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Biology of the Pacific Pomfret (*Brama japonica*) in the North Pacific Ocean

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Abundances of Pacific pomfret (*Brama japonica*), an epipelagic fish of the North Pacific Ocean, were estimated from gillnet catches during the summers of 1978–1989. Two size modes were common: small pomfret <1 yr old, and large fish ages 1–6. Large and small fish moved northward as temperatures increased, but large fish migrated farther north, often into the cool, low-salinity waters of the Central Subarctic Pacific. Lengths of small fish were positively correlated with latitude and negatively correlated with summer surface temperature. Interannual variations in the latitude of catches correlated with surface temperatures. Large catches were made in the eastern Gulf of Alaska (51–55°N) but modes of small pomfret were absent here, and large fish were rare at these latitudes farther to the west. Pomfret grow rapidly during their first two years of life. They are pectoral fin swimmers that swim continuously. They prey largely on gonatid squids in the region of the Subarctic Current in the Gulf of Alaska during summer. No evidence was found for aggregations on a scale ≤1 km. Differences in the incidence of tapeworm, spawning seasons, and size distributions suggest the possibility of discrete populations in the North Pacific Ocean.

L'abondance de la casthagnole mince (*Brama japonica*), un poisson épipélagique du Pacifique nord, a été estimée à partir des prises par filets maillants des étés 1978 à 1989. Deux classes de taille étaient communément trouvées : la petite casthagnole de moins de 1 an et la grande de 1 à 6 ans. Les uns comme les autres migrent vers le nord à mesure que la température s'élève, mais les plus gros se rendent plus loin au nord, souvent dans les eaux fraîches et peu salines de la partie centrale du Pacifique subarctique. Il existe une corrélation positive avec la latitude et une corrélation négative avec la température de l'eau de surface en été, et la longueur des petits poissons. Les variations d'une année à l'autre de la latitude des prises sont en corrélation avec la température de surface. Les grosses prises ont été faites dans la partie est du Golfe d'Alaska (51–55°N), mais les petits casthagnoles ne sont pas trouvés dans ce secteur, et les gros sont rares à la même latitude, mais plus à l'ouest. La casthagnole grossit rapidement durant ses deux premières années. Ce poisson se propulse avec ses nageoires pectorales et nage continuellement. Il se nourrit abondamment l'été des calmars gonatidés dans le Golfe d'Alaska ou dans la région où passe le courant subarctique. Rien n'indique qu'il y ait des agrégations de cette espèce sur une échelle égale ou inférieure à 1 km. Les différences dans le taux d'infestation par le ténia soulèvent la possibilité qu'il existe des populations distinctes dans le Pacifique nord.

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The Pacific pomfret, *Brama japonica* Hilgendorf (family Bramidae), is an abundant and widely distributed epipelagic fish in the North Pacific Ocean. It migrates from subtropical waters into feeding grounds north of the Subarctic Boundary during late spring and summer periods of high productivity (Neave and Hanavan 1960; Sasaki et al. 1981; Wada and Murata 1985; Brodeur 1988; Shimazaki 1989). During fall and winter, pomfret migrate rapidly into waters south of the Subarctic Boundary (Shimazaki and Nakamura 1981) where spawning occurs during winter through early spring near the Subtropical Frontal Zone in the western Pacific (Yoon and Shimazaki 1981; Shimazaki and Nakamura 1981).

The abundance of pomfret in the North Pacific is documented by their huge bycatch in the Japanese, Taiwanese, and Korean drift gillnet fisheries for flying squid (*Ommastrephes bartrami*). The estimated total number of Pacific pomfret caught by vessels of these nations was 1329 million and 82 million in 1990 and 1991, respectively (DiNardo and Kwok, unpublished data). In some years, the catch of pomfret was about one-half that of flying squid (Yatsu et al. 1993). Moreover, these bycatches may be underestimates because pomfret drop out of the gill nets during retrieval and accurate counts are not possible when large numbers are caught (Int. North Pac. Fish. Comm. 1991). LeBrasseur et al. (1987) estimated that 100–300 million pomfret may have been discarded annually in the Japanese fishery alone. Drift gill nets fished for flying squid off British Columbia also caught large numbers of pomfret; sometimes it was the most abundant species (Robinson and Jamieson 1984; Jamieson and Heritage 1987).

Pacific pomfret is greatly underutilized as a food fish. Some are landed in countries bordering the western Pacific, and a few are marketed in United States. It has excellent flavor to the palate

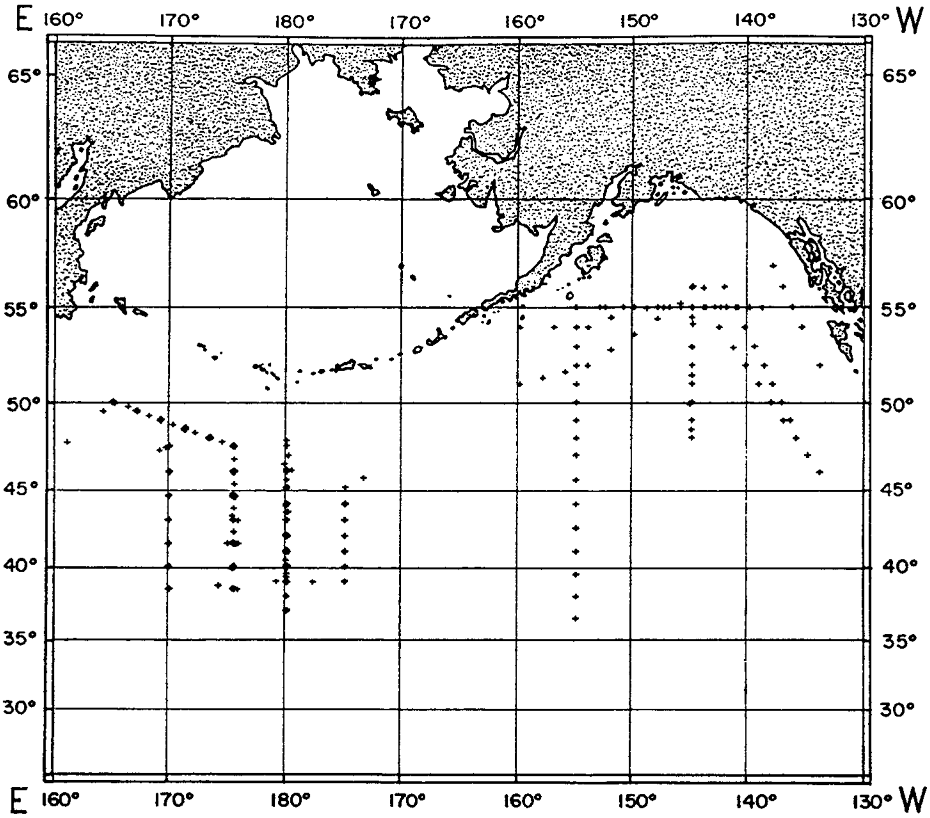

FIG. 1. Location of gillnet stations, 1978–89, by training ships from Hokkaido University. The transects along 180°, 175°E, and 170°E were repeated during most years (see text).

of North Americans (Elwell 1987).

Because of the abundance of Pacific pomfret, its important ecological role in these oceanic regions, and its potential for sustaining a large commercial fishery, better understanding of the biology and ecology of this species is needed (Shimazaki 1989). Based on results of 12 yr of gillnet cruises by Hokkaido University, we present information on geographic variations in size distributions, interannual trends in abundance relative to ocean conditions, patchiness of catches in gill nets, age and growth, food habits and parasites, and observations on swimming behavior of Pacific pomfret.

Methods

Data on catches of Pacific pomfret in gill nets together with oceanographic data were collected during summer cruises from 1978 to 1989, by the Hokkaido University Training Ships (T/S) Oshoro Maru along 180° and in the Gulf of Alaska (130°–165°W) and Hokusei Maru between 165°E and 180° (Fig. 1). Gill nets, 4550–6600 m long and 6.7 m deep, were fished overnight. Gill nets fished from the Oshoro Maru usually included 150–250 m (3–5 tans, one tan = 50 m) each of 29, 33, 37, 42, 48, 55, 63, 72, 82, 93, 106, 138, 157, 179, and 204 mm (stretched) mesh, 1000–1400 m (20–28 tans) each of 115 and 121 mm mesh, and 500–1000 m (10–20 tans) of 130 mm mesh. Gill nets fished from the Hokusei Maru usually included 50–150 m (1–3 tans) of 19, 22, 25, 29, 33, 42, 48, 55, 63, 72, 82, 93, 106, 138, 157, 179, 204, and 233 mm mesh, and 500–1000 m (10–20 tans) of 112, 115, 118, and 121 mm mesh (see Hokkaido University 1979–90 for details on gill nets, catches and oceanographic observations). Of the 385 sets that were completed during these years, 253 caught 92 439 pomfret. A total of 20 799 was measured to the nearest millimeter fork length (FL), including samples from each mesh size.

Temperature and salinity were measured at each gillnet station, and usually midway between gillnet stations, from the surface to a depth of at least 700 m. Dynamic height anomalies relative to 700 dbar were calculated by integrating specific volume anomalies (Fofonoff and Millard 1983) over pressure.

Estimating Abundance of Pacific Pomfret

A gill net fishing equal numbers of tans in a geometric size series of meshes, with each mesh approximately 14% larger than the preceeding one, is non-size-selective for Pacific pomfret from 160 to 520 mm FL (Shimazaki et al. 1981). The non-selective gill net described by Shimazaki et al. (1981) consisted

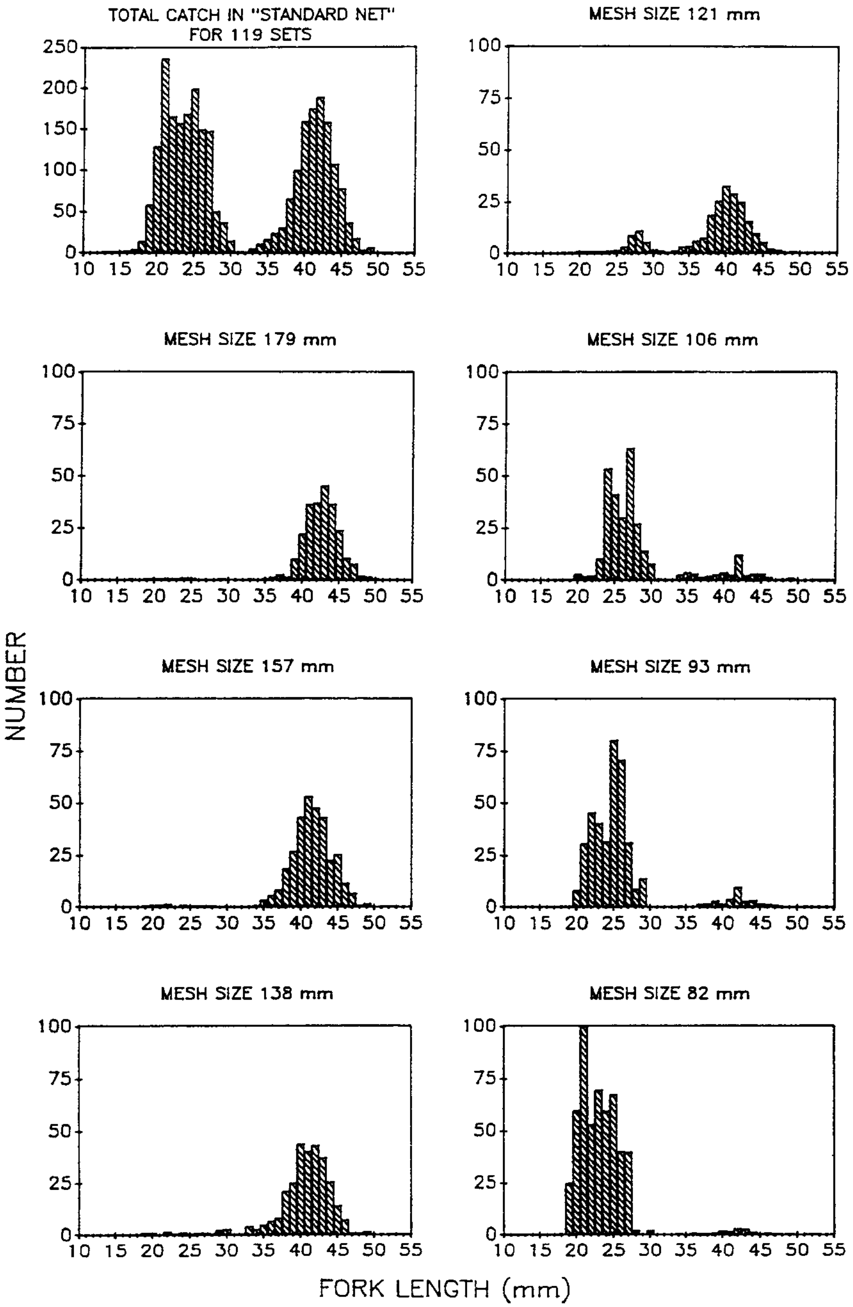

FIG. 2. Length–frequency distributions of pomfret caught in 119 sets of the "standard net" for the mesh sizes of Shimazaki et al's. (1981) non-selective gill net (excluding the 204 and 233 mm meshes). (*Fig. 2 concluded next page*)

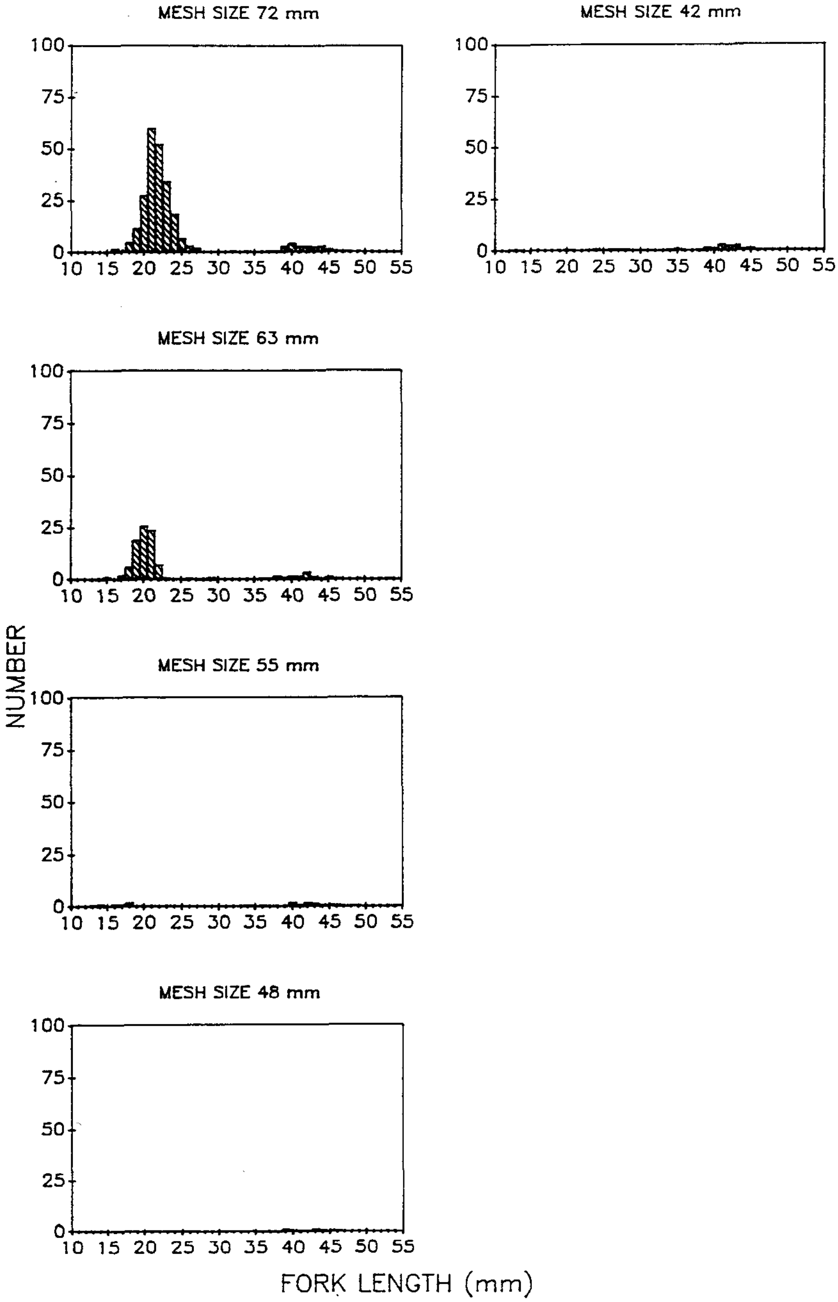

FIG. 2. (*Concluded*)

of 42, 48, 55, 63, 72, 82, 93, 106, 121, 138, 157, 179, 204, and 233 mm meshes. Standardized catches for each mesh size of this geometric series through 179 mm mesh (Fig. 2) show that small meshes (<106 mm) caught predominantly small (≤330 mm FL) pomfret and large meshes (121–179 mm) caught mainly large (>330 mm FL) pomfret. In our study, gill nets departed from the "research net" described by Shimazaki et al. (1981) chiefly in that many tans of 112, 115, 118, 121, and 130 mm mesh were

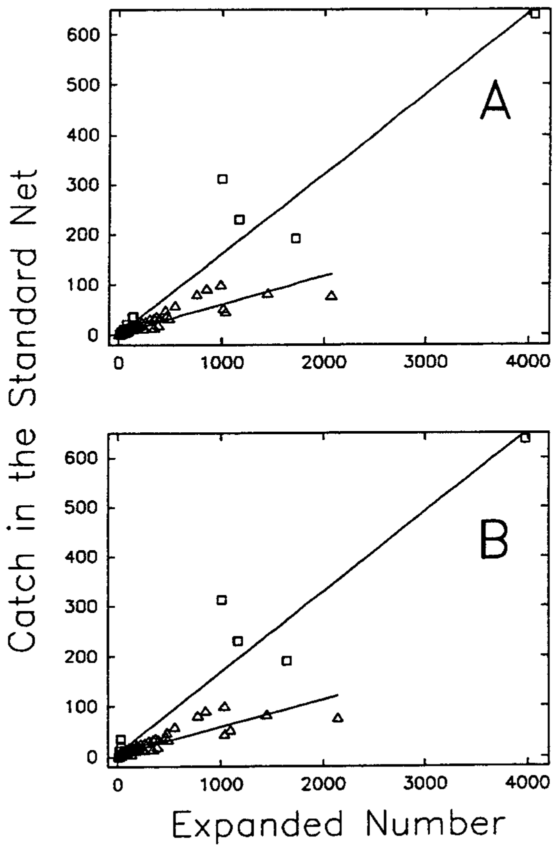

FIG. 3. (A) Regressions of catch of large and small pomfret in the standard net on the numbers of measured small and large pomfret expanded to equal the total catch in the set. Data are from 157 sets for which catch in the standard net could be determined directly (Method 1 in text). These regressions were used to estimate catch in the standard net in 69 sets where data were inadequate to determine catch directly, but where fish were measured from most mesh sizes (Method 2 in text). Small fish (squares), $n = 78$, $Y = 0.16X + 1.47$, $r = 0.97$. Large fish (triangles), $n = 137$, $Y = 0.06X + 3.41$, $r = 0.89$; (B) Same as 3(A), but expansions were based on the numbers of large and small fish in the 121 mm mesh only. Regression between catch in the standard net and the expanded numbers of small and large pomfret from 121 mm mesh were used to estimate catch in 22 sets where only fish from the 121 mm mesh were measured (Method 3 in text). Small fish (squares), $n = 29$, $Y = 0.16X + 5.69$, $r = 0.97$. Large fish (triangles), $n = 121$, $Y = 0.05X + 3.9$, $r = 0.88$.

fished in addition to the standard geometric series. Often these non-standard meshes accounted for over 50% of all tans in the gill net. In addition, small meshes between 19 and 37 mm were fished. Gillnet configurations consisted of as few as 12 and as many as 23 different sizes of mesh, and the total numbers of tans fished ranged from 63 to 133.

Because of the variability in net configuration, and the consequent variability in selectivity for different sizes of pomfret, raw catches in the different gill net sets were poor estimates of size-specific abundances of pomfret. To estimate relative abundance of small (≤330 mm FL) and large (>330 mm FL) pomfret caught in different sets and cruises, we converted raw catch in each gill net set to an estimated catch in the standard net described by Shimazaki et al. (1981). Depending on the completeness of catch data, one of three methods was used to make this conversion:

Method 1

Complete mesh-by-mesh catch data for pomfret were available for 157 sets. Total catches and size-frequency distributions of fish from subsamples were known for each mesh size in these gillnet sets. Total numbers of small and large fish caught in each mesh size were estimated by expanding the numbers in the measured subsample for each mesh. Catch data for each mesh were converted to catch/tan by dividing by the number of tans fished of the corresponding mesh. Catches/tan in each mesh in the geometric series described by Shimazaki et al. (1981), with the exception of the 204 and 233 mm meshes that were often missing, were added to give catch of large and small fish in a standard non-selective net in which one tan of each standard mesh was fished. This standardized catch, called "catch in the standard net," was the basis for our comparisons of abundance.

Method 2

In 69 gillnet sets, total catch of pomfret in the gill net and the size-frequency distributions of subsamples from the different meshes were known, but catch in each mesh was not known. Therefore, no estimate could be made of total catch of large and small fish in each mesh. Because catch in the standard net could not be calculated directly, it was estimated in two steps. The ratio of large and small fish in the measured sample from all meshes combined was expanded to the entire catch:

$$\text{No. small (large) fish} = \frac{\text{measured small (large) fish}}{\text{all measured fish}} \times \text{total catch.}$$

The expanded numbers of large and small fish were converted to catches in the standard net using regressions of these two abundance estimates for large and small fish from the 157 gillnet sets where catch in the standard net could be calculated directly (Method 1) (Fig. 3A). Because of the many extra meshes in the size range from 112 to 130 mm, the abundance of large fish relative to small fish in the measured sample was usually greater than that in the standard net. High selectivity of the gill nets for large fish and low selectivity for small fish are indicated by the lower slope of the regression for large fish than for small fish (Fig. 3A).

Method 3

In 22 sets, fish were measured in the 121-mm mesh and, at most, in one additional mesh. Catches in the standard net were converted from numbers of large and small fish in the 121-mm mesh expanded to equal the total catch in the set using regressions for large and small fish from the 157 complete sets, as in Method 2. The regressions are similar to those of Method 2 (Fig. 3B), indicating that the 121-mm mesh and the non-standard gill net caught similar ratios of large and small fish (see Fig. 2). In five sets, pomfret were caught, but none was measured and abundance was not estimated.

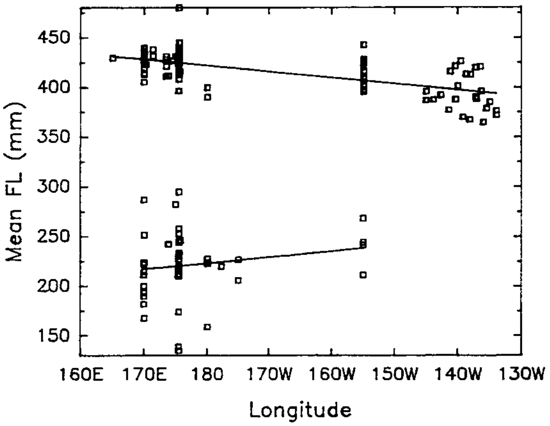

FIG. 4. Mean fork lengths of the distinct modes of small and large pomfret caught in the standard net during July vs. longitude of capture based on 157 sets with complete catch by mesh data.

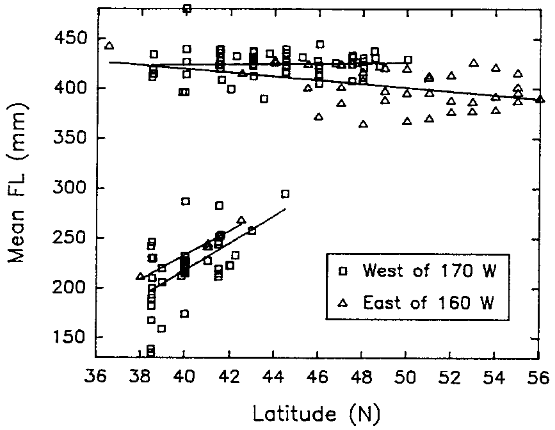

FIG. 5. Mean fork lengths of the distinct modes of small and large pomfret during July vs. latitude (squares, west of 170°W; triangles, east of 160°W) based on 157 sets with complete catch by mesh data.

Aggregation of Catches

The patchiness in abundance of pomfret caught within gill nets was examined from numbers of fish caught in contiguous tans of the same mesh size. In 26 instances, 10–20 tans of either 115, 121, or 130 mm mesh were fished in a continuous series. Coefficients of dispersion (variance/mean ratios) of the catch per tan were tested against a random distribution, assuming that they were distributed as a chi-square variate.

Age and Growth

Sagittal otoliths were removed from Pacific pomfret collected in the eastern North Pacific (135°–155°W) onboard the Oshoro Maru during the summers of 1985 and 1987, and stored dry (1985) or in a 50% glycerin-water solution with thymol added as a preservative (1987). A few small, whole pomfret were frozen in 1985 and otoliths were removed and fish lengths and sex recorded in the laboratory. All otoliths were cleaned in the laboratory and stored in 80% ethanol.

Otoliths were submerged in water on a black background, and distal surfaces were examined at 32–80× magnification under a Wild M3 dissecting microscope with reflected light. A white or opaque band, representing rapid growth, and an adjacent narrower dark or translucent band, deposited during periods of slow growth, were interpreted as 1 yr of growth, although increment periodicity remains unvalidated for this epipelagic species. The type of growth on the edge of the otolith was noted. Transverse and longitudinal sections were taken from many otoliths.

Narrow, fine-scale bands, presumed to represent daily growth increments, were counted on sagittal sections of otoliths from the smallest pomfret following the methodology of Boehlert and Yoklavich (1985). Increments were counted at 1000× magnification using a compound microscope and transmitted light. Increments appeared as distinct, concentric rings around the focus but became progressively smaller and less distinct toward the edge of the otolith.

Food Habits

Major prey taxa were determined from examination of stomach contents of 979 Pacific pomfret caught east of 180°. In 1980, stomachs were removed, frozen at sea, and preserved in 10% formalin ashore. Food items were identified and major prey taxa were weighed. In 1981, frequency of occurrence of major prey was calculated. In 1984, 1985, 1986, and 1987, percent composition of major prey taxa was estimated visually at sea. In all years, common prey taxa were preserved and identified. Indices of stomach fullness were estimated as 0 (empty), 1 (to $\frac{1}{4}$ full), 2 ($\frac{1}{4}$ to $\frac{1}{2}$ full), 3 ($\frac{1}{2}$ to $\frac{3}{4}$ full), and 4 (full, rugae of stomach not apparent, stomach lining thin). State of digestion of stomach contents was also noted as fresh (1), partially digested (2), and well-digested (3).

Parasites

Pacific pomfret from stations east and west of 180° were examined for larval tapeworms imbedded in the flesh. In all, 53 fish were frozen and examined in the laboratory ashore. Each fish was filleted and each of the four fillets from a fish, with skin removed, was candled with a lamp to detect tapeworms. When possible, the entire parasite was removed for identification.

Swimming Behavior

In 1987, pomfret caught on hook-and-line from a depth of about 20–30 m during the daytime were immediately placed in a 90 × 122 × 75 cm deep tank with circulating sea water on board the Oshoro Maru. Swimming behavior and gill ventilation were observed over 24 h.

Results and Discussion

I. Geographic Variations in Size Distribution

The size distribution of the catches was almost always unimodal or bimodal with clearly separated modes (see also Machidori and Nakamura 1971; Wada and Murata 1985; Shimazaki 1989), enabling classification of fish into two size groups: small fish (130–330 mm) and large fish (331–500 mm) (Fig. 2). Few fish of intermediate size were captured. Only 26 of over 20 000 pomfret measured were over 500 mm FL, and only three were over 600 mm FL. The largest was 614 mm FL.

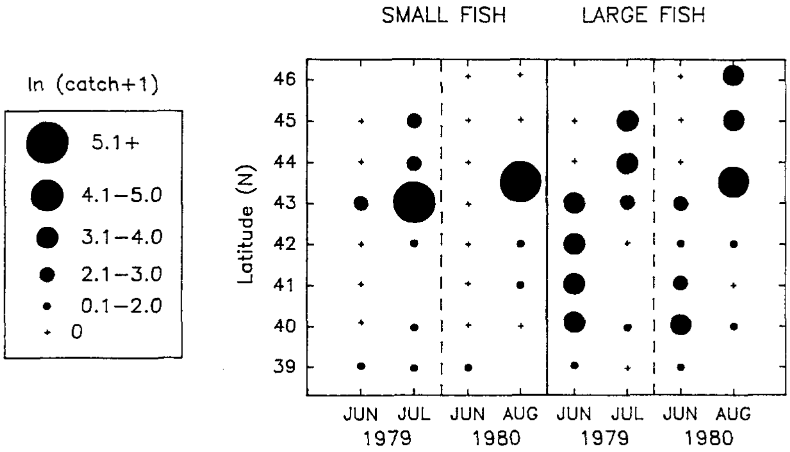

FIG. 6. Catches of small (≤330 mm FL) and large (>330 mm FL) pomfret in the standard net during early and late transects along 180°.

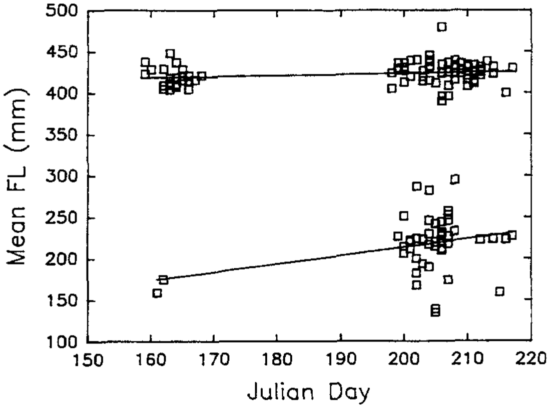

FIG. 7. Mean fork lengths of the distinct modes of small and large pomfret in the standard net vs. Julian date of capture for sets west of 170°W based on 117 sets with complete catch by mesh data.

The frequency of bimodal catches and the mean length of pomfret varied by location of capture. During July, when most sets were made, catches of small fish and bimodal catches of small and large fish were common in the western North Pacific (west of 170°W), whereas only four sets included modes of small pomfret in the Gulf of Alaska (Fig. 4). The mean lengths of the modes of large pomfret, but not small pomfret, decreased from the western Pacific to the Gulf of Alaska during July ($r = -0.65$, $P < 0.01$, $n = 81$, Fig. 4).

The size of pomfret in the standard net also varied with latitude. Modes of both small and large fish were common south of 44°N during July, but only large fish were caught north of 44°N. (Fig. 5). The largest percentage of sets with only modes of small pomfret occurred in southern waters, between 39° and 40°N. In addition, the mean FL of small fish was positively correlated with latitude ($P < 0.01$) both east of 160°W and west of 170°W, indicating that the smallest pomfret inhabited more southerly waters during the summer and did not migrate in high numbers into waters north of 44°N in this region. This trend was not found for large pomfret during July. Mean size of large pomfret decreased ($P < 0.05$) with latitude east of 160°W, but no

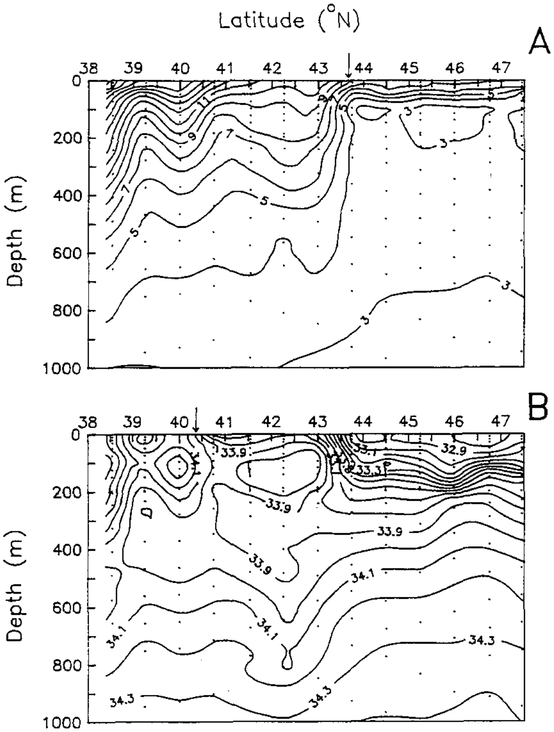

FIG. 8. Vertical section of (A) temperature and (B) salinity along 170°E during July 1983. The Subarctic Boundary is indicated by the intersection of the 34 ‰ isohaline with the surface, and the boundary between the Transitional and the Central Subarctic Domains of subarctic water is shown by the rapid descent of the 4°C isotherm below 100 m.

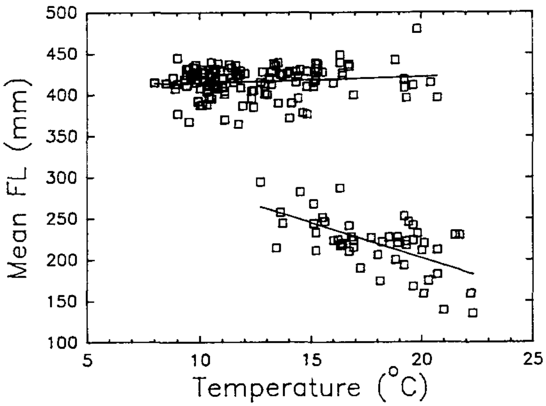

FIG. 9. Mean fork lengths of the distinct modes of small and large pomfret in the standard net vs. sea surface temperature based on 157 sets with complete catch by mesh data.

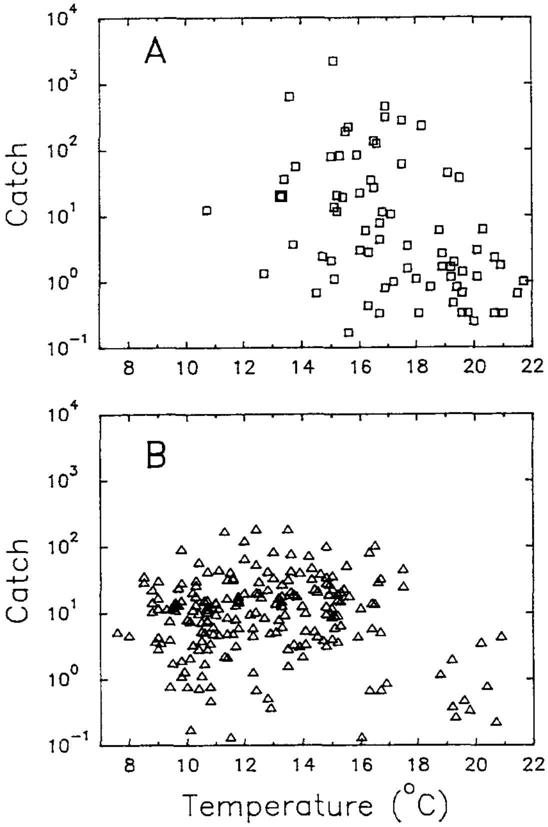

FIG. 10. Numbers of pomfret caught in the standard net vs. sea surface temperature for distinct modes of (A) small pomfret and (B) large pomfret.

significant trend with latitude was found for large pomfret west of 170°W.

Mean length of pomfret increases from south to north during the summer in subarctic waters (Sasaki et al. *1981*). Shimazaki (1989) reported that during the winter pomfret were only caught south of the Subarctic Boundary, whereas in early summer small pomfret (< 310 mm FL) were distributed south of the Subarctic Boundary (38°30′ to 43°N) while large pomfret were found in waters north of the boundary (45°30′ to 47°30′N, along 175°30′E). These trends indicate the more northerly migration of large fish during the summer.

North-south transects along 180°, conducted during June, July, or August, 1979 and 1980, clearly illustrate the northward movements of both small and large pomfret (Fig. 6). During these years, small pomfret (all fish ≤330 mm FL even if not in a distinct mode) were caught 2° farther to the north in July than in June 1979, and 4.5° farther to the north in August than in June 1980. These changes corresponded to movements northward of 2.7 and 5.1 miles per day, respectively. Large pomfret moved north by 2° in 1979 and 3.1° in 1980, corresponding to 2.7 and 3.8 miles per day, respectively.

Mean size of both small and large pomfret increased with date of capture ($P = 0.05$ and 0.07 respectively), although only two samples of small fish were measured in June (Fig. 7). The increase in size of small and large pomfret was about 1.0 mm and 0.15 mm/d, respectively. These rates are about twice the growth rates of age 0+ and 1+ pomfret estimated from otoliths (see Age and Growth section), and possibly result from size-selective migration of fish.

II. Pomfret Distribution in Relation to Oceanography

Pacific pomfret are associated with the Transitional Domain of the Subarctic Water Mass during the summer months (Shimazaki and Nakamura 1981; Shimazaki 1989; Pearcy 1991). This region is located north of the prominent Subarctic Boundary (often defined by the vertical ascent or the surface intersection of the 34 ‰ isohaline) and south of the boundary between the Transitional and Central Subarctic Domains (where the 4°C isotherm plunges below 100 m) (Dodimead et al. 1963; Favorite et al. 1976). These two boundaries often coincide with strong latitudinal gradients of both temperature and salinity (Fig. 8), and with regions of relatively strong gradients in dynamic height and hence strong geostrophic currents (see Fig. 11E, 12E).

Catches vs. sea surface temperature

The mean lengths of pomfret varied with sea surface temperatures (Fig. 9). The mean size of small fish decreased with increasing temperature ($r = -0.62$; $P < 0.01$), as expected if migration to the north is size-dependent. No trend in mean size with temperature was apparent for the large fish ($r = 0.12$; $P > 0.05$).

Small pomfret were rarely caught in waters where the sea-surface temperature was less than 13°C, whereas large fish were commonly found where temperatures were from 8 to 13°C (Fig. 10). Thus the 13°C isotherm may be a boundary to the northward migration of small fish. During June and July, small pomfret inhabited waters over 4°C warmer than large pomfret (mean 17.3°C vs. 12.8°C).

Wada and Murata (1985) also reported size segregation of pomfret by temperature with large fish most numerous at surface temperatures of 13–17°C, while small fish were mainly found in 17–21°C water. Large fish were usually more common in waters

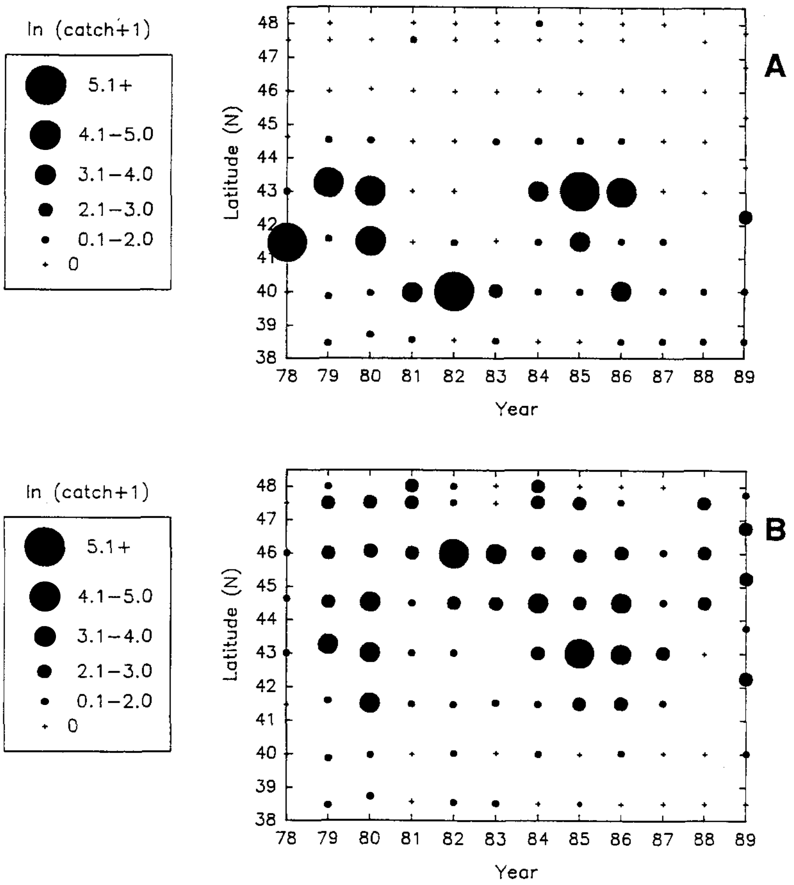

FIG. 11. Interannual variability along 175°E in the catches of (A) small (≤330 mm FL) and (B) large (>330 mm FL) pomfret, (C) sea surface temperature, (D) surface salinity, and (E) dynamic height of the sea surface relative to 700 m, the Subarctic Boundary (solid line) and the boundary between the Transitional and Central Subarctic Domains (dashed line). Stations along 175°E ± 2° of longitude are included. (*Fig. 11 concluded next page*)

with lower surface salinity, as expected in more northerly subarctic water. We found both large and small fish at higher temperatures (Fig. 10) than did Wada and Murata, probably because their collections were made in June whereas ours were made mainly in July.

Surface temperatures where pomfret were caught ranged from about 8° to 22°C, which is greater than the range reported by Hanavan and Tanonaka (1959), Neave and Hanavan (1960), and Hitz and French (1965). Machidori and Nakamura (1971) and Wada and Murata (1985) considered the 8.5–9.0°C isotherms to be close to the northern limit of distribution. We suggest that a surface temperature of 8.0°C is the thermal minimum for the occurrence of large Pacific pomfret. The southern limit of Pacific pomfret is associated with the 21°C isotherm (Mead 1972; Seki and Bigelow 1993), although we found small pomfret in water close to 22°C (Fig. 10).

Interannual trends in abundance

Interannual variations in the catches of small and large pomfret in the standard net were compared for the two most complete north-south transects, 175°E and 170°E, 1978–89.

The number of small pomfret caught at different latitudes along 175°E varied from year to year. Catches extended north of 42°N during 1978 through 1980, retreated south of 42°N in 1981 and 1982 (except one fish at 47°30′N), and then moved to the north of 44°N during 1983 through 1986 and to the south of 43°N in 1987 and 1988 (Fig. 11A). These trends generally conform to variations in sea surface temperatures. Temperatures were warm north of 42°N during northern excursions of small pomfret and cool during the intervening years when abundances were high to the south (Fig. 11C). The 13–14° isotherms generally defined the northern limits of small pomfret along this transect during July. Surface salinity (Fig. 11D) and dynamic height (Fig. 11E) did not correlate as well as temperature with catch rates. High catch rates of small pomfret were usually located north of the 34 ‰ isohaline, either at the surface or where it was vertical at 100 m (i.e., the Subarctic Boundary), and south of the northern boundary of the Transitional Domain as indicated by the salinity

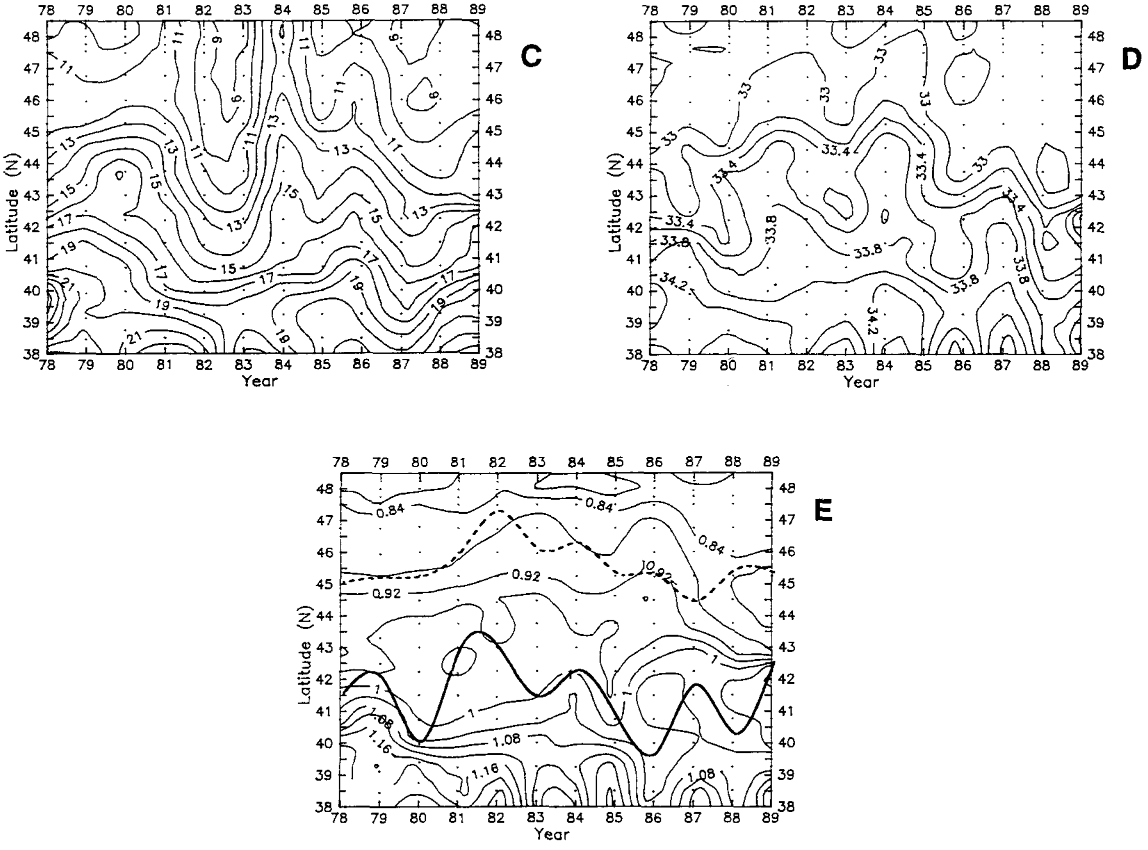

FIG. 11. (*Concluded*)

front centered between 33.2 and 33.4 ‰. During 1988 and 1989, when low surface salinities dipped to the south and strong currents were located at mid-latitudes (42–43°N) the catches of small pomfret were low at all latitudes.

Large pomfret along 175°E were distributed much farther to the north than small pomfret (Fig. 11A,B). However, both large and small pomfret were abundant at the same latitudes north of 42°N during 1980 and 1985–86. During 1982 and 1983, on the other hand, when small fish retreated to the south and sea surface temperatures declined, the highest catches of large pomfret were made at 46°N, in waters where surface temperatures were 9–10°C (Fig. 11C). This suggests that large pomfret are more eurythermal than small pomfret. Large pomfret often were common north of the front between the Transitional and Central Subarctic domains, and within the salinity front and region of accelerated currents (Fig. 11D,E).

Catch rates of small pomfret along 170°E were highest between 40° and 42°N during 1981–82 and 1984–85 (Fig. 12A), when warm surface temperatures bulged northward (Fig. 12C) and when the Subarctic Boundary extended northward (Fig. 12D). Catches were low during 1983, when low sea surface temperatures (13°C) intruded south of 41°N (Fig. 12C). Catches were generally low at all latitudes during 1986–1989, a period when unusual ocean conditions were not evident. These interannual trends have similarities to those at 175°E. Again, small pomfret were confined to waters south of the salinity front and accelerated currents associated with the northern boundary of the Transitional Domain.

High catches of large pomfret extended farthest to the north during 1984 (Fig. 12B), when warm surface waters (>10°C) occurred as far north as 47°30′N (Fig. 12C). Wada and Murata (1985) also found interannual variations in the size distribution of pomfret off northern Japan. In some years, such as 1980, the small size mode predominated in the catches. Fluctuations in the relative abundance of small pomfret suggest year-to-year variations in the year-class strength and recruitment of 0-age pomfret.

Catches in the Gulf of Alaska

Small pomfret were much less common in the eastern than the western North Pacific during July. In contrast with transects to the west, distinct modes of small pomfret were evident from size distributions of only four sets between 38°–42°30′N along 155°W (Fig. 4). Modes of small fish were not evident in the numerous sets farther to the east in the Gulf of Alaska, although a few small pomfret sometimes made up the tail end of the size distribution of the large mode.

High catches of large-sized pomfret were made during July in the Gulf of Alaska, especially from 48°–50°N along 145°W, from

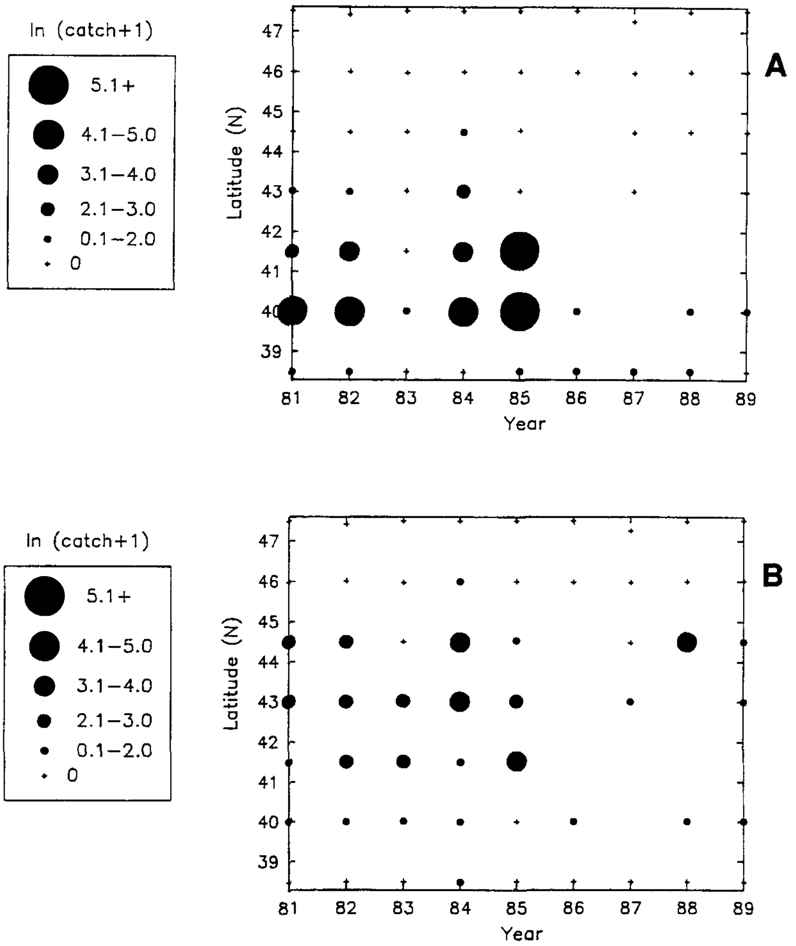

FIG. 12. Interannual variability along 170°E in the catches of (A) small (≤330 mm FL) and (B) large pomfret (>330 mm FL), (C) sea surface temperature, (D) surface salinity, and (E) dynamic height of the sea surface relative to 700 m and the Subarctic Boundary (solid line) and the boundary between the Transitional and Central Subarctic Domains (dashed line). Stations along 170°E ± 2 longitude were included. (*Fig. 12 concluded next page*)

136°–141°W along 55°N, and 52°–54°N along the coast of British Columbia (Fig. 13). Large pomfret were found in all but one set east of 141°W. The higher catches of pomfret in the eastern than the western Gulf of Alaska north of 50°N were associated with relatively high temperatures compared to waters at the same latitude to the west (11.4–12.0° vs. 8.7–10.7°C during 1982 and 13.6° vs. 10.4–11.8°C during 1983 along 55°N). These relatively warm temperatures in the eastern Gulf of Alaska may be associated with the Alaska Current.

Although sea surface temperatures in the region of low catches were lower than those farther to the east, they were always above the thermal minimum for large fish (Fig. 10). Surface temperatures at stations of zero catches were below 9°C at only 9 of 44 stations. These low or zero pomfret catches occurred in the region of the Alaska Stream at the northern stations along 155°W and where isotherms dome near the center of the Alaska Gyre (Ridge Domain) farther to the east (see Pearcy et al. 1988). Hitz and French (1965) also caught few pomfret in numerous gillnet and purse seine sets between 140°–149°W and north of 54°N in the Gulf of Alaska, but they did catch pomfret north of 55°N along 150°W. These trends suggest a possible discontinuity in the distribution of Pacific pomfret between the eastern and western Gulf of Alaska.

III. Patchiness within Gill Nets

Coefficients of dispersion of the number of pomfret caught in

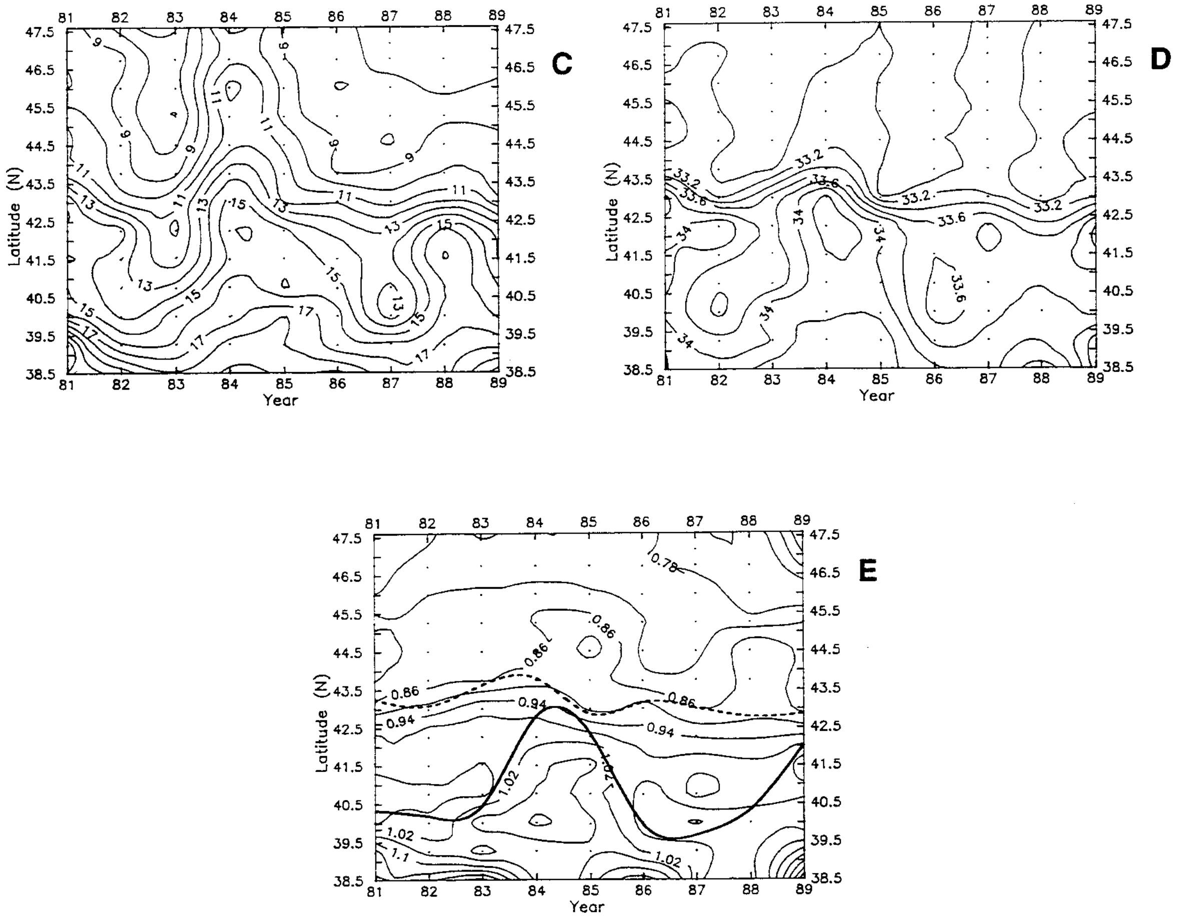

FIG. 12. (*Concluded*)

contiguous tans of the same mesh were, with one exception, close to 1.0 (0.87–3.0), for 26 comparisons. Low coefficients indicate that pomfret did not form compact aggregations or schools on a scale of a kilometer or less, but were randomly dispersed near the surface at night when they were entangled in the gill nets. Interception of many small schools at different times during the night could increase the impression of randomness. Conversely, patchiness could occur at large spatial scales that would not be detected.

IV. Age and Growth

Ages of 184 Pacific pomfret, from 211 to 500 mm FL, ranged from 0+ (young-of-the-year) to 6+ years (fish in the seventh year of life) based on otoliths. All otoliths had an opaque band of relatively rapid growth along the edge, as expected because fish were collected during summer. This was reported as "+" following the estimated age. The age of small fish was estimated from 49 whole otoliths, and confirmed by 18 sagittal or transverse sections. Ages of young-of-the-year Pacific pomfret estimated from sections and from whole otoliths did not differ. All otoliths having a surface age over 2 yr were sectioned (Fig. 14).

Pacific pomfret grow rapidly during their first 2 yr of life (Fig. 15). Growth was described with a von Bertalanffy function:

$$l_t = L_\infty (1 - e^{-k(t-t_0)}),$$

where L_∞ was estimated at 468 mm FL, k was 0.76 and t_0 was −0.52 yr. Lengths of our 6+ yr-old fish (i.e., 494 and 500 mm FL) were above the asymptote of the fitted curve, which underestimated the maximum length of pomfret. Although Pinckard (1957) suggested that Pacific pomfret reach a total length of 1220 mm, the largest previously reported sizes were 500–550 mm FL (Wada and Murata 1985). In this study, only 26 fish >500 mm FL and three fish >600 mm FL were measured. The largest was 614 mm FL, suggesting a maximum size of about 600–620 mm FL.

Our estimates of size-specific age agree with those based on annuli-like structures on scales from the caudal peduncle through age 3 (Shimazaki 1989). He reported fork lengths of 180–240 mm for age 0+, rapid growth to 360–400 mm by age 1+, and then slower growth to 380–480 mm for fish of age groups 2 and 3. However, he did not find annuli-like patterns on

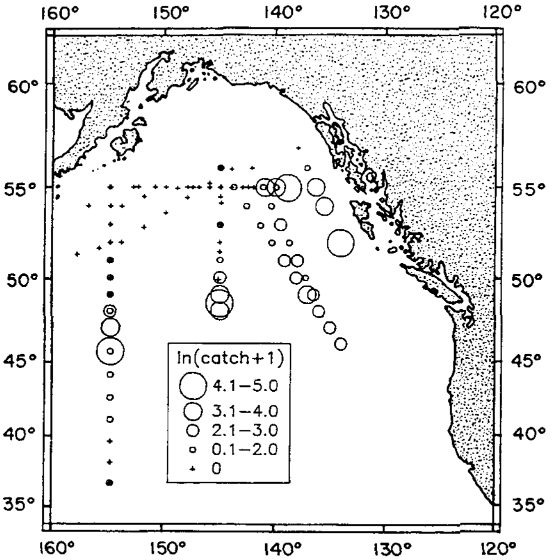

FIG. 13. Catches of large pomfret in the standard net in the Gulf of Alaska for all years.

TABLE 1. Food items identified from the stomachs of Pacific pomfret in the Gulf of Alaska and along 180°.

	Gulf of Alaska	180°
Euphausiids		
Thysanoessa spinifera	×	
Euphausia pacifica	×	
Gnathophausia	×	
Amphipods		
Cystisoma	×	×
Phronima	×	×
Themisto	×	
Shrimp		
Sergestes similis	×	
Barnacles		
Lepas		×
Pteropods		
Euclio		×
Heteropods	×	
Carinaria	×	×
Squids		
Berryteuthis anonychus	×	
Gonatus	×	×
Chiroteuthis	×	
Onychoteuthis	×	
Fishes		
Tarletonbeania	×	×
Myctophids		×
Lestidiops ringens	×	
Hemilepidotus	×	
Pleurogrammus monopterygius		×
Cololabis saira		×
Sebastes	×	

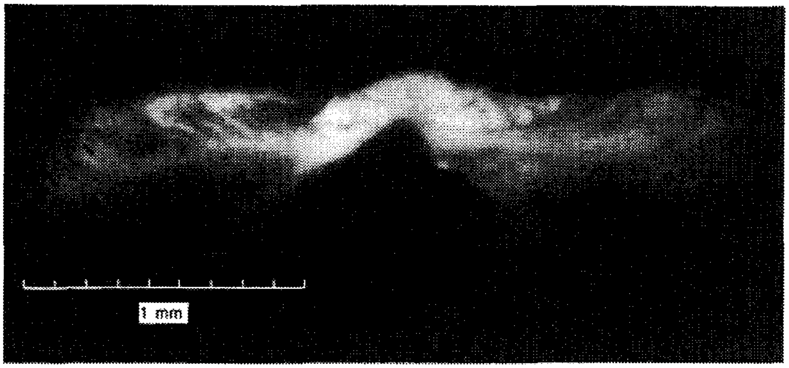

FIG. 14. Transverse section of an otolith of a Pacific pomfret, 494 mm FL. Age is estimated at 6+ yr, each yearly increment denoted by a dark line.

scales indicating age groups older than 3 yr, or minute growth increments in otolith sections indicating ages over 2 yr. Thus Shimazaki's estimates suggest that Pacific pomfret grow rapidly to 400–500 mm FL in less that four years, similar to our estimates based on otoliths.

Both our estimates and Shimazaki's differ from the much slower growth suggested by Machidori and Nakamura (1971). From otoliths and length frequencies they estimated that fish of two modal fork lengths groups, 350 and 405 mm, were age 4 and 5, respectively. Thus, we explain the absence of intermediate size modes (290–350 mm FL, Fig. 2) of Pacific pomfret during spring and summer surveys, ascribed previously to inadequate areal coverage or selectivity of gear (see Wada and Murata 1985), by the rapid growth of age 0+ fish to a large mode of slower growing fish, with intermediate sizes (300–350 mm FL) present only in the fall and winter. Based on our growth curve (Fig. 15), small fish (≤330 mm FL) in our catches were age 0+ and large fish (331–500 mm FL) were ages 1+ to 6+.

The number of fine-scale increments in sagittal sections of otoliths corroborate the rapid growth of young pomfret. Otoliths

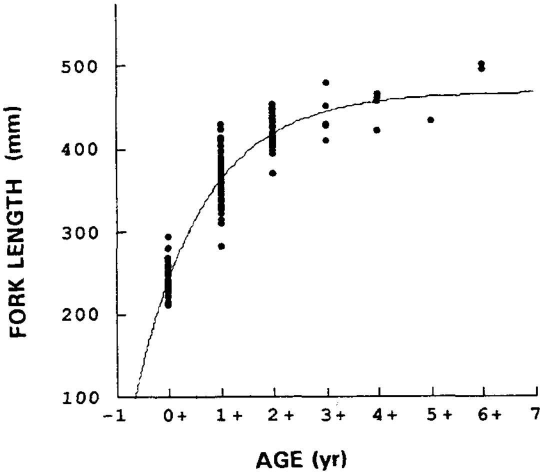

FIG. 15. Estimated age vs. fork length for Pacific pomfret. The line is a von Bertalanffy growth equation ($l_t = L_\infty (1 - e^{-k(t-t_0)})$) fitted to these estimates.

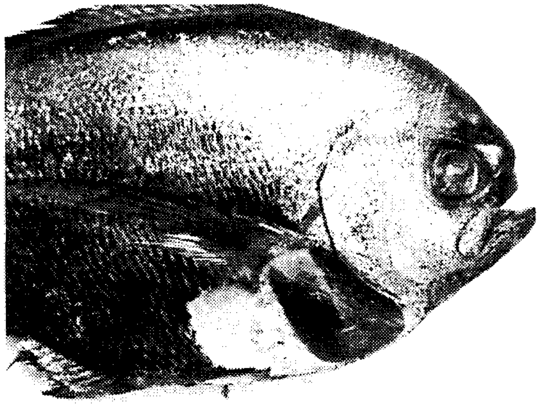

FIG. 16. Photograph of pomfret with skin removed from pectoral girdle and posterior area showing the dark coloration of the musculature of the lateral muscles associated with the pectoral fin.

from 0+ fish (200–260 mm FL) had 130–221 increments. Number of increments was positively correlated with fork length (r = 0.63). Assuming these are daily increments, hatch dates ranged from January to April. This supports the findings of Shimazaki (1989) that small pomfret (200–250 mm FL) caught in late July had less than 160-min growth increments, indicating than they hatched during February, again assuming that these increments are daily. Similarly, larval and juvenile pomfret caught in early March near the Hawaiian Archipelago were estimated to have hatched during January based on otolith microstructure (Seki and Bigelow 1993). It should be noted that none of the methods for ageing Pacific pomfret has been validated.

Rapid growth early in the life history of pomfret is similar to that of other epipelagic fishes, such as juvenile sablefish (*Anoplopoma fimbria*), a subarctic fish that is pelagic during its first year of life (Boehlert and Yoklavich 1985). Albacore (*Thunnus alalunga*), a highly migratory epipelagic fish of transitional waters, also has rapid growth during the first three years of life (Beamish 1981).

V. Food Habits

Pacific pomfret prey include a variety of pelagic crustaceans, mollusks, and fishes (Table 1). Gonatid squids were common in stomachs collected in the Gulf of Alaska where they dominated the stomach contents at 24 of 28 stations and usually comprised 75% or more of the prey (Table 2A,B,C,D,G). When squids were principal prey, the percentage of empty stomachs was usually low and stomach fullness was high.

Small *Gonatus* spp. squids (dorsal mantle length-DML <60 mm) were most important in the northern Gulf of Alaska where cold, saline waters protrude toward the surface (i.e., the Ridge Domain of Favorite et al. (1976)) and waters of the Alaska Current (55–53°N), whereas larger (DML >70–80 mm) *Berryteuthis anonychus* comprised most of the squid biomass consumed farther to the south in the region of the Subarctic Current (52–49°N). This species was the primary prey and contributed to the high stomach fullness of pomfret, as well as salmonids (Pearcy et al. 1988), in this region. Even farther to the south (48–44°N), in the Transitional Domain, other small squids (often gonatids) were present in pomfret stomachs but were of lesser importance. Gonatid squids were identified from pomfret caught along 180°, but no *B. anonychus* were found.

In our study, euphausiids were the major prey for large pomfret only at one station (50°N) in the Gulf of Alaska and at two stations along 180° (Table 2E,F,G). Pteropods were only found in fish from stations along 180°, but are sometimes important as food for epipelagic fishes in the subarctic eastern Pacific (Pearcy 1991). Among fishes found in pomfret stomachs, the myctophid *Tarletonbeania crenularis* occurred most frequently in the Gulf of Alaska (north of 45°N) and along 180°. The slender barracudina, *Lestidiops ringens*, occurred only in stomachs from the Gulf of Alaska, and the Pacific saury (*Cololabis saira*) was only found along 180° (Table 1).

Other investigators found that squids were important prey for large pomfret in the Gulf of Alaska, as elsewhere in the Central Subarctic Pacific (Pinckard 1957; Machidori and Nakamura 1971; Wada and Murata 1985; Shimazaki 1989). Shimazaki and Nakamura (1981) reported that squids and fishes were the most frequent food items for large pomfret during most months of the year. Kubodera and Shimazaki (1989) found that the gonatids (*Gonatus middendorffi*, *G. berryi*, and *G. pyros*) were more numerous than *B. anonychus* in stomachs of large pomfret caught west of 175°W. This is explained by the more easterly distribution of *B. anonychus* in the subarctic Pacific (Kubodera and Jefferts 1984; Kubodera and Shimazaki 1989).

Crustaceans were important prey for small pomfret off Japan during June (Wada and Murata 1985) and for large pomfret during the winter south of the Subarctic Boundary (Shimazaki and Nakamura 1981; Seki and Bigelow 1993). Euphausiids were important in the spring when other prey items were less abundant (Shimazaki 1989).

Shimazaki and Nakamura (1981) found that stomach fullness of Pacific pomfret was highest in the Subarctic Domain, where the catch per effort in gill nets was the highest, and decreased markedly to the south in the transition and subtropic regions. This high availability of pomfret prey in northern waters during the summer results in a 30% increase in body weight compared to that in the winter (Shimazaki 1989). Pomfret not only take advantage of increased secondary production of food in subarctic waters during the summer, but also follow small migratory fishes such as Pacific saury, sardine, and Pacific mackerel northward during the summer (Taniguchi 1981; Shimazaki 1986).

In the western Pacific, fishes rather than squids are often reported as the most important prey taxon for pomfret. Here the Japanese sardine (*Sardinops melanostictus*) was often the principal prey of large pomfret (Kohno 1983; Wada and Murata 1985), but in 1991, following a decline in Japanese sardine, pomfret fed on Japanese anchovy (*Engraulis japonicus*) and squids (Wada and Honda 1992), demonstrating their opportunistic feeding behavior.

VI. Parasites, Predators, and Populations

The only large parasite found in the flesh of pomfret was the larval stage of the trypanorynch tapeworm *Molicula* sp., that burrows into the muscle of the fish and eventually reproduces in the digestive tract of its final host. Two and one-half times more larval *Molicula* were found in pomfret caught in the western than the eastern Pacific (mean (std. dev.) 4.3 (2.53)) tapeworms per fish vs. 1.7 (1.4); $P < 0.005$).

These observations on parasites are important for two reasons. First, because all adult trypanorynchs occur only in elasmobranchs (Rohde 1984), sharks may be the major predator of Pacific pomfret. The blue shark and the Pacific pomfret have broadly overlapping distributions in the Transitional Domain of the subarctic Pacific during the summer (Mishima 1981; Pearcy 1991). Pomfret remains have been reported in the stomachs of the blue shark (*Prionace glauca*) in the Gulf of Alaska (LeBrasseur 1964), and in the Subarctic Frontal Zone north of the Hawaiian Islands (Seki 1993).

Second, this difference in parasite loads, as well as postulated differences in the spawning season of Pacific pomfret in the eastern and western Pacific, the absence of distinct modes of small pomfret in the eastern Gulf of Alaska, and the hiatus in distribution of large pomfret in the central Gulf of Alaska, all suggest geographic differences in stock structure.

Yoon and Shimazaki (1981) reported seasonal peaks in the gonosomatic indices that suggested the main spawning season of Pacific pomfret was early June and July between 140–177°W and during the winter and early spring (December–April) farther to the east (160–170°E) (see also Shimazaki 1989; Seki and Mundy 1991). The few data on the occurrence of larval and juvenile pomfret, however, indicate that the subtropic region in the mid-Pacific (29°47′N, 179°E) is a winter spawning area (Seki and Mundy 1991). At 28°N, 155°W, Loeb (1979) collected 49 larval pomfret during January–February and three during September, again suggesting primarily winter spawning in this region. These studies suggest that pomfret spawn during the winter in the central and eastern Pacific, not during June and July as postulated by Yoon and Shimazaki (1981).

Farther to the east in the southern region of the California Current (ca. 27–35°N and east of 125°W), *Brama* spp. larvae are rare (Stevens et al. 1990), but *B. japonica* larvae were collected during most months of the year, indicating year-around spawning, with the highest average abundance during October–December (G. Moser personal communication). Four of the five Pacific pomfret caught by Berry and Perkins (1966) off California (30°07′–34°47′N, 124°31′–129°16′W) appeared to be from spawning in the winter (15.5 mm standard length (SL) in March and 215–220 mm SL (similar to our age 0+) during August). However another specimen of 52.5 mm SL was collected during August, suggesting spring spawning. Thus it seems premature to conclude that Pacific pomfret has different spawning seasons in the eastern and western Pacific. We agree with Shimazaki (1989) that more research is needed on the seasonality of spawning and occurrence of eggs and larvae of Pacific pomfret to determine the existence of separate populations in the North Pacific.

VII. Swimming Behavior

During several cruises of the Oshoro Maru, it was noted that Pacific pomfret caught in gill nets set overnight and retrieved during the early morning were always dead, whereas other fishes (e.g., salmonids), were sometimes alive. This observation led to the hypothesis that Pacific pomfret swim continuously to ventilate their gills, and that entanglement in gill nets interferes with respiration and causes death. To test this idea, live pomfret were observed in tanks with running sea water aboard the ship.

Pacific pomfret (35–40 cm FL) swam continuously in tanks at speeds of about one body length per second. Propulsion was exclusively by their long, falcate pectoral fins (34–38% of standard length; Mead 1972) that flapped in unison about once per second. The forces of buoyancy and lift were about equal because the axis of body motion was nearly horizontal during pectoral swimming. The pectorals were also used to dive rapidly and to change vertical position in the tank. The caudal fin was used to accelerate and to turn at the ends of the tank. Bending of the relatively rigid dorsal and anal fins was also observed during turns, but these fins did not flap. Pomfret were very maneuverable and seldom collided with the walls of the tank. Their maneuverability in nature may assist in capturing squids which accelerate rapidly.

At swimming speeds of about 30–40 cm/s, the mouth was open and the opercle was slightly open. Opercular pumping was not seen. These observations indicate ramjet ventilation of the gills. Gape distance appeared to vary inversely with swimming speed. However, two fish that were on their sides on the bottom of the tank remained alive after 24 h and used opercular pumping to ventilate their gills. This suggests that ramjet ventilation is not obligatory, and that the death of Pacific pomfret in gill nets was due to interference with opercular movements, as well as prevention of ramjet ventilation, their normal means of gill ventilation.

Dissection of several fish at sea revealed that both the abductor and adductor muscles of the pectoral fin consisted of dark red muscle fibers, presumably enriched in capillaries and myoglobin. Red muscle is used for continuous propulsion in other fishes (Webb 1975). These dark red muscles contrasted with the white muscle fibers seen throughout the rest of the body (Fig. 16). No red muscle was associated with the lateral muscle mass of the body as in tunas and other fast swimming pelagic fishes.

Pectoral fin muscles of one specimen (355 mm FL, 759 g total weight) were dissected and weighed. The paired abductors (superficialis and profundus) located on the lateral face of the pectoral girdle (see Winterbottom 1974 for muscle morphology)

TABLE 2. Food habits of pomfret collected in the Northeast Pacific from the T/V *Oshoro Maru*, 1980–87. (A) percent of wet-preserved weights of taxa, (B) percent frequency of occurrence, and (C–G) percent by volume.

A. 1980, along 145°W

	Latitude north	
	50°	48°30′
Euphausiids	0	2
Amphipods	0	T
Squids	86	91
Fishes	4	3
Unidentified	10	5
No. examined	10	50
% empty	10	20

D. 1985, along 155°W

	Latitude north								
	48°	47°	45°30′	44°	42°30′	41°	39°30′	38°	36°30′
Squids	98	100	95	100	100	5			58
Fishes	2	0	5	0	0	21			38
Other	0	0	0	0	0	74			5
No. examined	38	20	30	6	1	25	0	0	6
% empty	0	5	10	17	0	40			33
Fullness	2.9	3.0	2.2	2.2	1.0	1.3			2.0

B. 1981, along 145°W

	Latitude north		
	51°	50°	49°
Amphipods	0	5	8
Squids	88	69	90
Fishes	38	0	6
No. examined	8	42	50
% empty	0	12	2
Fullness	1	2	2

E. 1986, along 180°

	Latitude north					
	37°	38°	39°	40°	41°	42°
Euphausiids	11	24	26	59	34	4
Amphipods	0	4	2	<1	16	8
Squids	11	15	1	7	17	35
Fishes	78	38	36	23	16	46
Other	0	18	35	11	18	6
No. examined	26	23	31	27	28	27
% empty	34	4	22	4	11	7
Fullness	2.4	1.9	2.1	1.9	1.3	1.8

C. 1984, along 155°W

	Latitude north				
	49°	48°	47°	45°	44°
Euphausiids	0	0	<1	0	0
Amphipods	0	0	7	15	2
Squids	92	64	80	73	23
Fishes	8	36	5	7	50
Other	0	0	7	5	25
No. examined	14	25	30	30	33
% empty	14	60	13	33	36
Fullness	3.43	0.8	2.53	0.5	1.5

F. 1987, along 180°

	Latitude north			
	39°	40°	41°	42°
Euphausiids	<1	53	12	11
Amphipods	0	9	3	0
Squids	12	<1	25	74
Fishes	72	37	36	10
Other	5	9	25	5
No. examined	20	58	39	10
% empty	60	16	48	0

G. 1987, on a diagonal from 56°N to 45°59′N

	Latitude north, longitude west										
	56°00′ 145°00′	55°00′ 143°48′	54°00′ 142°38′	52°27′ 141°23′	52°60′ 140°20′	51°00′ 139°12′	50°00′ 138°08′	49°00′ 137°05′	48°00′ 136°00′	47°00′ 135°00′	45°59′ 133°58′
Euphausiids	0	27	0	<1	0	0	60	0	0	<1	0
Squids	47	68	95	66	100	75	32	62	74	97	91
Fishes	53	5	2	5	0	25	8	16	12	2	9
Other	0	0	3	29	0	0	0	22	14	<1	0
No. examined	3	23	28	30	11	29	30	35	31	31	32
% empty	0	17	4	30	18	58	60	17	16	26	66
Fullness	1.0	1.7	1.8	1.3	2.9	1.6	1.5	2.3	1.6	1.2	1.4

had about the same mass as the adductor muscles on the medial face of the pectoral girdle. The combined weight of these muscles (9.8 g) from one pectoral girdle was 4.5% of the combined white (210 g) and red muscles mass from the same side of the body. This is about the same ratio of red muscle to total musculature reported for the labrid *Oxyjulis californica*, that relies on pectoral fins for normal swimming (Rosenblatt and Johnson 1976), but less than the ratio of red to white muscles found in myotomal musculature of rainbow trout (*Oncorhynchus mykiss*) (Webb 1971) and of red muscle to body mass in most of the scombrids studied by Magnuson (1973). It is far less than the ratio reported for the ocean opah (*Lampris guttatus*), that swims with its comparatively short pectoral fins and has large red adductor and abductor muscles comprising 37% of the total propulsive musculature (Rosenblatt and Johnson 1976).

Conclusions

Pacific pomfret has attracted attention as an underutilized resource because of its high abundance in fisheries for other species. Often it is the dominant nonsalmonid fish in gill net and purse seine catches in the subarctic region during the summer (Neave and Hanavan 1960; Hitz and French 1965; Machidori and Nakamura 1971; Yatsu et al. 1993). High abundance throughout much of the epipelagic waters of the North Pacific, rapid growth rate, and segregation of large and small individuals during northward migrations are favorable characteristics of a potentially productive fishery. In addition, we found no decrease in either catch per standard set of large pomfret or mean size of pomfret during our study that was coincident with the large-scale drift net fishery for flying squid. This indicates that the population of Pacific pomfret had not been adversely affected by its incidental catch in the flying squid fishery.

Although much is known about the biology of pomfret (see Shimazaki 1989), important features of their biology and ecology need to be evaluated. Differences in parasite loads and age structure suggest different stocks in the eastern and western North Pacific. The discreteness of stocks is an important management consideration and should be resolved, possibly by biochemical or genetic studies or larval surveys, before intensive exploitation.

Reliable methods of ageing need to be further developed, including an age-specific study to validate growth increment periodicity. Age determination is vital to estimates of growth, mortality, age at first spawning, and ages of large and small fish during the summer season. Information on reproduction in the Northeast Pacific is also needed.

Little is known about the early life history of Pacific pomfret, and nothing about factors affecting survival and year-class success. Better understanding also is needed on the role of Pacific pomfret in the North Pacific pelagic ecosystem and how a fishery would affect other species, including salmonids.

Finally, fishing techniques to catch pomfret may be problematical. Drift gill nets are not an acceptable option unless bycatch of other species is minimal. To target pomfret with purse seines or trawls, more information is needed on gear selection, schooling behavior, and oceanographic and geographic factors that may result in dense, available concentrations.

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