of some Alaskan fishes and squids. NOAA Tech. Mem. NMFS-AFSC-32. 32 p.
- Rogers, D.E. 1980. Density-dependent growth of Bristol Bay sockeye salmon. Pages 267-283 in W. McNeil and D. Himsworth (eds.). Salmonid ecosystems of the North Pacific. Oregon State Univ. Press, Corvallis.
- Rogers, D.E., and G.T. Ruggerone. 1993. Factors affecting marine growth of Bristol Bay sockeye salmon. Fish. Res. 18:89-103.
- Ruggerone, G.T., M. Zimmermann, K.W. Myers, J.L. Nielsen, and D.E. Rogers. 2003. Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaska sockeye salmon (*O. nerka*) in the North Pacific Ocean. Fish. Oceanogr. 12:209-219.
- Satterfield, F.R., and B.P. Finney. 2002. Stable isotope analysis of Pacific salmon: insight into trophic status and oceanographic conditions over the last 20 years. Prog. Oceanogr. 53:231-246.
- Seeb, L.W., P.A. Crane, C.M. Kondzela, R.L. Wilmot, S. Urawa, N.V. Varnavskaya, and J.E. Seeb. 2004. Migration of Pacific Rim salmon on the high seas: insights from genetic data. Environmental Biol. Fishes 69:21-36.
- Steimle, F.W., Jr., and R.J. Terranova. 1985. Energy equivalents of marine organisms from the continental shelf of the temperate Northwest Atlantic. J. Northw. Atl. Fish. Sci. 6:117-124.

- Tadokoro, K., Y. Ishida, N.D. Davis, S. Ueyanagi, and T. Sugimoto. 1996. Change in chum salmon (*Oncorhynchus keta*) stomach contents associated with fluctuations of pink salmon (*O. gorbuscha*) abundance in the central subarctic Pacific and Bering Sea. *Fish. Oceanogr.* 5:89-99.
- Takagi, K., K.V. Aro, A.C. Hartt, and M.B. Dell. 1981. Distribution and origin of pink salmon (*Oncorhynchus gorbuscha*) in offshore waters of the North Pacific Ocean. *Int. N. Pac. Fish. Comm. Bull.* 40. 195 p.
- Thayer, G.W., W.E. Schaff, J.W. Angelovic, and M.W. LaCroix. 1973. Caloric measurements of some estuarine organisms. *Fish. Bull., U.S.*, 71:289-296.
- Tyler, A.V. 1973. Caloric values of some North Atlantic invertebrates. *Marine Biology* 19:258-261.
- Urawa, S., M. Kawana, G. Anma, Y. Kamei, T. Shoji, M. Fukuwaka, K.M. Munk, K.W. Myers, and E.V. Farley, Jr. 2000. Geographic origin of high-seas chum salmon determined by genetic and thermal otolith markers. *N. Pac. Anadr. Fish Comm. Bull.* 2:283-290.
- Urawa, S. 2004. Stock identification studies of high seas salmon in Japan: a review and future plan. *N. Pac. Anadr. Fish Comm. Tech. Rep.* 5:9-10.
- Walker, R.V., K.W. Myers, and S. Ito. 1998. Growth studies from 1956-1995 collections of pink and chum salmon scales in the central North Pacific Ocean. *N. Pac. Anadr. Fish Comm. Bull.* 1:54-65.
- Walker, R.V., N.D. Davis, K.W. Myers, and J. Helle. In press. New information from archival tags from Bering Sea tagging, 1998-2003. *N. Pac. Anadr. Fish Comm. Tech. Rep.* 6.
- Welch, D.W. 1997. Anatomical specialization in the gut of Pacific salmon (*Oncorhynchus*): evidence for oceanic limits to salmon production? *Can. J. Zool.* 75: 936-942.

Table 1. Preliminary 2003 hatchery releases of juvenile salmon in Canada, Japan, Korea, Russia, and the United States in millions of fish. Data source: North Pacific Anadromous Fish Commission (2004).

	Sockeye	Pink	Chum	Coho	Chinook	Cherry	Total
Canada*	234.69	15.75	137.69	18.34	50.20	-	456.66
Japan	0.16	144.03	1,840.60	-	-	15.05	1,999.83
Korea	-	-	14.74	-	-	-	14.74
Russia	10.29	236.52	363.18	3.45	0.74	1.93	616.10
USA	85.61	962.46	496.25	67.13	210.57	0.00	1,822.01
Alaska	66.11	962.46	435.57	23.10	9.29	-	1,496.53
WOCI	19.50	-	60.68	44.03	201.28	-	325.48
<b>Total</b>	<b>330.74</b>	<b>1,358.76</b>	<b>2,852.45</b>	<b>88.92</b>	<b>261.50</b>	<b>16.97</b>	<b>4,909.34</b>

\*Not including releases from facilities that operate outside the direction of Oceans, Habitat, and Enhancement Branch.

Table 2. Percentage prey composition by prey wet weight (W, grams) in the stomach contents of three size groups of chum, sockeye, and pink salmon caught in six regions of the Gulf of Alaska in summer 1993-2003. Mean calories consumed per fish is an index of diet quality (Q, see methods section). Study area regions are shown in Fig. 2. Salmon body weight categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. n = total sample size, including fish with empty stomachs. % empty = percentage of fish with empty stomachs. Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

Species	Study area regions	Salmon body weight	n	% Empty	Total Prey W (g)	Mean calories per fish	% Prey composition by total prey wet weight									
							EU	CO	AM	CR	SQ	PT	FI	PO	CH	GE
Chum	Northwest	Small	19	10.5	50.9	2,386	0.0	2.5	12.4	7.7	10.5	37.4	20.8	0.0	6.9	1.7
Chum	Northwest	Medium	100	14.0	404.1	2,825	9.6	7.2	22.3	4.2	3.1	45.3	0.5	0.2	0.9	6.6
Chum	Northwest	Large	71	2.8	377.0	4,118	10.5	1.3	10.5	22.5	5.7	38.0	5.1	3.9	0.0	2.4
Chum	Southwest	Small	47	17.0	89.8	1,408	0.0	5.2	38.7	0.0	7.6	20.6	0.0	0.0	24.0	3.8
Chum	Southwest	Medium	70	8.6	265.4	1,599	0.0	12.0	25.3	0.0	1.0	8.3	0.3	0.0	0.4	52.6
Chum	Southwest	Large	30	6.7	149.4	3,488	66.4	12.6	9.6	0.0	0.0	0.1	0.0	0.0	0.0	11.4
Chum	North Mid	Small	7	14.3	13.5	1,503	0.4	2.8	36.3	1.8	3.2	50.5	3.2	1.8	0.0	0.0
Chum	North Mid	Medium	64	12.5	253.5	2,706	4.6	0.7	6.3	31.3	11.3	23.2	0.7	1.5	0.2	20.2
Chum	North Mid	Large	55	12.7	277.0	3,328	5.4	0.0	7.4	11.5	4.5	40.8	5.5	6.2	0.0	18.6
Chum	South Mid	Small	5	0.0	17.0	3,001	0.4	0.9	98.3	0.0	0.0	0.0	0.0	0.0	0.4	0.0
Chum	South Mid	Medium	24	0.0	96.5	3,557	0.1	1.2	98.5	0.0	0.1	0.1	0.0	0.0	0.0	0.0
Chum	South Mid	Large	2	0.0	8.0	6,109	0.0	0.0	5.0	0.0	95.0	0.0	0.0	0.0	0.0	0.0
Chum	Northeast	Small	44	22.7	67.6	1,058	50.7	4.0	6.4	0.0	0.2	21.7	0.3	6.1	0.0	10.7
Chum	Northeast	Medium	343	21.3	1,135.2	2,209	27.6	4.0	26.0	0.1	0.5	19.5	0.5	4.5	0.4	17.0
Chum	Northeast	Large	450	23.8	2,228.0	2,335	10.7	3.4	15.8	0.3	0.7	18.9	1.6	3.6	0.0	45.0
Chum	Southeast	Small	50	24.0	80.0	1,231	2.1	0.2	48.4	0.0	2.2	37.6	0.0	5.7	0.0	3.8

Table 2. Continued.

Species	Study area regions	Salmon body weight	n	% Empty	Total Prey W (g)	Mean calories per fish	% Prey composition by total prey wet weight									
							EU	CO	AM	CR	SQ	PT	FI	PO	CH	GE
Chum	Southeast	Medium	190	28.9	529.6	1,933	2.4	12.1	41.1	0.0	0.3	11.9	6.0	6.4	0.0	19.7
Chum	Southeast	Large	148	26.4	673.2	3,025	5.9	3.5	11.6	0.0	4.3	31.2	14.3	1.7	0.0	27.5
Sockeye	Northwest	Small	50	18.0	92.9	1,804	0.5	9.1	41.9	2.1	11.2	17.4	18.0	0.0	0.0	0.0
Sockeye	Northwest	Medium	88	17.0	462.4	6,223	1.8	3.9	20.1	4.7	46.6	13.7	8.7	0.4	0.0	0.0
Sockeye	Northwest	Large	92	17.4	1,592.9	22,930	14.3	8.9	3.4	0.6	69.7	1.2	2.0	0.0	0.0	0.0
Sockeye	Southwest	Small	13	7.7	20.0	1,458	2.7	3.7	76.8	0.0	12.5	4.2	0.0	0.0	0.0	0.0
Sockeye	Southwest	Medium	9	0.0	92.7	14,191	0.3	3.0	21.9	0.0	74.4	0.1	0.0	0.0	0.0	0.3
Sockeye	Southwest	Large	31	19.4	577.4	27,423	0.1	0.8	11.3	0.0	87.3	0.1	0.0	0.2	0.0	0.1
Sockeye	North Mid	Small	17	5.9	32.9	1,549	8.3	7.5	14.2	3.6	6.8	51.4	8.1	0.0	0.0	0.0
Sockeye	North Mid	Medium	44	2.3	127.8	2,869	5.6	3.2	14.4	9.8	23.5	31.1	12.1	0.4	0.0	0.0
Sockeye	North Mid	Large	53	11.3	422.4	8,571	14.4	12.8	5.7	9.5	41.1	13.2	2.9	0.0	0.0	0.4
Sockeye	South Mid	Small	0													
Sockeye	South Mid	Medium	8	0.0	187.9	33,816	0.0	0.0	17.8	0.1	82.0	0.0	0.0	0.0	0.0	0.0
Sockeye	South Mid	Large	4	0.0	251.4	96,117	0.0	0.0	4.7	0.0	95.3	0.0	0.0	0.0	0.0	0.0
Sockeye	Northeast	Small	122	18.0	218.9	1,542	4.8	15.6	31.2	0.5	8.7	29.6	9.0	0.0	0.2	0.3
Sockeye	Northeast	Medium	70	17.1	330.9	4,854	16.8	8.6	33.9	0.1	29.6	9.7	1.1	0.2	0.0	0.1
Sockeye	Northeast	Large	732	21.0	9,904.5	17,390	10.1	13.1	2.5	0.0	66.0	3.5	2.9	0.9	0.0	0.9
Sockeye	Southeast	Small	17	29.4	92.5	5,779	29.5	0.2	35.9	0.0	31.1	2.8	0.3	0.0	0.0	0.0
Sockeye	Southeast	Medium	15	46.7	50.5	3,416	44.0	0.9	27.0	0.0	26.2	1.9	0.0	0.0	0.0	0.0
Sockeye	Southeast	Large	413	15.3	11,222.8	39,846	1.1	1.8	6.0	0.0	87.3	2.5	1.1	0.0	0.0	0.2
Pink	Northwest	Small	2	0.0	16.5	8,426	0.0	0.0	0.0	1.1	0.9	43.9	54.1	0.0	0.0	0.0
Pink	Northwest	Medium	74	4.1	898.0	8,665	23.3	56.1	7.8	0.0	2.6	8.5	0.8	0.0	0.8	0.0
Pink	Northwest	Large	75	5.3	1,204.9	17,563	6.5	28.1	4.8	6.8	43.9	5.4	4.0	0.0	0.5	0.0
Pink	Southwest	Small	0													

Table 2. Continued.

Species	Study area regions	Salmon body weight	n	% Empty	Total Prey W (g)	Mean calories per fish	% Prey composition by total prey wet weight									
							EU	CO	AM	CR	SQ	PT	FI	PO	CH	GE
Pink	Southwest	Medium	44	20.5	234.0	4,923	0.0	32.0	33.1	0.0	21.9	1.9	3.0	0.0	8.0	0.0
Pink	Southwest	Large	30	16.7	188.0	8,359	0.0	0.9	16.0	0.0	69.0	11.2	3.0	0.0	0.0	0.0
Pink	North Mid	Small	2	0.0	10.0	3,975	0.0	0.0	0.9	86.4	5.6	1.5	5.6	0.0	0.0	0.0
Pink	North Mid	Medium	23	17.4	139.2	4,323	9.0	50.6	12.1	9.9	1.3	14.1	2.9	0.0	0.0	0.0
Pink	North Mid	Large	59	10.2	755.1	12,757	1.2	15.3	3.7	30.3	34.9	13.6	0.9	0.0	0.0	0.0
Pink	South Mid	Small	0													
Pink	South Mid	Medium	0													
Pink	South Mid	Large	0													
Pink	Northeast	Small	1	100.0	0.0											
Pink	Northeast	Medium	313	13.1	1,835.3	4,886	15.0	40.9	16.5	0.3	14.1	12.2	1.0	0.0	0.0	0.0
Pink	Northeast	Large	496	22.2	3,862.1	7,800	19.0	23.5	9.2	0.7	32.5	12.7	2.2	0.0	0.1	0.0
Pink	Southeast	Small	0													
Pink	Southeast	Medium	91	20.9	534.3	6,412	0.8	9.1	38.5	0.1	38.2	11.8	1.1	0.0	0.0	0.3
Pink	Southeast	Large	289	16.6	5,213.6	26,379	0.4	0.7	3.9	0.1	86.1	6.0	2.9	0.0	0.0	0.0
Total Sample Size			4996													

Table 3. Mean caloric values (cal/g wet weight) of prey categories used to calculate an index of salmon diet quality (Q, mean calories per fish, Table 2).

Group	Species	Sample Month	Body Part & Size	Sample Area	Reference	cal/g wet wt
EU: Euphausiids						
	<i>Thysanoessa spinifera</i>	Jul	whole, 23 mm TL	Gulf of Alaska	Davis 2003	840
	<i>Thysanoessa</i> spp.	Jun-Jul	whole, 11-26 mm TL	N Pacific & Bering Sea	Davis et al. 1998	743
	mean					792
	std dev					69
CO: Copepods						
	<i>Neocalanus cristatus</i>	Jun-Jul	whole; 7-8 mm TL	N Pacific & Bering Sea	Davis et al. 1998	627
	mean					627
	std dev					
AM: Amphipods						
	<i>Themisto pacifica</i>	Jul	whole; 4 mm TL	Gulf of Alaska	Davis 2003	887
	mean					887
	std dev					

Table 3. Continued.

Group	Species	Sample Month	Body Part & Size	Sample Area	Reference	cal/g wet wt
CR: Crabs						
	crab zoea	Jun-Jul	whole	Bering Sea	Nishiyama 1977	712
	mean					712
	std dev					
SQ: Squids						
	<i>Berryteuthis anonychus</i>	Jul	whole; 40 mm ML	Gulf of Alaska	Davis 2003	1307
	<i>Berryteuthis anonychus</i>	Jul	whole; 82 mm ML	Gulf of Alaska	Davis 2003	1737
	<i>Berryteuthis anonychus</i>	Jul	whole; 86 mm ML	Gulf of Alaska	Davis 2003	1562
	<i>Berryteuthis anonychus</i>	Jul	whole; 90 mm ML	Gulf of Alaska	Davis 2003	1636
	mean					1561
	std dev					184
PT: Pteropods						
	<i>Limacina</i> spp.	Jun-Jul	whole; 3 mm TL	N Pacific, Gulf of Alaska, Bering Sea	Davis et al. 1998	624
	mean					624

Table 3. Continued.

Group	Species	Sample Month	Body Part & Size	Sample Area	Reference	cal/g wet wt
FI: Fish						
	<i>Gasterosteus aculeatus</i> (threespine stickleback)	Oct	whole; 32-44 mm SL	Gulf of Alaska	Davis et al. 1998	1166
	<i>Gasterosteus aculeatus</i>	Oct	whole; 56-62 mm SL	Gulf of Alaska	Davis et al. 1998	1533
	<i>Clupea pallasii</i> (Pacific herring)	Jul-Aug	whole	Gulf of Alaska & Bering Sea	Perez 1994 (mean value)	2050
	<i>Clupea pallasii</i>	Oct	whole; 97-104 mm SL	Gulf of Alaska	Davis et al. 1998	1914
	<i>Mallotus villosus</i> (capelin)	Jul-Aug	whole	Gulf of Alaska & Bering Sea	Perez 1994 (mean value)	1680
	<i>Mallotus villosus</i>	Oct	whole; 63-71 mm SL	Gulf of Alaska	Davis et al. 1998	1277
	<i>Thaleichthys pacificus</i> (eulachon)	Mar & Aug	whole	Gulf of Alaska	Perez 1994 (mean value)	2630
	<i>Theragra chalcogramma</i> (walleye pollock)	Oct	whole; 75-95 mm SL	Gulf of Alaska	Davis et al. 1998	1011
	<i>Theragra chalcogramma</i>	Summer	whole; 52 mm SL	Gulf of Alaska	Boldt 1997 (mean value)	908

Table 3. Continued.

Group	Species	Sample Month	Body Part & Size	Sample Area	Reference	cal/g wet wt
FI:Fish (cont'd)	<i>Theragra chalcogramma</i>	Summer	whole; 55 mm SL	Gulf of Alaska	Boldt 1997 (mean value)	927
	<i>Theragra chalcogramma</i>	Summer	whole; 53 mm SL	Gulf of Alaska	Boldt 1997 (mean value)	934
	<i>Tarletonbeania crenularis</i> (blue lanternfish)	Jun	whole; 43 mm SL	N Pacific	Davis 2003	1199
	<i>Tarletonbeania crenularis</i>	Jun	whole; 24-50 mm SL	N Pacific	Davis et al. 1998	896
	<i>Tarletonbeania crenularis</i>	Jun	whole; 65-75 mm SL	N Pacific	Davis et al. 1998	1283
	<i>Pleurogrammus monopterygius</i> (Atka mackerel)	Jun-Jul	whole; 42-70 mm SL	N Pacific, Gulf of Alaska, & Bering Sea	Davis et al. 1998	1186
	<i>Anoplopoma fimbria</i> (sablefish)	Feb & Aug	whole; 184-258 g BW	Gulf of Alaska	Perez 1994 (mean value)	1300
	<i>Malacocottus kincaidi</i> (blackfin sculpin)	Feb	whole; 50-59 g BW	Gulf of Alaska	Perez 1994 (mean value)	840
	<i>Hemilepidotus hemilepidotus</i> (red Irish lord)	Jul	whole; 21 mm mean SL	Gulf of Alaska	Davis 2003	1561

Table 3. Continued.

Group	Species	Sample Month	Body Part & Size	Sample Area	Reference	cal/g wet wt
FI: Fish (cont'd)	<i>Hemilepidotus</i> sp. (Irish lord)	Jul	whole; 18-31 mm SL	N Pacific & Bering Sea	Davis et al. 1998	1184
						1341
						465
			whole; mean for 11 species		Steimle & Terranova 1985	1094
PO: Polychaetes	Polychaetes	no data	species	NW Atlantic		
	Polychaetes	no data	no data	NW Atlantic	Tyler 1973	673
			whole; mean for 3 species		Thayer et al. 1973	849
	Polychaetes	no data		NW Atlantic		872
						211
CH: Chaetognaths	Chaetognaths	Jun-Jul	whole	Bering Sea	Nishiyama 1977	455
						455
GEL: Gelatinous zooplankton	Small medusae	Jun-Jul	whole; 10-13 mm TL	N Pacific & Bering Sea	Davis et al. 1998	136
	<i>Beroe</i> sp.(ctenophore)	Jun	whole; 100 mm TL	N Pacific	Davis 2003	47
						92
						63

Table 4. Maturity composition of three size groups of chum and sockeye salmon in six regions of the Gulf of Alaska in summer 1993-2003, collected for stomach content analysis. Salmon body weight categories: small=<600 g, medium=600-1200 g, and large=>1200 g. UN = unknown maturity, IM=immature, MT=maturing. Study area regions are shown in Fig. 2.

Species	Study Area Region		Small body weight				Medium body weight				Large body weight				
			UN	IM	MT	n	UN	IM	MT	n	UN	IM	MT	n	
Chum	Northwest	No.	0	19	0	19	6	81	13	100	1	48	22	71	
		%	0.0	100.0	0.0		6.0	81.0	13.0		1.4	67.6	31.0		
	Southwest	No.	0	47	0	47	0	64	6	70	0	14	16	30	
		%	0.0	100.0	0.0		0.0	91.4	8.6		0.0	46.7	53.3		
	North Mid	No.	0	7	0	7	1	61	2	64		39	16	55	
		%	0.0	100.0	0.0		1.6	95.3	3.1		0.0	70.9	29.1		
	South Mid	No.	0	5	0	5	0	24		24	0	2		2	
		%	0.0	100.0	0.0		0.0	100.0	0.0		0.0	100.0	0.0		
	Northeast	No.	1	43	0	44	22	312	9	343	29	344	77	450	
		%	2.3	97.7	0.0		6.4	91.0	2.6		6.4	76.4	17.1		
	Southeast	No.	4	46	0	50	23	165	2	190	11	120	17	148	
		%	8.0	92.0	0.0		12.1	86.8	1.1		7.4	81.1	11.5		
	Sockeye	Northwest	No.	0.0	47	3	50	2	75	11	88	2	28	62	92
			%	0.0	94.0	6.0		2.3	85.2	12.5		2.2	30.4	67.4	
		Southwest	No.	0.0	10	3	13	0	7	2	9	0	7	24	31
			%	0.0	76.9	23.1		0.0	77.8	22.2		0.0	22.6	77.4	
		North Mid	No.	0.0	17	0	17		42	2	44	0	26	27	53
			%	0.0	100.0	0.0		0.0	95.5	4.5		0.0	49.1	50.9	
South Mid		No.	0.0	0	0	0	0	8		8	0	4		4	
		%	0.0				0.0	100.0	0.0		0.0	100.0	0.0		
Northeast		No.	0.0	106	16	122	1	54	15	70	4	83	646	733	
		%	0.0	86.9	13.1		1.4	77.1	21.4		0.5	11.3	88.1		
Southeast		No.	0.0	16	1	17	0	15		15	1	33	379	413	
		%	0.0	94.1	5.9		0.0	100.0	0.0		0.2	8.0	91.8		

Table 5. Number of otolith-marked salmon released from Pacific Rim hatcheries in 2003 (A), and preliminary number of otolith-marked salmon released from Pacific Rim hatcheries in 2004 (B). WOCI = Washington, Oregon, California, and Idaho. Data source: North Pacific Anadromous Fish Commission (2004).

A. 2003 releases of otolith-marked salmon

	Sockeye	Pink	Chum	Chinook	Coho	Masu	Total
Canada*							
Japan	0	3,078,000	64,783,000	0	0	32,000	67,893,000
Korea	0	0	0	0	0	0	0
Russia	8,745,060	271,050	46,869,070	524,207	3,702,000	0	60,111,387
USA	54,338,000	736,752,763	450,840,665	9,490,000	7,124,000	0	1,258,545,428
Alaska	31,481,000	736,752,763	449,379,665	6,535,000	6,680,000	0	1,230,828,428
WOCI	22,857,000	0	1,461,000	2,955,000	444,000	0	27,717,000
Total	63,083,060	740,101,813	562,492,735	10,014,207	10,826,000	32,000	1,386,549,815

\*Data not available

B. Preliminary 2004 releases of otolith-marked salmon

	Sockeye	Pink	Chum	Chinook	Coho	Masu	Total
Canada*							
Japan	0	1,400,000	78,800,000	0	0	2,310,000	82,510,000
Korea	0	0	0	0	0	0	0
Russia	11,424,000	17,918,000	49,785,000	1,800,000	4,457,000	0	85,384,000
USA	31,181,000	695,000,000	448,000,000	6,640,000	6,680,000	0	1,187,501,000
Alaska	31,181,000	695,000,000	448,000,000	6,640,000	6,680,000	0	1,187,501,000
WOCI*							0
Total	42,605,000	714,318,000	576,585,000	8,440,000	11,137,000	2,310,000	1,355,395,000

\*Data not available

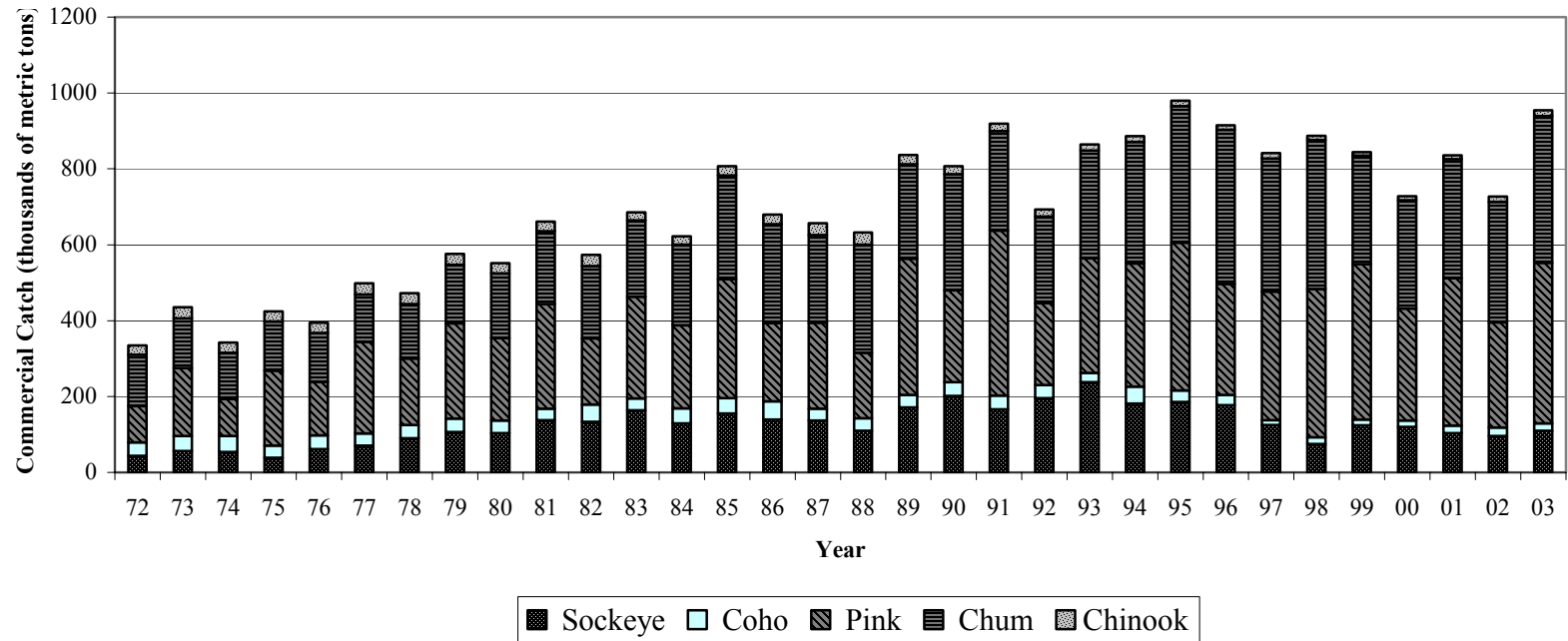


Fig. 1. Commercial salmon harvests, by species, in Canada, Korea, Japan, Russia, and the United States from 1972 to 2003 (round weight in metric tons). Source: North Pacific Anadromous Fish Commission (2004).

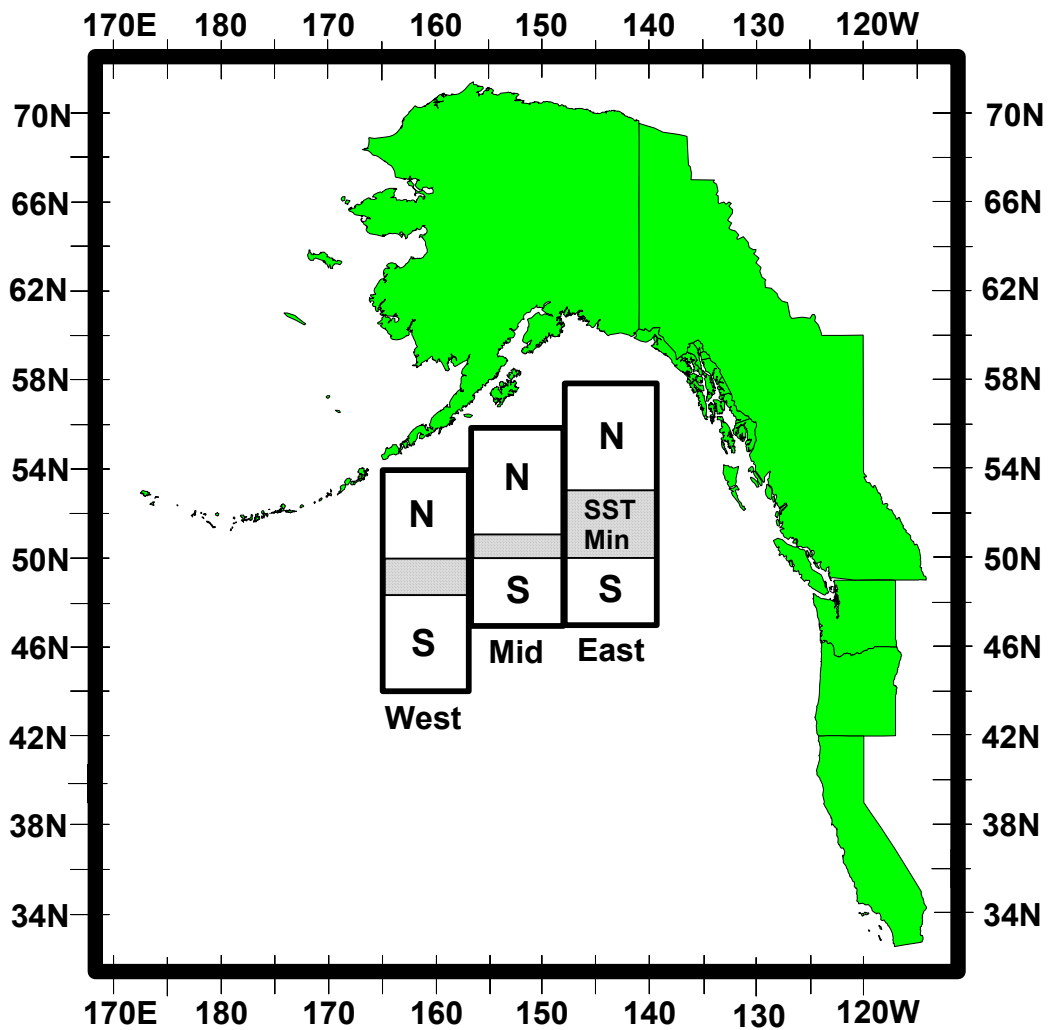


Fig. 2. Map of the study area in the Gulf of Alaska and adjacent North Pacific waters. The shaded areas indicate the approximate range of latitudes of the sea surface temperature minimum (SST Min) in 1993-2003. The data were stratified into six regions: three longitudinal regions (West, Mid, and East) and two latitudinal regions (S = south of the SST Min and N = north, including stations at the SST Min). N = north, S = south.

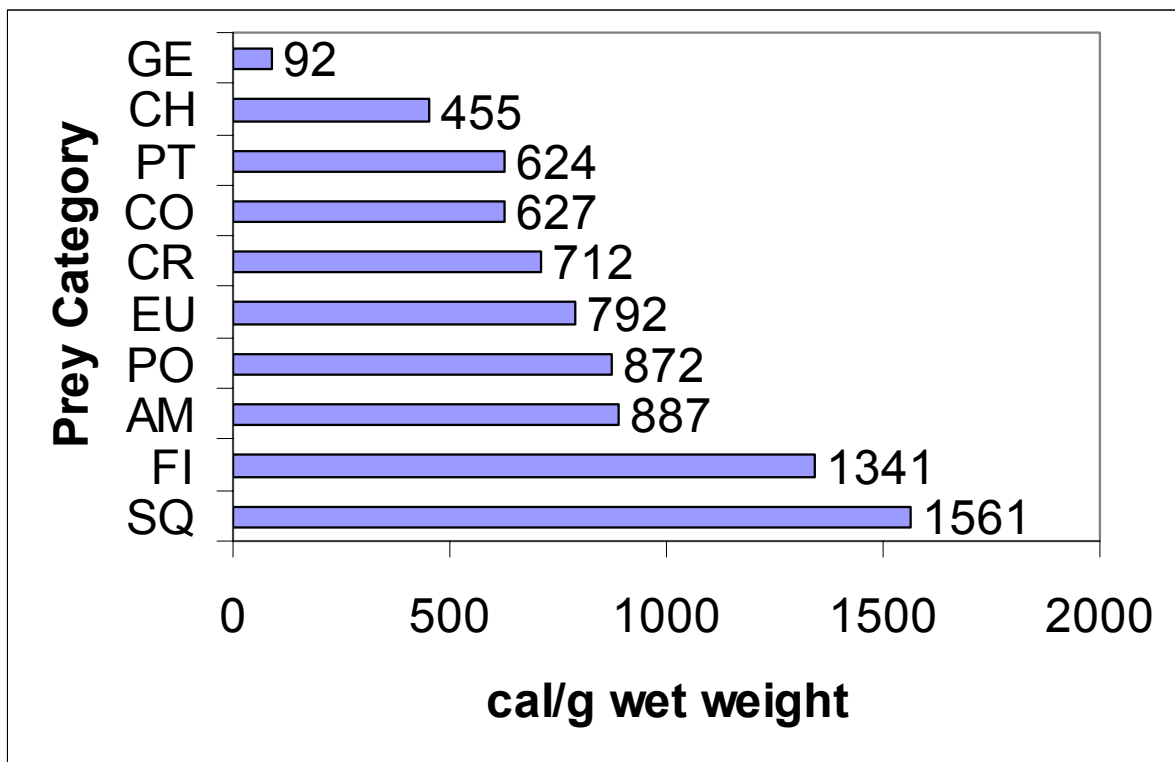


Fig. 3. Mean caloric content (cal/g wet weight) of prey categories used in analysis of salmon diet similarity (see Table 2 for data sources). Prey categories include: GE = gelatinous zooplankton (medusae and ctenophores), CH = chaetognaths, PT = pteropods, CO = copepods, CR = larval crab, EU = euphausiids, PO = polychaetes, AM = amphipods, FI = fish, and SQ = squid.

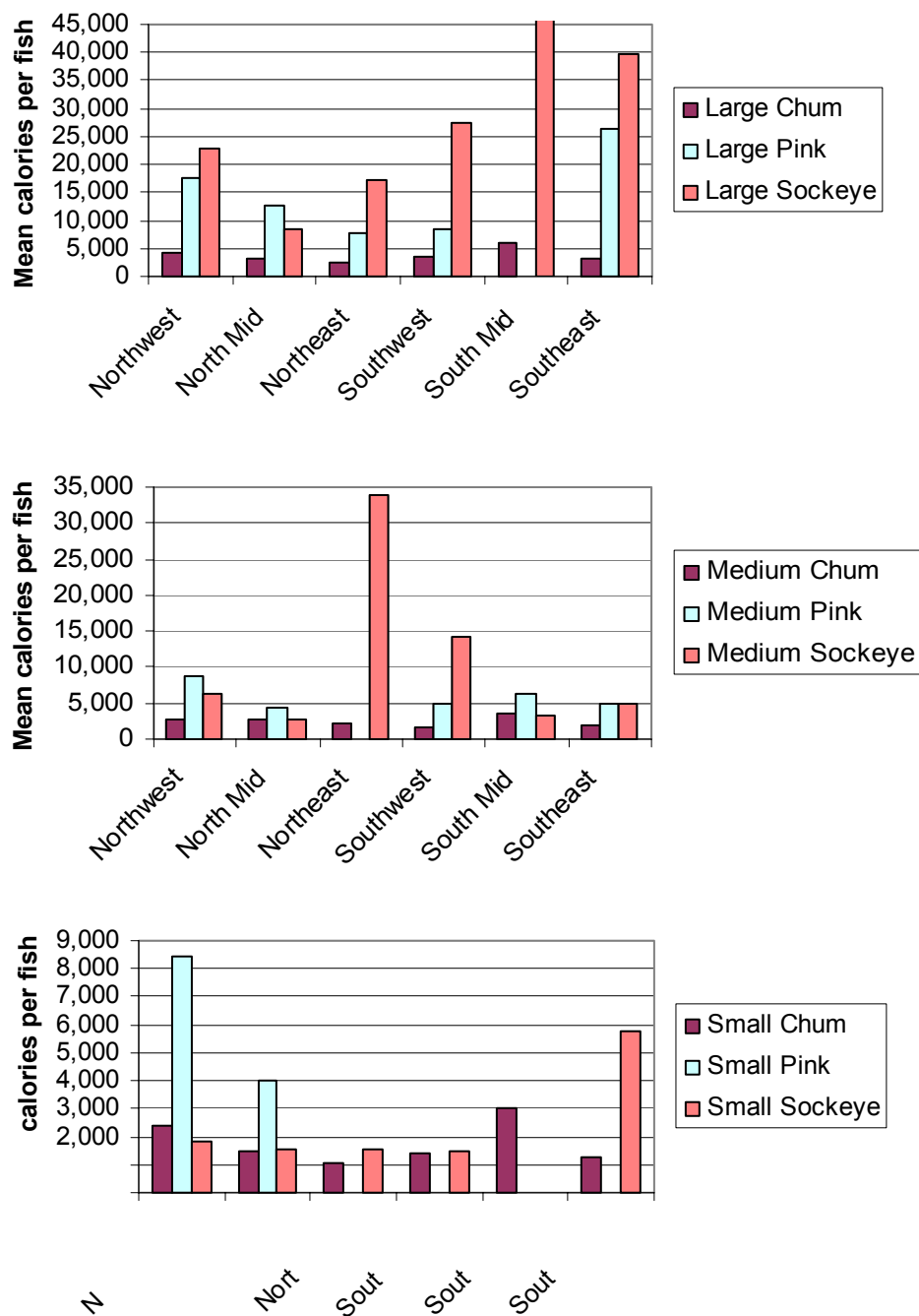


Fig. 4. Mean number of calories per fish in the diets of large (top panel), medium (middle panel), and small (bottom panel) body weight categories of chum, pink, and sockeye salmon in the Gulf of Alaska food habits study area by region (Fig. 2). Salmon size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g.

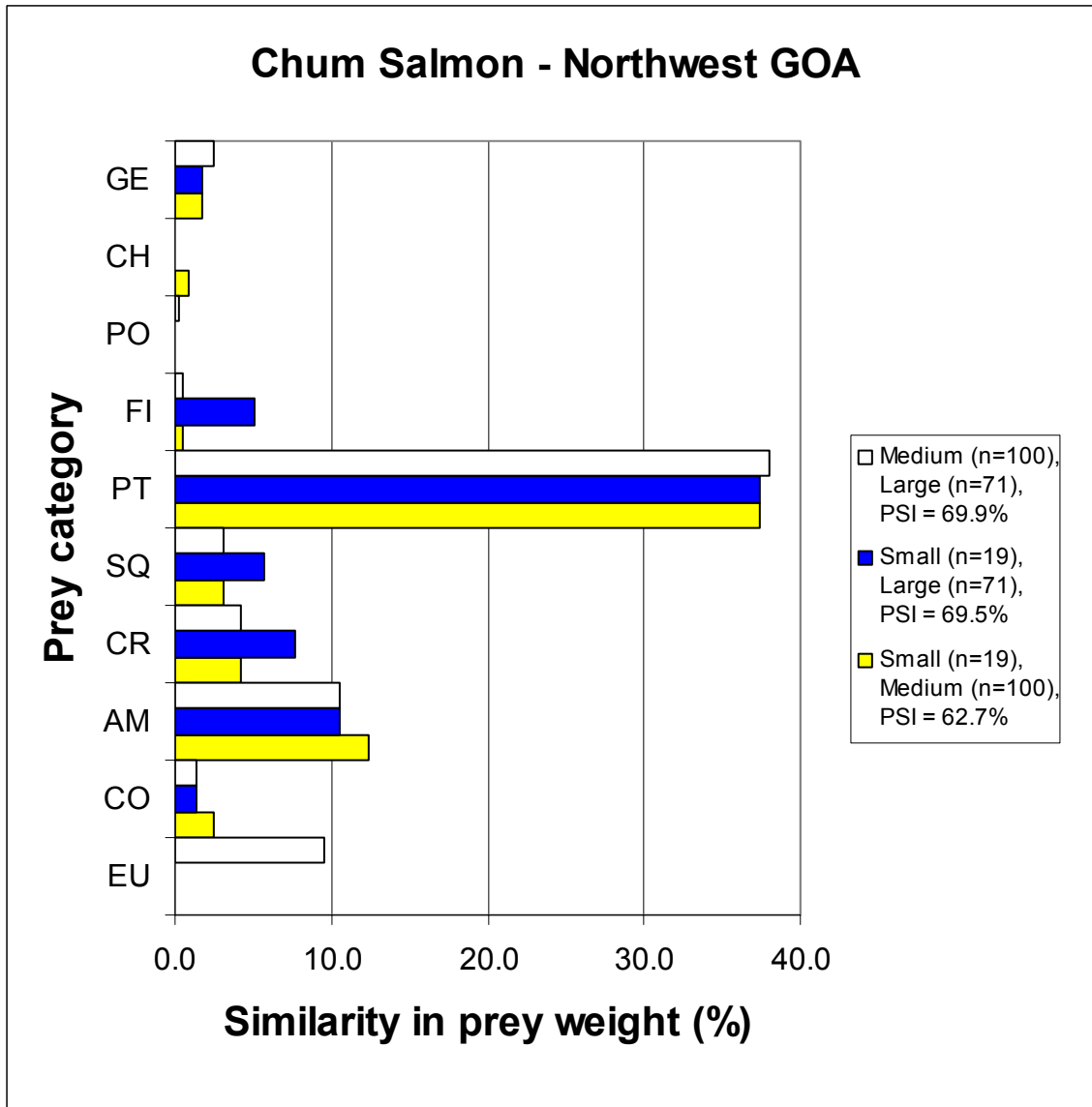


Fig. 5. Percent Similarity Index (PSI; values shown in figure legend) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon in the Northwest region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 157°-165°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

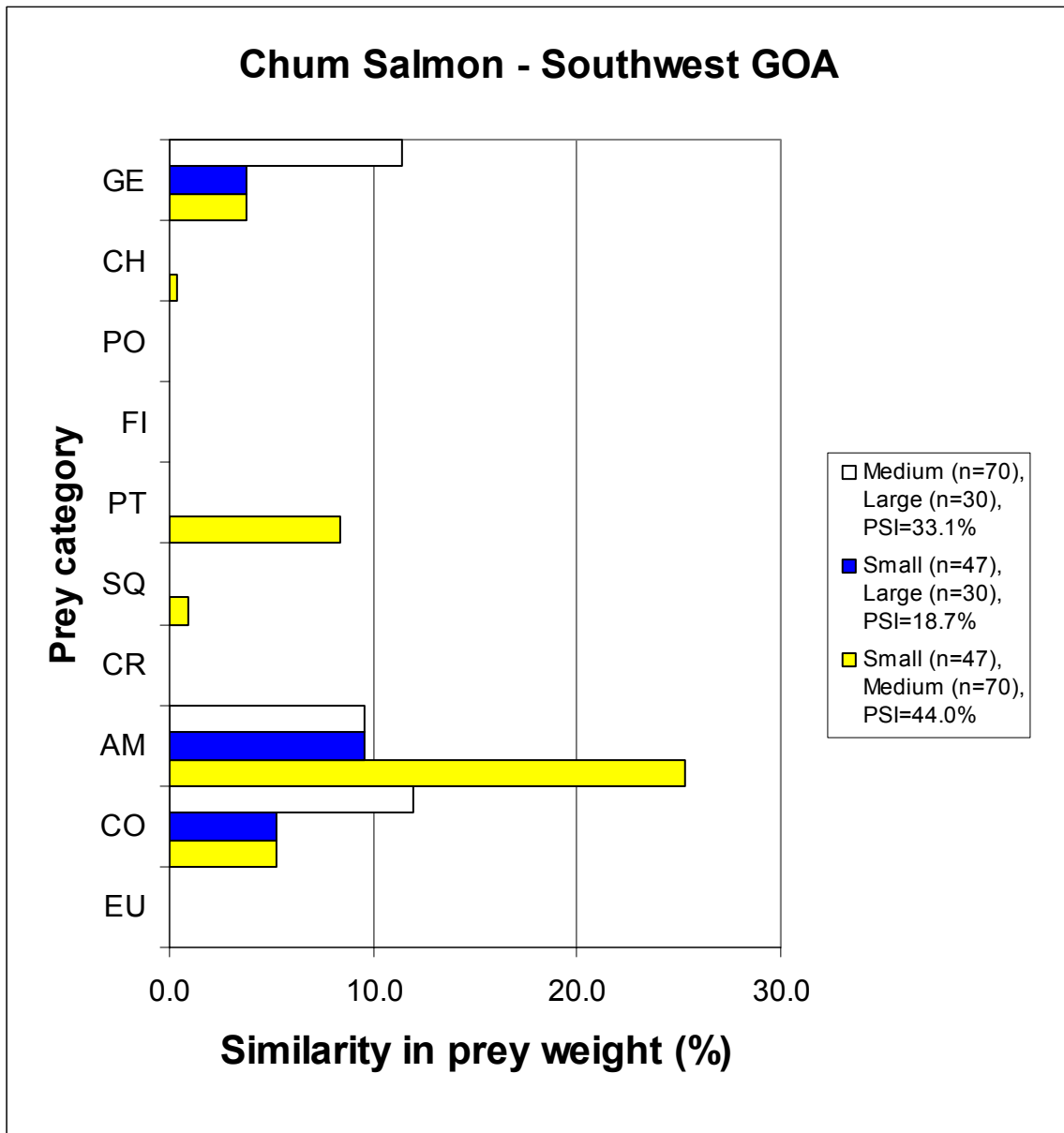


Fig. 6. Percent Similarity Index (PSI; values shown in figure legend) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon in the Southwest region of the Gulf of Alaska (GOA; south of the sea surface temperature minimum and between 157°-165°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

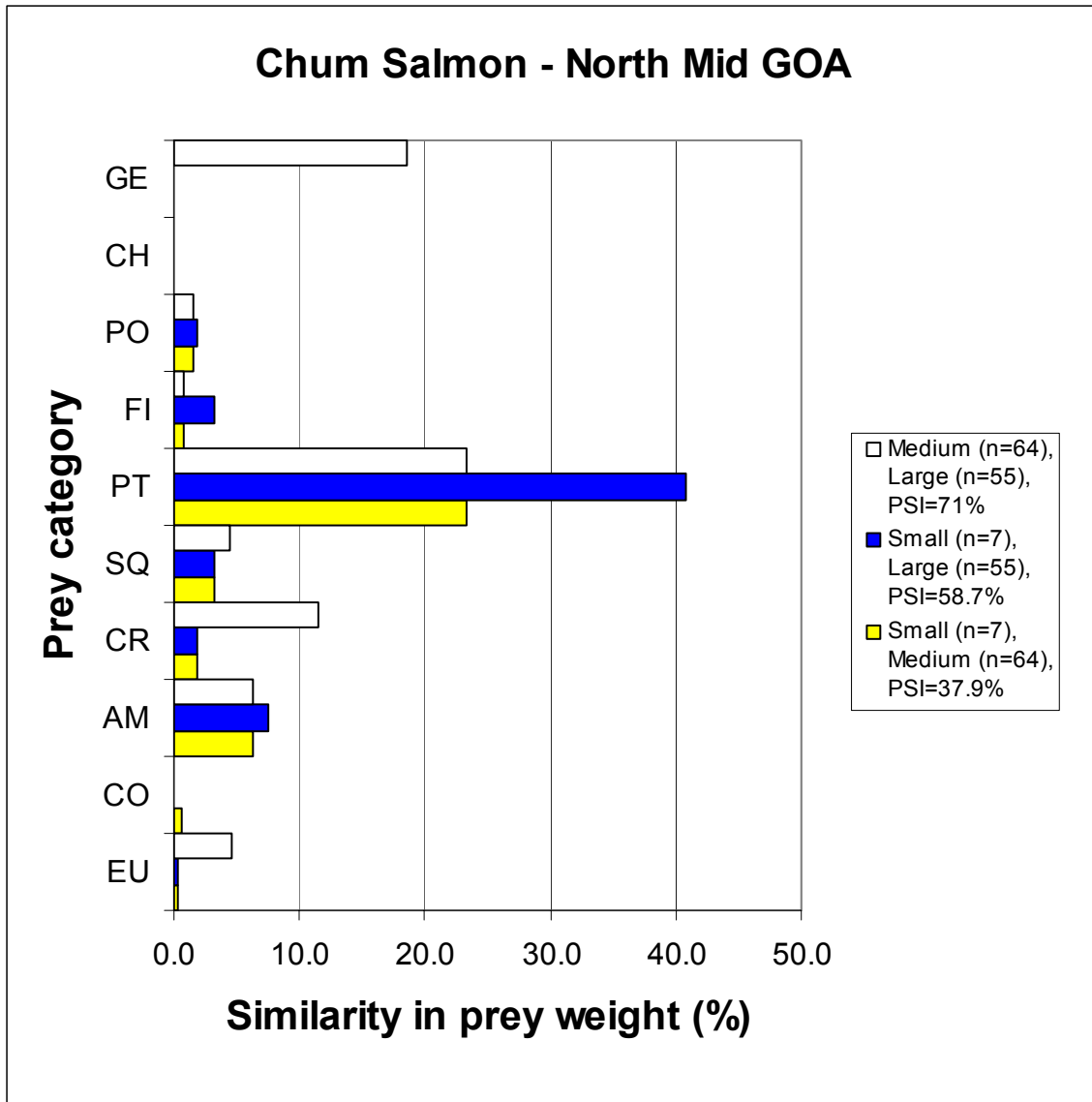


Fig. 7. Percent Similarity Index (PSI; values shown in figure legend) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon in the North Mid region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 149°-156°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

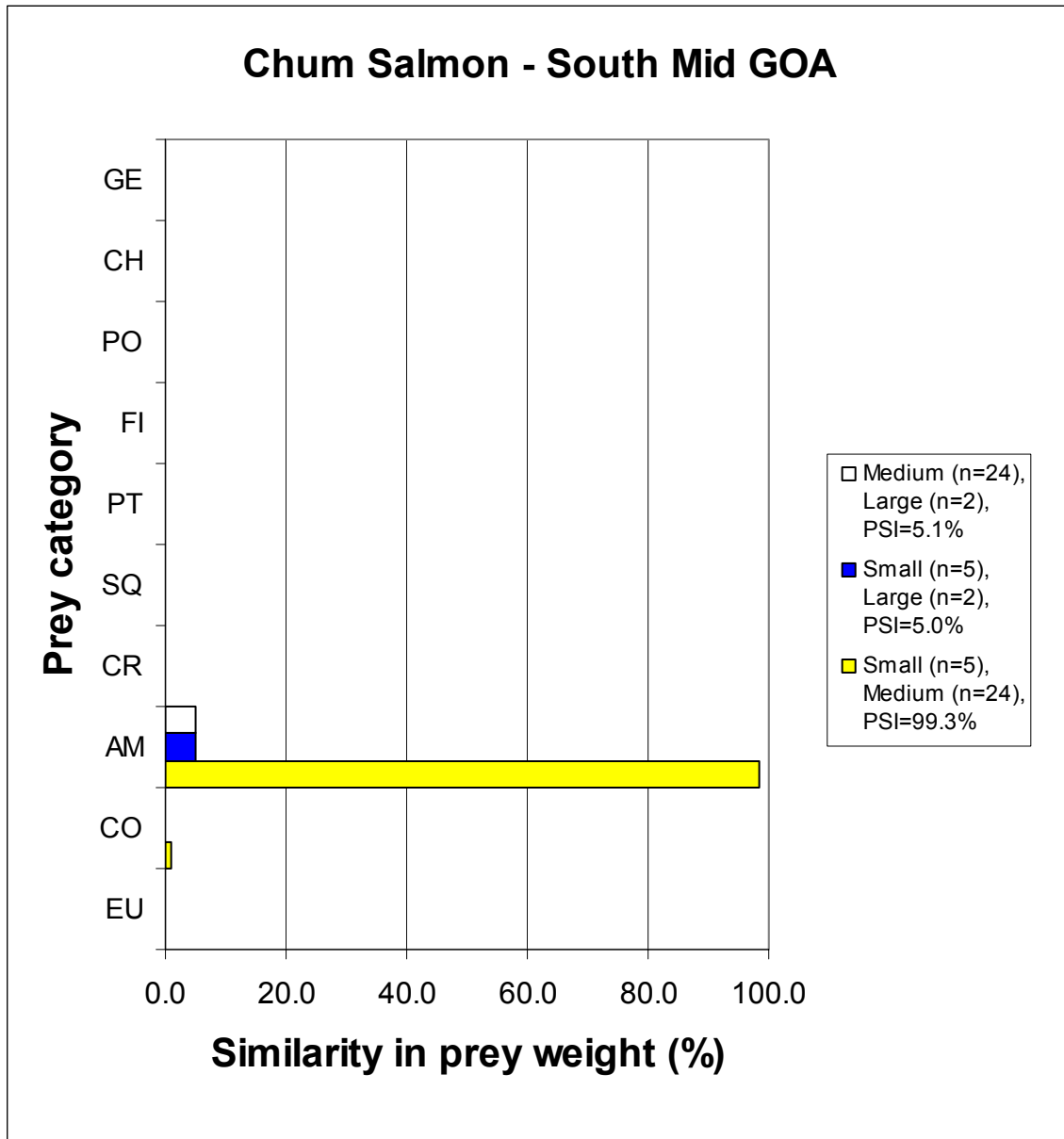


Fig. 8. Percent Similarity Index (PSI; values shown in figure legend) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon in the South Mid region of the Gulf of Alaska (GOA; south of the sea surface temperature minimum and between 149°-156°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

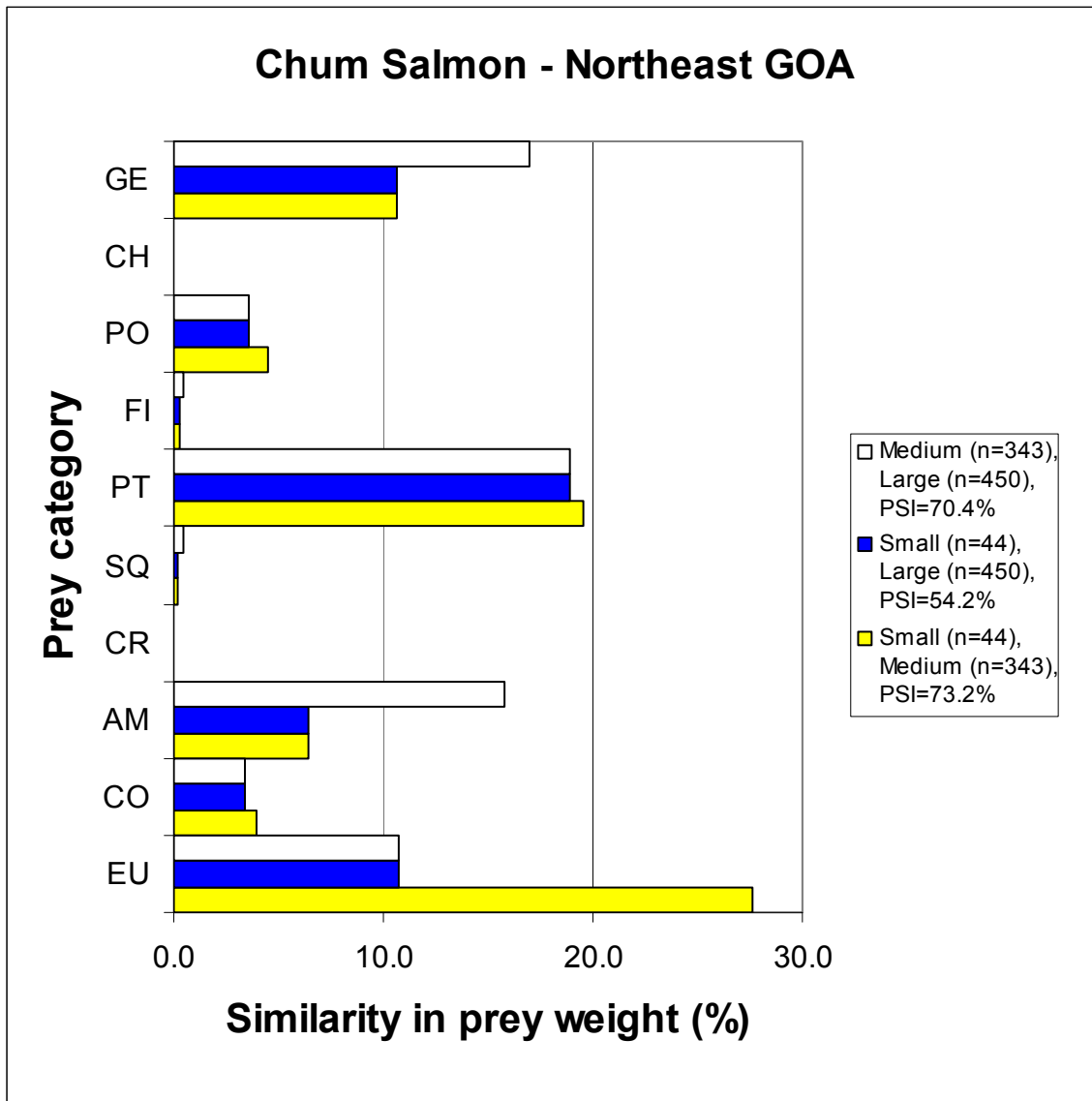


Fig. 9. Percent Similarity Index (PSI; values shown in figure legend) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon in the Northeast region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 139°-148°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

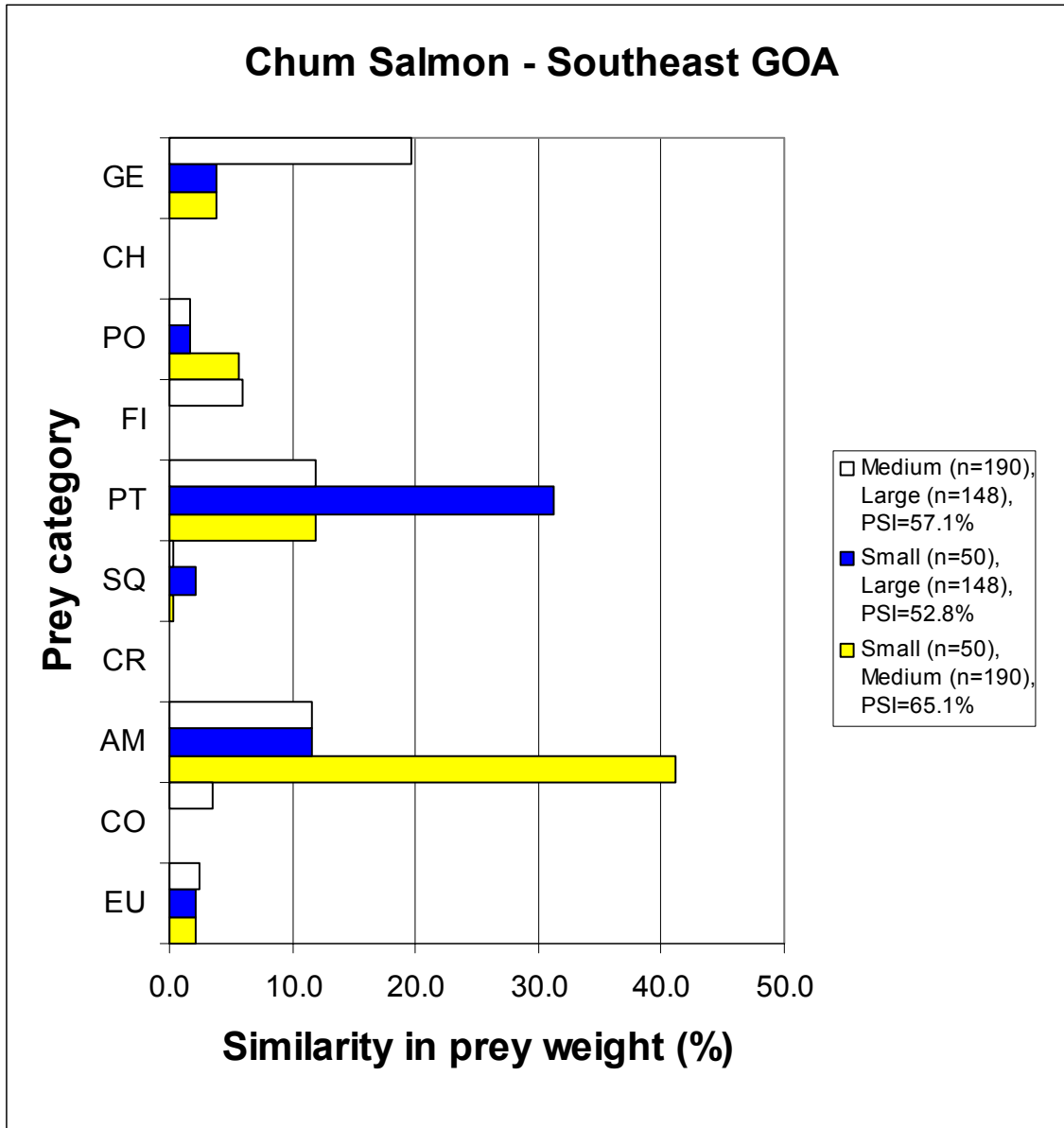


Fig. 10. Percent Similarity Index (PSI; values shown in figure legend) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon in the Southeast region of the Gulf of Alaska (GOA; south of the sea surface temperature minimum and between 139°-148°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

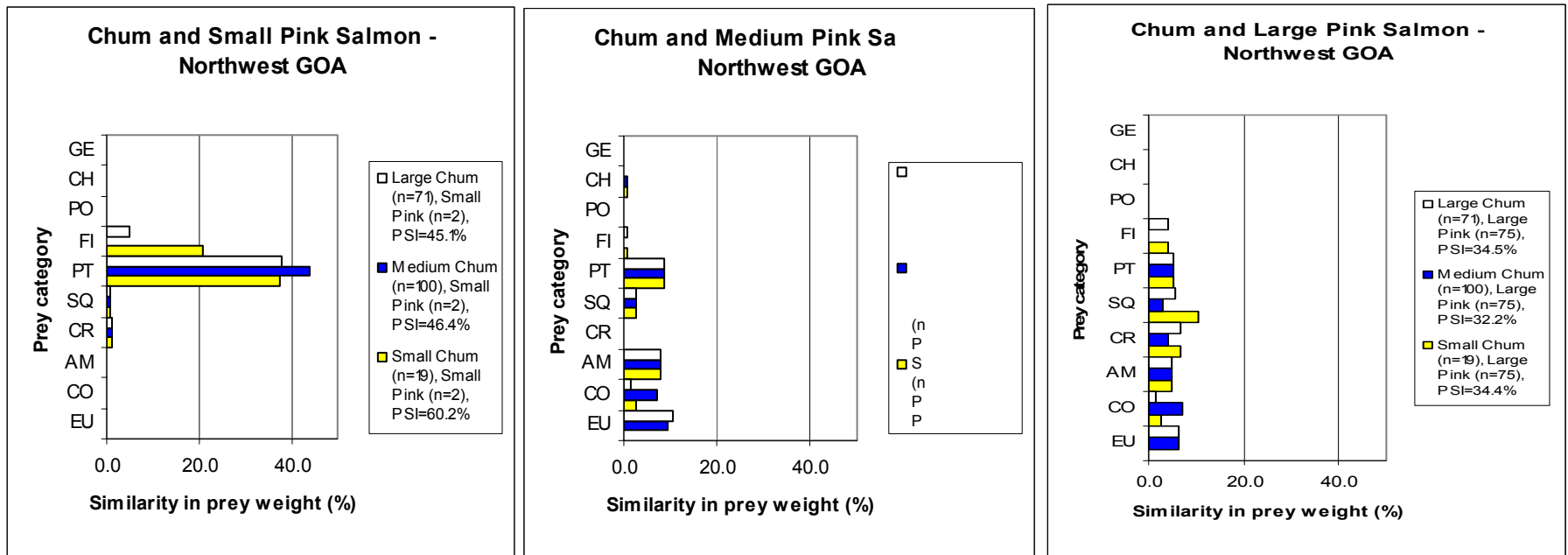


Fig. 11. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum and pink salmon in the Northwest region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 157°-165°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

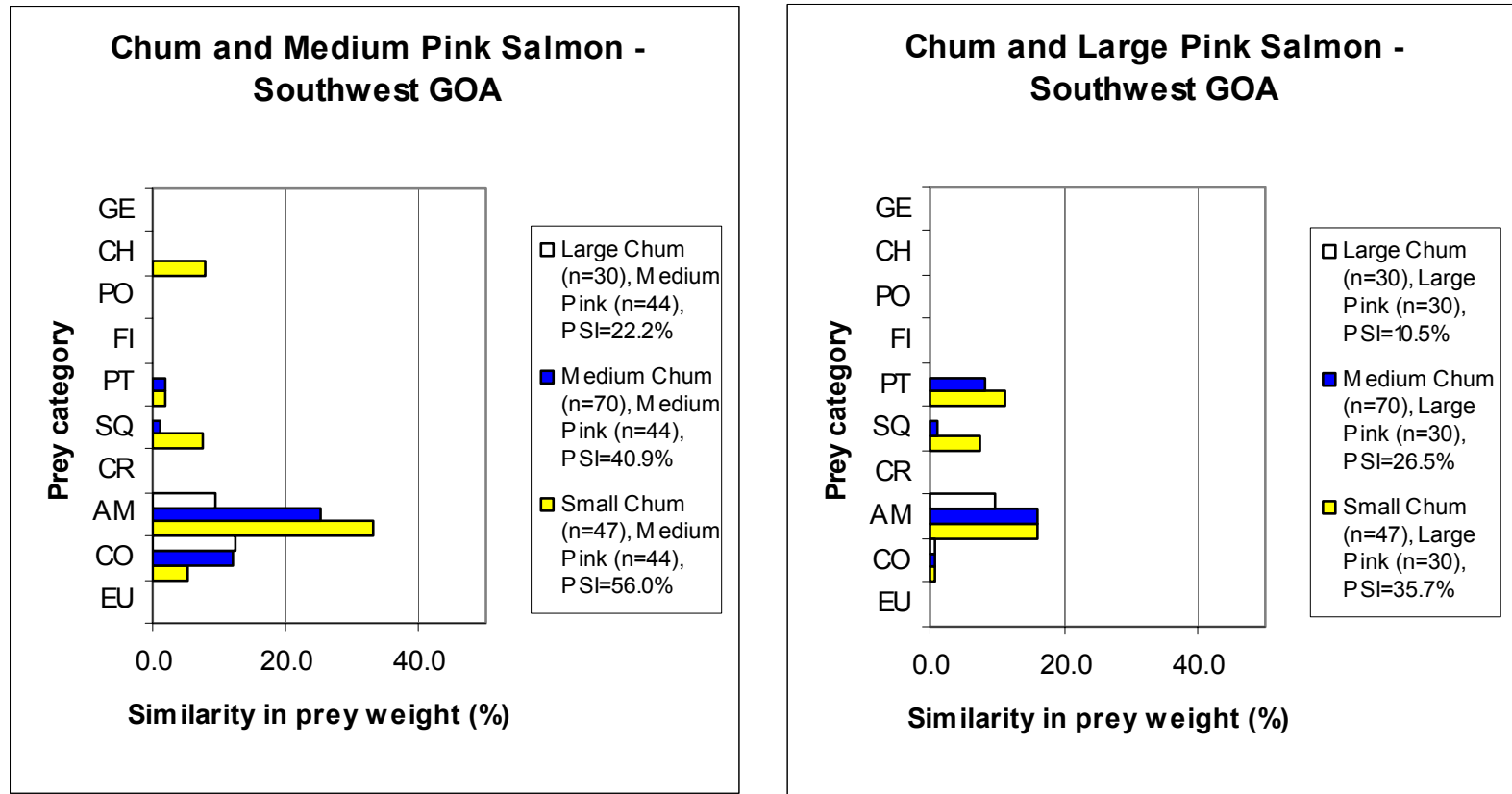


Fig. 12. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon and two size groups of pink salmon in the Southwest region of the Gulf of Alaska (GOA; south of the sea surface temperature minimum and between 157°-165°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

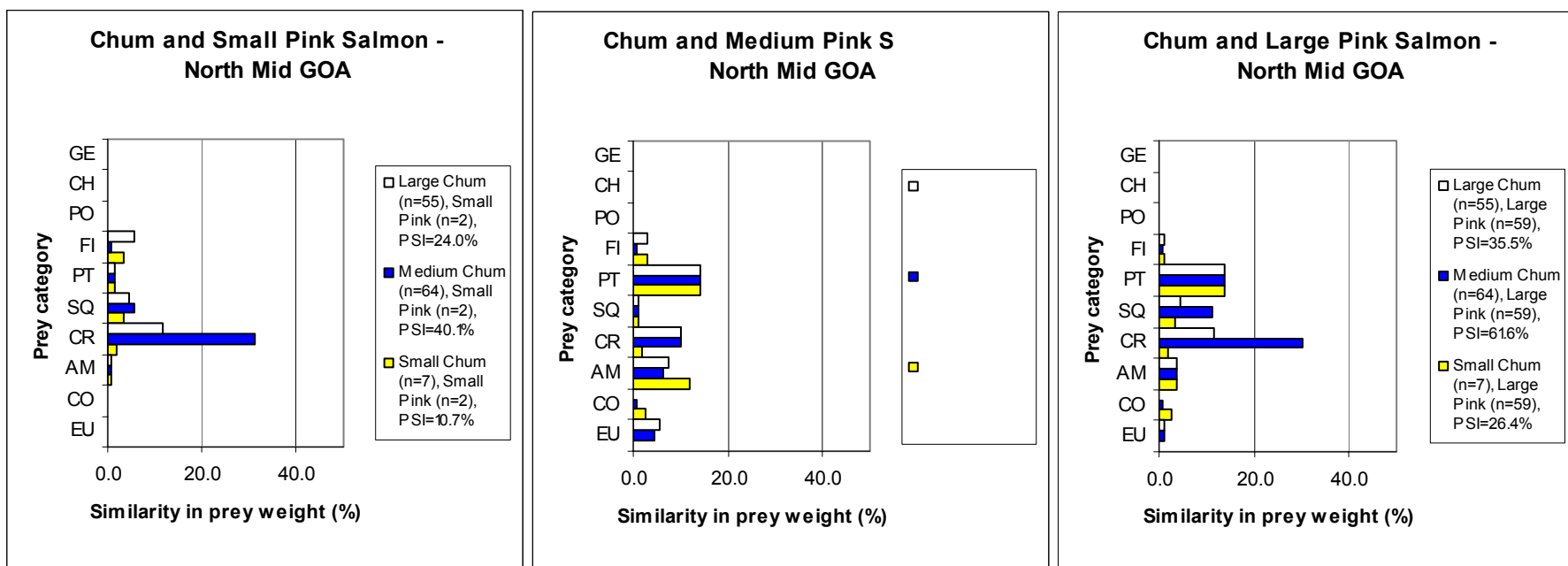


Fig. 13. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum and pink salmon in the North Mid region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 149°-156°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

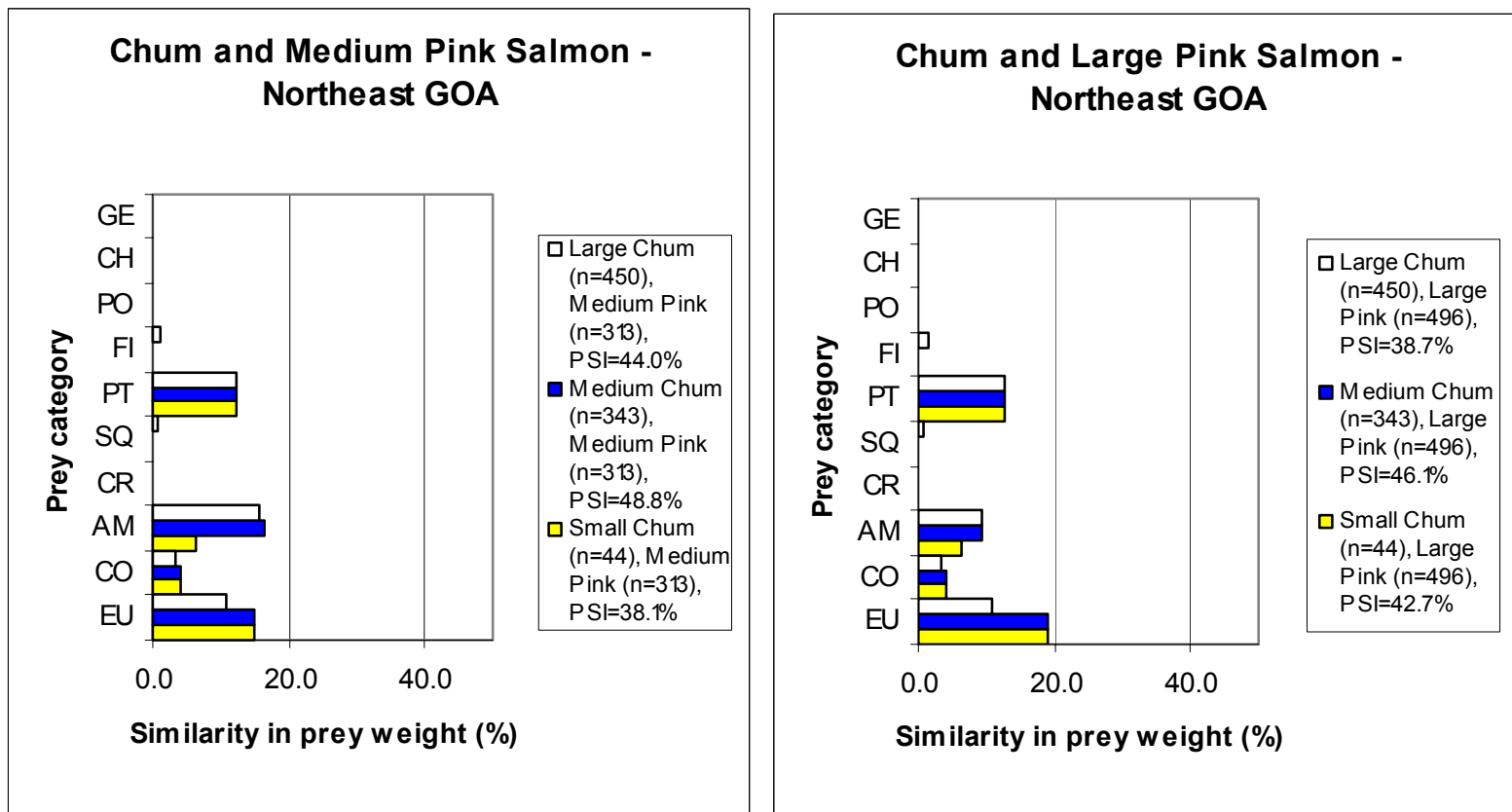


Fig. 14. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon and two size groups of pink salmon in the Northeast region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 139°-148°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

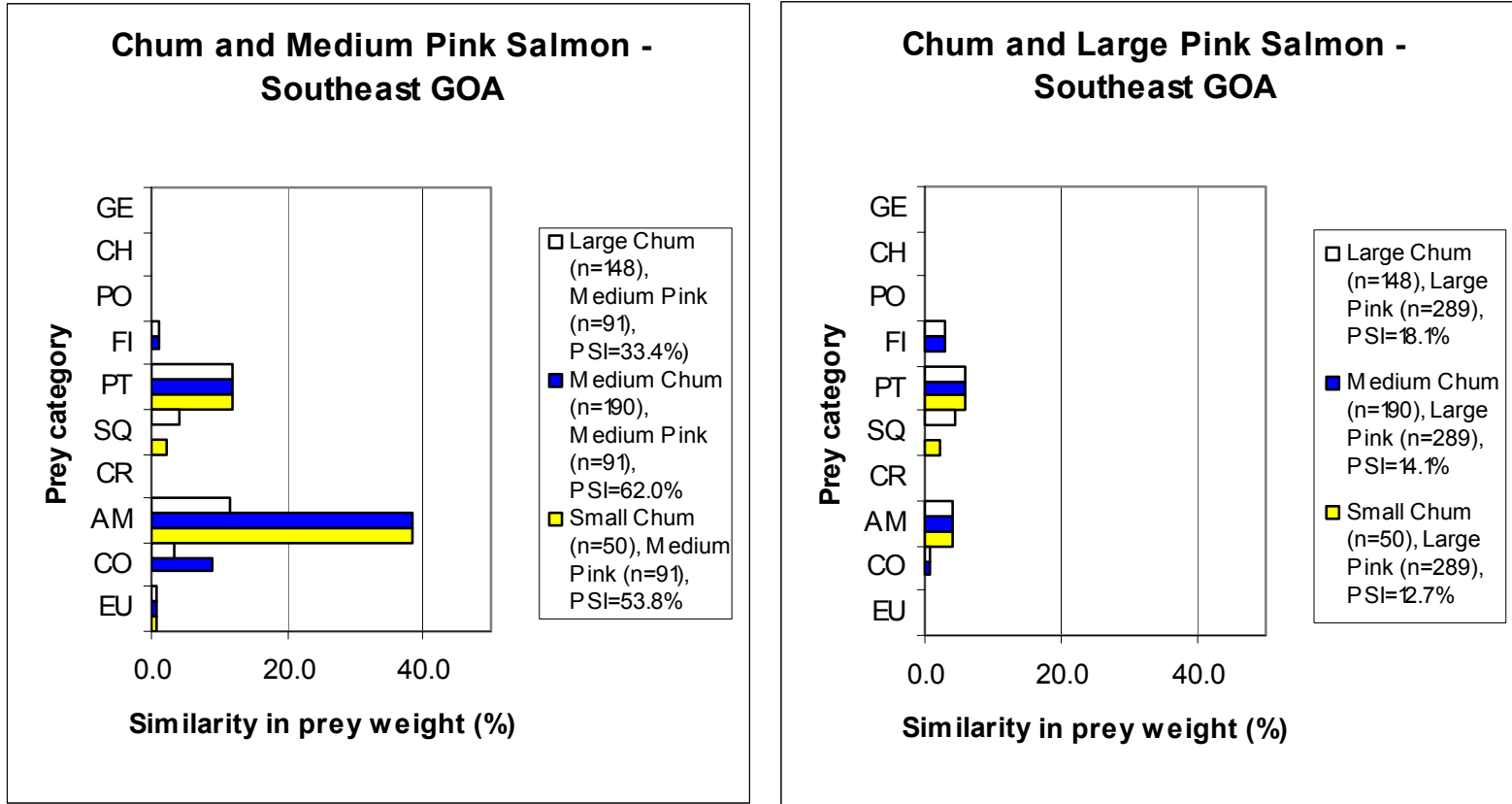


Fig. 15. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon and two size groups of pink salmon in the Southeast region of the Gulf of Alaska (GOA; south of the sea surface temperature minimum and between 139°-148°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

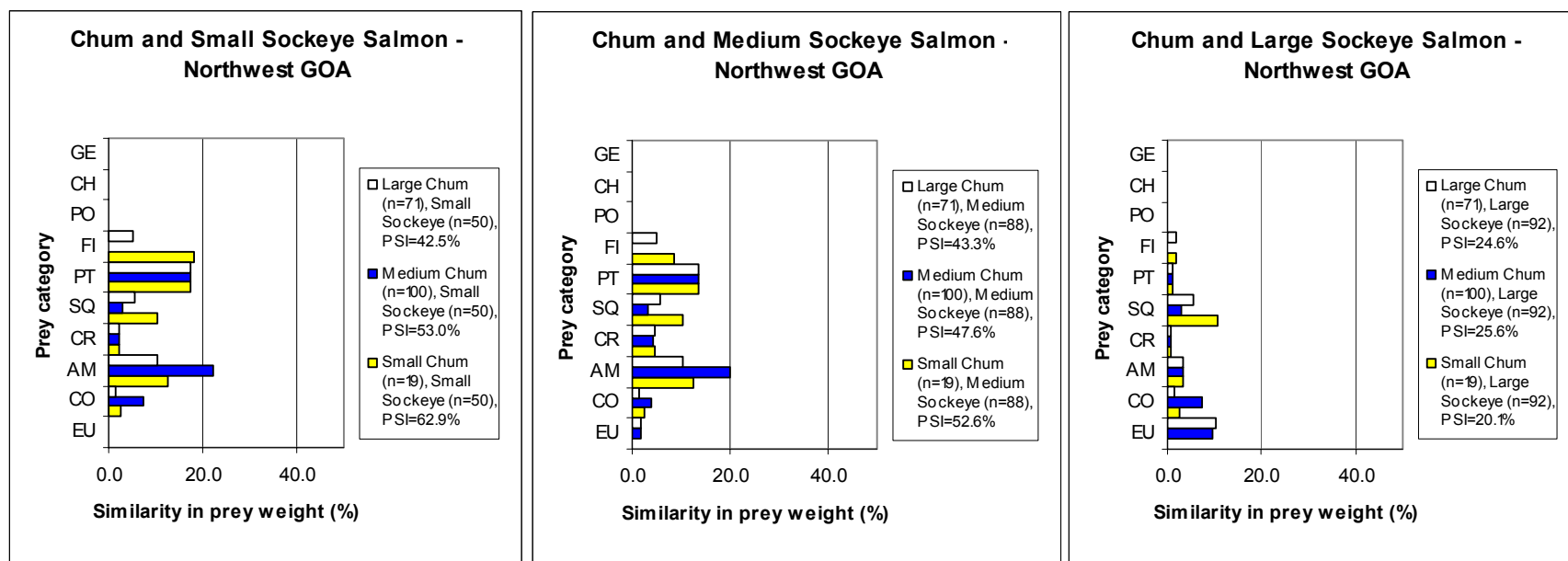


Fig. 16. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum and sockeye salmon in the Northwest region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 157°-165°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

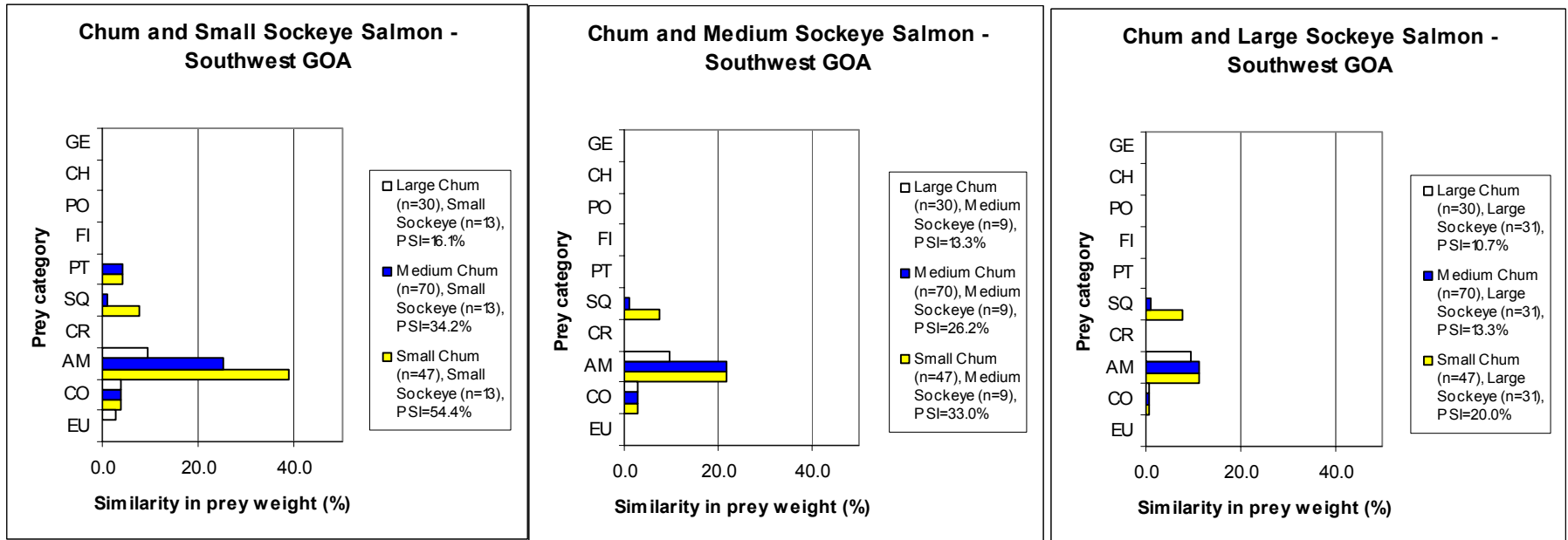


Fig. 17. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum and sockeye salmon in the Southwest region of the Gulf of Alaska (GOA; south of the sea surface temperature minimum and between 157°-165°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999); low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

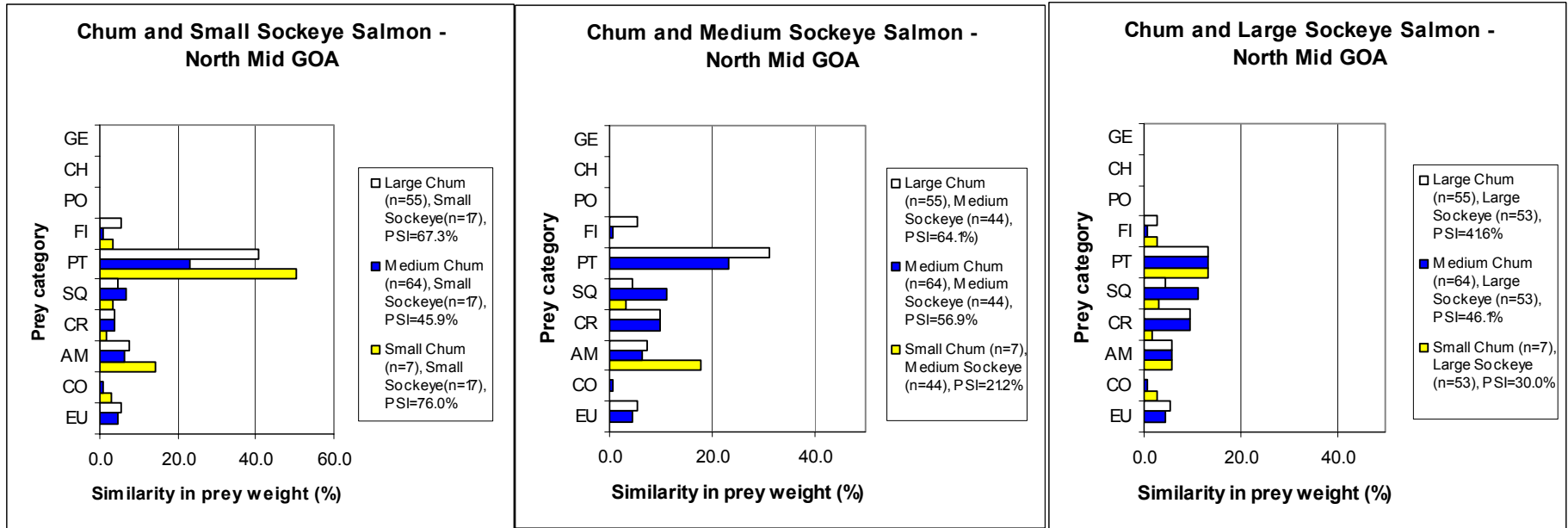


Fig. 18. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum and sockeye salmon in the North Mid region of the Gulf of Alaska (GOA; north of and including the sea surface temperature minimum and between 149°-156°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

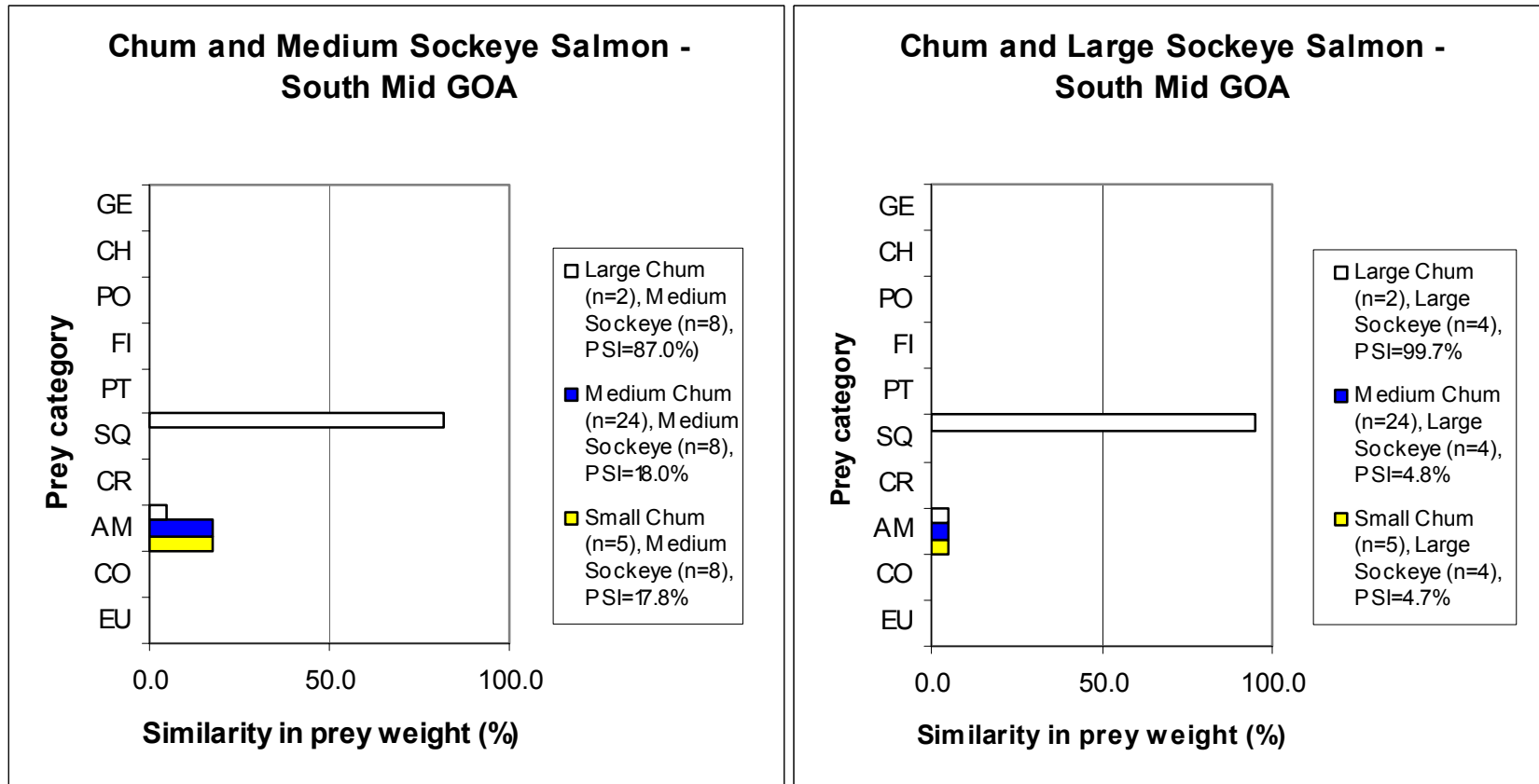


Fig. 19. Percent Similarity Index (PSI; values shown in figure legends) and pairwise comparisons of similarity in the summer diets of three size groups of chum salmon and two size groups of sockeye salmon in the South Mid region of the Gulf of Alaska (GOA; south of the sea surface temperature minimum and between 149°-156°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

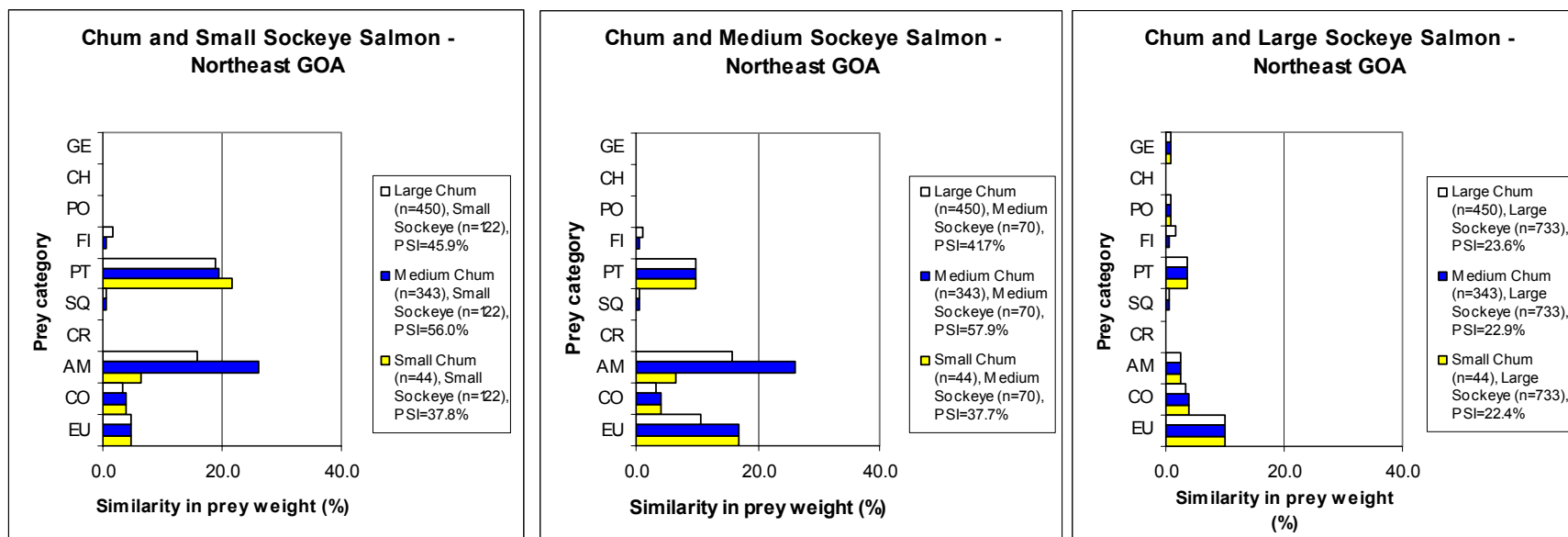


Fig. 20. Pairwise comparisons of similarity in the summer diets of three size groups of chum and sockeye salmon in the Northeast region of the Gulf of Alaska (GOA; north of the sea surface temperature minimum and between 139°-148°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

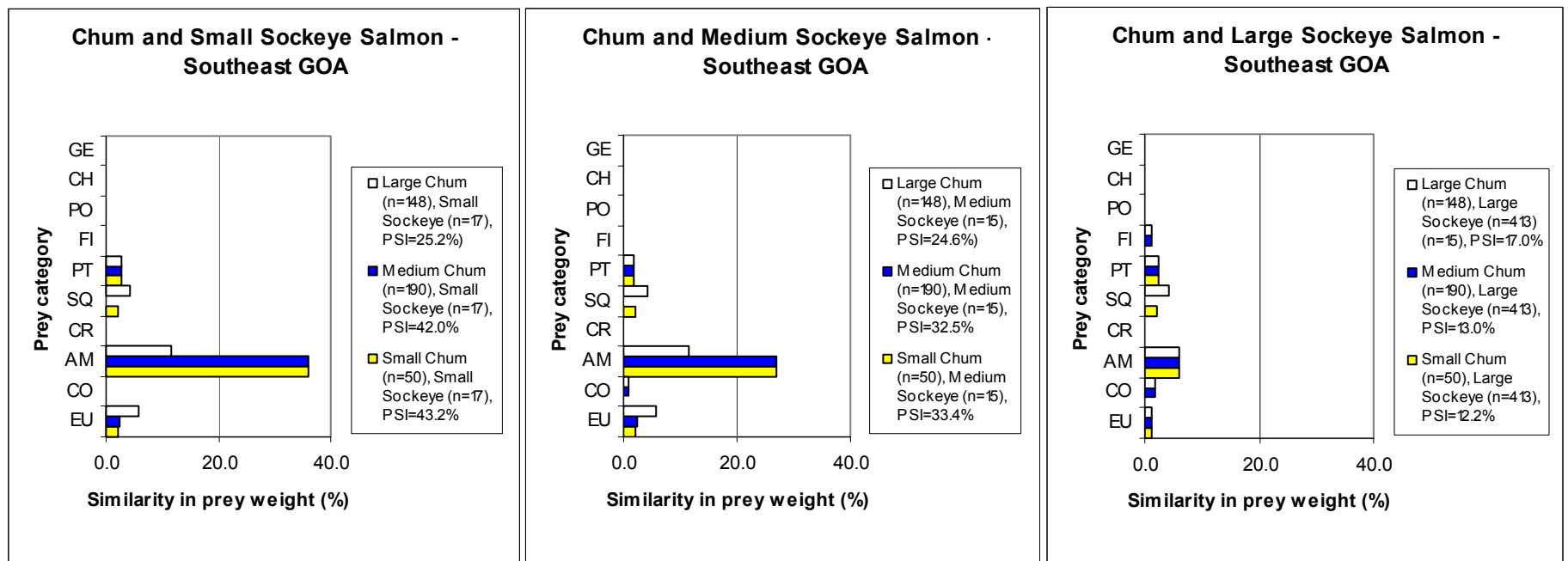


Fig. 21. Pairwise comparisons of similarity in the summer diets of three size groups of chum and sockeye salmon in the Southeast region of the Gulf of Alaska (GOA; south of the sea surface temperature minimum and between 139°-148°W longitude, Fig. 2). Size group categories: small = <600 g body weight, medium = 600-1200 g, and large = >1200 g. PSI = Percent Similarity Index (Buckley et al. 1999; low similarity = 0-24%, moderate = 25-49%; high = 50-74%, very high = 75-100%). Prey categories include: EU = euphausiids, CO = copepods, AM = amphipods, CR = larval crab, SQ = squid, PT = pteropods, FI = fish, PO = polychaetes, CH = chaetognaths, GE = gelatinous zooplankton (medusae and ctenophores).

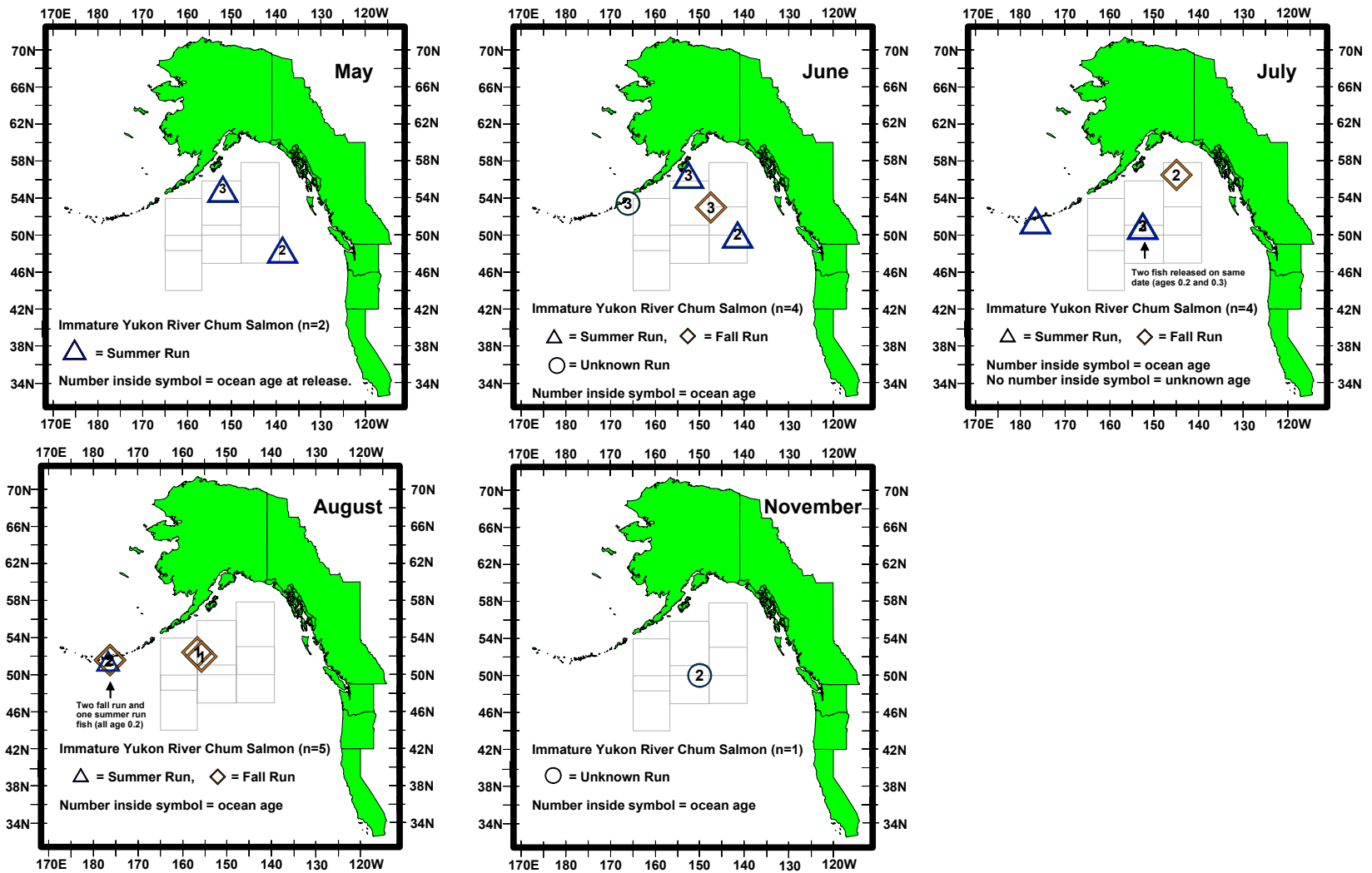


Fig. 22. The high seas distribution of seasonal races (summer and fall) of immature Yukon River chum salmon by month, as shown by tagging experiments (1956-2003). The symbols indicate the ocean release locations (May-November; no data for September and October) of tagged fish that were recovered one or more years later in the Yukon River. Summer-run chum salmon were caught in the Yukon River on or before July 15, and fall-run chum salmon were caught in the river after July 15. The food habits study area is indicated by dotted lines (Fig. 2). n = total number of tagged fish recovered.

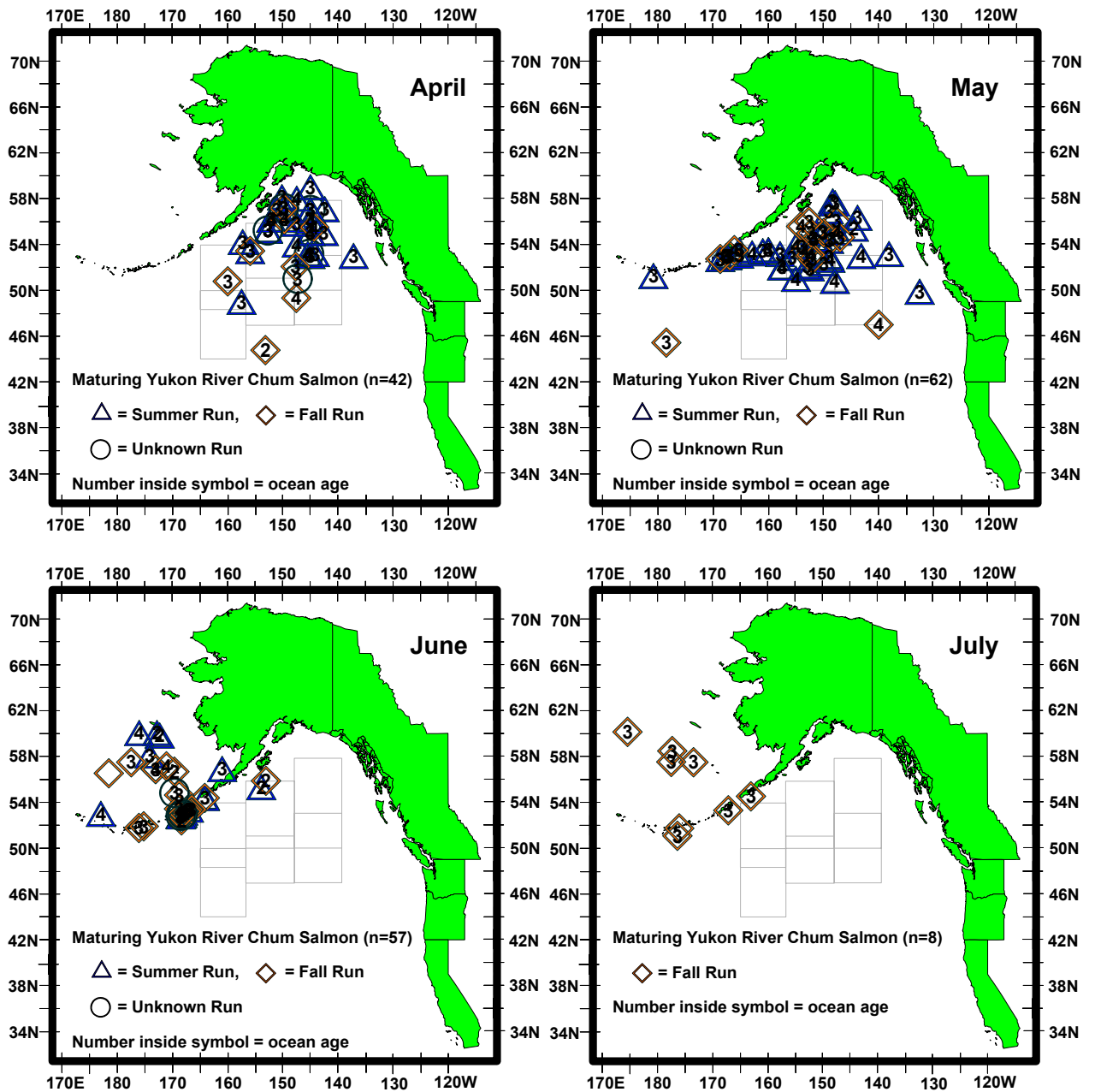


Fig. 23. The high seas distribution of seasonal races (summer and fall) of maturing Yukon River chum salmon by month, as shown by tagging experiments (1956-2003). The symbols indicate the ocean release locations (April-July) of tagged fish that were recovered during the same year in the Yukon River. Summer-run chum salmon were caught in the Yukon River on or before July 15, and fall-run chum salmon were caught in the river after July 15. The food habits study area is indicated by dotted lines (Fig. 2). n = total number of tagged fish recovered.



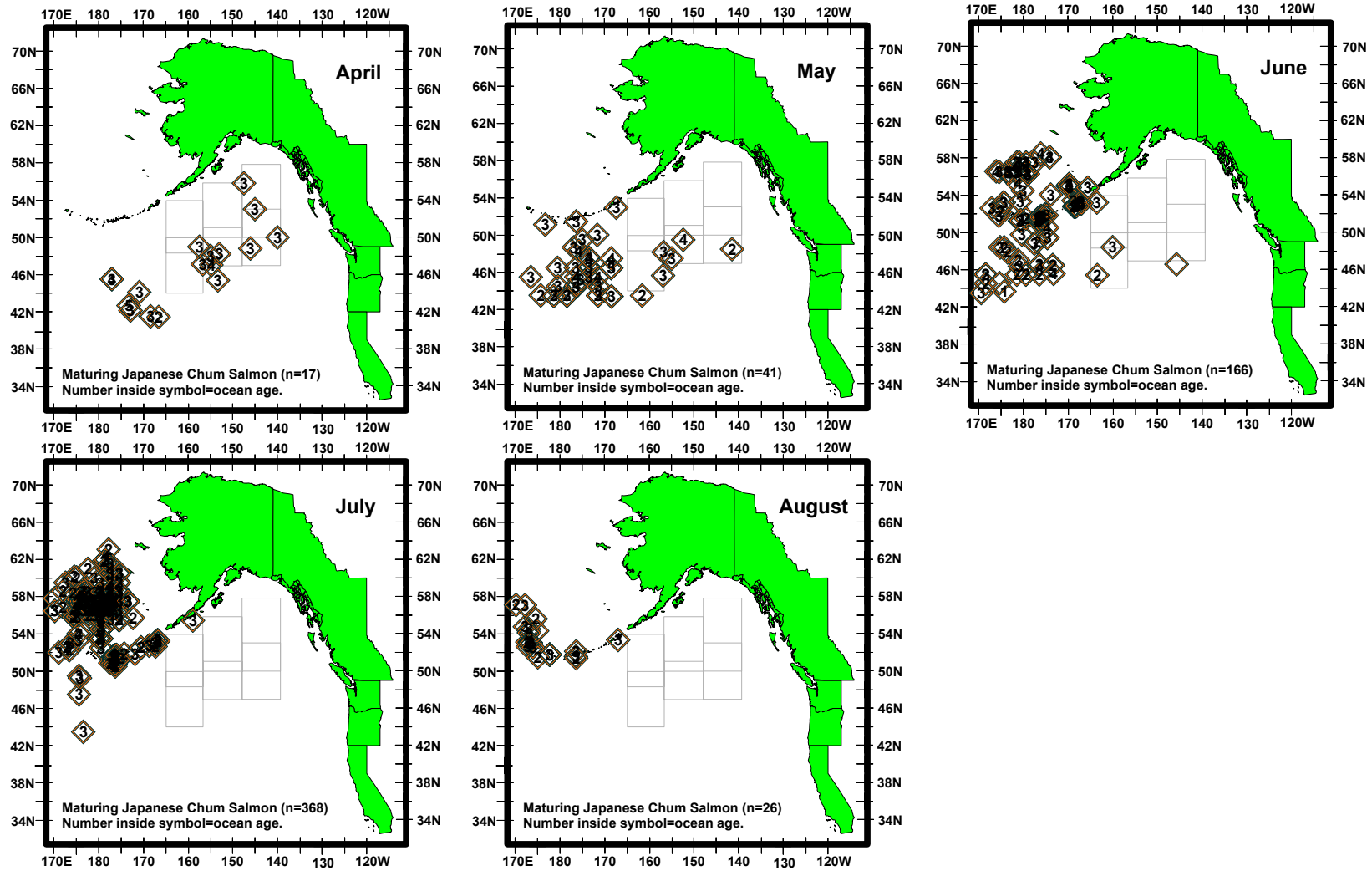


Fig. 25. The high seas distribution of maturing Japanese chum salmon by month, as shown by tagging experiments (1956-2003). The symbols indicate the ocean release locations (April-August) of tagged fish. The food habits study area is indicated by dotted lines (Fig. 2). n = total number of tagged fish recovered.

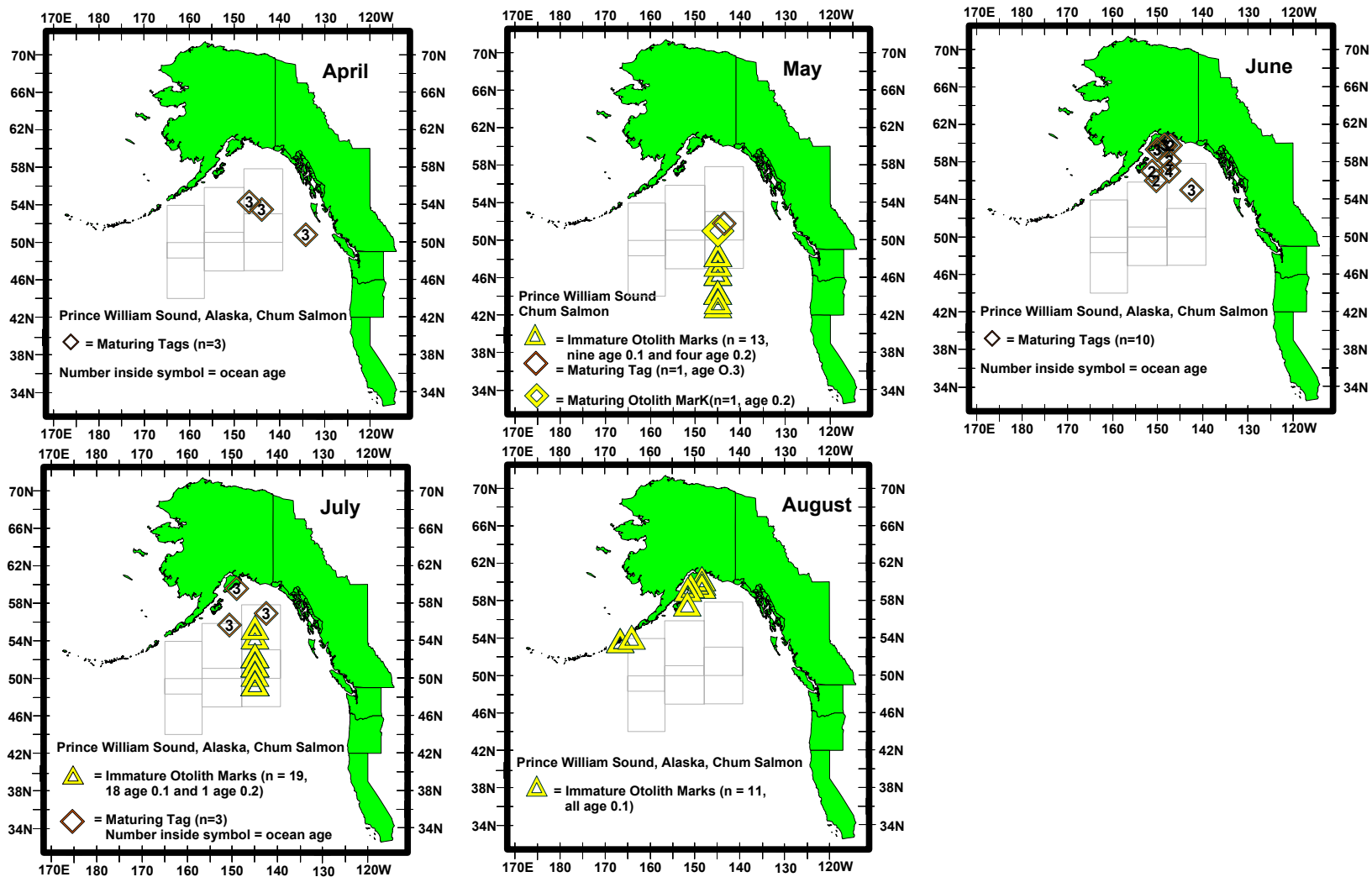


Fig. 26. The high seas distribution of immature and maturing Prince William Sound, Alaska, chum salmon by month, as shown by tagging experiments (1956-2003) and otolith mark recovery experiments (1997-2002). The symbols indicate the ocean release locations (April-August) of tagged fish or recovery locations of otolith marked fish. The food habits study area is indicated by dotted lines (Fig. 2). n = total number of tagged or otolith marked fish recovered.

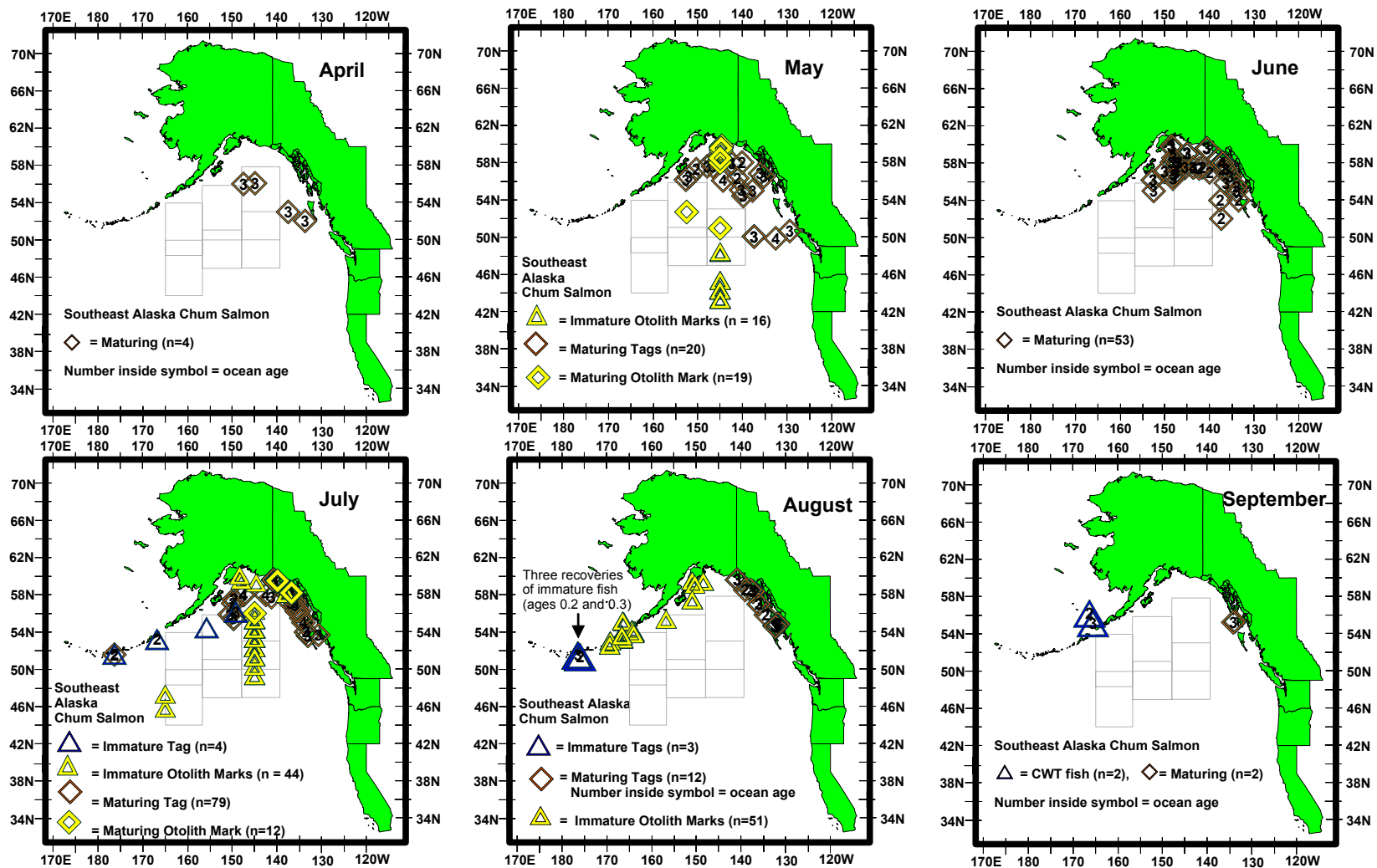


Fig. 27. The high seas distribution of immature and maturing southeastern Alaska chum salmon by month, as shown by tagging experiments (1956-2003) and otolith mark recovery experiments (1997-2000). The symbols indicate the ocean release locations (April-August) of tagged fish and recovery locations of otolith marked fish. The food habits study area is indicated by dotted lines (Fig. 2). n = total number of tagged or otolith marked fish recovered. CWT = recovery locations of two coded-wire tagged hatchery chum salmon in the Bering Sea in September.

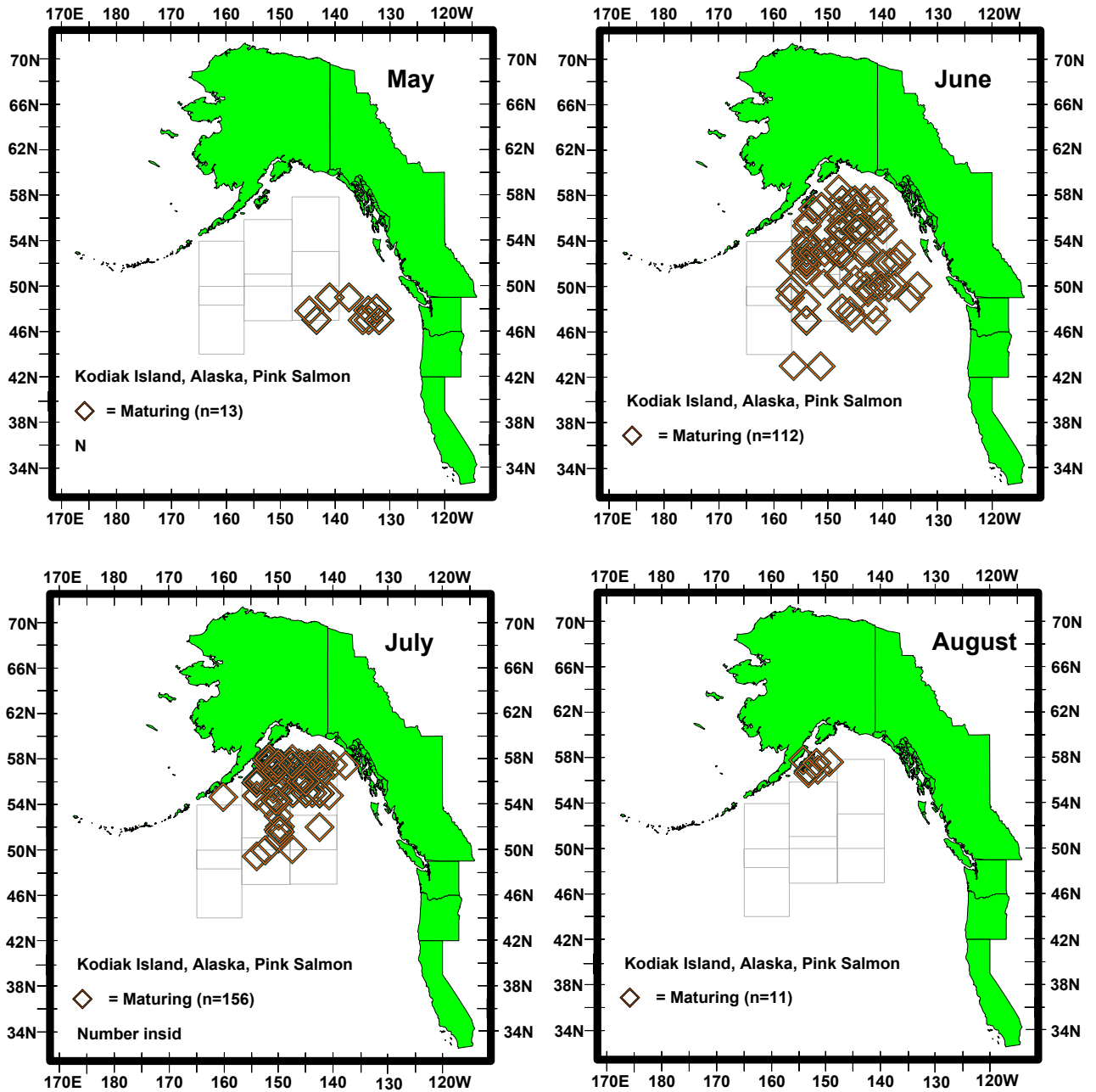


Fig. 28. The high seas distribution of maturing Kodiak Island, Alaska, pink salmon by month, as shown by tagging experiments (1956-2003). The symbols indicate the ocean release locations (May-August) of tagged fish. The food habits study area is indicated by dotted lines (Fig. 2). n = total number of tagged fish recovered.

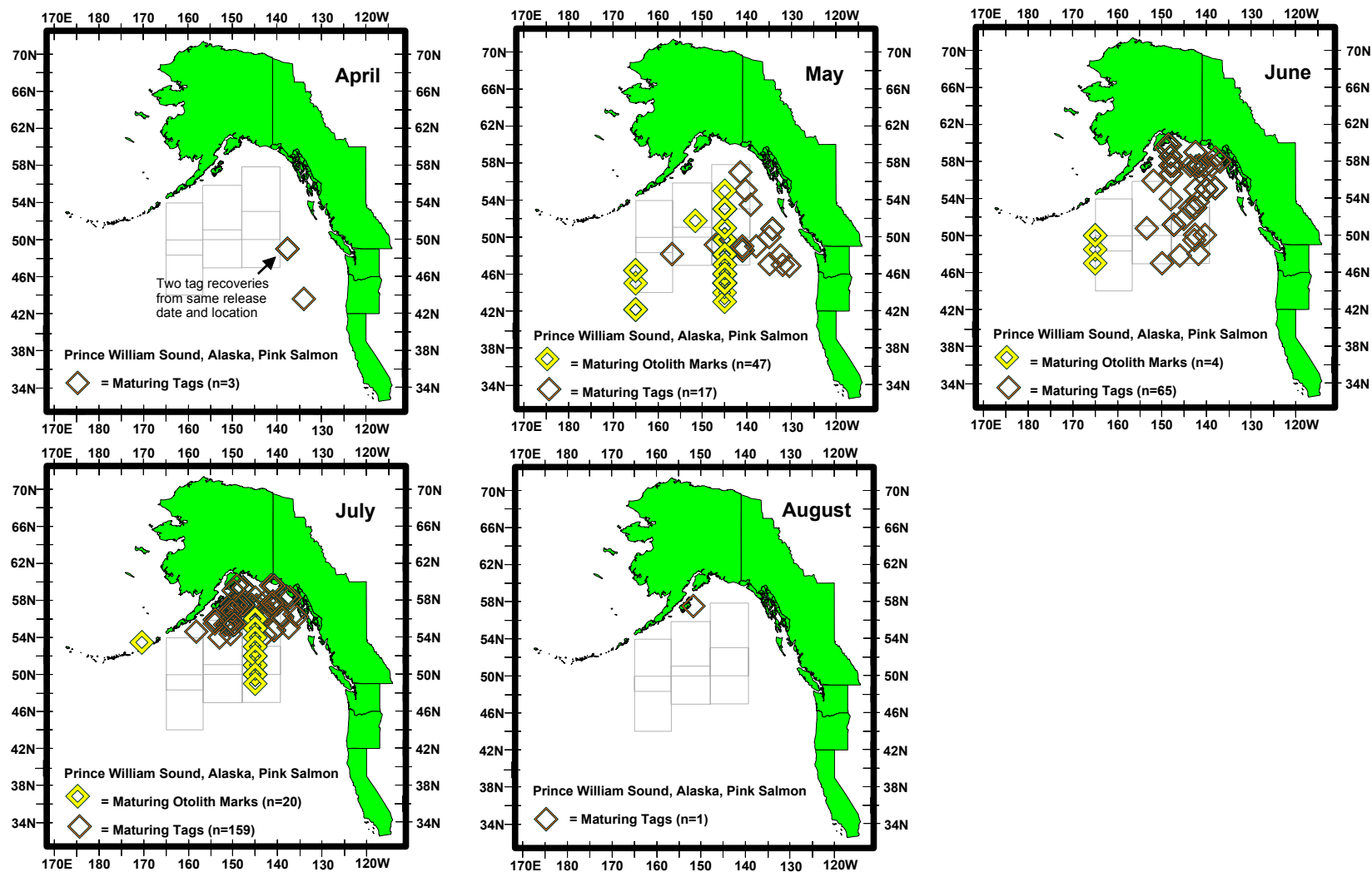


Fig. 29. The high seas distribution of maturing Prince William Sound, Alaska, pink salmon by month, as shown by tagging experiments (1956-2003) and otolith mark recovery experiments (1998-2002). The symbols indicate the ocean release locations (April-August) of tagged fish and recovery locations of otolith-marked fish. The food habits study area is indicated by dotted lines (Fig. 2). n = total number of tagged and otolith marked fish recovered.

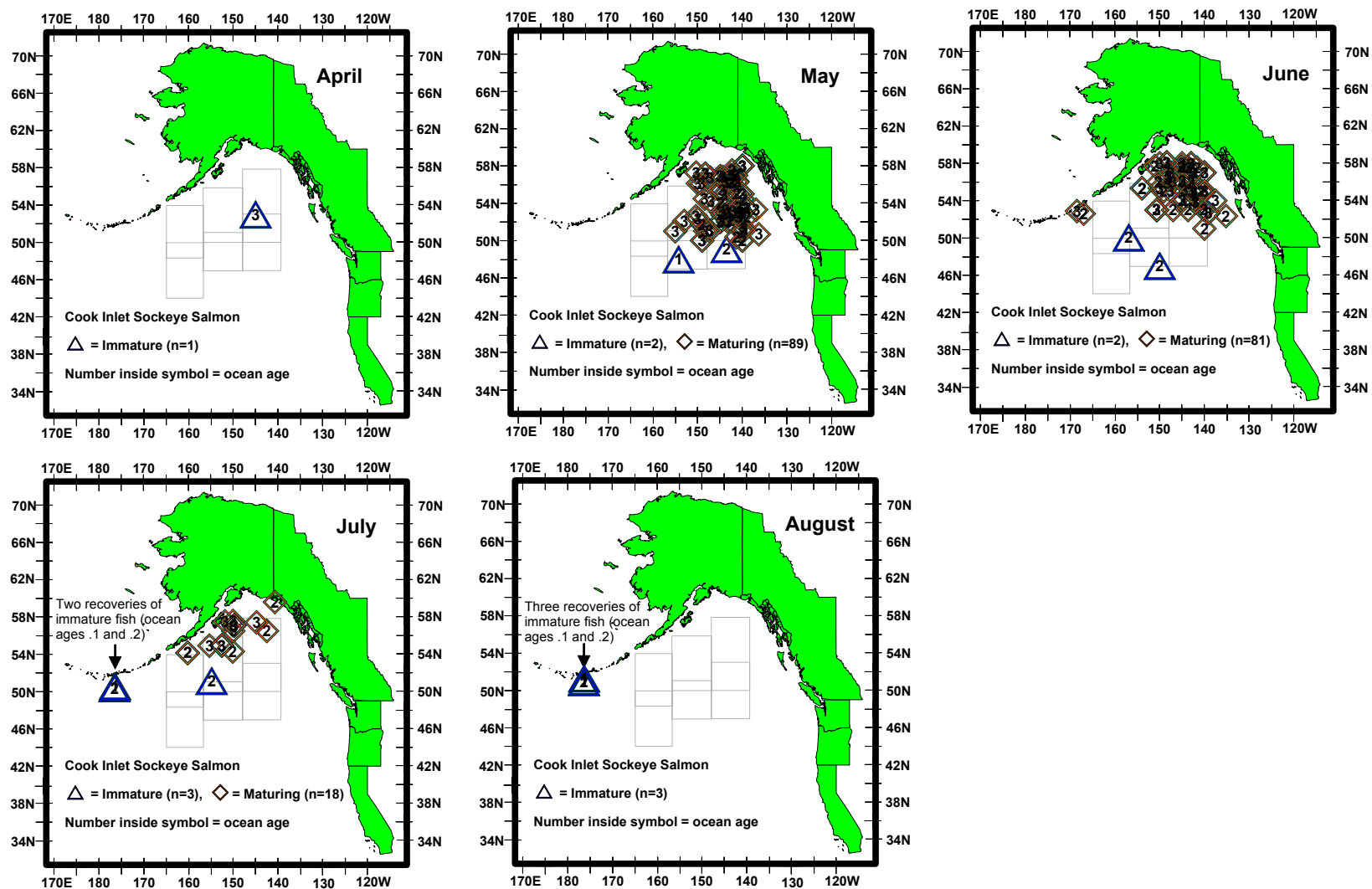


Fig. 30. The high seas distribution of Cook Inlet, Alaska, sockeye salmon by month, as shown by tagging experiments (1956-2003). The symbols indicate the ocean release locations (April-August) of tagged fish. The food habits study area is indicated by dotted lines (Fig. 2). n = total number of tagged fish recovered.

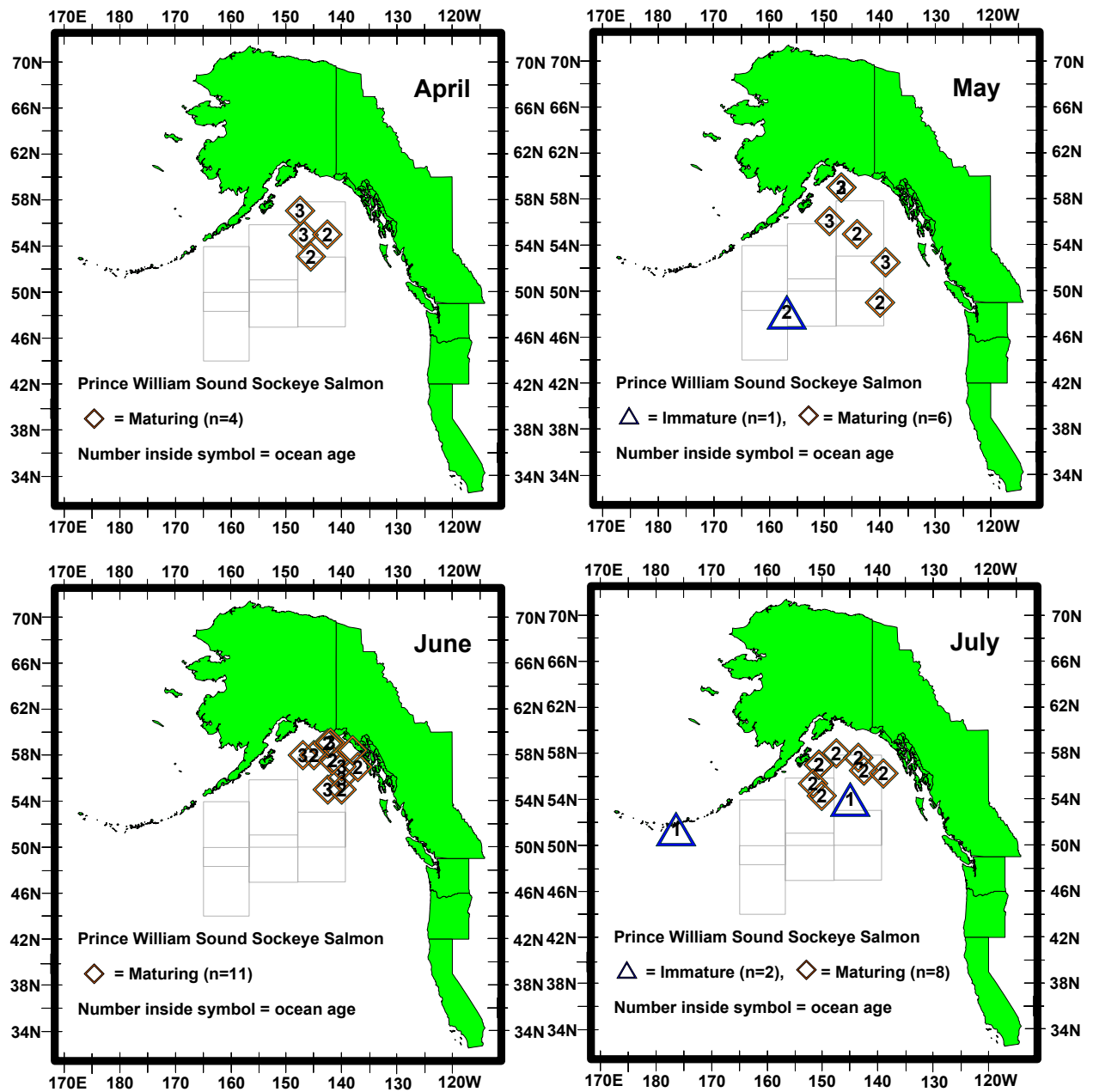


Fig. 31. The high seas distribution of Prince William Sound, Alaska, sockeye salmon by month, as shown by tagging experiments (1956-2003). The symbols indicate the ocean release locations (April-August) of tagged fish. The food habits study area is indicated by dotted lines (Fig. 2). In July, one immature fish is a CWT hatchery fish recovered in the northeast sector of the study area. n = total number of tagged fish recovered.

Appendix Table 1. List of prey animals and food items of Pacific salmon in the Gulf of Alaska in 1994-2000. Source: Kaeriyama et al. (2004).

<b>EU</b>	Euphausiids		
	<i>Thysanoessa longipes</i>	<b>PT</b>	Pteropods
	<i>Thysanoessa inermis</i>		<i>Limacina</i> spp.
	<i>Thysanoessa</i> spp.		<i>Clio</i> spp.
	<i>Euphausia</i> spp.		<i>Clione</i> spp.
	Other euphausiids	<b>FI</b>	Fishes
<b>CO</b>	Copepods		<i>Anoplopoma fimbria</i>
	<i>Neocalanus cristatus</i>		Myctophids
	<i>Eucalanus bungii</i>		Other fish eggs and larvae
	Other copepods	<b>PO</b>	Polychaetes
<b>AM</b>	Amphipods		Polychaetes
	<i>Hyperia medusarum</i>	<b>CH</b>	Chaetognaths
	<i>Hyperia</i> spp.		Chaetognaths
	<i>Themisto pacifica</i>	<b>GE</b>	Gelatinous zooplankton
	<i>Themisto japonica</i>		Coelenterates
	<i>Themisto</i> spp.		Ctenophores
	<i>Primno macropa</i>		Salps
	<i>Phronima sedentaria</i>	<b>OT</b>	Other animals
	Other amphipods		Halocypridids
<b>DE</b>	Decapods		Cumacea
	Decapods		Octopoda
<b>SQ</b>	Squids		Ostracods
	<i>Berryteuthis anonychus</i>		Barnacles
	<i>Gonatus middendorffi</i>		Debris
	Other squids		