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FOOD AND FEEDING OF STEELHEAD TROUT IN THE EPIPELAGIC WATERS OF THE NORTH PACIFIC OCEAN

by

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INTRODUCTION

Previous studies of stomach contents and feeding habits of salmonids which occupy epipelagic waters of the North Pacific Ocean have dealt mainly with salmon (*Oncorhynchus* spp.), with only marginal emphasis on steelhead (*Salmo gairdneri*) (Allen and Aron 1958, Andrievskaya 1957, Ito 1964, LeBrasseur 1966, Manzer 1968, Pearcy et al. 1984). In the few works that mention steelhead (LeBrasseur 1966, Manzer 1968, Pearcy et al. 1984), sampling was confined to the northeastern Pacific Ocean. The primary factor responsible for the scarcity of steelhead data is the low numbers of this species encountered during research cruises.

In recent years, steelhead collected by Japanese research vessels operating throughout the North Pacific Ocean have been retained for detailed biological analysis. This report describes the results of stomach content analyses for steelhead collected in 1983 by salmon research vessels and also for steelhead caught by the Japanese mothership salmon fishery in 1984.

METHODS

In 1983 eight salmon research vessels of the Fisheries Agency of Japan fished with surface gillnets and longlines from April to mid-August in the Gulf of Alaska, Bering Sea, and west-central North Pacific Ocean. Fishing effort south of the Aleutian Islands was concentrated between 150°E and 175°W. longitude. No sets were made below 40°N latitude. Gillnets had mesh varying in size (stretched) from 48 mm to 157 mm. The most common mesh sizes were 112 mm and 121 mm (commercial mesh). Gillnets were fished overnight for a period of approximately 8 hrs, and longlines were fished in the early morning.

In 1984, four commercial fleets of the Japanese mothership salmon fishery operated in the northwestern Pacific, roughly between 47°N - 56°N latitude and 165°E - 175°E longitude. All vessels used surface gillnets with 112 and 121 mm mesh. Nets were set at night, fished for approximately 8 hrs, and retrieved at dawn. The fleets fished from early June to late July.

In 1983, freshly caught steelhead were weighed (body and gonad wt.), measured for fork length, and sampled for scales. The fish were then labelled and stored frozen. In 1984, the same procedures were followed, only there were longer delays between catch and freezing due to the time involved in transporting the fish from the catcherboats to the motherships. Mothership samples were frozen whole.

At the end of the season the samples were shipped to the Pacific Biological Station in Nanaimo, B.C. (1983 samples), and the Fisheries Research Institute (FRI), Seattle, Washington (1984 samples), where they were kept frozen for up to nine months before processing.

Initial processing consisted of removing the stomachs from freshly defrosted fish, then preserving the contents in a 10% buffered formalin solution. At this point the 1983 stomach samples were sent to FRI for final analysis.

The total weight of the stomach contents was determined by blotting, then weighing the combined contents of each stomach to the nearest 0.01 g. Individual prey items were examined under a dissecting microscope and identified to the finest phylogenetic level possible given the current state of the taxonomic literature. The prey were sorted into taxonomic categories, counted, and weighed.

Stomach content data were organized and analyzed with computer software developed by Swanson and Simenstad (1984) of FRI. The programs provide a complete statistical description of the prey spectra, including measures of the trophic diversity of the diet.

A modification of Pinkas' et al. (1971) Index of Relative Importance (IRI) was used to rank the importance of prey taxa. This index is based on a combination of the percent occurrence of prey organism i, and the organism's numerical and gravimetric contribution to the diet. The IRI value is computed as follows:

$$\text{IRI} = \text{\% frequency of occurrence} \left[\text{\% numerical composition} + \text{\% gravimetric composition} \right]$$

To compare IRI values among prey spectra of different sample sizes, the importance of prey taxa were expressed as a percent of the total IRI (Swanson and Simenstad 1984).

Diversity was measured with four indices, based on the numerical and gravimetric diversity of the prey spectra (Pielou 1977):

1) Percent dominance index:

$$\text{\% dominance} = \Sigma(p_i)^2$$

where p_i is the ratio of the number, biomass, or % IRI of prey i to the total prey abundance, biomass, or IRI.

2) Shannon-Wiener diversity index:

$$H' = - \Sigma (p_i \log_2 p_i)$$

where pi's are the same as above.

3) Brillouin's diversity index (Hurtubia 1973):

$$H = (1/N)(\ln N! - \ln ni!)$$

where N is the total abundance of all organisms and ni is the abundance of organism taxa i.

4) Evenness index:

$$e = H/\ln S$$

where H = mean H, S = number of species, and lnS is equivalent to H_{max}.

All statistics related to prey spectra were performed on adjusted sample sizes that included only those fish with food in their stomachs.

Dietary overlap for steelhead in different times and areas was measured using a Percent Similarity Index (PSI, Sanders 1960) based on the sum of minimum percent of total IRI values for a given prey taxon.

Capture locations were used to assign steelhead to one of four oceanographic domains (Dodimead et al. 1963, Favorite et al. 1976): Transitional, Western Subarctic, Central Subarctic, and Alaskan Stream. Because steelhead were taken from two distinctly different areas of the Central Subarctic domain, these areas were treated separately in the analysis. These subsamples are referred to as the 'West-Central' Subarctic and 'East-Central' Subarctic, and the term 'Central Subarctic' signifies a pooled sample. The Western Subarctic sample is also subdivided based on the year of sampling. The subsamples in this domain will be referred to as '1983' and '1984' Western Subarctic samples. All subsequent time and area comparisons refer to the samples within these major areas.

RESULTS

Sample Characteristics

A total of 1,436 steelhead was caught by all Japanese salmon research vessels in 1983. Of these, 294 were retained for use in this study. Four domains were represented by these samples: Transitional, Western Subarctic, Central Subarctic, and Alaskan Stream. No steelhead were caught in the Coastal domain. In 1984, 345 steelhead were caught and kept for analysis. All of these were from the Western Subarctic domain. Figure 1 shows the number and approximate sampling location of steelhead within each domain. The two fish taken below the Subarctic

Boundary in the area 160° E to 170° E were not included in the analysis.

Most of the steelhead were captured in July, and fewer were taken in June (67), May (44), and April (2). Table 1 summarizes the biological characteristics of the steelhead from each domain, and provides general information on feeding habits (meal size, etc.). Appendix A provides a detailed monthly breakdown of this information.

Steelhead ranged in size between 195 mm (91 g) and 889 mm (7700 g). Mean lengths and weights did not vary greatly between domains. The largest individuals were found in the Western Subarctic domain, where they were larger in 1984 than in 1983. The smallest individuals were taken in the East-Central Subarctic and Alaskan Stream domains.

The highest percentages (56% to 58%) of empty stomachs were found in steelhead of the Eastern Subarctic and Alaskan Stream domains. Steelhead of the Transitional, Western Subarctic (1983), and West-Central Subarctic domains had the highest percentage of stomachs containing food (71% to 75%). More fish had empty stomachs in 1984 than in 1983. The average number of prey categories per stomach was 2 (range of means 1.5 to 2.1). The highest number of distinct prey categories in any one stomach was 4.

Diet Composition

Steelhead in all domains consumed prey from five major taxonomic groupings: fish, squid, polychaetes, crustaceans, and a group that contains miscellaneous taxa and unidentifiable contents. The prominent organisms in the miscellaneous group were pteropods (probably *Limacina*). There were notable differences, however, in the frequency of occurrence of these taxon groups, in the species that comprised them, and in their overall contribution to the diet. As a result, the relative importance of each taxon group differed considerably from domain to domain, and even within domains. Table 2 summarizes the characteristics of these major taxon groups by domain. A detailed taxonomic listing of all identified prey organisms is presented in Table 3.

Overall, fish were the most significant numerical component of the diet for steelhead. Collectively, this taxon accounted for 29% of the total prey abundance (all samples combined), and provided nearly half (47%) of the total biomass. Between and within domains, the percent composition and relative importance of this taxon were notably different. In 1983, fish were most frequent in stomachs of Alaskan Stream steelhead, and ranked highest in prey importance for this domain. They occurred less frequently in steelhead from the Western Subarctic domain, and contributed the least biomass to the diet in this region. In this same area in 1984, however, they were consumed more often and contributed eight times the biomass of the previous year. Numerical abundance changed little between years.

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Juvenile Atka mackerel (Pleurogrammus monopterygius) were the most important fish in the diet. The frequency of occurrence of this species decreased from highs of 36% and 29% in the 1984 Western Subarctic and Alaskan Stream samples to an apparent total absence in stomachs from the Transitional domain. A large proportion of the unidentified fish category is believed to be composed of P. monopterygius (Doug Milward, FRI, pers. comm., 1985), and thus their significance in the diet of steelhead is undoubtedly underestimated in this study.

Threespine sticklebacks (Gasterosteus aculeatus) were present in 8% of the samples, and were consumed most commonly by steelhead in the Transitional, Alaskan Stream, and 1983 Western Subarctic domains. They were least frequent in steelhead stomachs from the East-Central Subarctic. They were most numerous in the Transitional domain (21% of the stomachs), and averaged between 4% and 8% of the numerical prey composition. A single steelhead from the 1984 Western Subarctic domain had fed on 74 sticklebacks.

Fish of the family Myctophidae (lanternfishes) were also common in the diet. Stenobrachius leucopsarus was the most abundant representative of this family. Tarletonbeania crenularis and Protomyctophum thompsoni were present but occurred in the samples infrequently.

Gonatid squids were the second most common prey category in the total sample (all domains combined). They were strongly represented in diets of steelhead from the Transitional, 1983 Western Subarctic, and West-Central Subarctic regions. Berryteuthis magister was the most abundant species in this taxon (14% occurrence overall; 50% in the 1983 Western Subarctic), and was the largest squid found in the diet. This species represented 39% of the overall mean biomass of the stomach contents (83% of the 1983 Western Subarctic total). Gonatus middendorfii represented 7.5% of the overall mean biomass, and occurred in 3% of the stomachs. None of the other squid species were identified in more than 2% of the stomachs.

The presence of squid was much lower in the East-Central Subarctic and Alaskan Stream samples (Table 2). In these areas, the frequency of occurrence was one-third to one-fifth what it was farther to the south and west. B. magister abundance reflects this decrease, whereas G. middendorfii abundance showed only a slight reduction in percent occurence. In contrast, Gonadus madokai was found exclusively in Gulf of Alaska (Alaskan stream and East-Central Subarctic) stomach samples. Between 1983 and 1984 the occurrence of squid in stomach samples from the Western Subarctic decreased dramatically to one-third of its former level. B. magister occurrence dropped seven-fold, whereas G. middendorfii occurrence changed little.

The mean percent composition of squid in the diet, and the consequent importance of this taxon as food of steelhead in different areas and years generally followed the trends in percent occurrence.

In the Western Subarctic domain in 1983, squid so dominated the diet that they constituted one- third of the total number of prey categories and over 92% of the biomass.

Fish and squid collectively contributed 98% of the total prey biomass, and accounted for 38% of prey abundance. The remaining biomass was distributed among taxa that consist of numerous individuals that exhibit low average biomass per individual, such as crustaceans and pelagic polychaetes.

Crustaceans (mainly hyperiid amphipods) were found in 28% of the stomachs, and individual species of this taxon contributed between 2% and 46% of total prey numbers. In terms of biomass, however, crustaceans were not an important contributor to the diet (less than 1% overall; no greater than 2.4% in any one domain). Because of their strong numerical representation, they were important to steelhead feeding in the East-Central Subarctic (37.8% IRI), but in the remaining domains they comprised less than 12% of the total IRI. Once again, area differences were apparent; crustaceans in the Western Subarctic were nearly absent in 1983 stomachs, yet comprised 11.7% of the IRI in 1984.

Parathemisto pacifica and Hyperia medusarum dominated the crustacean fraction of the diet. Other hyperiid amphipods and euphausiids were noticable in the diet, but the majority of other crustacean taxa were rare.

Pelagic polychaetes (family Alciopidae) were another prey category with high abundance and low biomass. They occurred in 19% of the stomachs and averaged 3 per stomach. In one case, 129 were found in a single stomach. Numerically, they accounted for 32% of total prey numbers. Gravimetrically, however, they represented less than 2% of the total prey biomass. Their presence in the diet was highly variable, and trends were unclear or absent, suggesting these prey were patchily distributed.

In both 1983 and 1984, the frequency of occurrence of polychaetes was the same (6%), but both relative abundance and biomass differed substantially. Their importance in the diet was equally variable, from an IRI value of 0.1% in the Western Subarctic to 38.5% in the West-Central Subarctic.

Diet Diversity

Prey diversity in the diet of steelhead from the four domains can be compared using results from Table 4. Based on fish with stomachs containing prey, these results indicate that the most diverse prey spectrum, both numerically and gravimetrically, occurs in the diet of steelhead from the 1984 Western Subarctic domain. This is contrasted by the 1983 prey spectrum in the same area which shows the least gravimetric diversity and exhibits the most heterogeneous prey distribution. The diets of steelhead from the other domains were intermediate in diversity. Numerical diet diversity in 1983 was highest in the Transitional, East-Central Subarctic and Alaskan Stream domains, followed by the Western Subarctic and West-Central Subarctic.

Gravimetrically-based diversity results were somewhat different, especially for the Central Subarctic samples. Within this domain, gravimetric and numerical diversity in the eastern and western subsamples were inversely related. Whenever the East-Central Subarctic samples had a greater numerical diversity than those of the West-Central Subarctic, gravimetric diversity of the two areas showed the reverse trend. The gravimetric diet diversity of the Transitional and Alaskan Stream domains was consistently high, and generally mirrored the numerically-based diversity results.

Diversity based on the percent of total IRI, which incorporates both numerical and gravimetric abundance of the prey and accounts for unequal sample sizes, produced slightly different results than when diversity was measured on the basis of biomass or abundance alone. Regardless of which index was used, the prey spectrum from the Transitional domain was the most diverse, and had the most even distribution of prey within the 15 categories identified. The Alaskan Stream domain had nearly as diverse a prey spectrum, but prey were less evenly distributed among the 13 categories identified. The 1984 Western Subarctic and East-Central Subarctic diets were similarly diverse. Only 9 prey categories were found in the 1983 Western Subarctic sample, which was consequently the least diverse and least evenly distributed of any of the prey spectra.

Dietary Overlap

Dietary overlap was measured with prey grouped by two methods. In the first grouping, prey were divided into as many distinct taxa as could be identified (Table 5a). By the second method, prey were divided into five major taxon groups (Table 5b). It is immediately apparent that, at the higher taxonomic resolution (Table 5a), there is a low degree of overlap between any of the domains. The high overlap values for within-domain subsamples result from unequal sample sizes. The larger of the two subsamples contains a disproportionately large percentage of the total prey taxa in that domain, so that when compared to the combined sample, the larger subsample is, in effect, being compared to itself. The highest between-domain overlap occurs among the Alaskan Stream - Western Subarctic (1984), Transitional-West-Central Subarctic, and Transitional-Western Subarctic (1983) combinations (68%, 55%, and 44% overlap, respectively). The least overlap, and hence most different prey spectra, was between the Alaskan Stream-Western Subarctic (1983) domains, because squid were nearly absent from the diet of Alaskan Stream steelhead. The same relationships persist with the broader taxonomic groupings (Table 5b), but the magnitudes of the overlap increased.

Table 6 presents monthly comparisons of prey overlap within and between domains. These results reveal the extreme variability in dietary overlap for steelhead collected in different areas and at different times. Although there are some fairly high overlap values, no trends are apparent, and between-month differences for a given domain are often as great as between-domain differences for the same month. Sample sizes differ considerably between months, and because sample size apparently influences dietary overlap measures, this may obscure any trends in time and area differences.

DISCUSSION

Steelhead trout are widely distributed in the North Pacific Ocean (Sutherland 1973, Okazaki 1983), and the major prey taxa they feed on are similarly widespread (Frost and McCrone 1979, Jefferts 1985, Motoda and Minoda 1974, Pearcy 1976, Pearcy et al. 1977; 1979, Roper et al. 1984). However, the details of the seasonal occurrence and relative abundance for most of the prey species are not well known. Since planktonic communities are no doubt strongly influenced by prevailing oceanographic conditions, the environment surrounding prey communities should be considered before any time and area comparisons are made. Grouping steelhead by oceanographic domain proved to be an effective way of evaluating qualitative and quantitative differences in the composition of their diet.

By examining stomach contents from areas where the physical environment is relatively consistent, environmentally-induced differences in prey assemblages are reduced, and comparisons are more meaningful. The results of comparisons between and within domains show that steelhead feed on a variety of organisms, of which only a few are represented in the stomach of any one steelhead. The occasional superabundance or absence of prey in stomachs of steelhead taken together in the same haul suggests either that prey are evenly distributed and are selectively consumed by individual fish, or that prey are patchily distributed and steelhead feed opportunistically.

Allen and Aron (1958) found that stomach contents of Pacific salmon were often stratified and contained two prey types, one in each half of the stomach. They suggested that food organisms were patchily distributed, and that salmon fed intensively on swarms of different prey as they were encountered. The findings of Pearcy et al. (1984) support this idea of opportunistic feeding on prey patches. They found distinct diel changes in the composition of salmon prey; when euphausiid abundance increased in surface waters at night, salmon fed almost exclusively on these organisms. Without complete knowledge of prey abundance and distribution in the waters where steelhead were collected, it is nearly impossible to say how selective they were in their choice of prey, but results of this study and studies on salmon suggest that steelhead exploit their food resources on an opportunistic basis. An examination of the literature also indicates that diet variability is a feature shared by steelhead and Pacific salmon in the North Pacific Ocean.

Although oceanographic domains were useful in subdividing the samples collected in this study, they merely represent large-scale subdivisions of the pelagic environment. Within these zones, the micro-environments of prey communities probably undergo rapid changes that dictate when, where, and what types of prey will be available to foraging steelhead. Prey behavior, such as vertical migration and swarming, will also influence prey availability (Charles Simenstad, FRI, pers. comm., 1985). Additionally, the boundaries of the domains are indistinct and fluctuate continuously (Favorite et al. 1976), such that, without exact information on the oceanic conditions in 1983 and 1984, it is uncertain whether some samples were assigned to the wrong domains.

The principle difference between the diets of steelhead and salmon is the relative importance of different taxonomic groups, which is species specific. In general, steelhead were found to feed on the same types of organisms as the five species of co-occurring Pacific salmon. Some taxa, such as euphausiids, are known to be principle components of salmon diets in the same regions (Allen and Aron 1958, Ito 1964, LeBrasseur 1966), yet are of minor importance to steelhead (LeBrasseur 1966, Manzer 1968, Pearcy et al. 1984, this study).

In the Western Subarctic domain, steelhead primarily fed on fish and squid. Salmon studies in this same area suggest that, in addition to fish and squid, euphausiids and copepods are primary prey organisms of salmon. Allen and Aron (1958) studied the diet of salmon in the Western Subarctic domain in the area of the mothership salmon fishery. They found that copepods and euphausiids were the most common prey of sockeye and pinks, and fish and euphausiids dominated the diet of chum salmon. Squid were present in 25% of the salmon stomachs (all species combined), which compares favorably with my findings for steelhead. Fish were less frequent in salmon than in steelhead, whereas amphipods were about twice as common in salmon stomachs as they were in steelhead stomachs.

Ito (1964) conducted a comprehensive eight year study over a broad area of the western North Pacific which included the area of my samples. He concluded that salmon could be classified into 3 major groups based on their food preferences. Chinook (Oncorhynchus tshawytscha) and coho (O. kisutch) salmon ate primarily squid and fish. Sockeye (O. nerka) and pinks (O. gorbuscha) ate squid and fish, but also consumed an assortment of small zooplankton, such as euphausiids and amphipods. Chum (O. keta) ate mainly euphausiids, along with some pteropods and jellyfish. Based on the frequency of occurrence of squid and fish, steelhead in this study were intermediate between the chinook-coho and sockeye-pink groups.

Machidori (1968) and Simenstad (1980) also studied salmon from the area of the mothership fishery. They found that pinks and chums ate amphipods, fish, euphausiids, pteropods, and jellyfish (chums only), whereas sockeye and coho had fed on euphausiids, fish, amphipods, and squid. The relative importance of each prey group to these two salmon species varied from study to study. Chinook salmon ate mainly rockfish (Scorpaenidae) larvae.

Machidori (1972) examined the stomachs of coho from an area contiguous with the West-Central Subarctic and Transitional domains. He found that squid were the exclusive prey of coho (99% by wt.), which compares to this study's results of 80% (by wt.) for steelhead in the West-Central Subarctic, and 85% (by wt.) for steelhead in the Transitional domain.

In the Gulf of Alaska, LeBrasseur (1966) investigated the feeding habits of sockeye, pinks, coho, and steelhead collected from the East-Central Subarctic, Transitional, and Coastal domains. Steelhead fed mainly on fish, squid, and amphipods. Euphausiids and copepods were present only in trace amounts. He found no pteropods in steelhead stomachs. Salmon were found to feed mainly on euphausiids, with secondary emphasis on squid or fish, and occasionally amphipods.

To compare diets between species, LeBrasseur weighted his results to obtain a constant sample size of 100 fish. By this method, he estimated that the total biomass contribution to the diet from squid was 1740 g per 100 steelhead, and for fish was 25 g per 100 steelhead. In a weighted sample of 100 steelhead from my study, squid contribute 372 g and fish provide 101 g. The squid-dominated diet of steelhead was distinctly different from that of salmon.

Pearcy et al. (1984) sampled continuously for twenty-four hours in the north-central Gulf of Alaska at approximately the same location as the East-Central Subarctic samples in this study. He reported euphausiids as the principle prey for sockeye, pinks, and coho. Significant amounts of squid and fish were also noted in stomachs of coho and sockeye, depending on when the fish were caught.

The wealth of evidence presented above clearly demonstrates that steelhead feed on the same general types of organisms as Pacific salmon. The evidence presented herein goes further to suggest that, in addition to the dietary differences noted above, steelhead feed on several prey that are not found in the diets of any of the Pacific salmon.

Nowhere in the literature are there accounts of threespine sticklebacks (Gasterosteus aculeatus) in the stomachs of salmonids in epipelagic waters of the North Pacific. This is surprising, because they appeared in stomachs of steelhead in all domains, and were not rare when encountered. The marine form of the threespine stickleback is known to occur in neritic and epipelagic waters of the North Pacific Ocean from the Gulf of Alaska to the Bering Sea (Hart 1973, McPhail and Lindsey 1970, Quast and Hall 1972). Clemens and Wilby (1961) report that as many as 4000 sticklebacks were taken in a single haul of a surface townet in the Gulf of Alaska. If, as the literature suggests, sticklebacks are present in appreciable numbers in the areas inhabited by salmon, it is reasonable to assume that they would appear in the salmon diet. Perhaps G. aculeatus was unusually abundant in the times and areas sampled in this study. Unfortunately, most studies of salmonid diets that include steelhead do not provide complete species listings, so it is unkown whether G. aculeatus was actually present, but not in the quantities discovered herein.

Pelagic polychaetes, which in some areas contributed appreciably to the diet of steelhead, were also notably absent in the findings of other researchers. Takeuchi (1972) reported the presence of the polychaete Tomopteris septentrionalis in stomachs of salmon in the western and central Bering Sea. Synkova (1951) found polychaetes in 5% of chum stomachs taken near the northern Kuril Islands.

Sockeye and pink salmon, which are known to prey predominantly on smaller zooplankton (Ito 1964), might be expected to feed on polychaetes, but this is evidently not so. The fact that threespine sticklebacks have not been mentioned in diet studies of salmonids in the marine environment, and only passing references are made to polycheates, leaves the impression that neither of these organisms are particularly important members of salmonid prey spectra in most years. Either they are rarely encountered by salmon, or are largely ignored when found. The results of this study on steelhead counter this notion, by showing that steelhead feed extensively on both polychaetes and threespine sticklebacks.

SUMMARY

1) In the summer of 1983 and 1984, Japanese salmon research vessels and commercial salmon fishing fleets sampled 639 steelhead in four oceanographic domains in the North Pacific Ocean.

2) The stomachs were removed from these fish, and the contents were sorted, counted, and weighed. The resulting data were compiled and analyzed by specialized computer software designed for stomach content analysis.

3) The composition of the diet varied between oceanographic domains. In the Transitional domain, squid were the primary component of the prey spectra, followed by fish and pelagic polychaetes. In the Western Subarctic, squid dominated in 1983, and fish dominated in 1984. In the East-Central Subarctic, steelhead preyed most heavily on fish, squid, and crustaceans. In the West-Central Subarctic, squid and polychaetes dominated the diet. The diet of steelhead from the Alaskan Stream domain was principly composed of fish, and to a lesser degree, polychaetes, crustaceans, and pteropods.

4) The diversity of the diet also varied between domains. Steelhead from the Transitional domain had the most diverse diet, while steelhead from the 1983 Western Subarctic sample had the least

diverse diet which was dominated by squid. Differences between years were as large as differences between domains within years.

5) Dietary overlap was generally low (usually <35%) among steelhead in the different domains, but depended upon how the prey taxa were grouped. Overlap based on the highest phylogenetic identification of taxa was greatest in the Alaskan Stream-Western Subarctic (1984), Transitional-West-Central Subarctic, and Transitional-Western Subarctic (1983) combinations (68%, 55%, and 44% overlap, respectively). Alaskan Stream and 1983 Western Subarctic steelhead shared the fewest prey in their diet compositions. Grouping of the prey taxa into five major categories (fish, squid, crustaceans, polychaetes, and miscellaneous) reflected the same trends but increased the magnitude of the overlap, as would be expected. Overlap values were also presented for monthly comparisons within and between domains.

6) Results of this study were compared to similar studies on steelhead and Pacific salmon in epipelagic waters of the same regions. Steelhead and salmon were found to feed on prey from the same general taxonomic groups, but the species within these groups were often distinct. The most striking difference between the diets of salmon and steelhead was that steelhead were found to feed on substantial amounts of threespine sticklebacks and pelagic polychaetes, whereas the literature indicates that salmon do not eat these prey.

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Doug Milward of FRI identified the stomach contents and prepared the preliminary computer analysis. Charles Simenstad provided the computer software and made helpful suggestions on its utilization. Thanks are also due to Kathy Jefferts of the National Marine Fisheries Service for her help in identifying the squid species.

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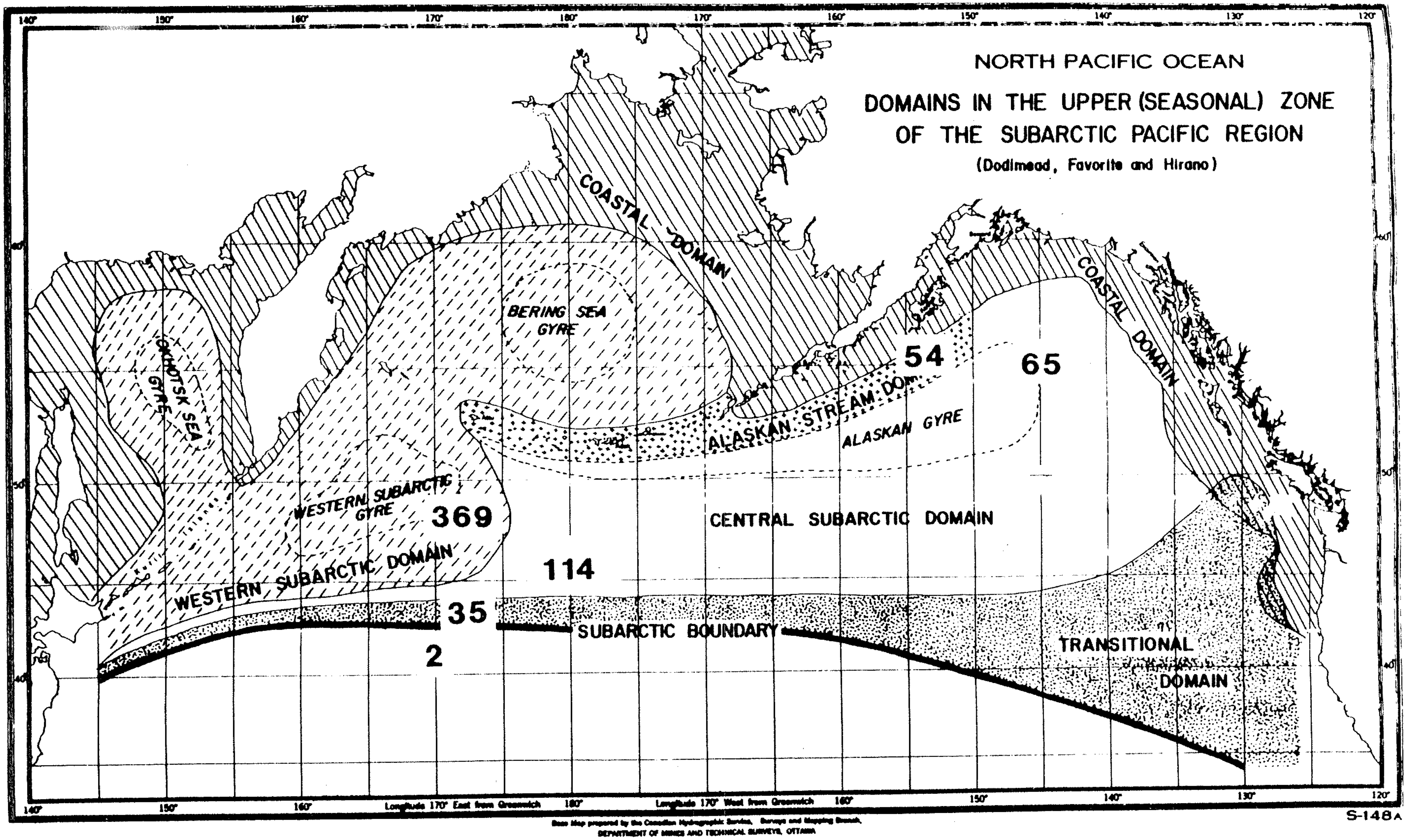

Figure 1. Number and approximate location of steelhead trout sampled from major oceanographic domains[1] within the North Pacific Ocean in 1933 and 1984[2].

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[1] Described by Dodimead et al. (1963).
[2] All 1984 samples were taken in the Western Subarctic domain.

Table 1. Biological characteristics and stomach-content parameters of steelhead trout taken in the North Pacific Ocean in summer, 1983[3] and 1984[4]. Data shown are means (± 1 S.D.).

Domain	No. of steelhead	Fork length (mm)	Weight (g)	Percent with empty stomachs	No. of prey categories per stomach	Total wt. of contents per stomach (g)	Total no. of contents per stomach	Percent ratio of contents wt. to steelhead wt.
Transitional	35	615 (±98)	2743 (±1047)	29	1.8 (±0.9)	11.9 (±19.0)	8.4 (±6.8)	0.52 (±0.81)
Western Subarctic								
1983	24	650 (±75)	3138 (±1046)	25	1.4 (±0.9)	30.0 (±36.2)	2.8 (±2.0)	0.95 (±0.98)
1984	345	707 (±78)	3999 (±1230)	42	1.5 (±0.7)	15.1 (±25.2)	10.7 (±22.2)	0.43 (±0.81)
Comb.	369	703 (±79)	3943 (±1236)	41	1.8 (±1.0)	16.3 (±26.5)	10.0 (±21.3)	0.47 (±0.84)
Central Subarctic								
West	114	627 (±87)	2584 (±1019)	29	2.0 (±0.9)	12.0 (±20.5)	12.3 (±21.2)	0.47 (±0.63)
East	65	582 (±138)	2100 (±1056)	58	1.6 (±0.7)	4.9 (±11.0)	4.3 (±4.8)	0.33 (±0.55)
Comb.	179	610 (±110)	2412 (±1055)	40	2.1 (±1.2)	10.2 (±18.8)	10.3 (±18.8)	0.44 (±0.61)
Alaskan Stream	54	655 (±107)	2651 (±1005)	56	2.1 (±1.2)	4.3 (±5.2)	6.1 (±7.1)	0.18 (±0.21)

[3] Steelhead taken by Japanese research vessels, Fisheries Agency of Japan.

[4] Steelhead taken incidentally to salmon by the Japanese mothership salmon fishery, and retained for the purposes of this and other scientific studies.

Table 2. Frequency of occurrence, mean percent composition, and percent of total Index of Relative Importance (IRI)[5] of the four major prey types for steelhead from four oceanographic domains[6] in the North Pacific Ocean, 1983 and 1984.

Prey type	Domain	Frequency of occurrence	Mean percent composition Numerical	Gravimetric	Percent of total IRI
FISH	Transitional	44	33.3	11.3	20.0
	West. Subarctic				
	1983	39	36.0	7.9	13.4
	1984	86	36.1	68.7	79.0
	Comb.	82	36.1	59.4	74.2
	Cent. Subarctic				
	West	54	11.4	12.7	13.2
	East	59	19.8	20.8	32.4
	Comb.	56	12.3	13.7	16.7
	Alaskan stream	79	36.0	88.9	83.3
SQUID	Transitional	64	24.8	85.3	68.0
	West. Subarctic				
	1983	72	60.0	92.0	86.4
	1984	26	5.9	30.4	8.3
	Comb.	30	7.1	39.8	13.3
	Cent. Subarctic				
	West	51	8.0	80.5	45.2
	East	22	19.0	76.7	28.6
	Comb.	44	9.2	80.1	45.1
	Alaskan stream	12	2.7	6.5	1.0
CRUSTACEANS	Transitional	36	12.4	2.1	5.0
	West. Subarctic				
	1983	6	2.0	tr[7]	0.1
	1984	33	39.2	0.4	11.7
	Comb.	31	38.4	0.4	11.4
	Cent. Subarctic				
	West	36	7.3	1.0	3.0
	East	59	45.7	1.8	37.8
	Comb.	42	11.3	1.1	6.0
	Alaskan stream	46	10.9	2.4	5.1
POLYCHAETES	Transitional	28	28.1	1.3	8.0
	West. Subarctic				
	1983	6	2.0	tr	0.1
	1984	6	17.1	0.5	1.0
	Comb.	6	16.7	0.4	1.0
	Cent. Subarctic				
	West	49	71.9	5.6	38.5
	East	11	3.4	0.3	0.6
	Comb.	40	64.8	4.9	32.2
	Alaskan stream	33	21.1	1.6	6.4

[5] Modified from Pinkas et al. (1971).
[6] Described by Dodimead et al. (1963).
[7] tr = trace, where prey biomass totalled less than 0.1 g.

Table 3. Taxonomic listing and associated statistics of organisms found in stomachs of steelhead trout (Salmo gairdneri) collected in the North Pacific Ocean in April through July 1983, and in June and July 1984. All samples combined. Data are percentages based on total number of stomachs containing prey items.

Prey item	Frequency of occurrence	Mean percent composition Numerical	Mean percent composition Gravimetric	% I.R.I.[8,9]
FISH				
Teleostei (misc. unidentified)	46	10.1	12.5	28.1
Hexagrammidae				
Pleurogrammus monopterygius (Atka mackerel)	24	11.0	28.3	25.1
Gasterosteidae				
Gasterosteus aculeatus (3-spine stickleback)	8	6.7	3.8	2.3
Myctophidae (misc. unidentified genera) (lampfishes)	2	0.2	0.6	
Stenobrachius leucopsarus	3	0.4	1.5	0.1
Tarletonbeania crenularis	1	0.1	0.2	
Protomyctophum thompsoni	<1	0.1	0.1	
Engraulidae				
Engraulis mordax (Northern anchovy)	1	0.1	0.1	
SQUID				
Teuthoidea (misc. unidentified)	3	0.3	0.2	
Gonatidae (misc. unidentified genera)	13	1.7	7.6	3.2
Berryteuthis magister	14	4.0	38.6	16.5
Gonatus middendorfii	3	0.7	7.5	0.2
Gonatus (unidentified sp.)	2	0.7	0.5	
Gonatus madokai	2	0.9	0.2	
Gonatus tinro	1	0.2	0.2	
Gonatopsis borealis	1	0.1	0.8	
POLYCHAETES				
Alciopidae	19	32.2	1.5	17.4
AMPHIPODS				
Hyperiidae (misc. genera)	2	0.9	0.0	
Hyperia medusarum	15	3.3	0.2	1.4
Parathemisto pacifica	9	18.6	0.1	4.6
Hyperia galba	1	0.1	0.0	
Lysianassidae				
Paracallisoma sp.	9	1.2	0.1	0.3
Oxycephalidae (misc. genera)	<1	0.2	0.0	
Paraphronima sp.	<1	<0.1	0.0	
Vibilia sp.	<1	<0.1	0.0	

Table 3. Taxonomic listing and associated statistics of organisms found in stomachs of steelhead trout (Salmo gairdneri) collected in the North Pacific Ocean in April through July 1983, and in June and July 1984 - continued.

Prey item	Frequency of occurrence	Mean percent composition Numerical	Mean percent composition Gravimetric	% I.R.I.[8,9]
AMPHIPODS				
Calliopiidae			0.0	
Calliopius sp.	2	0.2	0.0	
Gammaridae (misc. genera)	<1	0.1	0.0	
COPEPODS				
Aetideidae				
Euchaeta sp.	<1	<0.1	0.0	
Calanidae				
Calanus cristatus	<1	<0.1	0.0	
Monstrilloidae (misc. genera)	<1	<0.1	0.0	
MISCELLANEOUS CRUSTACEA				
Isopoda	<1	<0.1	0.0	
Mysidacea				
Gnathophausia gigas	1	0.1	0.1	
Eucarida				
Euphausiidae	2	2.1	<0.1	0.1
Decapoda	1	0.1	0.1	
Pandalidae	<1	<0.1	<0.1	
Brachyura	1	0.2	0.0	
Chionoecetes sp.	<1	<0.1	0.0	
Cancridae				
Cancer sp.	<1	<0.1	0.0	
PTEROPODS				
Thecosomata	3	2.6	<0.1	0.2
INSECTS				
Lepidoptera	<1	0.1	<0.1	

[8]Modified from Pinkas et al. (1971).

[9]IRI values were not computed for prey items with a frequency of occurrence less than 5 and both numerical and gravimetric composition less than 1.

Table 4. Diet diversity and the distribution of prey of steelhead caught in four oceanographic domains of the North Pacific Ocean in 1983 and 1984. See text for descriptions of indices.

Domain	Effective sample size[10]	Number of prey categories	Shannon-Weiner Diversity Index			Brillouin's Index	Percent Dominance Index			Eveness Index		
			Nos.	Biomass	% IRI		Nos.	Biomass	% IRI	Nos.	Biomass	% IRI
Transi-tional	24	15	2.89	1.88	2.3	2.73	0.17	0.37	0.25	0.74	0.48	0.59
Western Subarctic												
1983	18	9	2.25	0.95	0.94	1.96	0.30	0.70	0.71	0.71	0.30	0.30
1984	200	25	3.03	2.42	2.02	2.99	0.18	0.27	0.34	0.65	0.52	0.43
Comb.	218	25	3.07	2.40	2.17	3.03	0.17	0.26	0.30	0.66	0.52	0.47
Central Subarctic												
West	81	31	1.93	1.99	1.64	1.86	0.53	0.44	0.42	0.39	0.40	0.33
East	27	16	2.75	1.34	1.87	2.50	0.23	0.59	0.34	0.69	0.33	0.47
Comb.	108	35	2.31	1.97	1.85	2.23	0.43	0.45	0.36	0.45	0.38	0.36
Alaskan Stream	24	13	2.70	1.77	2.04	2.52	0.19	0.42	0.31	0.73	0.48	0.55

[10] Steelhead with stomachs containing prey.

Table 5. Dietary overlap (Percent Similarity Index[11]) of prey for steelhead trout sampled from four oceanographic domains in the North Pacific Ocean in 1983 and 1984.[12] Data shown are percent prey overlap based on percent of total Index of Relative Importance (IRI)[13].

(a) Prey identified to finest taxonomic level possible.

Domain		Trans.	Western Subarctic 1983	Western Subarctic 1984	Western Subarctic Comb.	Central Subarctic West	Central Subarctic East	Central Subarctic Comb.	Alaskan Stream
Transitional									
Western Subarctic	1983	44.5							
	1984	16.6	14.9						
	Comb.	21.9	20.0	94.4					
Central Subarctic	West	55.1	34.1	15.7	20.9				
	East	26.8	20.7	34.4	39.1	27.8			
	Comb.	56.1	35.0	19.9	25.1	91.0	33.8		
Alaskan Stream		21.5	10.8	68.2	66.1	21.3	31.4	26.7	

(b) Prey grouped into five major taxon groups (fish, squid, crustaceans, polychaetes, and miscellaneous).

Domain		Trans.	Western Subarctic 1983	Western Subarctic 1984	Western Subarctic Comb.	Central Subarctic West	Central Subarctic East	Central Subarctic Comb.	Alaskan Stream
Transitional									
Western Subarctic	1983	81.6							
	1984	33.3	21.9						
	Comb.	38.3	26.9	95.0					
Central Subarctic	West	69.4	58.6	25.5	30.5				
	East	53.1	42.2	52.9	57.7	45.3			
	Comb.	74.8	58.6	32.0	37.0	93.4	51.9		
Alaskan Stream		31.3	14.6	86.2	81.4	23.5	39.6	29.2	

[11] Modified from Sanders (1960).
[12] All samples from 1983 unless otherwise noted.
[13] Modified from Pinkas et al. (1971).

Table 6. Time and area comparisons of dietary overlap (Percent Similarity Index[14]) of the four major prey types (fish, squid, crustaceans, polychaetes) for steelhead from four oceanographic domains in the North Pacific Ocean in 1983 and 1984. Data shown are percent prey overlap based on percent of total Index of Relative Importance (IRI)[15].

Domain	Period[16]	Effective sample size[17]	Transitional May	Transitional June	Transitional July	Transitional Comb.	Western Subarctic June 1984	Western Subarctic July 1983	Western Subarctic July 1984	Western Subarctic Comb.	Central Subarctic May W.	Central Subarctic June W.	Central Subarctic July E.	Central Subarctic July W.	Central Subarctic July Comb	Central Subarctic Comb.	Alaskan Stream July
Trans-tional	May	15															
	June	3	37.9														
	July	6	40.0	86.6													
	Combined	24															
Western Subarctic	June 1984	5	50.7	85.4	86.1												
	July 1983	18	49.2	86.6	85.8		98.4										
	1984	195	57.6	8.1	17.9		20.9	19.4									
	Combined	218				**38.3**											
Central Subarctic	May West	12	90.9	2.3	29.7		44.2	42.6	55.3								
	June West	42	62.4	55.3	56.6		64.0	63.7	20.2		63.6						
	July East	27	65.3	30.7	43.6		43.8	42.2	50.2		63.5	42.5					
	West	27	62.9	38.8	41.1		47.1	46.7	20.7		63.2	83.1	43.1				
	Comb.	54	70.9	40.9	50.0		53.7	52.2	35.7		71.3	84.4	58.1	83.0			
	Combined	108				**74.8**				**37.0**							
Alaskan Stream	July	24	58.2	2.3	6.8	**31.3**	16.1	14.6	88.9	**81.4**	55.8	20.7	39.6	58.5		**29.2**	

[14] Modified from Sanders (1960).
[15] Modified from Pinkas et al. (1971).
[16] All samples from 1983 unless otherwise noted.
[17] No. of fish with prey in stomachs.

Appendix A. Biological characteristics and stomach-content parameters of steelhead trout taken in the North Pacific Ocean in April through July 1983,[1] and June through July 1984.[2] Data shown are means with ranges in parentheses.

Domain	Month	No. of steelhead	Fork length (mm)	Weight (g)	Percent with empty stomachs	No. of prey categories per stomach	Total wt. of contents per stomach (g)	Percent ratio of contents wt. to steelhead wt.
Transitional	April	1	417	970	0	2.0	0.1	0.1
	May	22	628 (336-750)	2806 (947-4545)	32	1.7 (1-4)	5.7 (0.5-21.0)	0.3 (0.0-1.4)
	June	4	592 (550-645)	2135 (1136-3016)	25	1.7 (1-2)	41.1 (18.8-81.9)	1.6 (0.8-2.7)
	July	8	659 (545-740)	3096 (1938-4012)	25	1.8 (1-3)	14.7 (1.5-57.0)	0.6 (0.1-2.9)
	Combined	35	625 (336-750)	2743 (947-4545)	29	1.8 (1-4)	11.9 (0.5-81.9)	0.5 (0.0-2.9)
Western Subarctic	June 1984	6	741 (700-787)	3648 (440-5700)	17	1.8 (1-3)	62.9 (0.2-244.9)	3.0 (0.0-8.1)
	July 1983	24 (492-750)	649 (1371-4704)	3138	25 (1-3)	1.2 (0.6-137.0)	30.4 (0.0-3.1)	1.0
	July 1984	339	706 (495-889)	4005 (350-7700)	42	1.9 (1-6)	13.8 (0.1-141.0)	0.4 (0.0-2.6)
	Combined (1983-1984)	369	703 (492-889)	3943 (350-7700)	41	1.5 (1-4)	16.3 (0.1-244.9)	0.5 (0.0-8.1)

Appendix A. Biological characteristics and stomach-content parameters of steelhead trout taken in the North Pacific Ocean in April through July 1983,[1] and June through July 1984.[2] Data shown are means with ranges in parentheses - continued.

Domain	Month	No. of steelhead	Fork length (mm)	Weight (g)	Percent with empty stomachs	No. of prey categories per stomach	Total wt. of contents per stomach (g)	Percent ratio of contents wt. to steelhead wt.
Central Subarctic	May	22	681 (600-762)	3243 (2165-4701)	45	2.0 (1-3)	7.8 (0.6-27.8)	0.3 (0.0-0.9)
	June	57	630 (440-810)	2613 (1032-4989)	26	1.7 (1-4)	16.2 (0.1-120.4)	0.6 (0.0-3.3)
	July	100	584 (195-830)	2108 (91-5347)	46	2.0 (1.4)	6.1 (0.1-50.3)	0.4 (0.0-3.3)
	Combined	179	610 (195-830)	2412 (91-5347)	40	1.9 (1-4)	10.2 (0.1-120.4)	0.4 (0.0-1.7)
Alaskan stream	July	54	655 (305-835)	2651 (280-4597)	56	1.9 (1.4)	4.3 (3.0-5.0)	0.2 (0.0-0.8)

[1]Steelhead taken by Japanese research vessels, Fisheries Agency of Japan.

[2]Steelhead taken incidental to salmon by the Japanese mothership salmon fishery, and retained for the purposes of this and other scientific studies.