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Title: ZOOGEOGRAPHY AND SYSTEMATICS OF CEPHALOPODS OF THE

NORTHEASTERN PACIFIC OCEAN

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Collections of cephalopods from the northeastern Pacific
north of 20°N and east of 170°E were examined in order to
elucidate zoogeographic patterns for the region. Sixty-four
species were identified, including two new species of Gonatus.

The distributions of Subarctic and Transitional (including
California Current) species are now fairly well understood. Less
clearly defined are the distributions of central and equatorial
species. This is in great part due to the lower sampling density
in those areas. In several instances, species have been
identified for the first time from North Pacific waters, primarily
within the central gyre.

Ten pelagic distributional types are defined for cephalopods
in this area; most coincide with water masses or portions or
combinations thereof. In many cases, good correlation is seen
with the work of others on other taxonomic groups.

The relative abundance of cephalopods in main water mass
types is considered, using diversity and evenness statistics. The
central water mass is dominated by Enoploteuthidae, and the
Subarctic by Gonatidae. The dominant taxa of the Transition Zone

and California Current show a mixture of these two families. The Transition Zone fauna is more closely allied to that of central waters, and the California Current fauna is more similar to that of the Subarctic.

Possible mechanisms for population maintenance are discussed, and consideration is given to speciation processes relative to the observed distributions.

The phylogeny of the Gonatidae is explored on the basis of primitive vs. derived characters and the observed zoogeographic distribution.

It is proposed that the subgenus _Boreoteuthis_ be elevated to generic status.

Zoogeography and Systematics of Cephalopods of the

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ZOOGEOGRAPHY AND SYSTEMATICS OF CEPHALOPODS OF THE NORTHEASTERN PACIFIC

INTRODUCTION

Cephalopods represent several trophic levels in the marine ecosystem, from first to the highest level of invertebrate carnivore. They are, in turn, important in the diets of fishes, marine mammals, and birds. This paper summarizes the species composition and zoogeography of cephalopods in the northeastern Pacific Ocean.

Previous reports on the cephalopod fauna of the northeastern Pacific have been few. One of the first was Dall (1873), describing Moroteuthis robusta. The first attempt to define the fauna of this region was that of Berry (1912b), who listed twenty species, including five of Polypus or Octopus, from nearshore waters between Bering Strait and southern California. Sasaki (1929) discussed several Japanese species which also occur in the eastern Pacific. Akimushkin (1963) detailed the systematics of Russian cephalopods; several northeastern Pacific forms were included. Pearcy (1965) listed seventeen species (not including Octopodidae) from the waters off Oregon. The larval cephalopods of the California Current were examined by Okutani and McGowan (1969), and Young (1972) considered the cephalopods from the seas off southern California and northern Baja California. Anderson (1978) recorded several cephalopods from Monterey Bay, California. Young's (1972) work has certainly been the most comprehensive to

date, but he encountered only a small portion of the Subarctic fauna.

In the North Pacific, the zoogeography of cephalopods has been studied rather infrequently and usually only in relatively restricted areas. Clarke (1966) gave distributional data for a number of pelagic oegopsids, but his data were few for this area, and the systematics of this group has since changed markedly. Okutani and McGowan (1969) described the zoogeography of larval forms in the California Current; again, the systematics has recently changed significantly. Young (1972), in a primarily taxonomic work, gave summaries of the known distributions of the forms he treated, but his own data covered a very restricted area off southern California and northern Baja California. He discussed the affinities of the species he encountered for Subarctic, Transitional (including California Current in his terminology), central, and eastern tropical Pacific distributions, and noted a fourth group with cosmopolitan tropical-subtropical distributions. He was not always able to distinguish between Subarctic, Transitional, and Subarctic-Transitional distributions.

Nesis (1973b) was the first to address the zoogeography of cephalopods in the Pacific in light of many recent taxonomic changes, but documentation of his data sources is generally unclear. He concluded that five zoogeographic regions or subregions exist for cephalopods in the North Pacific: Arctic; Boreal (including north and south boreal subregions); and Tropical (including Californian subtropical and eastern tropical subregions

in the eastern Pacific). His classificatory scheme was based on
one used for benthic molluscs (Golikov and Kusakin, 1962; Golikov,
1963). He did not distinguish clearly between central and
equatorial distributions; this and the general lack of data in his
paper is the basis for a number of differences between his and my
conclusions. There are also, in a number of instances, taxonomic
differences or difficulties which prevent strict comparison
between his and my results.

The systematics of many of the groups reported have undergone
more or less major revision in the years since Berry's (1912b)
work, and many species new to science or to this area have been
described. The family Gonatidae forms, numerically, by far the
most important group of cephalopods in the subarctic Pacific.
Recent years have seen a rapid and continued increase in the
number of species recognized in the family. Young (1972) began
the subdivision of the genus *Gonatus* by describing three new
species (*onyx*, *pyros*, and *californiensis*), and resurrecting *G.*
berryi Naef, 1923, which had apparently been lost in the synonymy
of *G. fabricii*. The description of another species, *G. madokai*,
from the western Pacific (Kubodera and Okutani, 1977) followed.
Kubodera's (1978) thesis thoroughly described several larval
types. Three of these were subsequently identified with adult
forms, one of which (type A) is probably identical with a specimen
described by Middendorff (1849) as *Onychoteuthis kamtschatica*.
This has been redescribed, and named *G. middendorffi* (Kubodera and
Okutani, 1981). Kubodera's type B is identical with *G. onyx*, and

type D with _G. berryi_; his type C is distinct, and remains unnamed.

Nesis (1972b) described and named an additional species, _G. tinro_, which proved to be identical with an unusual specimen reported by Fields and Gauley (1971). The most recent systematic results are those of Bublitz (1981); he has apparently discovered a ninth species, based on larval individuals from the eastern Bering Sea. With the inclusion of two new forms described here, there are thus eleven species in the genus _Gonatus_ in the North Pacific.

There are apparently at least two species of _Gonatus_ in the North Atlantic: _G. fabricii_ (sensu stricto) and another, as yet undescribed (Okutani, 1981). Young (1972) reported that the collections he had examined indicated that at least two species were present in the Antarctic (_G. antarcticus_ Lönnberg 1899, and another, undescribed).

The genus _Gonatopsis_ has been less exhaustively examined; at least five species are present in the North Pacific: _G. makko_ Okutani and Nemoto, 1964; _G. octopedatus_ Sasaki, 1920; _G. borealis_ Sasaki, 1923; _G. japonicus_ Okiyama, 1969; and _G. okutanii_ Nesis, 1972. Two forms of _G. borealis_ are known which mature at different sizes; it is as yet unknown whether these represent distinct species. _Gonatopsis japonicus_ is known only from immature specimens.

Berryteuthis at present comprises only two species: _magister_ (Berry, 1913) and _anonychus_ (Pearcy and Voss, 1963).

The family Gonatidae consists of three genera and at least twenty-one species, limited to high temperate and polar latitudes. Gonatus occurs in the North Pacific and North Atlantic as well as in Antarctic waters, and exhibits a relatively high degree of speciation in the Pacific. Individuals belonging to this genus are known to occur in the Arctic Ocean; but they have been identified only as G. fabricii, which in the past has been treated as a portemanteau species. The extent of Atlantic-Pacific communication, or lack thereof, is thus unknown. Berryteuthis and Gonatopsis are limited to North Pacific waters.

OCEANOGRAPHY OF THE NORTHEASTERN PACIFIC

An understanding of at least the general oceanographic
features of the northeastern Pacific is essential to an
investigation of the zoogeography of organisms from that region.
The North Pacific embraces two large gyral systems: a subtropical
anticyclone and a high latitude cyclone. Primary features of
interest in the anticyclonic gyre are the easterly Subarctic
Current, southerly California Current, and westerly North
Equatorial Current, and in the cyclonic gyre, the Alaskan Stream
and Bering Sea current system (see Figure 1).

Central North Pacific

The temperate-subtropical North Pacific is characterized by a
broadly anticyclonic circulation. The boundaries of this central
gyre are seen, in the north as the North Pacific Current, in the
east as the California Current, in the south as the North
Equatorial Current, and in the west as the Kuroshio (Beklemishev
and Nakonechnaya, 1972; Kitano, 1972; Smith, 1976; Venrick, 1979).
The central waters of this gyre are oligotrophic, a result of the
stable thermocline and nutrient-poor, deep mixed layer (Bogorov,
1958; Reid et al., 1958). Essentially no mixing occurs through
the thermocline (Reid et al., 1958). This mixed layer is warmer
and more saline than Subarctic and Central Intermediate waters,
but cooler and less saline than equatorial waters. North Pacific
Central water in the east generally has the following properties:

Figure 1. Major surface current systems (0-125 m) of the
northeastern Pacific (after Favorite et al., 1976, north of 34° N,
and Wyrtki, 1965, eastern tropical Pacific).
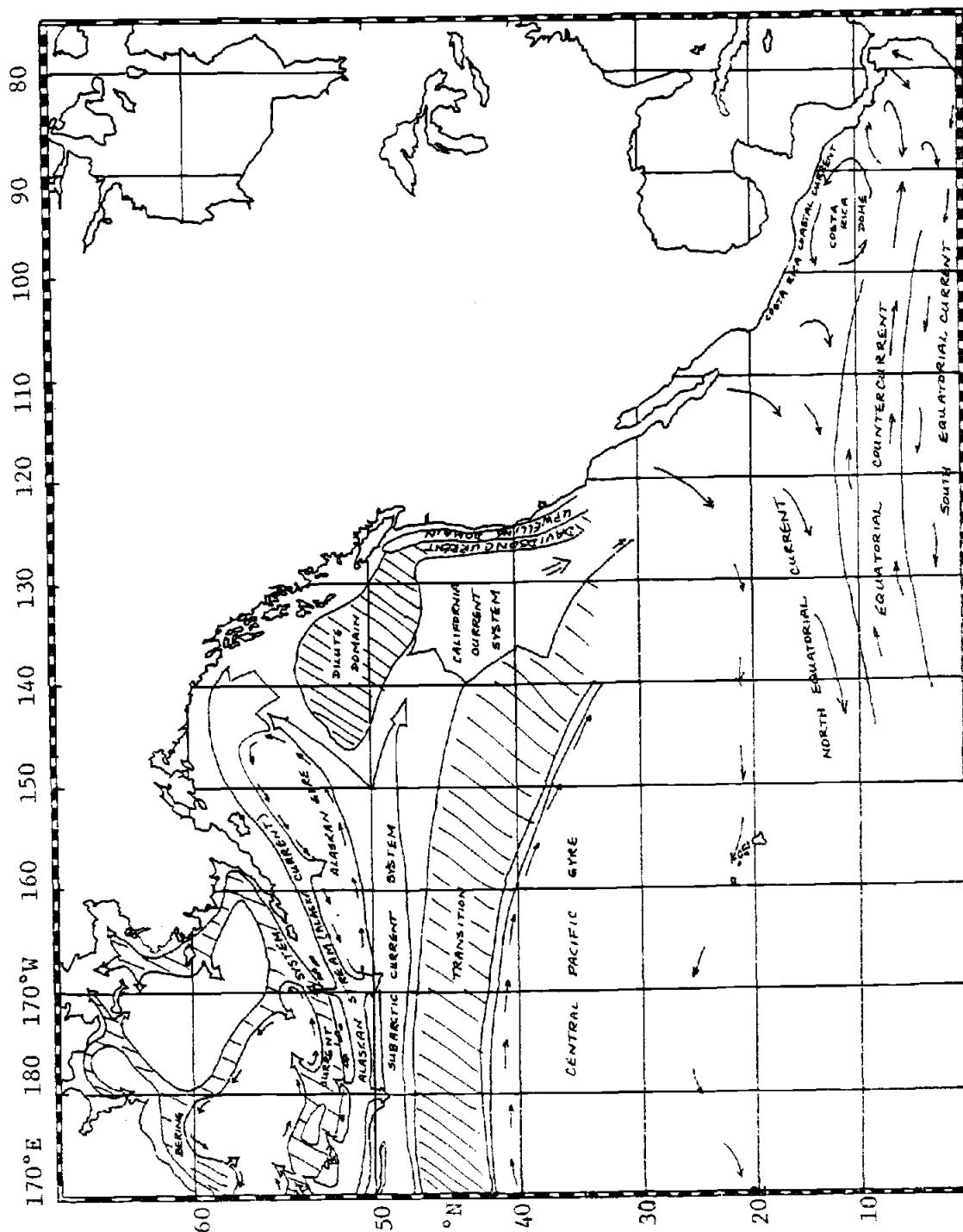
at 10°C, 34.0‰, at 15°C, 34.5‰; and in the west, at 10°C, 34.3‰ and at 15°C, 34.6‰ (Smith, 1976).

Central gyres generally harbour many endemic and rare species and usually have a low total biomass (Reid et al., 1978). In the North Pacific central gyre, plankton biomass is about one-tenth that of the Subarctic. This may, however, be offset by higher reproductive rates (Bogorov, 1958). Omnivores and carnivores are relatively more abundant in subtropical regions, apparently as an adaptation to the lower level of trophic resources (Reid et al., 1978).

Equatorial

A sharp, stable boundary separates Transitional and Central waters from Equatorial water, at about 20-25°N near the American coast, and at about 10°N in mid-ocean (south of the Hawaiian chain). This warm and saline Equatorial water (34.7‰ at 10°C, 35.1‰ at 15°C, Smith, 1976) is formed *in situ*, by subsurface mixing of central and intermediate waters (Sverdrup et al., 1942). The thermocline and other isolines approach the surface in this area of divergence between the westerly North Equatorial Current and the easterly Equatorial Countercurrent (Wooster and Cromwell, 1958; Austin, 1960). This and another divergence within the South Equatorial Current induce upwelling leading to the characteristically increased productivity of the equatorial region (Fleming and Laevastu, 1956; Wooster and Cromwell, 1958; Cromwell, 1958; Sette, 1958; Austin, 1960; Raymont, 1963). An associated

oxygen minimum often occurs below the wind-mixed layer (Ebeling, 1967).

The North and South Equatorial Currents are westerly, may extend as deep as 1500 m, and bracket the easterly Equatorial Countercurrent, which flows between 5° and 10° N and may also extend as deep as 1500 m. Another easterly current, the Cromwell or Equatorial Undercurrent, subtends a shallow surface layer of the South Equatorial Current. This undercurrent is located symmetrically about the equator, and may extend from 50 to 500 m, with the maximum velocity of 3.5 kt occurring at about 100 m. It is about 240 miles wide north of the Marquesas (Knauss and King, 1958).

The circulation of the eastern tropical Pacific lies outside the influence of the North and South Pacific central gyres. The Equatorial Countercurrent is fully developed only from May to December, during the rest of the year ending west of 120° W. Seasonal features of the eastern tropical circulation include cyclonic flow around the Costa Rica Dome, and anticyclonic flow to the southeast. A strong easterly flow between these is present year round. The northwesterly Costa Rica Coastal Current is present seasonally as far north as 20° N, at other times turning west south of the gulf of Tehuantepec. A cyclonic eddy is seasonally developed near the Gulf of Panama and the coast of Colombia (all of the foregoing is based on Wyrtki, 1965).

The eastern tropical Pacific is an area of high biological productivity. Areas of low oxygen tension occur relatively close

to the surface (100-500 m), the result of this high production.
This region holds a relatively depauperate, but highly endemic,
fauna.

Transitional

Oceanographic "fronts", or areas of major and rapid change in
various physicochemical properties (temperature, salinity, oxygen,
etc.) define the boundaries between water masses and major gyres.
The North Polar Front (Wust, 1929) marks the boundary between the
central or subtropical gyre and the subarctic gyre. The subarctic
gyre circulates in a cyclonic fashion. It is delimited by the
Subarctic Current to the south, Alaska Current to the east,
Alaskan Stream to the north, and the Oyashio or Kurile-Kamchatka
Current to the west (Kitano, 1972; Ohtani et al., 1972). The
polar front in the North Pacific covers a fairly broad
"transitional region" and may consist of two or three component
thermal or salinity fronts (Suda, 1936; Uda, 1938; Sverdrup et
al., 1942; Kawaii, 1955; Tully and Barber, 1960; Favorite and
Hanavan, 1963; Kitano, 1972). This transitional region broadens
from west to east; convergent flow dominates in the west and
divergent flow in the east. The transition region marks a change
from species-poor, high biomass subarctic waters to speciose but
low biomass subtropical waters, and harbours a characteristic
mixed fauna, which may show changes from west to east (Hida, 1957;
Bogorov, 1958; McGowan, 1960; Brinton, 1962; Fager and McGowan,
1963;   Lang, 1965; Beklemishev and Nakonechnaya, 1972).

This transition region also constitutes a major biological boundary (Aron and McCrery, 1958; Aron, 1959; Bieri, 1959; Beklemishev and Parin, 1960).

The separation line between subarctic and subtropical circulations is farther to the north in the eastern than in the western Pacific. On the basis of satellite-tracked drifter studies, Kirwan et al. (1978) showed a northward meander from about 43°N between 150° and 170°W, to about 50°N between 130° and 140°W (based on 1976-1977 conditions).

The transitional region of the North Pacific spans the change from oligotrophic central waters to highly productive subarctic waters. Boreal species, when present, live in ever deeper water south of the mixing zone, which oscillates seasonally between 40° and 42°N (Bogorov, 1958).

Transitional waters of the eastern Pacific often overlie deep northward intrusions of equatorial water (Sverdrup et al., 1942; Reid et al., 1958; Wooster and Gilmartin, 1961; Lavenberg, 1964; Bussing, 1965). Transitional waters are widespread in the eastern Pacific, encompassing the California Current, and harbour some endemic species, including several euphausiids (Brinton, 1962), and Melamphaes parvus (Ebeling, 1962).

The transitional region of the North Pacific is a zone of variable biomass, representing a mixed, secondary oceanic community (Kitano, 1972; Beklemishev and Nakonechnaya, 1972). The members of this community may perhaps derive primarily from a "neutral col" in the western Pacific located between the central

gyres and the coast of Japan (Beklemishev and Nakonechnaya, 1972).

Individual species may show changes in morphology and/or relative

abundance from west to east, and diversity patterns may change

(Beklemishev and Nakonechnaya, 1972).

Transitional water is physicochemically distinguished from

central and subarctic waters by its intermediate temperature

(4-9°C) and low salinity (less than 34‰; see Figure 2). The

offshore Transition Zone (South Boreal Region of some authours,

e.g., Briggs, 1974) is defined in the area of the West Wind

Drift - North Pacific Current subarctic convergence in mid-ocean,

or where the 34.00‰ isohaline intersects the surface (Dodimead et

al., 1963).

California Current

The transitional waters of the North Pacific give rise in the

east to the complicated California Current system. Near the U.S.

- Canadian border, the North Pacific Drift splits into two parts:

one flowing north into the Gulf of Alaska, and the other turning

south. This southward flowing body is the California Current; the

name applies only to the shallow (200 m) offshore flow, which

averages 20 cm/sec (Smith, 1976). Deeper than 200 m, the current

is southward offshore and northerly inshore, the year round. In

inshore waters the surface current is generally northerly in the

winter months and is known as the Davidson Current. Off southern

California the southward flow turns west to merge with the North

Figure 2. Temperature-salinity characteristics of North Pacific
Central Water (NPCW), Transitional Water (TR), and Subarctic Water
(SA) (after Tebble, 1962).
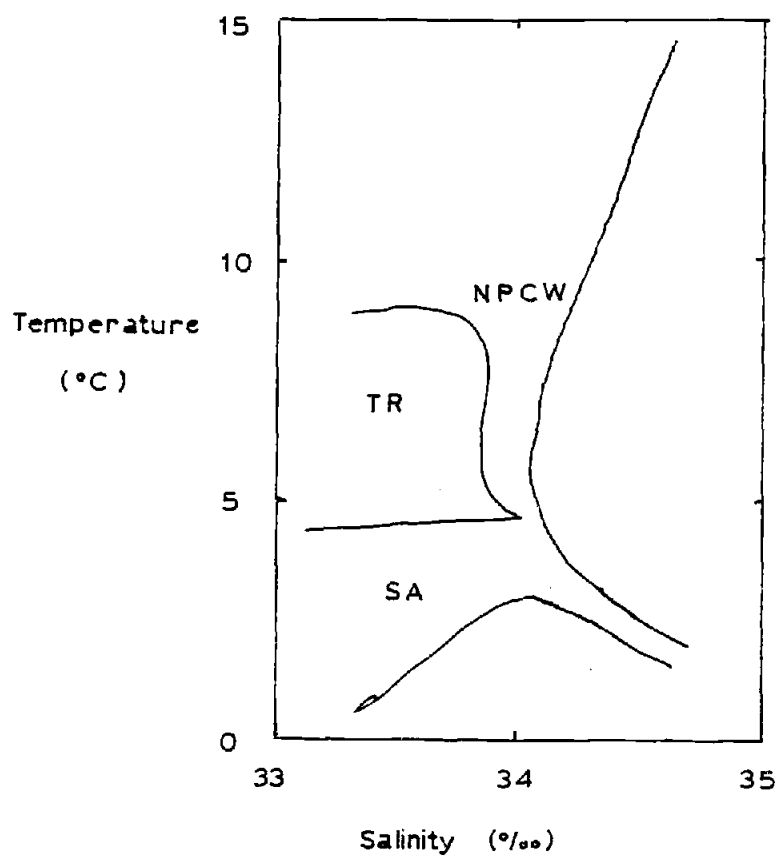
Equatorial Current at about 24°N (Reid et al., 1958; Emery, 1960; Ricketts et al., 1968; Okutani and McGowan, 1969).

The California Current is largely derived from the Subarctic Water Mass, and acquires its final character through admixture of central water, and equatorial water flowing northward as a countercurrent below 200 m (Reid et al., 1958; Huyer, 1976). A similar countercurrent exists bvelow the Peru Current (Brandhorst, 1959b). Coastal upwelling along the western boundary of North America provides nutrients from its component subarctic and equatorial waters (Reid et al., 1958). Species diversity is somewhat higher than in the Subarctic Water Mass due to admixture of low latitude species (Alvariño, 1965b; Brinton, 1967; Fleminger, 1967; McGowan, 1974). The California Current is here treated as part of the transitional region (but zoogeographically distinct from the offshore Transition Zone), and as a derivative of the Subarctic Water Mass.

Subarctic

The Subarctic Pacific encompasses an area of approximately 6×10^6 square miles north of about 40°N (Johnson and Brinton, 1963). The most noticeable biological feature of the Subarctic Pacific is its high productivity. Vertical mixing replenishes surface waters with nutrients from below, which are derived from waters beneath the photic zone of the North Pacific central gyre, resulting in high primary production, especially near the Aleutians and the western coast of North America (Fleming, 1955;

McGowan and Williams, 1973; Hood and Kelley, 1974; Reid et al., 1978). Large seasonal variations in vertical mixing and illumination are reflected in seasonal changes in primary production (Reid et al., 1978); summer stratification is accompanied by development of a pronounced oxygen minimum layer (0.5-0.9 ml/l - Okubo, 1958). These cold, nutrient-rich waters have relatively few, but often large species of plankton and nekton, and a high biomass (Ebeling, 1962; Reid et al., 1978).

Subarctic Water originates in the convergence of the cold, low salinity Oyashio and the warmer, more saline Kuroshio (Kitano, 1958). The Subarctic system may be divided into an eastern and western gyre, although neither is completely closed. The eastern gyre is situated in the Gulf of Alaska (Gulf of Alaska Central Water), and the western in the Bering Sea (west of Bowers Ridge - Bering Sea Water) and northwestern Pacific and Sea of Okhotsk, separated by the Aleutian Islands (Fleming, 1955; Uda, 1959). The Bering Sea represents the northernmost reaches of the Subarctic environment. The Subarctic is also the source of North Pacific Intermediate Water, formed by mixing through the pycnocline (Reid, 1965).

Subarctic Water is characterized by the presence of a dichothermal layer (subsurface temperature minimum) at 100-150 m. This layer is most strongly developed in the west, where the temperature minimum is about 3°C; the temperature gradient weakens west to east, and the minimum temperature rises to about 4°C at 165°W as a result of warming through mixing with southern portions

of the Alaskan Stream (Kitano, 1972). This water type is also characterized by a halocline near or below the dichothermal layer (between 100 and 300 m), bridging the difference between low salinity (< 33.6‰) surface water and higher salinity intermediate waters (> 34.5‰). It should be noted that winter overturn destroys the surface water types characteristic of the Subarctic, Transitional, and Central regions (Kitano, 1972).

Bering Sea and Alaskan Stream

The portion of the North Pacific Drift which turns north continues along the coast north and west to the Aleutian Peninsula where a portion of the flow turns south into the Alaskan Gyre. The westerly coastwise flow is termed the Alaskan Stream (Favorite, 1967); it is characteristically dilute (less than 32.8‰), and continues at least as far west as 165° E (Favorite and Ingraham, 1972). Its southern boundary is at about 50° N at 175° E (Favorite, 1974). The Alaskan Stream is driven by seasonal intensification of cyclonic flow in the Gulf of Alaska (Favorite, 1970). It has the temperature structure (warm mesothermal layer) characteristic of most of the Subarctic Pacific: a temperature maximum (over 4 °C) below a temperature minimum layer produced by winter overturn (Favorite and Ingraham, 1972). The characteristic low salinity is the result of spring and summer meltwater runoff from the coastal mountain ranges of the Gulf of Alaska (Callaway, 1963; Favorite, 1969) and persists during all seasons (Favorite et al., 1964; Ingraham and Favorite, 1968; McAlister et al., 1970).

Nearly all flow into the Bering Sea is derived from the Alaskan Stream (Arsen'ev, 1967; Ohtani, 1970; Ohtani et al., 1972), and passes through five major groups of passes in the Aleutian-Commander Island chain (Favorite, 1967, 1974; Hood and Kelley, 1974; Sayles et al., 1979). The northward transport through these various passes has both been measured and calculated on geostrophic assumptions (Reid, 1966; Hughes et al., 1974; Favorite, 1974; Sayles et al., 1979). A general pattern is evident, although not all authours agree on specifics: northerly flow through most of the Aleutian passes, Commander-Near Strait, and Kamchatka Strait (near the surface in the east, and deep in the east and west); and southerly flow through Buldir and Kiska passes (at least in summer)[1] and the western portion of Kamchatka Strait. This is coupled with an overall cyclonic circulation in the surface waters (to about 600 m) of the western basin of the Bering Sea: northeast in the southeastern Bering Sea, turning northwest at the edge of the broad Alaskan shelf (this is the Bering Slope Current of Kinder et al., 1975) and southwest along the Siberian shelf (Hughes et al., 1974; Sayles et al., 1979).

The main characteristics of Subarctic water on entering the Bering Sea (upper-level stratification) are destroyed by turbulence in the dissipation of tidal energy on flowing through the passes (Ohtani et al., 1972). Warm and relatively fresh water is advected northward through Amukta, Amchitka, and Buldir passes,

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[1]Sayles et al. (1979) cite northward flow through Buldir Pass.

and Near Strait. Below 150 to 200 m, the Bering Sea is characterized by well-oxygenated (2.5-3.0 ml/l) near-bottom inflow through passes east of Bowers Ridge (mostly through Amukta and Amchitka passes). The passes west of Bowers Ridge are deeper; their flows are denser and less well oxygenated (Sayles et al., 1979). Favorite and Ingraham (1972) discuss flows around Bowers Ridge.

Surface waters in the Bering Sea range from $-1.3°C$ to at least $10°C$ and from 32.12%o to 33.00%o. A temperature minimum occurs at 100-150 m and 33.2%o, and a temperature maximum of $3-4°C$ at 300-400 m. Below the maximum, temperature decreases with increasing depth (Sayles et al., 1979). This structure is established through convective overturn to 150-200 m in winter (i.e., surface cooling and admixture of relatively fresh shelf water - Sayles et al., 1979), and upwelling associated with cyclonic eddies (Ohtani et al., 1972). After a residence time of approximately one year, and outflow through western Kamchatka Strait, Western Subarctic Pacific Water results from mixing of this Bering Sea water with cold, less saline Okhotsk water near the Kuriles. Part of this outflow turns east, parallel to the West Wind Drift, as the Subarctic Current; the rest flows southwest as the Oyashio (Ohtani et al., 1972).

Bering Strait

The Bering Sea connects with the Arctic Ocean (proximately, the Chukchi Sea) through the narrow (85 km) and shallow (45 m)

Bering Strait (Hood and Kelley, 1974). The northward transport through Bering Strait is about 1.4 Sv (Coachman and Aagaard, 1966). About one-half of this volume passes through the eastern channel (between Cape Prince of Wales and Little Diomede Island) and half through the western channel (between Cape Dezhneva and Ratmanov Island). Occasional southerly flow may occur through the eastern channel, but the volume is probably minimal (Coachman and Aagaard, 1966). The three water masses in the strait are discussed by Saur et al. (1954), Coachman and Aagaard (1966), and Coachman et al. (1975). Flow in the western channel is slow and uniform (one-quarter to one-third the speed in the eastern channel); in the eastern channel, upper level flow is strong (over 100 cm/sec) and deeper flow less so (30-60 cm/sec). The regional distribution of wind stress in summer produces a downward slope of the sea surface to the north, and a nearly continuous northward flow. In winter, temperatures at all depths are very close to freezing (within 0.02° C) and flows are about twice as rapid as in summer (Coachman et al., 1975).

In the Chukchi Sea, Anadyr and Bering Shelf waters combine to form Bering Sea Water, most of which moves west through the Hope Submarine Valley into the Arctic Ocean. Alaskan Coastal Water remains distinct, and most moves east into the Beaufort Sea (Coachman et al., 1975).

SAMPLING METHODS

Cephalopods were collected with a wide variety of sampling devices, ranging from a Nansen bottle to trawls which have effective mouth openings of nearly 125 m2. These devices are divisible into two broad groups: those which generally capture one individual at a time, and which are usually manually operated from the deck of a ship; and those which are designed to filter large volumes of water, extracting animals of various sizes depending on the mesh size of the filter (i.e., nets). The latter group may be further divided into sampling devices which collect organisms from discrete subsurface depth horizons (opening-closing or discrete-depth samplers), and collectors which sample all depth horizons from the surface to the maximum depth encountered (open or non-discrete depth samplers).

Single-organism samplers

In this group are included dipnets, Nansen bottle, bow and arrow, hook and line, strandings, squid jigs, and long-lines. The dipnet is an important sampling device in the study of cephalopods, especially for agile surface-dwelling animals which are seldom or never collected in trawls. The primary use of this device is under night lights in a moderately calm sea. Sixty-eight individuals were examined from twenty-nine dipnetting sessions (several dipnet samples were considered part of the same session when all were obtained as the result of one night's endeavours at a single station).

One cephalopod was captured in a Hansen bottle cast. This should not be considered a testimonial to the efficacy of this device for cephalopod sampling.

One cephalopod was captured with each of the following devices: bow and arrow, squid jig, and hook and line. These methods are often suitable for sampling large, highly visible specimens, and may yield the investigator important data on large individuals of various species.

One individual was recovered in the process of stranding, reportedly having been chased onto the beach by harbour seals (Phoca vitulina).

Two individuals were taken on Japanese surface salmon long-lines.

The above-mentioned collection techniques rarely provide the central basis of an investigation, but can be invaluable to taxonomic or life-history researches.

Midwater trawls

The various towed nets employed had mouth openings ranging from 0.8 to nearly 125 m2 (see Table 1); I shall treat them generally in order of increasing mouth cross-section.

A one-metre diameter ring net, with 0-mesh (0.571 mm) plankton netting throughout, was used in three sampling modes: attached to the trawl wire just above an IKMT (Isaacs-Kidd Midwater Trawl, Isaacs and Kidd, 1953); an oblique haul to depths

Table 1. Collection devices, showing mouth area in square metres (where applicable or known), the number of hauls which collected cephalopods, and the number of cephalopods collected.

GEAR TYPE	MOUTH AREA	□ HAULS	INDIVIDUALS
dipnet	0.8	29	68
Nansen bottle		1	1
bow and arrow		1	1
squid jig		1	1
hook and line		1	1
stranding		1	1
long-line		1	2
metre net (on IKMT)[a]	0.8	30	91
metre net (oblique)	0.8	12	34
metre net (vertical)	0.8	4	5
MPS [b]	1.0	19	68
0.9 m IKMT (BB)[c]	0.7	72	363
1.8 m IKMT (BB)	2.94	429	2936
0.9 m IKMT (OSU)[d]	0.7	7	29
1.8 m IKMT (OSU)	2.94	805	8189
3.0 m IKMT	8.17	109	1215
1.8 m IKMT + MPS	2.94	162	603
2.4 m IKMT + MPS	5.4	619	3239
3.0 m IKMT + MPS	8.17	15	79
RMT - 4 pt. bridle [e]	11.3	4	35
RMT - 2 pt. bridle	11.3	3	56
RMT	11.3	7	51
Cobb - rockfish	65.	31	1126
Midwater trawl + MPS	50.	122	14,377
Engels	30.	1	24
Beam trawl	2.3	52	103
Otter trawl	12.	12	22
Gulf shrimp trawl (ODFW)	25.	22	524
Eastern - 71/94	25.6	14	28
Eastern - 83/112	39.	8	9
Nor'Eastern - 90/105	123.6	287	9715
Commercial shrimp trawl	?25.	2	2
Purse seine		7	84

a IKMT: Isaacs-Kidd Midwater Trawl
b MPS: Multiple Plankton Sampler
c BB: R/V Brown Bear
d OSU: Oregon State University sampling program
e RMT: Rectangular Midwater Trawl

of up to 200 m; and towed vertically. Because of its small mouth opening and mesh size, the metre net caught primarily larvae and small individuals which are seldom retained by larger nets and mesh sizes.

The multiple plankton sampler (MPS), originally developed by Bé (1962), was modified by Pearcy and Hubbard (1964), Pearcy and Mesecar (1971), and Pearcy et al. (1977) to fish three or five nets at variable depth intervals. These devices have a square mouth opening of 0.12 m2 (three-net MPS) or 1.0 m2 (five-net MPS). They were generally used as opening-closing cod ends on 1.8, 2.4, or 3.0 m IKMT nets, but sometimes the 1.0 m2 MPS was fished alone with 0.571 mm Nitex mesh. When the 1.0 m2 MPS was used as a cod end closure it had nets 4.6 m long, with 5 mm mesh in the first portion of each net, and 0.571 mm netting in the terminal section. The nets are opened and closed consecutively by a pressure actuated device (three-net system), or an electrically or timer activated shaft and cam system (five-net MPS). This device constituted the closing apparatus on all of the nets mentioned below, with the exception of the Rectangular Midwater Trawl.

The Isaacs-Kidd Midwater Trawl, in various sizes and configurations, accounted for 78% of all hauls capturing cephalopods. In this study, four different sizes were used: 0.91 m, 1.83 m, 2.44 m, and 3.05 m. The dimension refers to the width of the depressor. In the Brown Bear investigations (sampling programs are discussed in the next section), 0.91 m and 1.83 m versions were used as open sampling devices. A one-half

metre plankton net with 3.2 mm mesh and attached collecting bucket formed the cod end. Mesh size in the net was 7.6 cm, with a 1.3 cm liner in the aft portion (Aron, 1958, 1962). A 3.05 m IKMT was also used by Nemoto; several collections made by him were available to me.

The IKMTs used by the O.S.U. (Oregon State University) Nekton sampling program had 0.571 mm Nitex mesh (0.91 m IKMT), and 5 mm (square measure) mesh (1.83, 2.44, and 3.05 m IKMTs). The physical dimensions were otherwise the same as for the nets used on the Brown Bear.

A Rectangular Midwater Trawl (RMT) was used briefly in the O.S.U. Nekton sampling program. The net measured approximately 3 m across the top and bottom of the rectangular mouth opening, and 4 m along the sides. The net is similar in design to that described by Clarke (1969). The net was fished either with a four point bridle, attached to the four front corners of the net, which permitted a fishing angle no greater than 20° (yielding a figure of 11.3 m^2 for area swept), or with a two point bridle, attached to the top corners of the net, permitting an unknown, and probably variable, fishing angle. The net was constructed of 6.4 mm bobbin netting.

Two different midwater trawls fished with otter boards were used in the sampling: the first, by the National Marine Fisheries Service (NMFS), in a rockfish survey, was a "modified standard Cobb trawl" with 20 cm mesh in the wings and first section, 10 cm mesh in the second section, and a 3.2 cm cod end liner. It was

fished with 55 m dandylines and 2.1 x 3.0 m steel 'V' doors, and positioned with a headrope netsounder with upward and downward looking capability. This equipment indicated an average vertical mouth opening of 7.3 m.

The other midwater trawl was used in the O.S.U. Nekton sampling program. Details of the net construction may be found in Willis (1980); Pearcy (1980); and Willis and Pearcy (1982). This net has a mouth opening of approximately 50 m2, and is equipped with a five-net MPS and a headrope transponder for continuous depth monitoring. The body of the 42 m long net is lined with 19 mm stretch mesh throughout, and the cod ends with 9 mm stretch mesh. This net was fished with 1.8 x 2.7 m or 1.5 x 2.1 m otter doors.

An Engels trawl, with a horizontal mouth opening of about 30 m, was used in one haul aboard a chartered trawler.

Bottom trawls

The last category of sampling devices includes seven bottom trawls, none of which was equipped with an opening-closing device.

A three-metre beam trawl has been used extensively in the benthic sampling program at O.S.U. The trawl net consists of 3.8 cm stretch mesh with a 1.3 cm stretch mesh liner. The skids are lined with 1.3 cm mesh (see Carney, 1977 and Carey and Heyomoto, 1972 for details and diagrams).

An otter trawl has been used in the Nekton and Benthos sampling programs at O.S.U. This is a 7 m semiballoon shrimp

shrimp trawl with 3.8 cm stretch mesh with a full or partial
1.3 cm liner. It has been fished with Hydro Flow trawl doors,
bridles 31 m on a side leading to single warp, at 1.5 to 2.0 kts
(Carney, 1977; Carey and Heyomoto, 1972).

A shrimp survey conducted by the Oregon Department of Fish
and Wildlife (ODFW) in 1977 used a Gulf semiballoon trawl with
12.5 m headrope and 15.8 m footrope, fished with 1.5 x 2.1 m steel
'V' type otter doors on 7.3 m bridles to single warp. The net was
constructed of 2.9 cm stretch mesh, with a 3.8 cm cod end
containing a 1.3 cm liner. Plastic rollers and eleven 20 cm
spherical floats were used on the headrope; a 25 m, 9.5 mm tickler
chain was attached to the ends of the footrope and 5.5 m doglegs
(Hosie, 1977).

Two Eastern trawls were used in the NMFS rockfish survey; the
smaller of the two had a 22 m headrope and a 29 m footrope (71/94
Eastern trawl). This net was constructed of 10.2 cm mesh in the
wings, square, and belly, and 8.9 cm mesh in the intermediate and
cod end. Eleven to fifteen 20 cm deep sea floats were used on the
headrope. The mean effective path width was 12.2 m and the mean
vertical opening was 1.7 m (measured with net-mounted acoustical
gear). The trawl was fished with 1.5 x 2.1 m steel 'V' doors,
46 m dandylines, no weight on the footrope, and a 3.2 cm liner in
the cod end.

The second Eastern trawl (83/112 Eastern trawl) had a 25 m
headrope, a 34 m footrope, and was fished with 2.1 x 3.0 m Astoria
type 'V' otter boards and 68 m double leg dandylines. The net had

10.2 cm mesh in the wings and body, and 8.9 cm mesh in the intermediate and cod end. Forty-one 20 cm floats were used on the headrope.

A Nor'Eastern trawl, with 27 m headrope and 32 m footrope, was used extensively in the NMFS rockfish survey. The net was composed of 12.7 cm mesh in the body and 8.9 cm mesh in the intermediate and cod end, with a 3.2 cm liner in the cod end. The trawl was fished with 1.5 x 2.1 m steel 'V' doors, 55 m triple dandylines and 31 m of roller gear on the footrope. The mean effective path width was 13.4 m, and the mean vertical opening was 9.2 m (measured with net-mounted acoustical gear).

SAMPLING PROGRAMS AND SAMPLE DISPOSITION

This study examined cephalopods gathered in a wide variety of sampling programs, over a period of twenty-three years (1957-1980), in an area bounded by lines between San Diego, the Hawaiian Islands, and Attu, Alaska. The Bering Sea east of about 180° and north to Bering Strait is also included. By far the largest portion of the samples came from the Nekton sampling program at O.S.U., conducted by W.G. Pearcy. This group of studies concentrated on the waters off the Oregon coast (mostly central Oregon) to a distance of 280 km. or farther, offshore. These collections sampled at most depths, from the surface to 1000 m, and most seasons (particularly in the early years of the program) (e.g., Pearcy, 1964). Various kinds of gear were employed: 0.91, 1.83, 2.44, and 3.05 m IKMTs, with and without the MPS; metre nets, especially early in the program; occasionally, dipnets; the 2.44 m RMT; a 7 m otter trawl; and the midwater trawl with MPS. The numbers of cephalopods caught in these nets are detailed in Table 1. Only hauls which captured cephalopods have been included in this study.

Samples from the O.S.U. program were preserved in 10 % buffered formalin-seawater solution at sea. In the weeks following a cruise, the samples were sorted to major taxon (fish, shrimp, euphausiids, cephalopods, etc.). The cephalopods were placed in 5 % buffered formalin for storage. They were later identified to lowest possible taxon, measured (dorsal mantle length, DML), and enumerated.

The following station data were generally available: position (latitude and longitude) at the beginning and end of each tow (or MPS net deployment); the times at which each haul (or net) began and ceased fishing; and the depth at which each net fished.

The second major sampling program was one conducted by the National Marine Fisheries Service (NMFS), its aim being to define the location and abundance of rockfish stocks off the western United States. The survey was restricted to relatively nearshore waters, and consisted of zig-zag transects from 91 to 457 m water depth, spaced at 18 km intervals (north of Cape Flattery, the inshore limit was the 55 m isobath). The midwater portion of the survey concentrated on echointegration estimation of stocks, with occasional trawling efforts to verify target identity. The demersal survey made hauls of thirty minutes duration, spaced along the transects according to a predetermined formula. Demersal trawling was restricted to daylight hours; some midwater trawls were made at night. The waters off California, Oregon, and Washington were surveyed in the summer of 1977 by FRS Miller Freeman (midwater) and the Polish R/V Professor Siedlecki, David Starr Jordan, R/V Commando, and M/V Pacific Raider (demersal). The waters from Dixon Entrance to Kodiak Island were surveyed in the summer of 1978 by FRS Miller Freeman, M/V Nore-Dick, and M/V Heidi J (demersal). In 1979, R/V Oregon and M/V Nore-Dick conducted demersal trawling in the area between Kodiak Island and Unimak Pass. The 1980 survey was performed by M/V Half Moon Bay

and M/V Ocean Harvester (both demersal), and encompassed the area between Attu Island and Unimak Pass (Figure 3).

The cephalopods from the rockfish survey were separated from other taxa, placed in muslin or perforated plastic bags, and preserved in 208 litre drums (1977) or 19 litre buckets (1978-1989), in ten percent formalin-seawater solution. The samples were delivered to Corvallis late in the fall and then rinsed and placed in smaller containers of fresh 5 % formalin. All samples were subsequently identified, measured (DML), and enumerated. In several cases the storage facilities on shipboard precluded the preservation of an entire sample. When the sample was a very large individual (Moroteuthis robusta or Octopus sp.), the specimen was weighed and a portion (the head of Moroteuthis or the taxonomically important arms of Octopus) was retained to confirm the species identification. When the sample consisted of a large number of smaller individuals (Loligo opalescens), a subsample was retained, after estimation of the weight of the total catch of cephalopods.

Station data were obtained from the data storage facility at Northwest Alaska Fisheries Center (NWAFC), NMFS, Seattle. Available data included latitude, longitude, hour at which the trawl was made, the duration of the trawl, the distance fished, gear and surface temperatures (occasionally), the water and gear depths, and the gear type. These data are summarized for the cephalopods in Jefferts and Pearcy (1978, 1979, 1980, 1981).

Figure 3. Location of rockfish surveys. Horizontal hatching, area of 1977 survey; single diagonal hatching, area of 1979 survey; double diagonal hatching, area of 1978 survey; vertical hatching, area of 1980 survey.
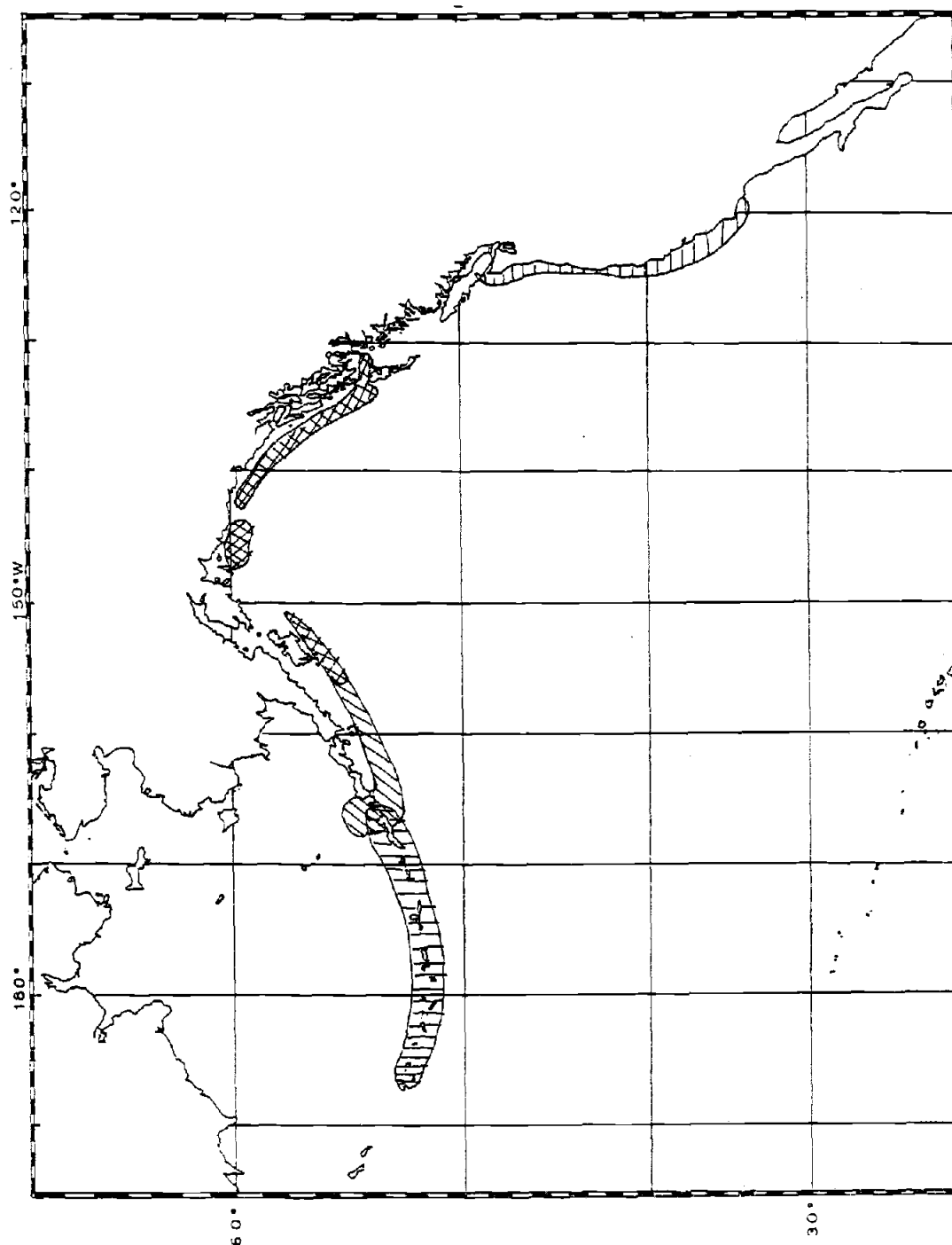
The midwater trawling was conducted with a "modified standard Cobb trawl"; demersal work utilized three trawl designs: 90/105 Nor'Eastern otter trawl; 71/94 Eastern trawl; and 83/112 Eastern trawl.

A third major sampling program was conducted aboard the R/V Brown Bear. Samples were available from cruise 176 in 1957, cruises 199 and 202 in 1958, cruises 235 and 236 in 1959, and cruise 254 in 1960. The collection of these samples was under the direction of W. Aron, University of Washington (Aron, 1958, 1962). Cruise 176 covered the waters between Seattle and Kodiak Island and westward through the Aleutian Islands to 160°E (Figure 4). Cruise 199 went west from Seattle to 140°W, southeast to San Diego, back to 140°W and returned to Seattle (Figure 5). Cruise 202 went due west from Seattle almost to 140°W and back. Samples from cruise 235 were collected along a roughly straight trackline between Seattle and the southern Bering Sea, just north of Unimak Pass. Cruise 236 samples are from Bering Strait. Cruise 254 sampled along a semicircular track from Los Angeles to Seattle, the westernmost extent of which was 132°W (see Figure 6 for cruise tracks from cruises 202, 235, 236, and 254). The samples from these cruises generally contained small juvenile or larval specimens, but they were invaluable for zoogeographic and taxonomic purposes.

A non-closing IKMT (either 0.91 or 1.83 m) was used on all Brown Bear cruises. Approximately thirty minute tows were made day and night, usually to depths of 30, 60, 120, 225, and 400 m (a

Figure 4. Cruise track, Brown Bear cruise 176, 1957. Circles
indicate all haul locations; filled circles indicate those hauls
which captured cephalopods. For purposes of clarity, only one
symbol is included per one degree square (one degree of latitude
by one degree of longitude) in this figure and all subsequent
ones.
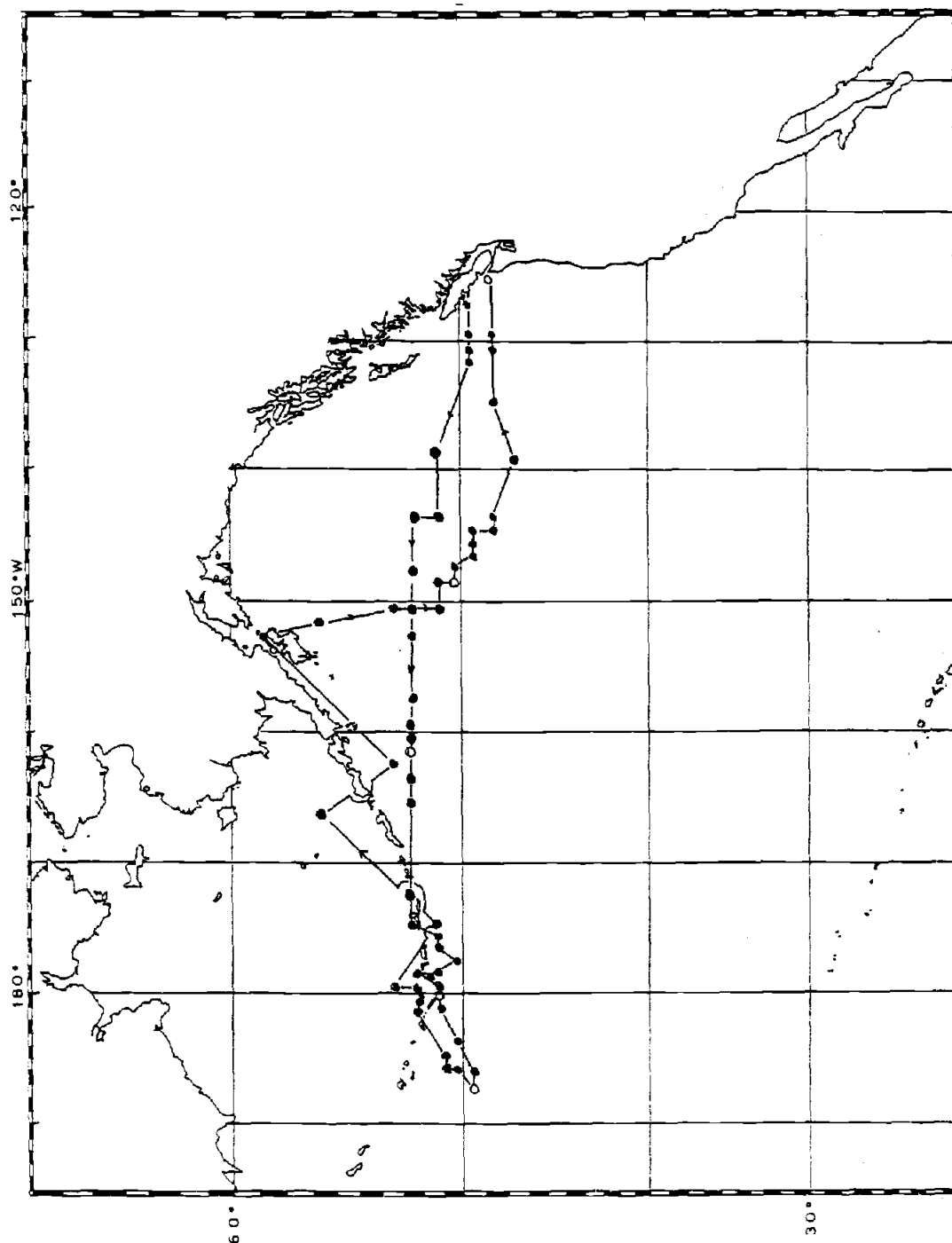
Figure 5. Cruise track, Brown Bear cruise 199, 1958. Symbols as
in Figure 4.
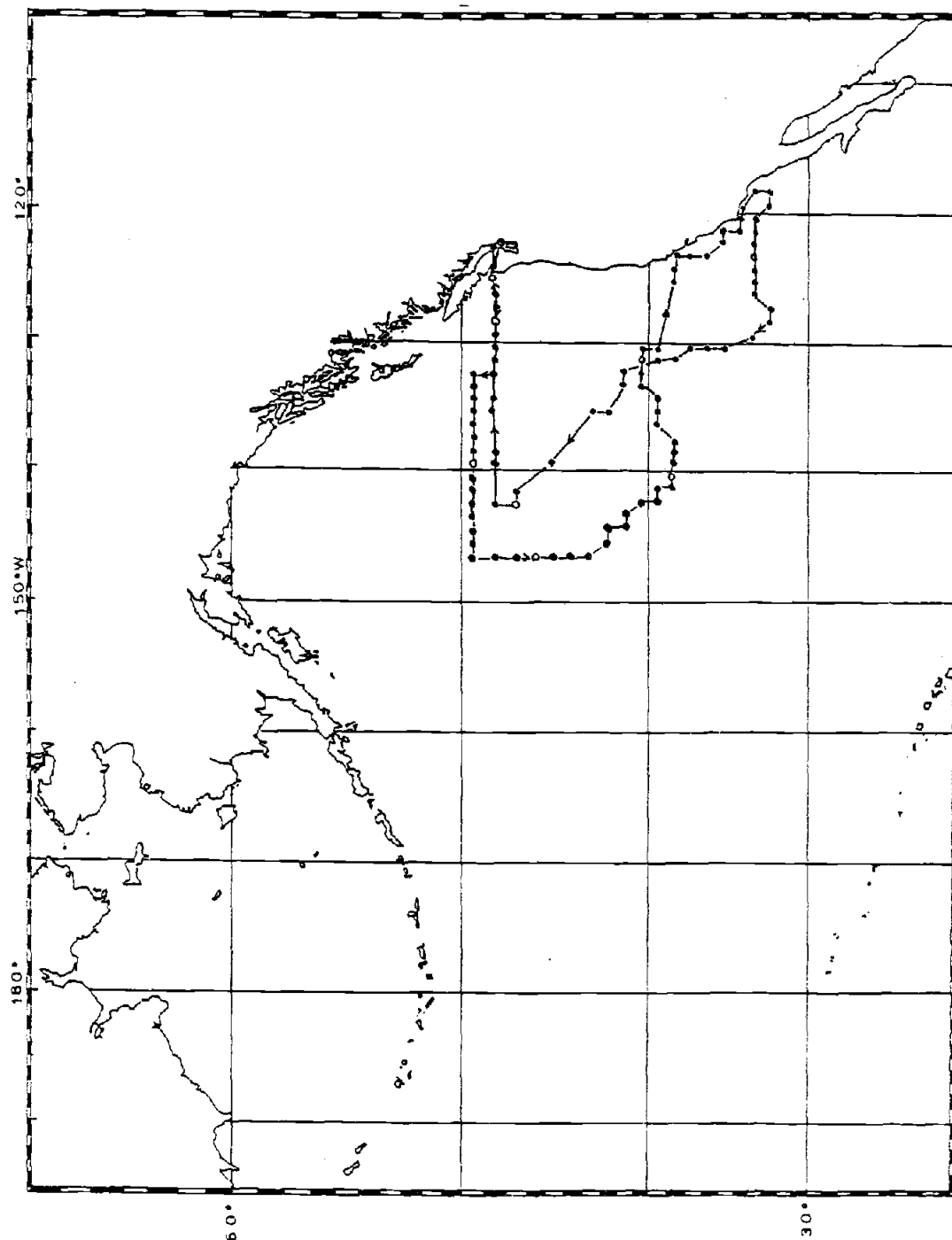
Figure 6. Locations of hauls capturing cephalopods, Brown Bear
cruises 202 (filled circles), 235 (triangles), 236 (filled
squares), and 254 (open circles).
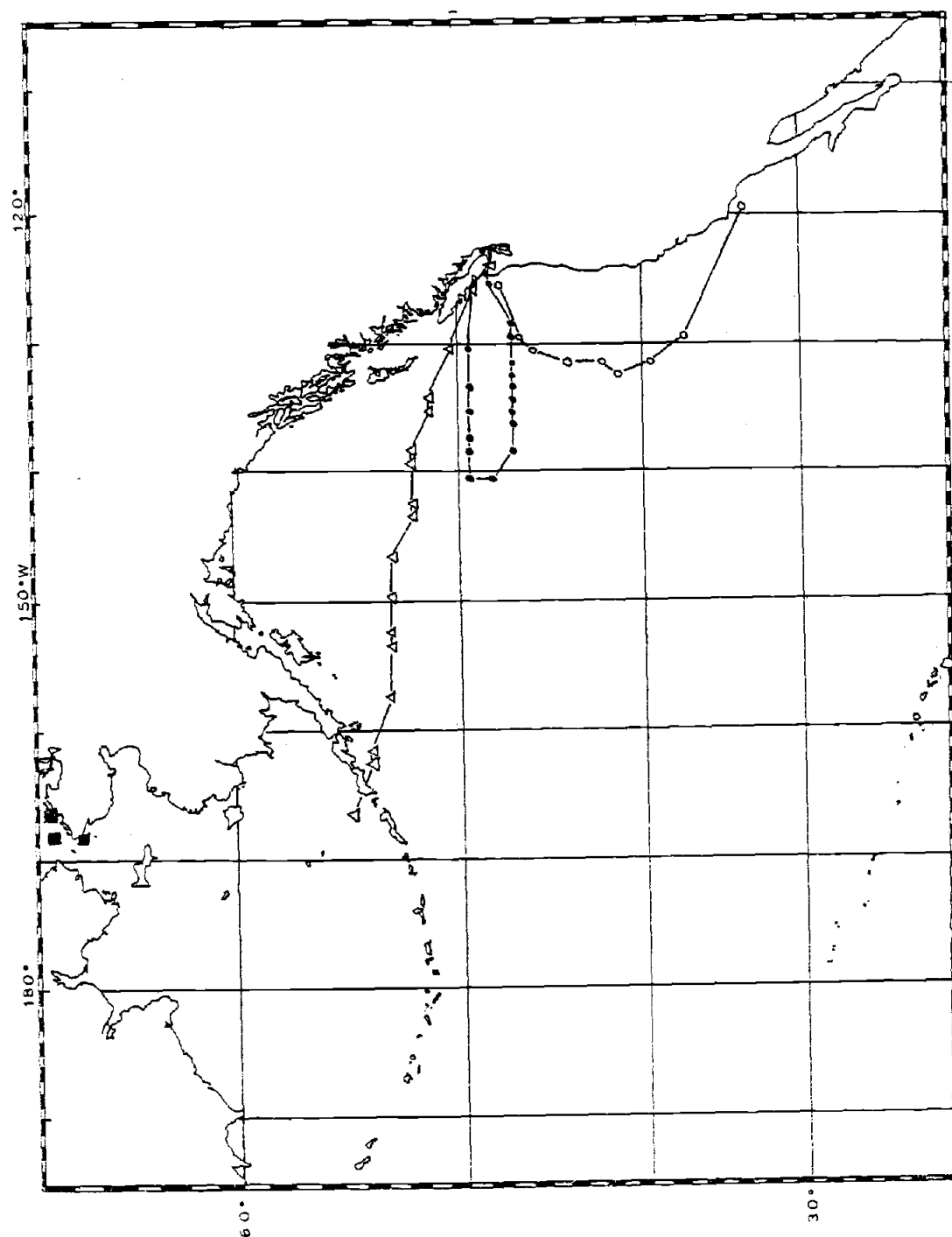
few other depths were sampled). The samples were preserved at sea in 10 % formalin-seawater solution. They were later sorted to major taxon and the cephalopods made available to me along with position, time, and depth information.

A fourth group of samples came from three long ocean cruises (Figure 7 shows cruise tracks). The YALOC 66 cruise (R/V YAquina Long Ocean Cruise, 1966) went northwest from Hawaii to the Aleutian Islands at 177°W, then east to 138°W, south to 44°N, and east to Newport, Oregon. A 1.83 m IKMT (non-closing) and a 3.05 m IKMT+MPS were used. The SICSPAC (Special Interval Cast Study, PACific, 1965), from Newport southwest to 34°N, 142°W, and back, utilized 1.83 m and 3.05 m non-closing IKMTs. The WELOC 76 (WEcoma Long Ocean Cruise, 1976) cruise proceeded west from Newport along 45°N to 160°W, and then south along 160°W to Oahu. Eleven nighttime hauls were made with a 1.83 m non-closing IKMT. Samples from all these cruises were preserved in ten percent formalin-seawater solution at sea and treated identically to samples from the rest of the O.S.U. Nekton sampling program.

A fifth group of samples was collected off the Oregon coast, from the David Starr Jordan during an anchovy survey in the summer of 1977. These animals were collected with a "modified standard Cobb trawl" identical to that used in the rockfish survey. The samples were collected and sorted by personnel from the Southwest Fisheries Center (SWFC), NMFS, La Jolla. They were preserved in 10 % formalin and made available to me along with position, time, and depth data.

Figure 7. Cruise tracks and locations of hauls capturing
cephalopods, long ocean cruises. Open circles YALOC 66; filled
circles, SICSPAC; squares, WELOC 76; filled triangles, FRONTS 80;
open triangles, Nemoto 1978.
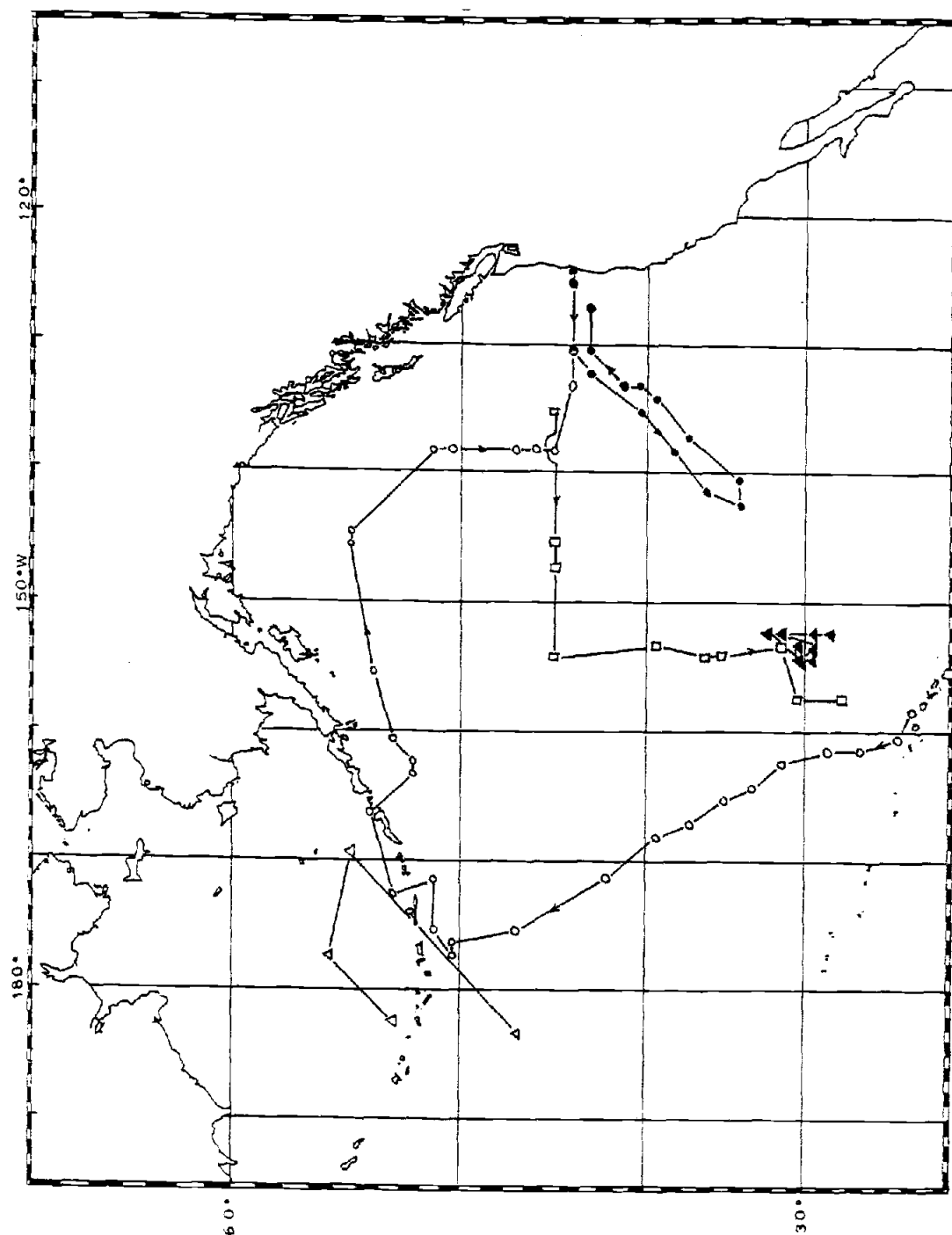
A final group of samples derives from other sampling projects
and occasional or incidental catches using many types of gear.
One sub-group includes a portion of those cephalopods collected by
the O.S.U. Benthos sampling program (A.G. Carey, Jr.) in otter
trawls or beam trawls off the Oregon coast, primarily from
Cascadia Basin and Tufts Abyssal Plain (see Carney, 1977 or
Ambler, 1980 for a description of the sampling program). Voss and
Pearcy (unpubl. MS) described the abyssal octopods; they were
unavailable to me.

A second sub-group includes those cephalopods collected by
the Oregon Department of Fish and Wildlife during their shrimp
survey in 1977. These consist almost entirely of _Loligo_
opalescens, and were collected with a Gulf semiballoon shrimp
trawl. These samples were frozen at sea, and later thawed in the
laboratory and fixed in ten percent formalin. It should be noted
that freezing is often a poor choice of preservational technique when
the whole animal is required for taxonomic work.

The last group is a gallimaufry including incidental and
occasional collections with dipnets, bow and arrow, hook and line,
squid jig, Nansen bottle, strandings, and individual animals saved
by fishermen from their trawl hauls. Included in this group are
cephalopods collected during the High Seas Chum Salmon Tagging
program conducted by T/V _Oshoro_ _Maru_ during the summers of 1967,
1977, and 1980. Squid were recovered from purse seine sets (both
free in the net, and as stomach contents of _Alepisaurus_ _ferox_) and
from surface long-lines. Strandings and those animals collected

by fishermen were already frozen when received, and were subsequently treated like the ODFW shrimp survey samples, above. All others were fixed in ten percent formalin at sea.

Individuals were generally counted on the basis of whole animals. However, if mantle-less heads, or clearly identifiable mantles were present, they were counted on the basis of heads plus excess mantles (that number of mantles greater than the number of heads).

SYSTEMATIC RESULTS

A total of 43,742 cephalopods was taken in 2890 hauls. A geographic survey of these hauls is given in Figure 8. Sampling intensity as a function of maximum depth of samples is shown in Figures 10-14. Total numbers of hauls at each depth interval are as follows: 0-500 m, 2177 hauls; 501-1000 m, 252 hauls; 1001-2000 m, 49 hauls; 2001 m and deeper, 20 hauls; demersal hauls, 390. Twenty-three families are represented, including forty-one genera and sixty-four species (Table 2). A summary of species collected and their length distributions is given in Table 3. Representative specimens have been placed in the Oregon State University Invertebrate reference collection (c/o W.G. Pearcy, School of Oceanography), and given OSUI numbers. A listing of all specimens so referred to is given in Appendix B.

In the following sections, a brief diagnosis is given for each species found, emphasizing the characters which distinguish it from its congeners, especially those occurring in the study area. Unless otherwise stated, family diagnoses for the Teuthoidea follow those of Roper et al. (1969). Specific diagnoses usually follow those of Young (1972); where he did not treat a species found here, or where my results differ from his, the appropriate authourity is cited. In several instances, the diagnoses given here represent a synthesis of several authours' work, in combination with new information. Those for the cirrate octopods are my compilation of information in Hoyle (1885a,b; 1904), Berry (1911), Robson (1926), Sasaki (1929), Grimpe (1933),

and Lipka (1975), with some new information on Opisthoteuthis.
Full descriptions are given for two new species of Gonatidae. The
geographic distributions found in this study are then discussed
and compared with the findings of other workers. A summary is
given of the number of collections made with midwater and demersal
gear, and the depth range of collection. General discussion of
the species within a family follows the specific discussions, with
special regard given to intercomparisons between congeners and
other morphologically similar species.

Figure 8. Density of hauls capturing cephalopods. Open circles, one haul per one degree square; single diagonal hatching, two or three hauls per one degree square; double diagonal hatching, four to six hauls; filled squares, seven or more hauls per one degree square. Triangles indicate locations of salmon gillnet catches of cephalopods (see Figure 9).
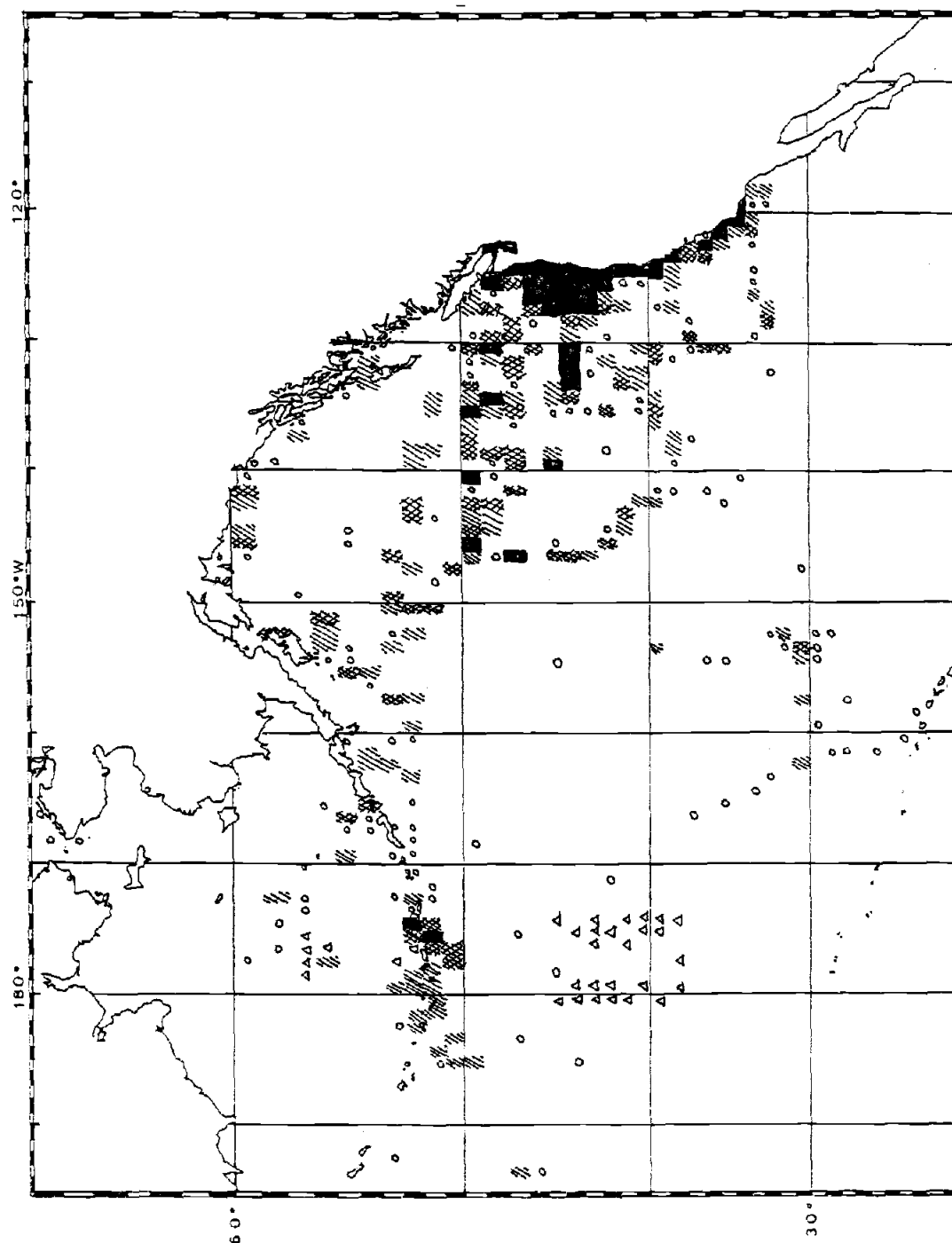
Figure 9. Location of salmon gill net sets by T/V Oshoro Maru
which captured cephalopods in 1978 and 1979 (see Faculty of
Fisheries, Hakodate, 1979, 1980 for more information). Hatching
from lower left to upper right, Onychoteuthis borealijaponicus;
from upper left to lower right, Ommastrephes bartramii; horizontal
hatching, Gonatopsis borealis.
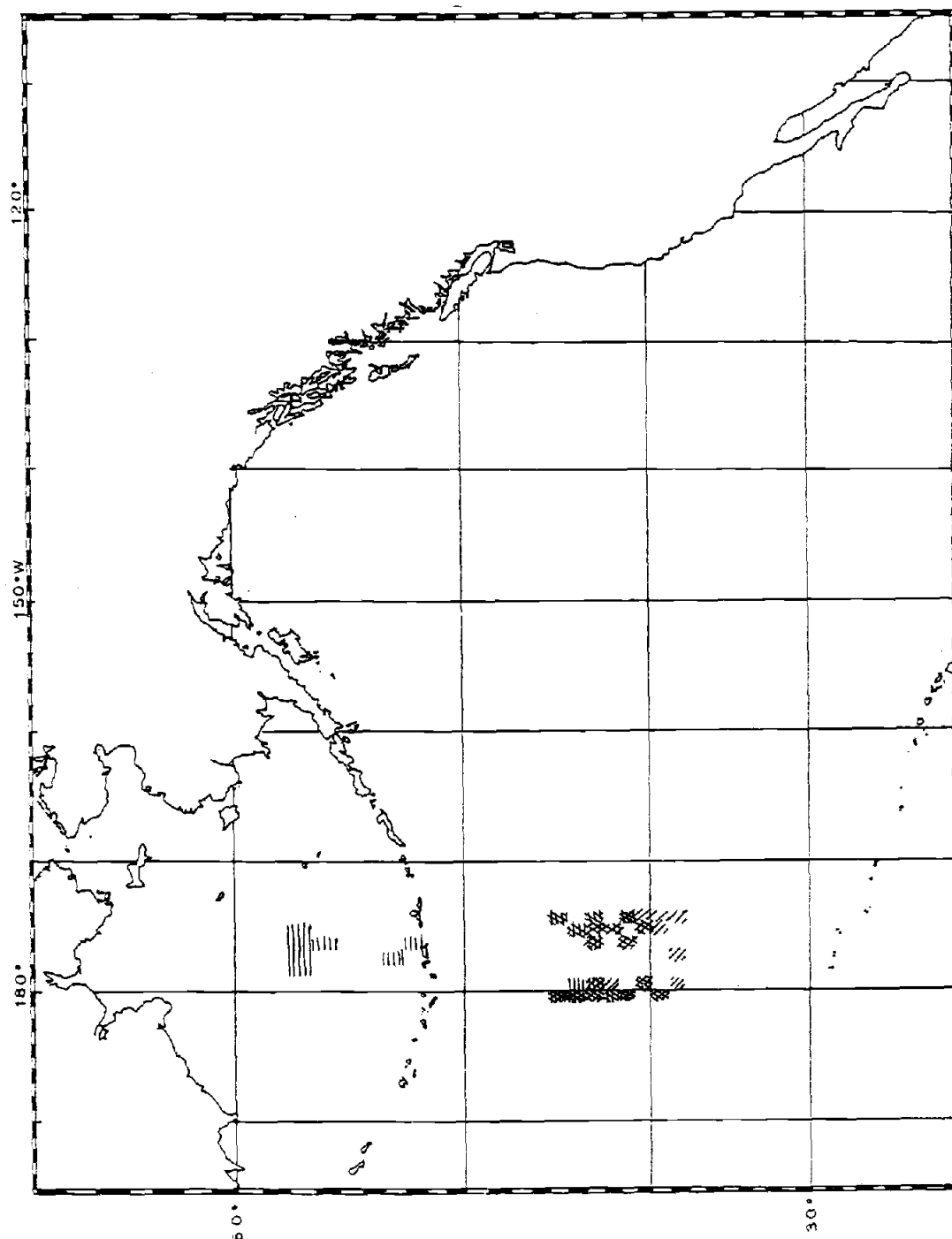
Figure 10. Density of hauls capturing cephalopods between 0 and 500 m (maximum depth of haul). Demersal hauls not included. Symbols as in Figure 8.
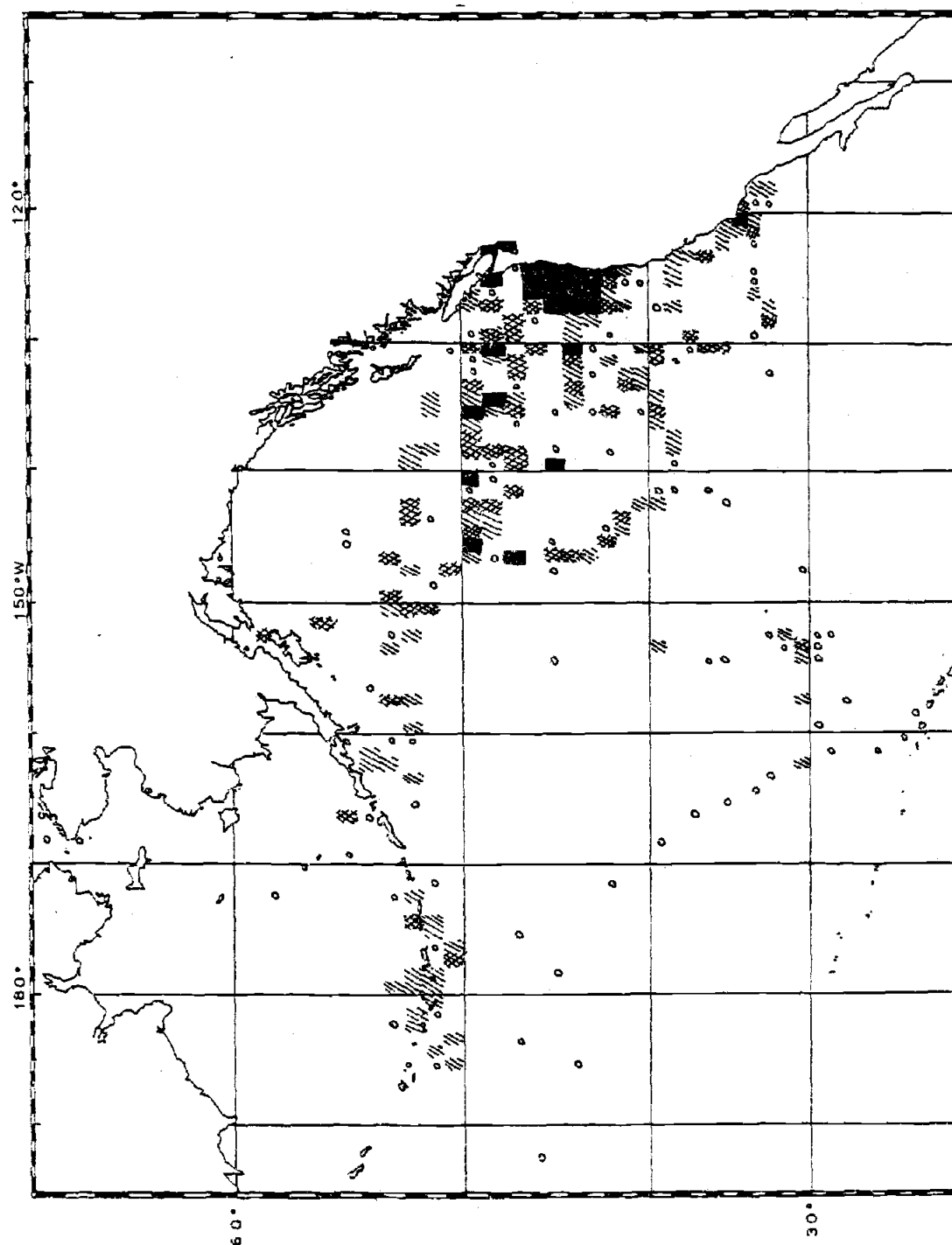
Figure 11. Density of hauls capturing cephalopods between 501 and
1000 m (maximum depth of haul). Demersal hauls not included.
Symbols as in Figure 8.
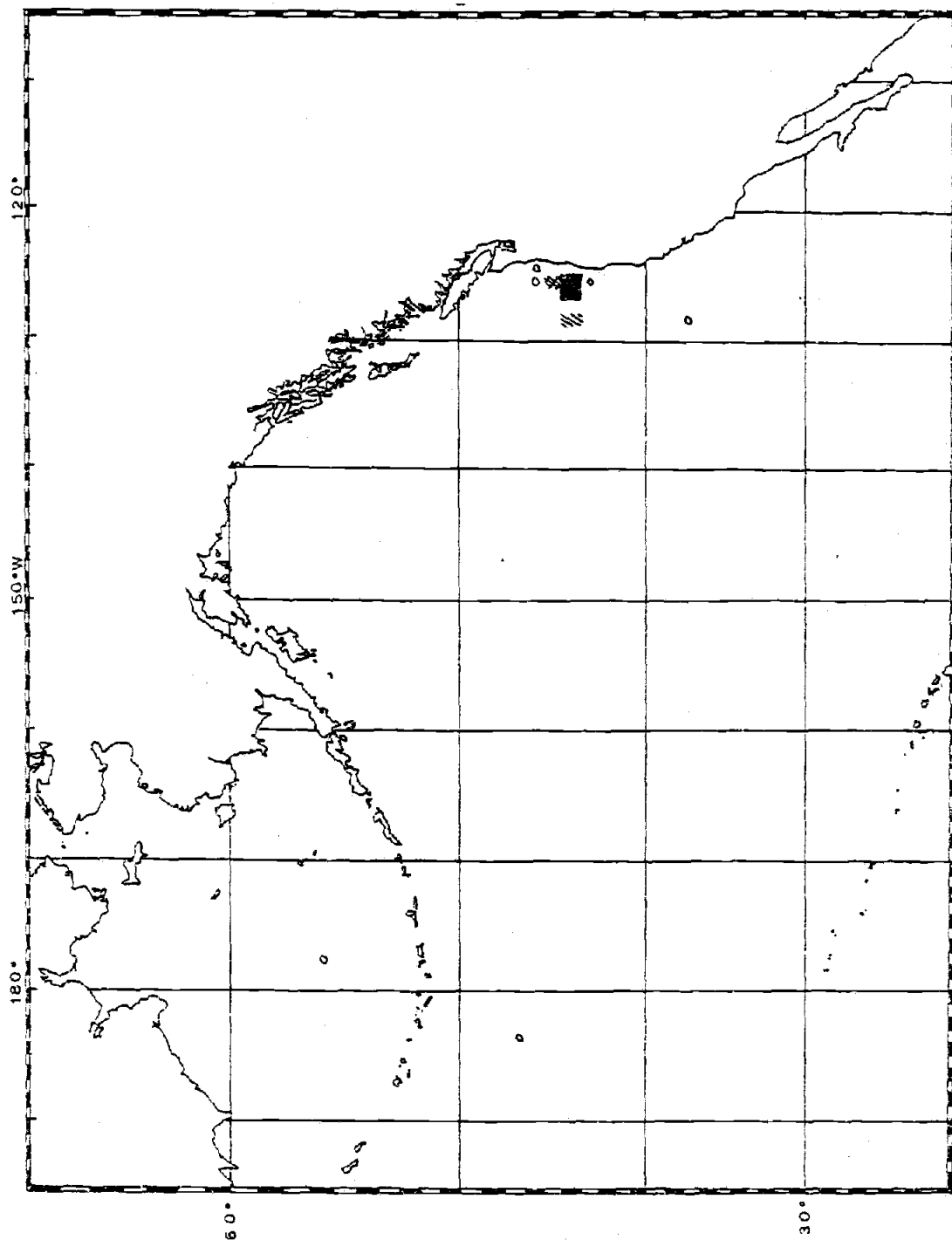
Figure 12. Density of hauls capturing cephalopods between 1001 and 2000 m (maximum depth of haul). Demersal hauls not included. Symbols as in Figure 8.
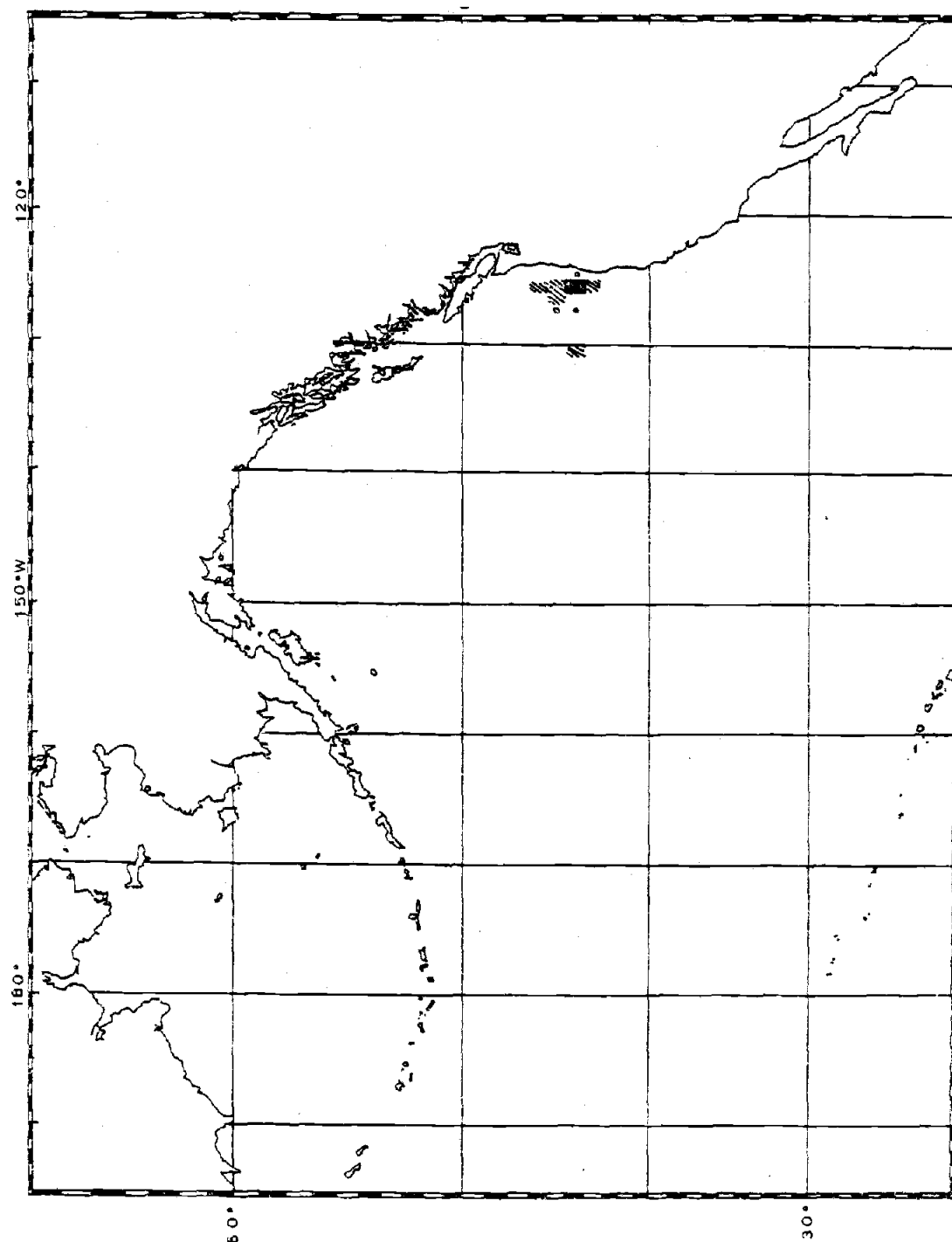
Figure 14. Density of demersal hauls capturing cephalopods.
Symbols as in Figure 8.
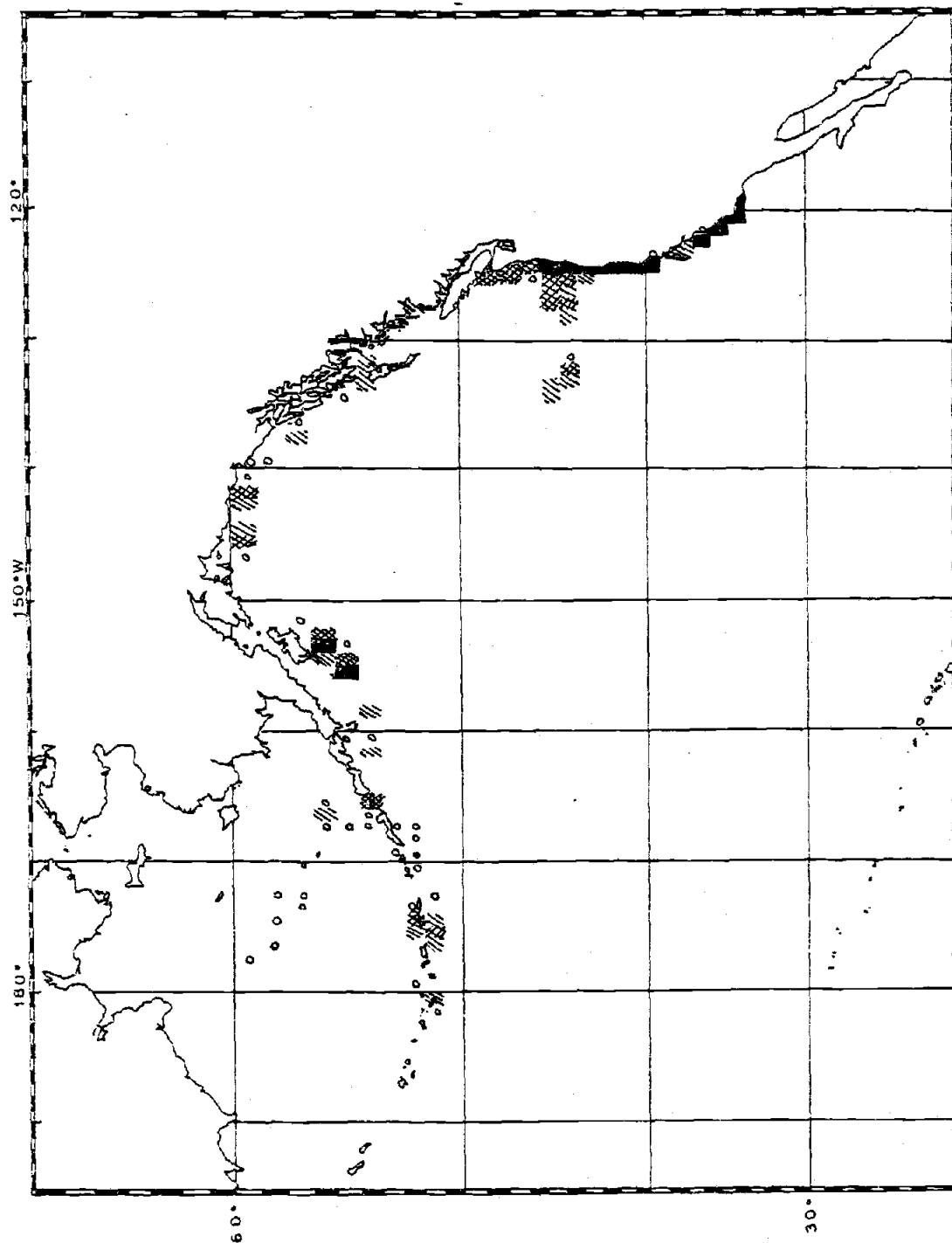
Table 2. Summary of the families and genera collected and
examined in this study.

Order
    Suborder
        Family - Genera

Sepioidea
        Sepiolidae - _Rossia_
Teuthoidea
    Myopsida
        Loliginidae - _Loligo_
    Oegopsida
        Enoploteuthidae - _Abraliopsis_, _Thelidioteuthis_, _Pyroteuthis_,
                          Pterygioteuthis
        Octopoteuthidae - _Octopoteuthis_
        Onychoteuthidae - _Onychoteuthis_, _Onykia_, _Moroteuthis_
        Gonatidae - _Gonatus_, _Gonatopsis_, _Berryteuthis_
        Histioteuthidae - _Histioteuthis_
        Neoteuthidae - _Neoteuthis_
        Bathyteuthidae - _Bathyteuthis_
        Ctenopterygidae - _Ctenopteryx_
        Brachioteuthidae - _Brachioteuthis_
        Ommastrephidae - _Ommastrephes_, _Dosidicus_, _Symplectoteuthis_
        Chiroteuthidae - _Chiroteuthis_, _Valbyteuthis_
        Mastigoteuthidae - _Mastigoteuthis_
        Cranchiidae - _Cranchia_, _Leachia_, _Taonius_, _Sandalops_,
                      Helicocranchia, _Galiteuthis_, _Megalocranchia_
Octopoda
    Cirrata
        Cirroteuthidae - _Cirroteuthis_, _Cirrothauma_
        Stauroteuthidae - _Stauroteuthis_
        Opisthoteuthidae - _Opisthoteuthis_
    Incirrata
        Bolitaenidae - _Japetella_, _Eledonella_
        Octopodidae - _Octopus_
        Tremoctopodidae - _Tremoctopus_
        Ocythoidae - _Ocythoe_
Vampyromorpha
        Vampyroteuthidae - _Vampyroteuthis_

Table 3. Species of cephalopods examined, and their size distribution.

Species	0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	101-110	111-120	121-130	131-140	141-150	150+	TOTAL[b]
Rossia pacifica	3	7	18	20	9	3				1							64
Loligo opalescens		1	3	9	71	116	230	301	248	123	72	42	34	6	4	4	8479
Abraliopsis falco	17	13	5	1													36
Abraliopsis felis	479	885	364	207	167	36											2318
Abraliopsis hoylei		3	2														5
Abraliopsis pfefferi		7	4														11
Thelidioteuthis alessandrinii			1														1
Pyroteuthis addolux	24	51	20	8													104
Pterygioteuthis gemmata	15	14	5	2													39
Octopoteuthis deletron	15	48	58	79	51	37	28	21	7	7	5	4	5	5	3	6	429
Onychoteuthis banksii								3	1								4
Onychoteuthis borealijaponicus	67	65	27	4	3	3	4	2	1	2	2	2	4	7	1	17	231
Onykia carribaea	4																4
Moroteuthis robusta																33	33
Gonatus berryi	26	77	40	15	3	4	2			1							180
Gonatus californiensis			5		1	1		1									8
Gonatus madokai	14	71	43	16	1	1		1					1			1	192
Gonatus middendorffi		2		21	15	5	7	1								3	54
Gonatus onyxa	631	3459	2405	1244	951	382	82	12	1	3	1				1		15,917
Gonatus pyros	13	468	481	153	53	16	9										1231
Gonatus sp. A		9	8														22
Gonatus sp. E		1	5	3	1												10
Gonatus type C	71	49															126
Gonatopsis borealis	181	331	113	40	21	7	2	2	2		2	1	5	1	6	10	755
Gonatopsis okutanii															1		1
Berryteuthis anonychus	190	437	16	6	17	1	10	17	16	6							757
Berryteuthis magister	47	118	35	4		6	14	8	9	8	12	7	5	9	2	81	478
Histioteuthis corona berryi			1														1
Histioteuthis dofleini	16	25	8	4	3	1	1			1		1	2	1	1	1	67
Histioteuthis heteropsis	2	12	2	3	5	11	34	25	8	2							108
Neoteuthis sp.			1														1
Bathyteuthis abyssicola		2	1														3
Bathyteuthis berryi		1			1												2
Bathyteuthis sp.		1															1
Ctenopteryx sicula	2	2	1		1												6
Brachioteuthis sp.	1	1															2
Ommastrephes bartramii									1					2	2		5
Dosidicus gigas															3		3
Symplectoteuthis luminosa			1	2		1					2		1				7
Chiroteuthis calyx	11	234	630	754	737	273	38	13	4	5	1	2					2865
Chiroteuthis joubini			2	1	1												4
Valbyteuthis oligobessa							3										3
Mastigoteuthis dentata					1			2									3
Mastigoteuthis pyrodes				1	2	1											4
Cranchia scabra	2	3	3	4													12
Leachia dislocata	5	21	19	12	9	5	7	8	3	1		1					93
Taonius pavo	18	189	213	125	50	40	34	24	29	59	85	47	19	8	10	23	1006
Sandalops melancholicus		1															1
Helicocranchia pfefferi	3	6	1		1												11
Galiteuthis phyllura	11	129	197	184	53	19	10	11	2	5	9	7	2	3		16	694
Megalocranchia speculator	1	1	7	5													14
Cirroteuthis sp.				1		1			1								3
Cirrothauma murrayi			1	1								1					3
Stauroteuthis sp.				1	1			1									3
Opisthoteuthis californiana		1	11	13	4	8	1	3		1							49
Japetella heathi	1169	849	265	124	67	51	15	18	6	5	3						2664
Japetella sp. Young 1972								1	1								2
Eledonella pygmaea				1				1									2
Octopus spp.	381	37	30	20	16	25	32	21	22	12	9	4	4	1	2	7	636
Octopus sp. A	26	1															27
Octopus sp. B	3																3
Tremoctopus violaceus	1																1
Ocythoe tuberculata	2																2
Vampyroteuthis infernalis	1	10	9	5	5	5	7	10	10	14	6	5	1	1			90

	39,892
Individuals not identifiable to species due to mutilation or larval condition:	3,850
GRAND TOTAL:	43,742

aSeveral large collections of G. onyx were subsampled; all individuals were counted, but only the subsamples measured.
bTotal includes heads and unmeasured individuals.

Order SEPIOIDEA Naef, 1916

Shell coiled and chambered (Spirulidae), straight with
vestigial chambering (Sepiidae), vestigial, or lacking; eyes
covered by a corneal membrane; eight arms armed with suckers only;
two retractile tentacles.

Family SEPIOLIDAE Leach, 1817

Internal shell rudimentary: gladius thin, straight, and
non-calcified, or absent. Fins round, separately dorsolaterally
attached. Tentacles retractile into sheaths. (See Akimushkin
(1963) for further details).

Rossia pacifica Berry, 1911

Both dorsal arms of male hectocotylized; no photophores;
brachial armature biserial proximally, quadriserial distally. Arm
suckers all of roughly equal size. Tentacle suckers smaller than
brachial suckers and arranged in six to eight rows. (See
Akimushkin, 1963).

Sixty-four animals were collected in forty-two hauls (six
midwater, close inshore; the remainder demersal) inshore of the
California and Alaska Currents, and in shallow waters of the
Bering Sea (Figure 15). The species is known around the Pacific
rim from Japan through the Bering Sea to California (Berry, 1911,
1912b; Sasaki, 1920,1929; Kondakov, 1941; Akimushkin, 1963).

Figure 15. Location of hauls capturing <u>Rossia</u> <u>pacifica</u>. In this
and all subsequent zoogeographic figures, only one symbol is
included for all hauls within a one degree square.
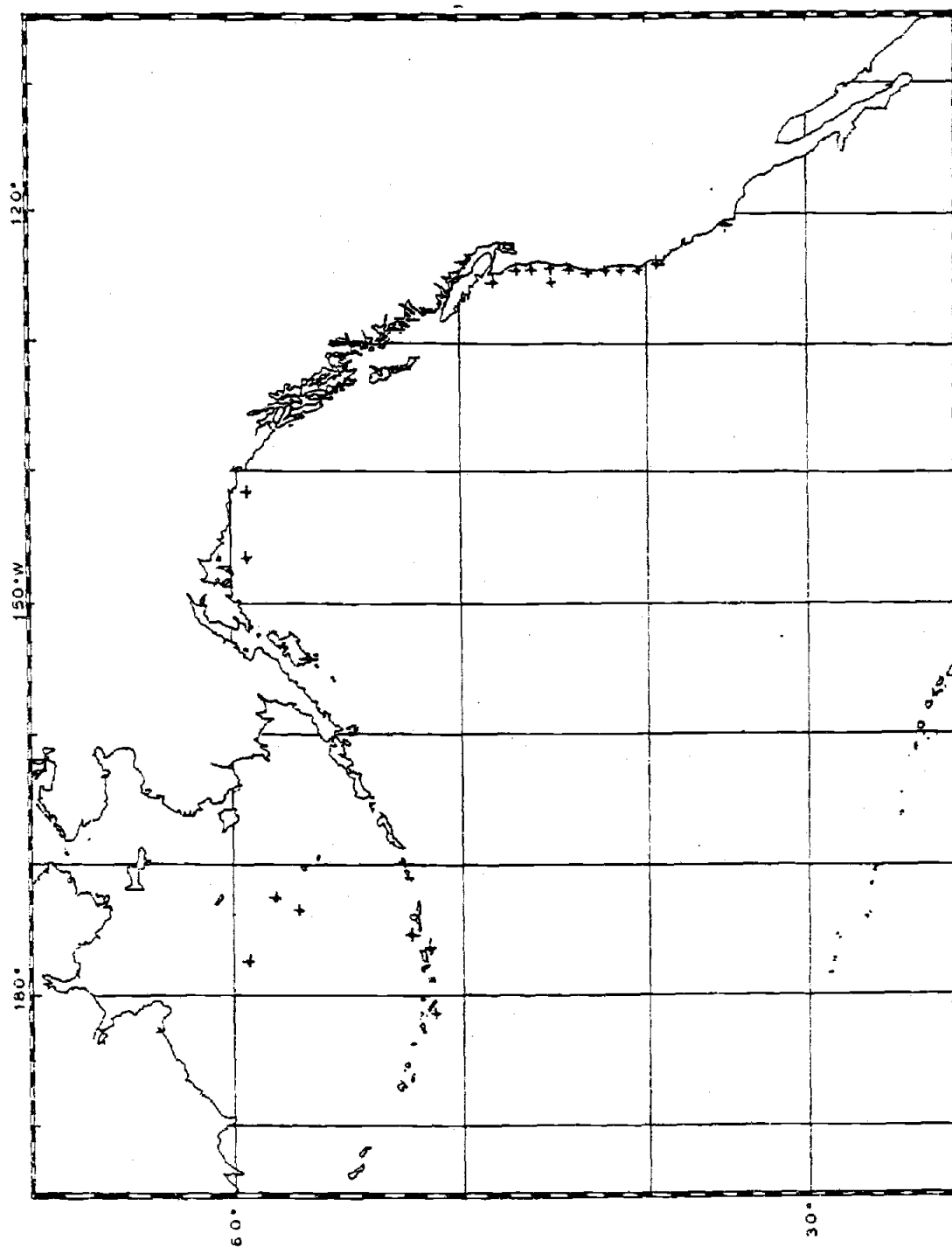
Order TEUTHOIDEA Naef, 1916

Shell reduced to a thin, horny gladius. Eight arms; two contractile tentacles.

Suborder MYOPSIDA d'Orbigny, 1845

Eyes covered by a corneal membrane. Neritic forms.

Family LOLIGINIDAE Steenstrup, 1861

Characterized by a corneal membrane covering the eyes; simple, straight funnel-locking cartilage; buccal connectives which attach ventrally to arms IV; biserial brachial and quadriserial manus armature; and posteriorly united fins.

Loligo opalescens Berry, 1911

Left ventral arm of male hectocotylized; only suckers of the distal third of the arm are modified by having elongate and flattened stalks, and being much reduced in size; dorsal row the most modified (see Berry, 1912b for figure and description).

A total of 8479 individuals was collected, in ninety-one hauls (both demersal and midwater) in coastal waters (Figure 16). This species is a neritic form, and was never taken in areas where the water depth exceeded 460 m. Its recorded distribution is from Baja California (Punta Eugenia) to Dixon Entrance (55°N) (Fields, 1965; Bernard, 1970).

Figure 16. Location of hauls capturing <u>Loligo opalescens</u>. The species has been recorded throughout the shaded area.

Suborder OEGOPSIDA d'Orbigny, 1845

Eye in direct contact with sea water, completely surrounded by a muscular eyelid. Open ocean forms inhabiting all depths.

Family ENOPLOTEUTHIDAE Pfeffer, 1900

Characterized by a simple, straight funnel-locking apparatus; biserial brachial armature, with hooks; tetraserial club armature, usually with hooks; buccal connectives which attach dorsally to arms IV; and the presence of photophores.

Subfamily ENOPLOTEUTHINAE Pfeffer, 1912

Characterized by the absence of nidamental glands; the presence of small photophores on the surface of the mantle, head, and arms, but not in the tentacles or on the viscera; and having fins with concave posterior borders.

Genus _Abraliopsis_ Joubin, 1896

Arms IV with two to four large dark photophores at tips. Clubs with two rows of hooks.

Subgenus _Micrabralia_ Pfeffer, 1900

Photophores on the ventral surface of head arranged in distinct rows.

Abraliopsis falco Young, 1972

A single row of photophores in the midventral area of the head; no keel or swimming membrane on the club, which bears five to eight hooks in two rows. Circumocular photophores number 48 to 63.

Thirty-five individuals (3-32 mm DML) were collected from nine hauls in central Pacific waters (all midwater hauls to 225 m or less) (Figure 17). An additional specimen (21 mm DML) was recovered at 9°58'S, 98°00'W (midwater trawl, 0-200 m). The species has previously been recorded (Young, 1972) from off Baja California (28-30°N, 114-122°W) and north of Hawaii (one specimen at 24°N, 151°W). The present collections therefore represent northward and southward range extensions, as well as a great increase in the number of known specimens (from eleven to forty-seven). Nesis (1973b) listed the southern limit of this species as Peru.

Subgenus *Abraliopsis* Joubin, 1896

Photophores arranged in a diffuse pattern on the ventral surface of the head.

Abraliopsis felis McGowan and Okutani, 1968

No semicircular membrane on the ventral margin of the club; indistinct keel on the distal half of the dactylus; six to eight hooks on the club; thirty to thirty-one circumocular photophores.

Figure 17. Capture locations of <u>Abraliopsis falco</u>. An additional specimen was taken at 10 °S, 98 °W. Previous records shown as triangle and shaded area (see text).
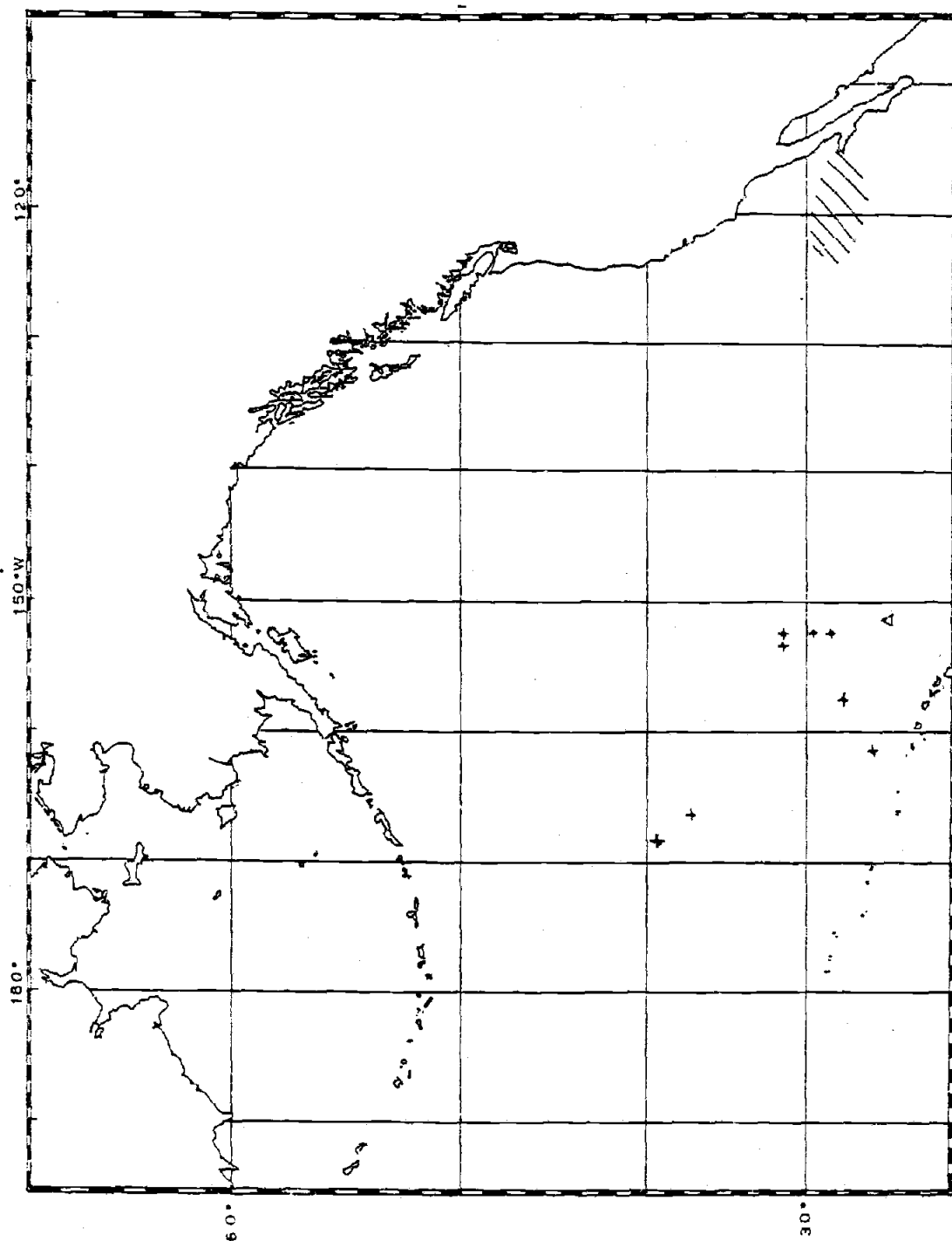
This species was collected in abundance in the California Current system and Transition Zone (Figure 18). A total of 2318 individuals (3-60 mm DML), representing 5.3% of all cephalopods, was collected in 704 hauls (25% of all hauls capturing cephalopods). All but four hauls were midwater; the species was consistently taken in closed nets as deep as 500-1000 m. It is obviously an important component of the cephalopod fauna of this area. The species has previously been recorded along the west coast of North America from 27° to 43° N (McGowan and Okutani, 1968; Anderson, 1978) and, in the southernmost part of its range, as far west as 147°W (Young, 1972). My samples did not include the southern limits of the species, but they do show marked extensions to the known geographic distribution: northward to at least 50°N and westward to 172°W.

Abraliopsis ? _hoylei_ (Pfeffer, 1884)

Diffuse photophores on the ventral surface of the head; club with keel. Known only from the original description (Pfeffer, 1884, 1912). The characters of my specimens do not precisely fit those of _A. pfefferi_, and the description of _A. hoylei_ is inadequate for positive identification. A semicircular membrane and keel are present on the club in my specimens, and the club bears eight hooks. The fins are 81% of the mantle in length, and 119% in width. Approximately 42 photophores surround the eye, and the midventral strip of the mantle lacking photophores does not extend to either the anterior or posterior end of the mantle.

Figure 18. Location of captures of _Abraliopsis felis_. Previous records shown as shaded area (see text).
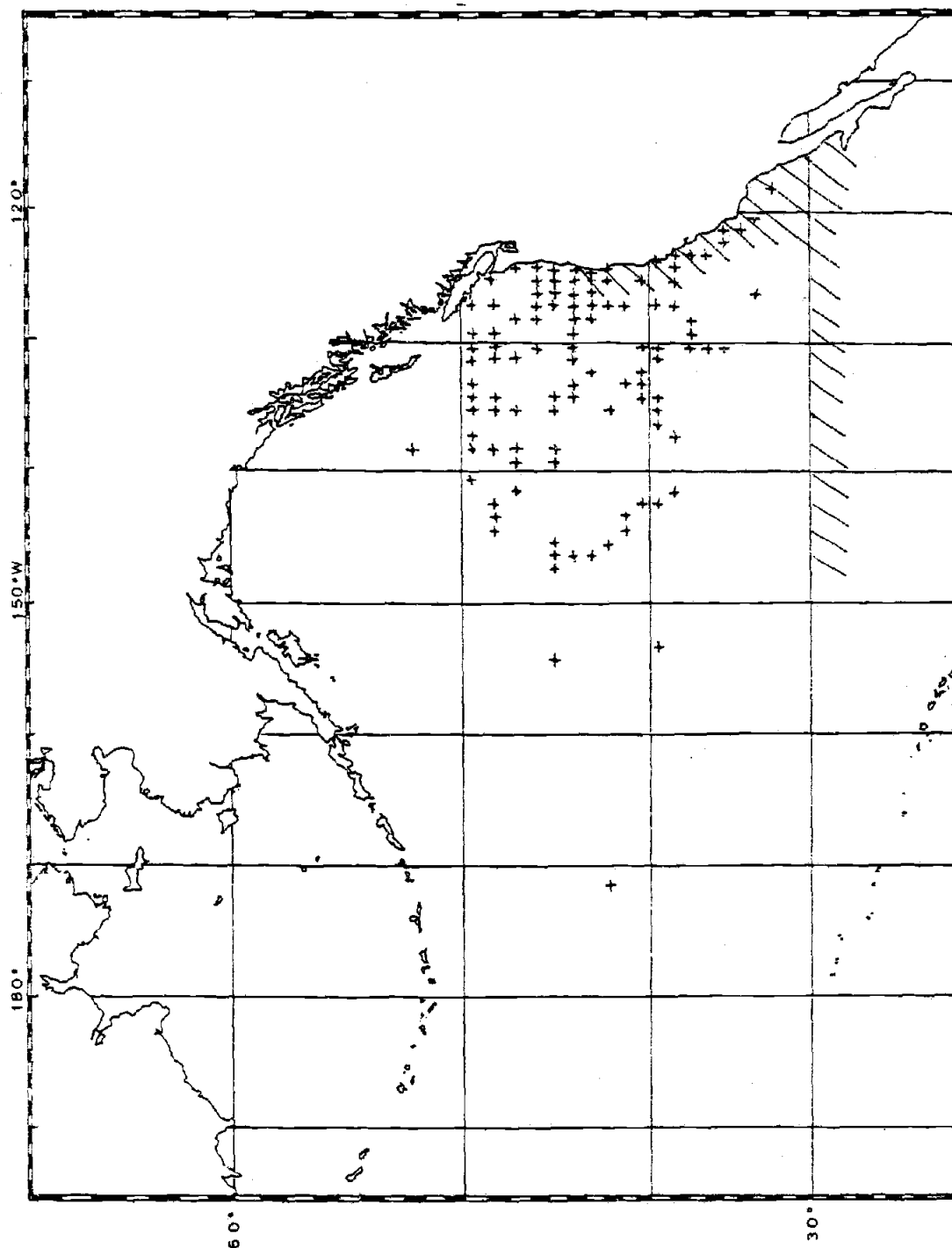
Young (1972) gave an elucidative discussion on the species.

Five specimens believed to belong to this species were collected in two central Pacific hauls (midwater, 0-250 m) (Figure 19). The species was originally described from the Indian Ocean; collections tentatively identified as A. hoylei have been made off eastern Australia, and in the Kermadec Islands (Clarke, 1966; Young, 1972).

These specimens ranged in length from 13 to 30 mm DML (OSUI 801-805); the original description listed a mantle length of 31 mm (Pfeffer, 1884).

<u>Abraliopsis</u> <u>pfefferi</u> Joubin, 1896

Diffuse pattern of photophores on the ventral surface of the head. Semicircular membrane and keel on tentacle club, which bears ten to twelve hooks. About 44 to 46 photophores around the margin of the eye.

Eleven individuals (12-29 mm DML; OSUI 806-816) were collected in three central Pacific hauls (midwater, 0-70, 0-200, 0-2400 m) (Figure 19). The species is known from the Mediterranean, Atlantic, and eastern Indian Oceans (Clarke, 1966; Young, 1972; Clarke and Lu, 1974; Cairns, 1976). If my specimens prove to belong to this species, they will represent the first records for the Pacific Ocean.

Figure 19. Capture sites of <u>Abraliopsis hoylei</u> (crosses), <u>A.</u>
<u>pfefferi</u> (circles), and <u>Thelidioteuthis alessandrinii</u> (square,
previous record shown as triangle).
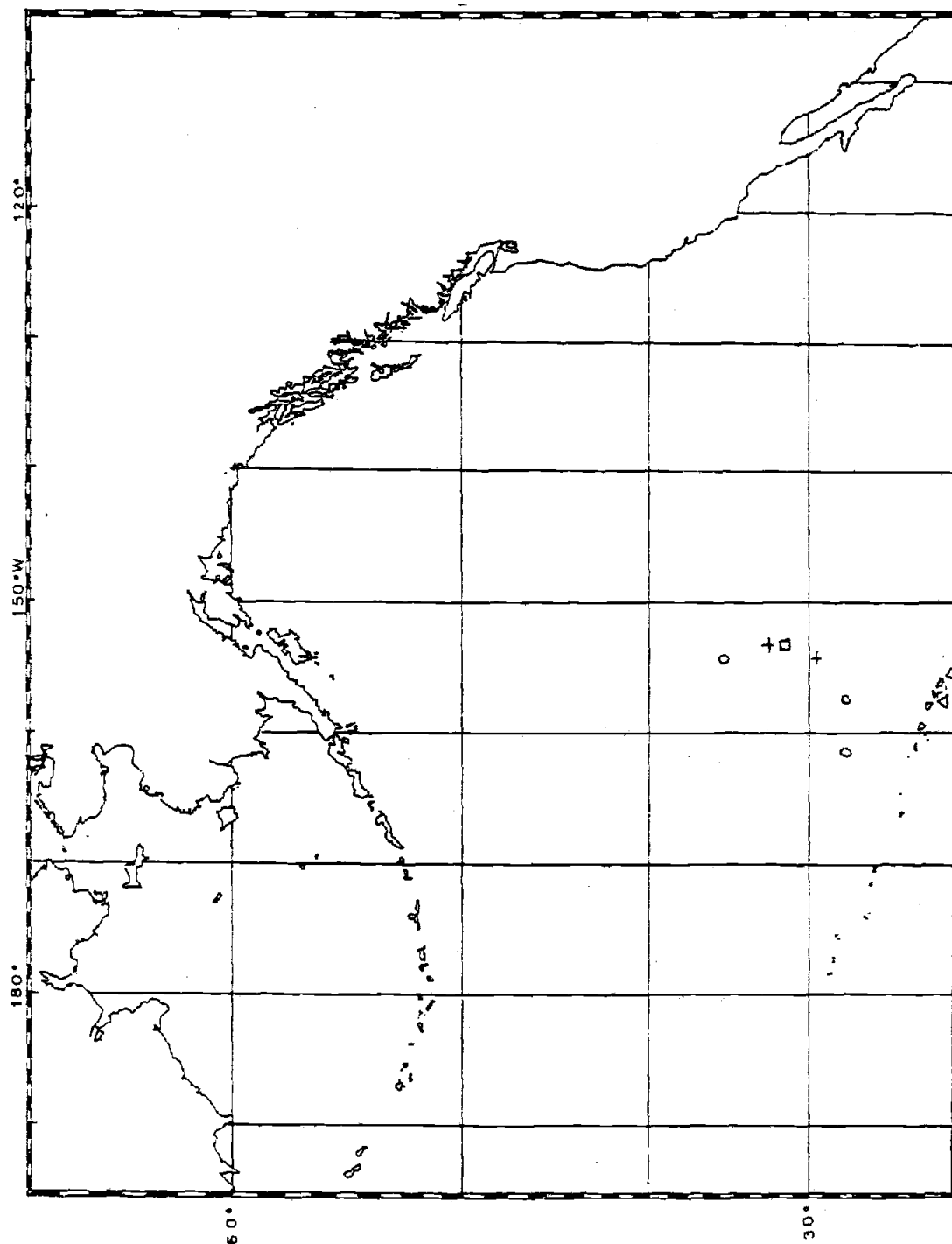
Subfamily ANCISTROCHEIRINAE Pfeffer, 1912

Characterized by the possession of nidamental glands; very large fins with convex posterior borders; and a few large photophores on the surface of the mantle, head, and tentacles, but not on the arms or viscera.

Thelidioteuthis alessandrinii (Vérany, 1851)

Very large fins, at least 80% of mantle length. Hooks on arms and tentacle clubs. Large ventral photophores on mantle number twenty, in seven transverse rows, alternating four and two photophores per row. Fourteen large photophores on head, and two on dorsal side of body. Tentacles and arms also with large and small photophores. See Chun (1910), Berry (1912d), Pfeffer (1912), and Sasaki (1929) for further information.

One specimen (29 mm DML; OSUI 757) was recovered from a haul in central Pacific waters (midwater tow, 0-70 m) (Figure 19). The species has previously been recorded from the Mediterranean Sea, North and South Atlantic, the Indian Ocean, near Malaysia, off Tahiti, off Japan (Clarke, 1966), and off Hawaii (Young, 1977). Its distribution is thus cosmopolitan in tropical and subtropical latitudes.

Subfamily Pyroteuthinae Pfeffer, 1912

Characterized by the presence of nidamental glands; photophores only on the viscera or embedded in the tentacles; and having fins with convex posterior borders.

Pyroteuthis addolux Young, 1972

Hooks present on clubs; seven photophores embedded in the tentacular stalk.

A total of 104 individuals (4-38 mm DML) was taken in 23 hauls in transitional and central Pacific waters (all midwater tows, mostly 0-225 m, two individuals in 0-2400 m hauls) (Figure 20). Relatively few specimens and collection locations were previously known: 20 from Young's (1972) southern California study area; one each at 26°N, 147°W and 32°N, 133°W; and 161 individuals from 21°N, 158°W (Young, 1978). The first 22 animals were taken in area south and east of the present collections and Young's (1978) samples; the latter are most likely closer to the centre of abundance for this species. Pyroteuthis addolux appears to be a major component of the cephalopod fauna in North Pacific central waters.

Pterygioteuthis gemmata Chun, 1908

No hooks on clubs; hooks only in ventral rows of arms I, II, and III. Fourteen ocular photophores.

Thirty-nine individuals (5-33 mm DML) were recovered in 24 hauls in the southern California Current and central Pacific waters (midwater tows, 0-225 m, night, and 0-400 m, day) (Figure 21). The species is known from the North, equatorial, and South Atlantic, the Indian Ocean, off southern California, off Hawaii (if P. microlampas proves to be synonymous), and in the

Figure 20. Location of hauls capturing _Pyroteuthis addolux_.
Previous records shown as triangles and shaded area.
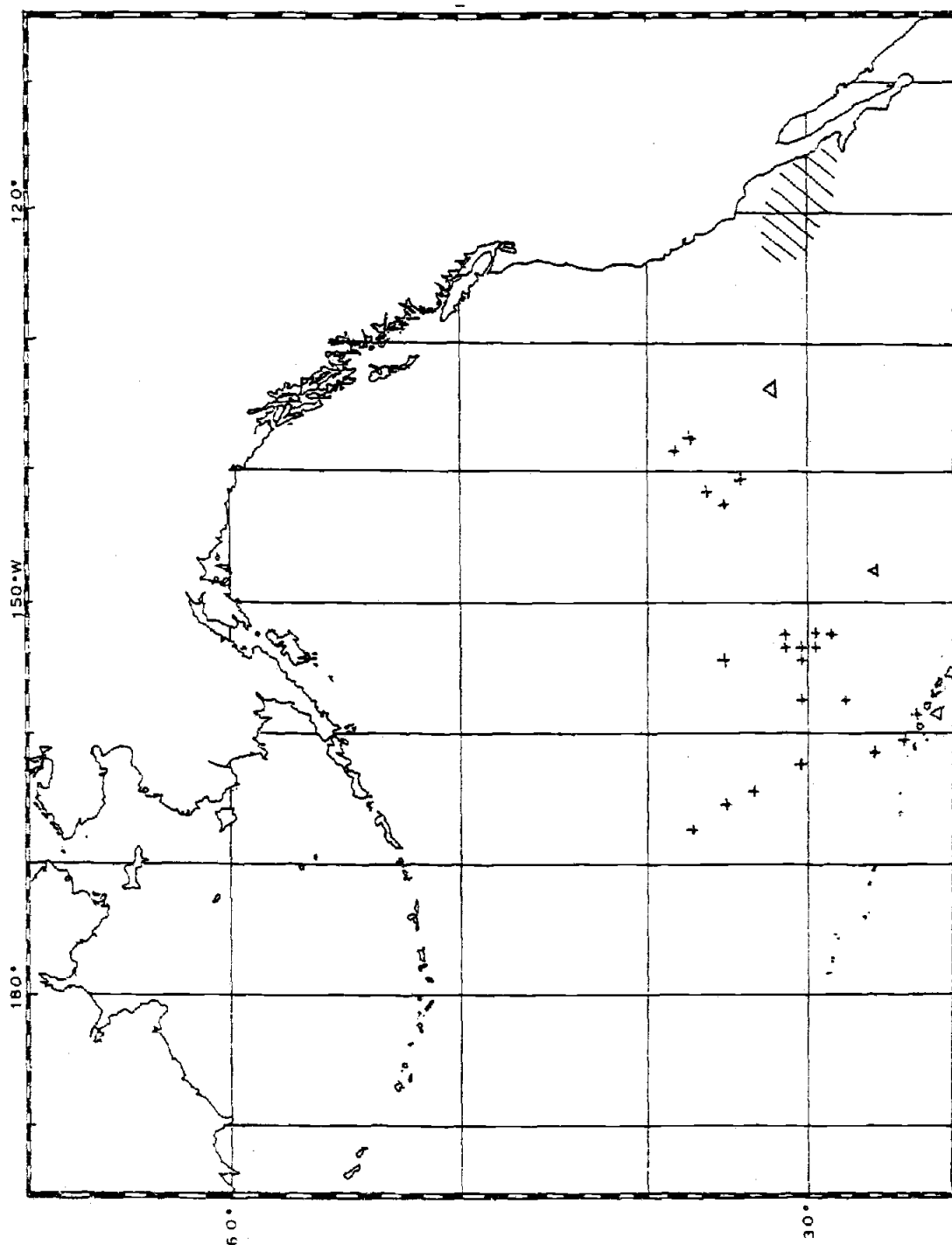
subtropical convergence of the South Pacific (Berry, 1914; Clarke, 1966; Young, 1972, 1978; Nesis, 1973a,b; Cairns, 1976). Its distribution is probably antitropical in the Pacific (Nesis, 1973a). The present specimens represent a slight northerly range extension.

Summary - Family ENOPLOTEUTHIDAE

Seven species, comprising 2526 individuals, were identified in this study. Abraliopsis felis was by far the most important numerically, occurring in 25% of all hauls which captured cephalopods. The second most abundant species, Pyroteuthis addolux, occurred in 57% of central Pacific hauls. Abraliopsis felis, like Chiroteuthis calyx, is limited to the California Current system and transitional waters, rarely occurring north of 50°N. On the other hand, Pyroteuthis addolux seems to be limited to North Pacific Central waters.

The genus Abraliopsis is represented by four species in this study: the three belonging to the subgenus Abraliopsis (felis, pfefferi, and hoylei); and one of three in the subgenus Micrabralia (falco). Abraliopsis falco, A. pfefferi, and A. hoylei all appear to be central water species; Abraliopsis falco appears to be an important component of that fauna. Abraliopsis falco is herein first reported from the South Pacific.

Pterygioteuthis gemmata and Pyroteuthis addolux have rather similar geographic distributions, being known from central waters

as well as off the southern California coast. _Thelidioteuthis_
alessandrinii probably occurs circumglobally in low latitudes.

Family OCTOPOTEUTHIDAE Berry, 1912
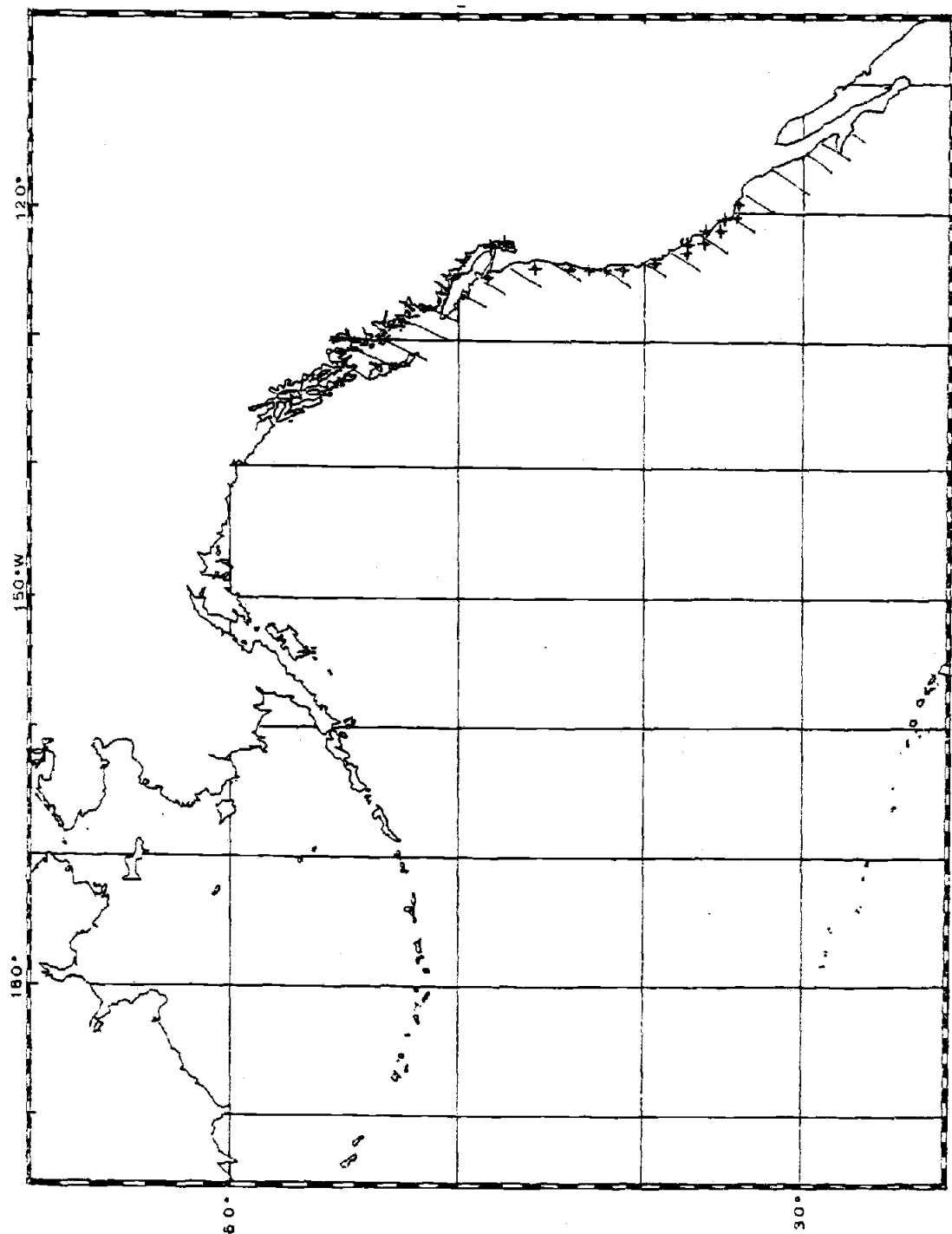
Characterized by a simple, straight funnel-locking cartilage;
buccal connectives which attach ventrally to arms IV; biserial
brachial armature (hooks, which are replaced by suckers at the arm
tips); the absence of tentacles in adults; and the presence of
photophores.

Octopoteuthis deletron Young, 1972

Possessing a single postero-abdominal photophore, a very
short tail (mantle does not project appreciably beyond the
posterior border of the fins), and well developed accessory teeth
on arm hooks.

A total of 429 individuals was collected, in 254 hauls (7
demersal tows, at 340-460 m, 1900 m maximum; in closed midwater
tows as deep as 1000-1600 m, and 0-2200 m in open tows) in the
California Current system and transitional waters (Figure 22).
This species has been recorded from the California Current between
30° and 34°N, and off Oregon (Young, 1972). One specimen from off
Peru (8°S, 82°W - Young, 1972) most likely belongs to this
species. There is thus some possibility that this species has a
bitemperate distribution. Another species, _O. nielseni_, is known
from waters off western Panama. _Octopoteuthis deletron_ has not
been recorded north of 48°N; it appears that the California

Figure 22.   Location of hauls which captured _Octopoteuthis deletron_.   Previous records shown as shaded area.

Current system proper defines its distribution in the northern hemisphere.

Family ONYCHOTEUTHIDAE Gray, 1849

Characterized by a simple, straight funnel-locking apparatus, buccal connectives which attach dorsally to arms IV, biserial brachial armature and (usually) tetraserial club armature, the median two rows of which are hooks. Nuchal (occipital) folds are present.

Onychoteuthis banksii (Leach, 1817)

A single photophore on the ventral surface of the eye; nineteen to twenty-three hooks on the club; two well separated anal and intestinal photophores with no intervening iridescent tissue.

Onychoteuthis banksii probably represents a species complex (Young, 1972); as such, published distributions are probably of little value. The "species" is reported to occur worldwide, from the Bering Sea to Cape Horn (Clarke, 1966).

Four individuals (70, 74, 76, 88 mm DML; OSUI 322, 323, 330, 398), clearly distinguishable from *O. borealijaponicus*, were collected at three dipnet stations north of Hawaii (Figure 23).

Figure 23. Location of hauls which captured Onychoteuthis banksii
(squares) and O. borealijaponicus (crosses; triangles represent
captures of O. borealijaponicus by T/V Oshoro Maru; other previous
records shown as shaded areas; salmon gillnet data represented by
x's).
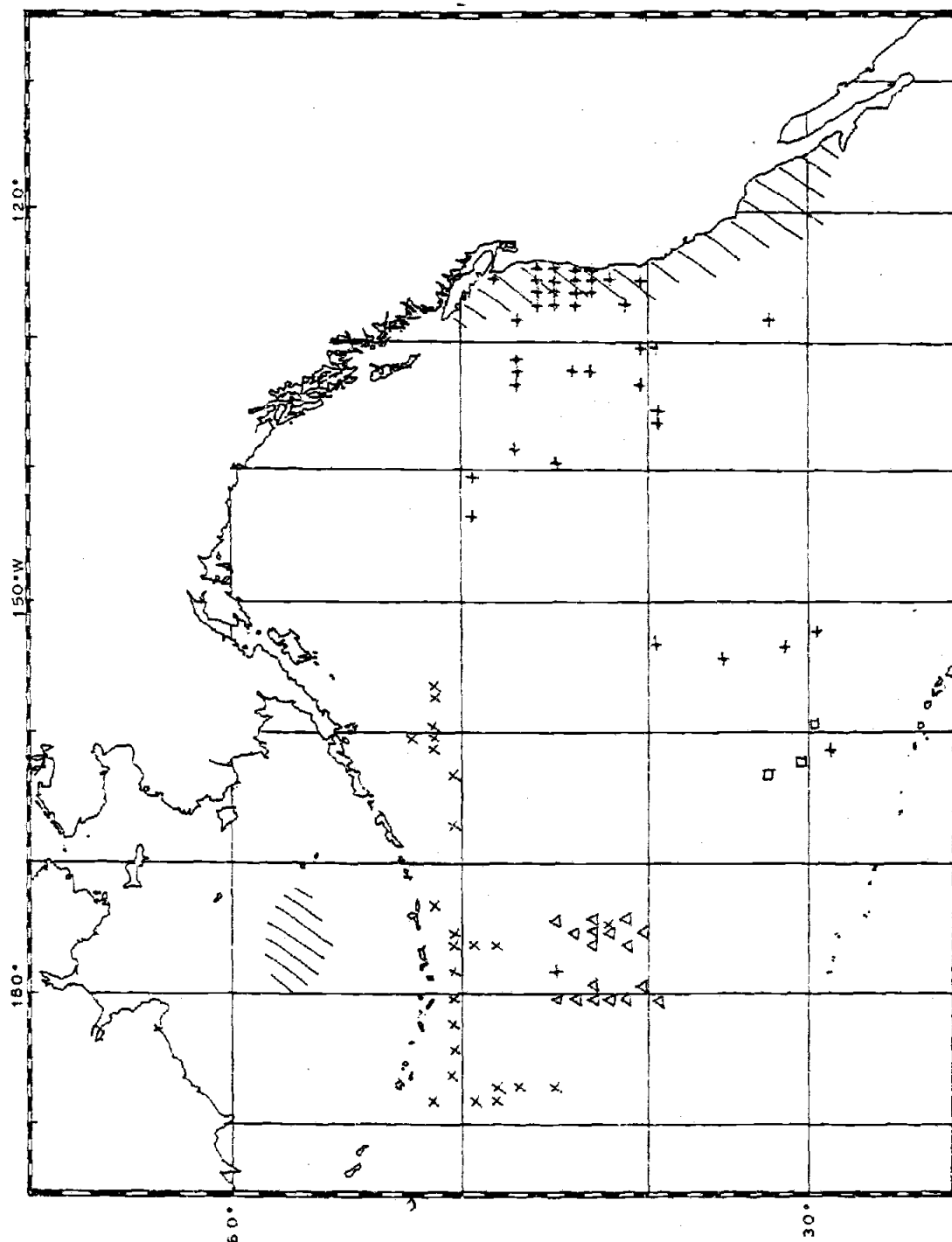
Onychoteuthis borealijaponicus Okada, 1927

Visceral photophores not clearly delineated, and with a band of iridescent tissue between them. Club with twenty-five to twenty-seven hooks.

A total of 231 individuals (0.53% of all cephalopods) was taken in 151 hauls (5.3% of all hauls capturing cephalopods) in the California Current, transitional, and central Pacific waters (midwater, open tows to 3000 m, closed tows as deep as 485-500 m) (Figure 23). Adults of this species are extremely difficult to capture with towed nets; it is probably much more important than the numbers collected would indicate. This species is known to occur in the California Current (Okutani and McGowan, 1969; Young, 1972); southwest of Japan (Okutani, 1969; Yamamoto and Okutani, 1975); and in the Bering Sea (Nesis, 1973b). In the western Pacific, it tends to find a northern limit off the southern Kuriles, in the southern portion of the Subarctic water mass in summer, with a southward migration in the winter (Murata et al., 1976; Murakami, 1976). In 1978 and 1979, T/V Oshoro Maru collected this species in salmon gillnets in an area bounded by 40° and 45°N, and 174° and 179°E (Faculty of Fisheries, Hakodate, 1979, 1980). Fiscus and Mercer (1982) reported gillnet collections in and north of this area (Figure 9).

Naito et al. (1977a) noted that O. borealijaponicus occurred in water temperatures of 1° to 20°C, but abundant catches occurred at 6° to 14°C. They also indicated (1977b) that maximum sizes were 370 mm DML for the female, 300 mm for the male, that the life span

was probably only one year, and that the growth rate decreased rapidly with the onset of sexual maturity.

Fiscus and Mercer (1982) captured this species at water temperatures of 6.9° to 12.8°C, primarily between 9° and 13°C. They postulated maturity for females at DMLs above 290 mm and nidamental gland length over 40 mm, and for males, when spermatophores were present in Needham's sac. They also gave length-weight relationships for animals over 200 mm DML and speculated that individuals mature "in late summer and early fall at about the same rate across the North Pacific."

The central Pacific collections of this species are noteworthy in indicating a zoogeographic overlap with O. banksii; Okutani (1981) has noted a similar overlap off Okinawa and Taiwan.

Onykia carribaea LeSueur, 1821

Characterized by tetraserial club armature and the absence of photophores. Very small (37 mm DML maximum known - Lipka, 1975) as adults. The genus may be monotypic.

Four individuals (3, 6, 6, 9 mm DML; OSUI 724-726) were collected in central Pacific waters (midwater tows, 0-170 m) (Figure 24). Hooks are not yet developed on the clubs of these specimens, which demonstrate biserial armature proximally and tetraserial armature distally. This epipelagic species is known circumglobally between about 40°N and 40°S (Clarke, 1966). In the northeastern Pacific, this species has been taken only off southern California and Baja California (Nesis, 1973b). The

Figure 24. Location of hauls capturing _Onykia_ _carribaea_ (circles;
triangles represent records of Nesis, 1973b) and _Moroteuthis_
robusta (crosses; previous records are from around the North
Pacific Rim, from Japan to southern California).
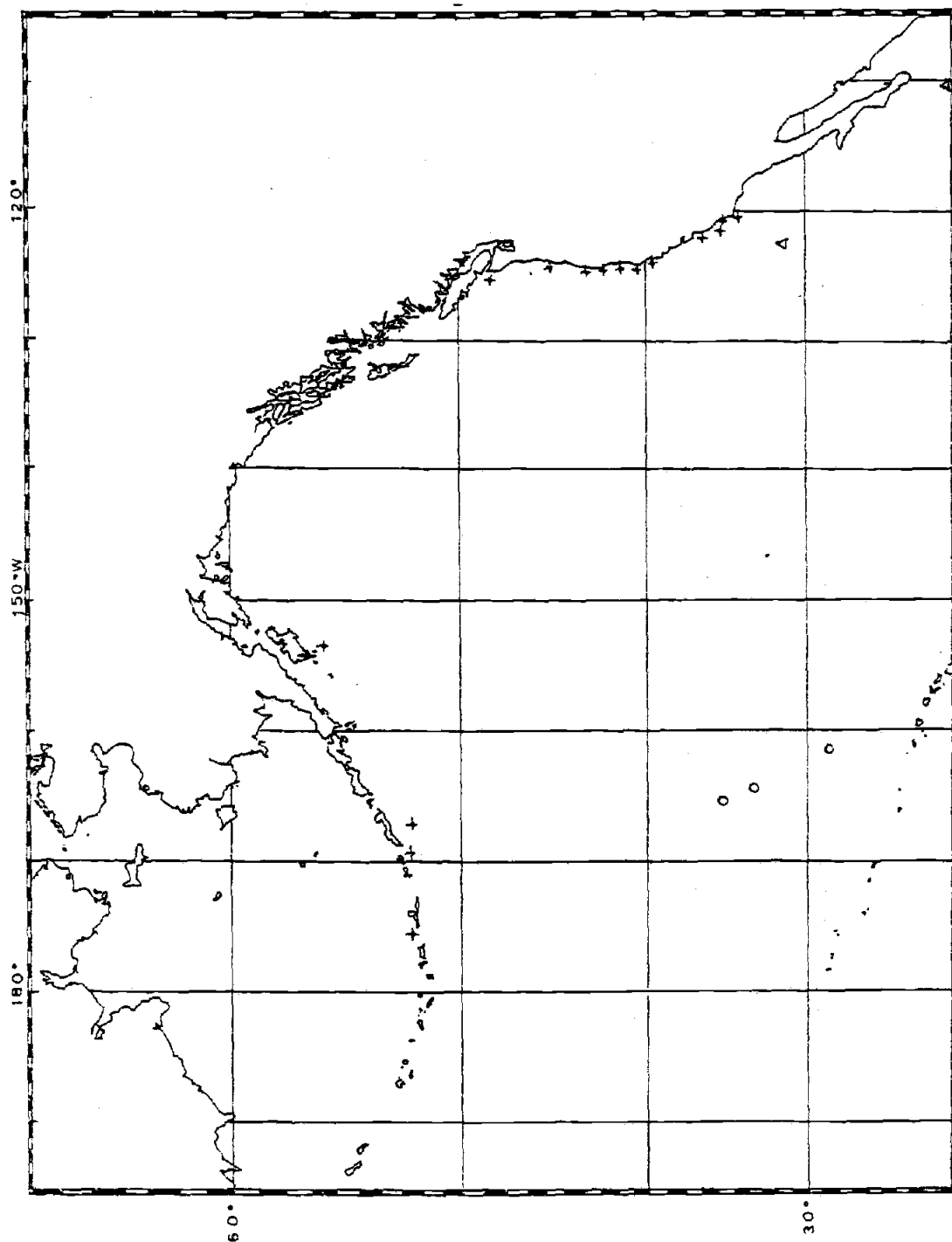
present specimens are thus the first records from the central
North Pacific.

<center>Moroteuthis robusta (Dall) Verrill, 1876</center>

No occipital folds. Gladius terminating in characteristic
cartilaginous cone. No photophores. Smooth funnel groove.
Approximately 36 biserial hooks on club. Connective apparatus of
club oval, with anterior margin raised.

Thirty-five individuals (327-1360 mm DML) were examined.
This species was collected in 31 demersal hauls; it was most
abundant at 200-400 m, and occurred as deep as 500 m. Although
this species is probably foremost in terms of biomass, it
represents less than 0.1% of the cephalopods examined, and
occurred in less than 1% of the hauls capturing cephalopods. The
larvae are unknown.

This species was taken only in coastal waters, from southern
California to Atka Island (Figure 24). It is known from the
neritic waters of the North Pacific rim from Japan, the Kuriles
and Aleutians, to central and southern California (Dall, 1873;
Verrill, 1876; Thompson, 1900; Ishikawa and Wakiya, 1914a; Sasaki,
1929; Classic, 1929, 1949; Croker, 1934; Phillips, 1933, 1961;
Robbins et al., 1937; Pike, 1950; Beteshava and Akimushkin, 1955;
Okutani and Nemoto, 1964; VanHyning and Magill, 1964; Smith, 1963;
Pearcy, 1965; Clarke, 1966; Hochberg, 1974).

Summary - Family ONYCHOTEUTHIDAE

Four species of this family, comprising 279 individuals, were identified. *Moroteuthis robusta* is limited to coastal waters (maximum depth of capture, 514 m). Although relatively few individuals were collected, it may rank first in terms of cephalopod biomass in that environment. The geographic ranges of *Onychoteuthis banksii* and *O. borealijaponicus* overlap but slightly; *O. banksii* is a tropical-subtropical cosmopolite, and may represent a species complex, while *O. borealijaponicus* is a south-boreal to subtropical species limited to the northeast and northwest Pacific, with occasional excursions into central waters. *Onykia carribaea* is a tropical-subtropical epipelagic form; the present specimens are the first records from the central North Pacific.

Family GONATIDAE Hoyle, 1886

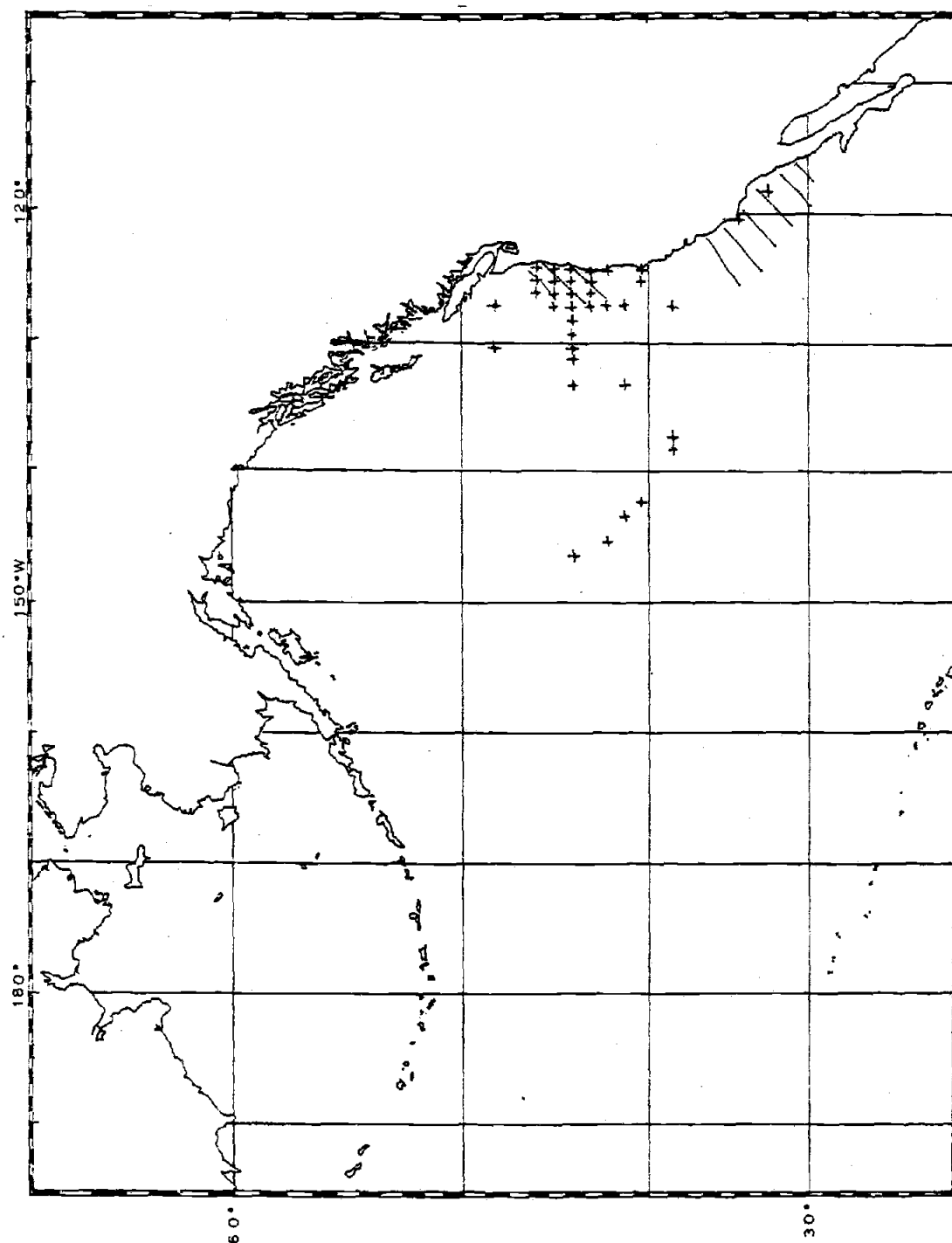Characterized by a simple, straight funnel-locking cartilage; buccal connectives which attach ventrally to arms IV; tetraserial brachial armature, including two medial rows of hooks (except male *Berryteuthis anonychus*, which lack hooks).

This family accounts for a majority of the cephalopods in the Subarctic Pacific; in this study gonatids represented 51% (22,189 individuals) of all cephalopods collected.

Genus _Gonatus_ Gray, 1849

Radula with five teeth in a transverse row; club usually with one to seven hooks.

Gonatus berryi Naef, 1923

Club with a large central hook, and one smaller hook distal to it. Proximal to the central hook are one or two suckers followed by several small hooks generally increasing in size cephalad. Larvae develop arm hooks at a DML of 7-10 mm.

The _Gonatus_ type D of Kubodera (1978) is closely allied to Young's (1972) description for this species, but the _Gonatus_ sp. cf. _berryi_ of Okutani and Satake (1978) probably represents a different species (the size of the fins and disposition of the suckers on the tentacular stalk are at variance with Young's description, and the distribution of hooks and suckers on the manus was not clear, owing to preservational condition). Kubodera's specimen was taken at 54°N, 177°W, while Okutani and Satake's animal was collected from the stomach of a sperm whale off Honshu between 36° and 39°N.

A total of 180 _G. berryi_ was collected; representing 0.41% of all cephalopods collected, this species was present in 4.7% of all hauls capturing cephalopods. It was taken in 175 midwater hauls (open, as deep as 2000 m; closed, as deep as 760-830 m), and three demersal hauls (375-450 m maximum). It was taken in the California Current system (and northern extensions thereof) and in the Alaska and Bering Current regions (Figure 25). There is one

Figure 25. Location of hauls capturing Gonatus berryi. Previous
records shown as triangle and shaded area.
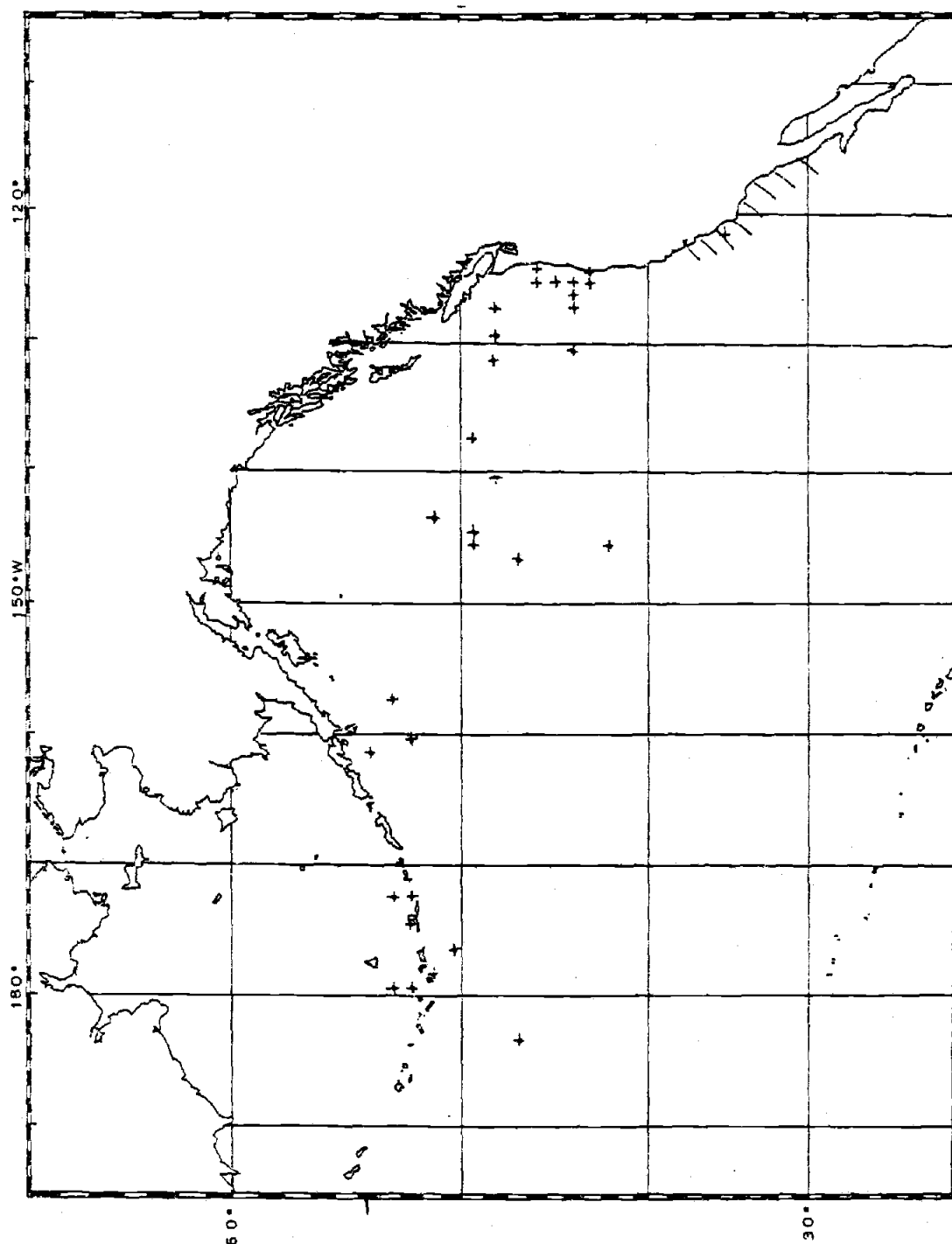
record from transitional waters at 42°N, 145°W. This species has
been previously reported from coastal waters of the Californias
between 30° and 37°N (Young, 1972; Anderson, 1978), and, as
Gonatus type D, from the southern Bering Sea (Kubodera, 1978).
The present specimens thus show a continuous distribution from
southern California throughout the California Current into the
Alaska Current and the southern reaches of the Bering Sea. The
westernmost extent of this species is 176°E, according to
presently available information.

Gonatus californiensis Young, 1972

Club with a large central hook, small distal hook, and three
to five proximal hooks. No suckers intervene between central and
proximal hooks.

Eight individuals (representatives: OSUI 680-682) were
collected in seven midwater hauls in the California Current region
(Figure 26). In the daytime, it was taken at 400-500 m; at night,
at 150-400 m. The species has been previously recorded from off
the coasts of California and Baja California between 28° and 34°N
(Young, 1972). My records thus represent northward and westward
extensions to the known distribution, but the species seems to be
confined to the California Current system. Imber (1978) believed
that _Gonatus californiensis_ represented the same species as _G.
antarcticus_ Lonnberg, 1898; if this is correct, the species shows
an intermittent distribution from the California Current through
the eastern Pacific to the Peru Current and subantarctic.

Figure 26. Location of hauls capturing Gonatus californiensis. Previous records shown as shaded area.
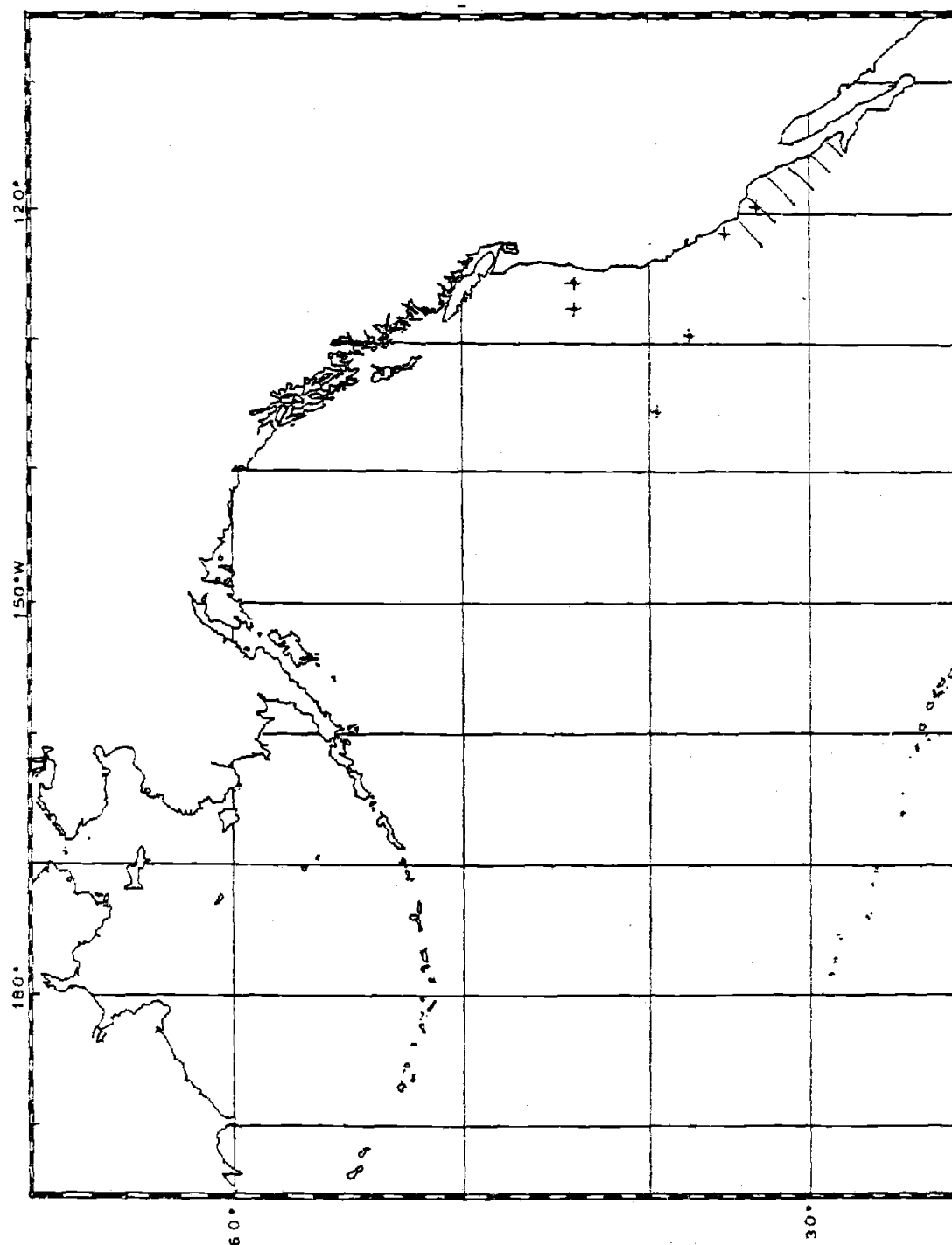
Gonatus madokai Kubodera and Okutani, 1977

Tentacular club with central, distal, and five proximal
hooks. Very long arms (90% DML), and soft mantle consistency.
Aboral keels on arms III and IV. See Kubodera and Okutani (1977)
for further details.

A total of 192 individuals (6-72, 129, 228 mm DML;
representatives: OSUI 702-706) was taken in 98 midwater hauls
from the northern reaches of the California Current into the
Alaska Current, Alaska Gyre, Bering Current, and Subarctic Current
(Figure 27). In open hauls, it occurred as deep as 2000 m; in
closed hauls, as deep as 450 m. At night, most individuals were
taken at 150-200 m. The only published records are those of
Okutani (1966), Kubodera and Okutani (1977), and Kubodera (1978),
which cite collections in the Sea of Okhotsk, around the Kuriles,
and southeast of Kamchatka, but none farther east than about
169°E. I have thus demonstrated a continuous distribution across
the Subarctic Pacific.

Gonatus middendorffi Kubodera and Okutani, 1981

Characterized by a long and slender mantle (MW/DML ratio =
15-18% in individuals over 30 mm, 20-24% in smaller animals).
Arms are quite short, 44-52% DML. Clubs and tentacles are short,
bear a central and distal hook, and five or six proximal suckers,
of which two or three may be modified into small hooks in adults.

Arm hooks first develop at about 30 mm DML; the central club
hook is present but immature at 45 mm; distal hook develops

Figure 27. Location of hauls capturing Gonatus madokai. Previous records are all east of 169°E; those in the area of the map are shown as triangles.
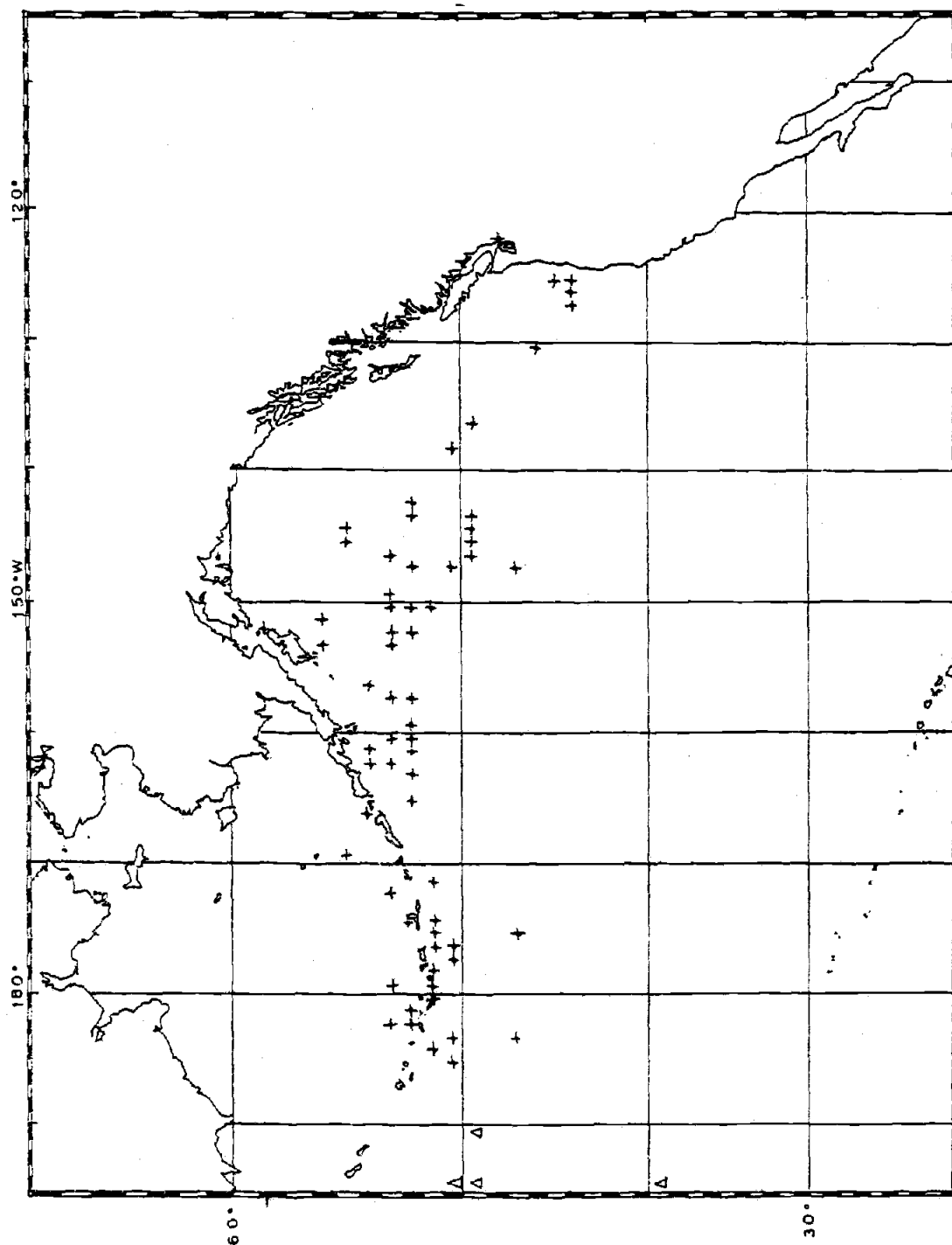
between 45 and about 60 mm; the proximal hooks are not evident until about 230 mm DML. Club with dorsoaboral keel beginning distal to hooks, extending to tip of dactylus. Dactylus with about eight rows of suckers just distal to hooks, decreasing to four rows about half to two-thirds of the way out on the dactylus.

Larvae are distinguished by the arrangement of suckers on the tentacular stalk: the distal portion of the tentacle has many small sucker buds, with four regular longitudinal rows of small suckers proximally, decreasing to two alternating rows. This pattern is evident until about 40-45 mm DML. For comparative purposes, measurements of a number of individuals, over a range of sizes, are given in Table 4.

Gonatus middendorffi was first described as Gonatus type A by Kubodera (1978), on the basis of larval specimens. It may be synonymous with G. kamtschatica (Middendorff, 1849), which has been declared a species dubia by Kubodera and Okutani (1981).

Fifty-four individuals (11-73, 231-241 mm DML; representatives: OSUI 707-714) were collected in seven hauls (two midwater trawls: 0-200 m, 0-500 m; five purse seine hauls) in transitional waters and the Alaska and Bering Current regions (Figure 28). This species is known from the central and southern Bering Sea and northwestern Pacific (Kubodera, 1978; Kubodera and Okutani, 1981). Bublitz (1981) has taken larvae in the central and eastern Bering Sea. The distribution is therefore northwestern and north central Pacific; as yet no individuals are known from the Gulf of Alaska or the eastern Pacific.

Table 4. Measurements (in mm) and counts for selected individuals of _Gonatus_ _middendorffi_. Abbreviations: DML, dorsal mantle length; MW, mantle width; HW, head width; FL, fin length; FW, fin width; AL, arm length; TL, tentacle length; CL, club length; AH, arm hooks (present/absent); CH, central hook (present/absent); DH, distal hook (present/absent); PH, proximal hooks (number present/absent). ES, enlarged sucker. ND, not differentiated.

Haul:	HST-5	HST-3	HST-3	HST-2	HST-2	HST-2	845	845
DML	231	73	69	66	52	45	20	11
MW	35	11	10	11	8.5	8	5	6
HW	28	11	11	9	7	6	4	3
FL	110	32	30	30	21	15	3	1.5
FW	90	37	39	35	23	20	6	4
AL I	102	32	33	32	22	17	6	2
AL II	109	34	36	33	25	20	8	4
AL III	113	38	38	34	26	18	8	3
AL IV	109	31	33	31	21	16	3	2
TL	188	63	62	48	38	23	8	8
CL	25	11	11	9	8	5	ND	ND
AH	+	+	+	+	+	+	-	-
CH	+	+	+	+	+	+	-	-
DH	+	+	+	+	+	ES	-	-
PH	3	-	-	-	-	-	-	-

Figure 28. Location of the hauls which captured *Gonatus middendorffi*. Previous records shown as triangles and hatched area.
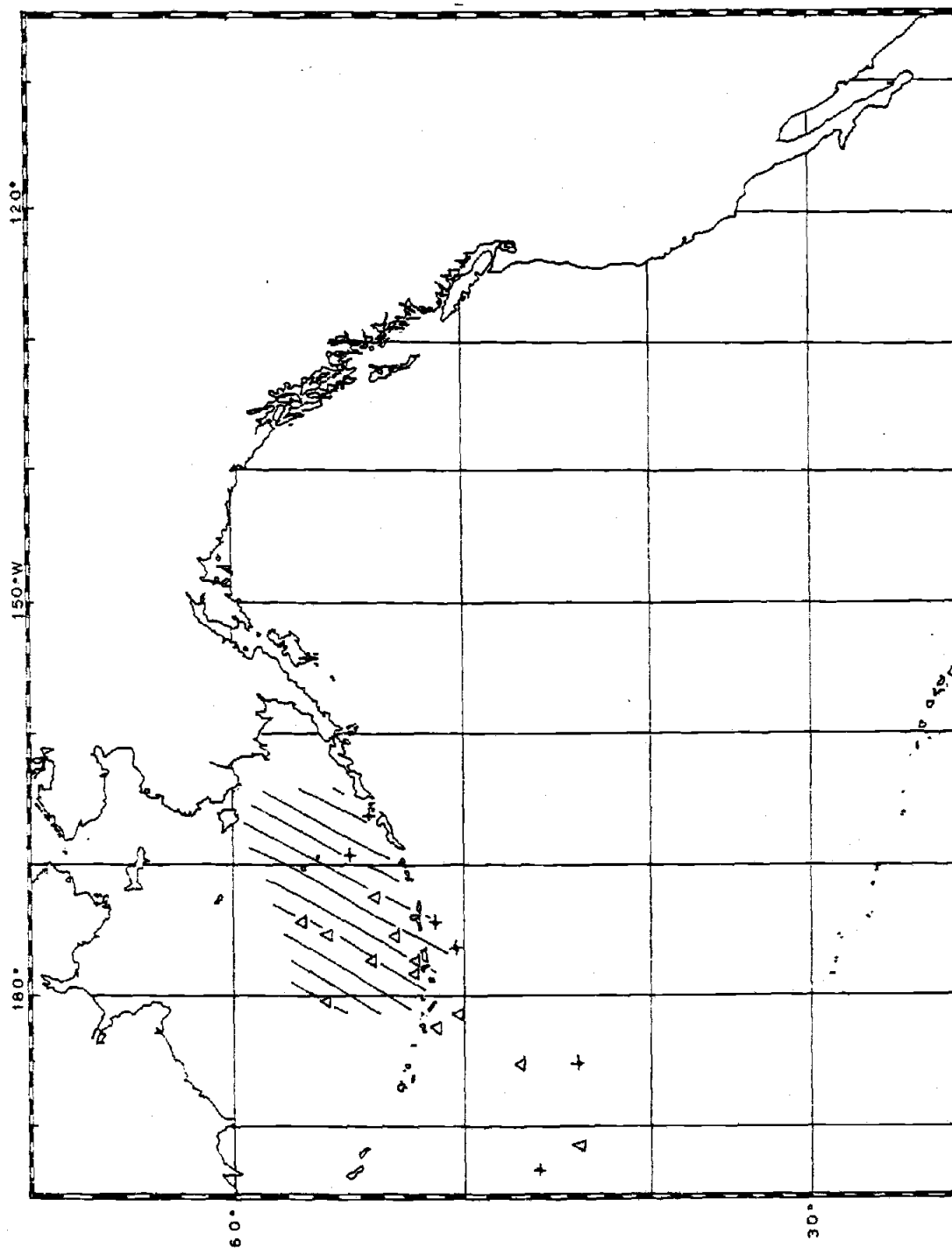
Gonatus onyx Young, 1972

Club with central hook, and occasionally with a distal hook on one or both tentacles, but never with proximal hooks.

A total of 15,917 individuals was collected, in 1037 hauls (69 demersal, 80-670 m maximum; midwater, as deep as 500-1125 m, closed tows, and 0-3000 m, open tows) (Figure 29). It occurred from southern California, north through the California Current into the Alaska Current and southern Bering Sea. The species has previously been recorded from inshore waters off North America between 30° and about 43°N. The present samples thus represent a notable northward and westward range extension. Kubodera's (1978) type B, which is identical with G. onyx, is known from the northwestern Pacific, particularly the southern Okhotsk Sea and Bering Sea.

Gonatus pyros Young, 1972

A large photophore on the ventral surface of each eye. Ventral margin of tentacular stalk with biserial suckers. Club with central, distal, and three to four proximal hooks decreasing in size cephalad.

A total of 1231 individuals was collected in 455 hauls (4 demersal, 440 m maximum; midwater, as deep as 750-790 m and 500-1000 m, closed tows, and 0-2120 m, open tows) from the southern reaches of the California Current northward into the Alaska Current and west to 175° E, but not into the Bering Sea (Figure 30). This species has been previously recorded only by

Figure 29. Location of hauls capturing Gonatus onyx. Previous records shown as shaded area.
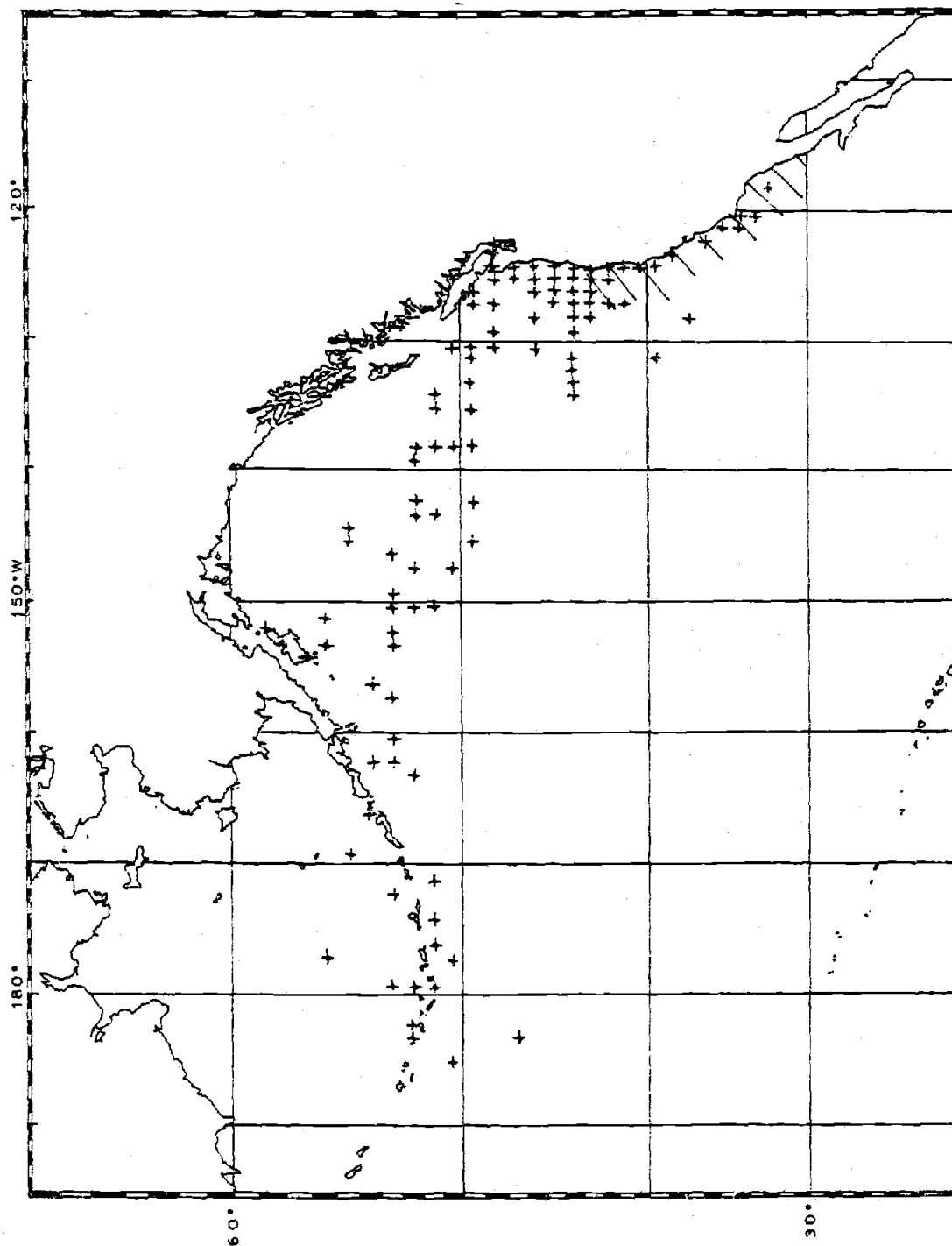
Figure 30. Location of hauls capturing Gonatus pyros. Previous records shown as shaded area.
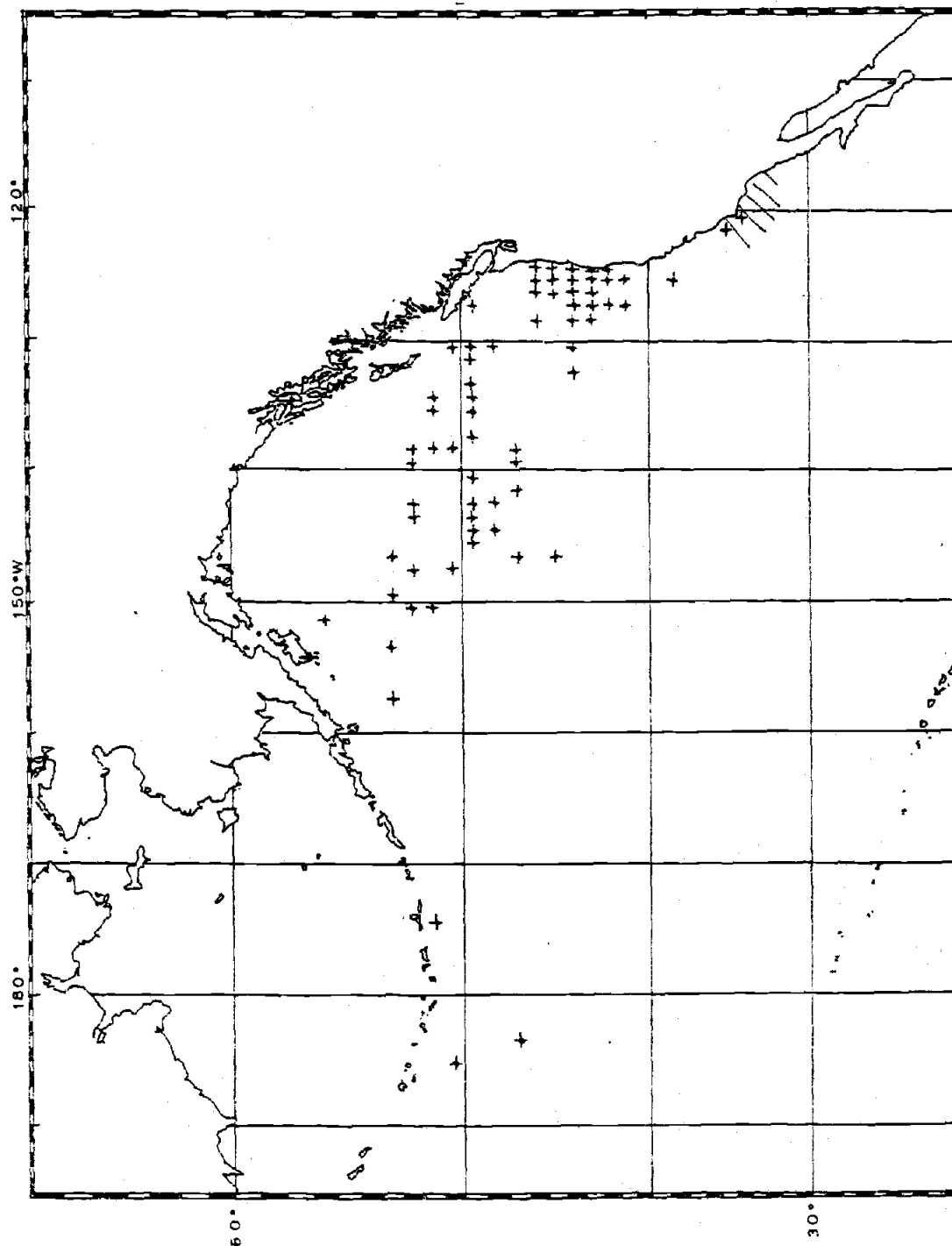
Young (1972) off the California coast between 32° and 34°N. The range has thus been extended to the north and west.

Gonatus sp. A (new species)

Body quite plump, widest at anterior margin (MW:DML = 30-53%, highest in small individuals). Mantle of soft consistency. Fins relatively small, FWI = 41-58%, FLI = 26-50%, very thin (FWI, fin width index, equals fin width divided by dorsal mantle length; FLI, fin length index, equals fin length divided by dorsal mantle length).

Arm formula generally III≥II>I≥IV. Arms fairly short: longest arms (III or II) 42-56% DML, shortest arms (IV) 25-44% DML. Aboral keels well developed on arms IV. Trabeculate protective membranes very well developed on arms I-III, especially in larger individuals. Brachial armature quadriserial; the two medial rows are small suckers in all individuals examined (largest, 24 mm DML). The two lateral rows of suckers are borne on trabeculae and consist of suckers which are very much enlarged (at least two or three times the diameter of the medial suckers) on the middle third of arms I-III. Arms IV bear four rows of equally sized suckers which are smaller than the medial suckers of arms I-III.

Tentacles are of moderate length, 53-79% DML, and the clubs are quite small, 13-25% DML. A dorsoaboral keel is present on the club from the level of the central hook to the tip of the dactylus. The medial zone contains a central hook in the 24 mm

specimen, and an enlarged central sucker in specimens of 19 and
20 mm DML. A locking zone consists of approximately five ridges
and suckers. The dorsal marginal zone contains suckers in four
rows, and the ventral marginal zone bears four to five rows. The
dactylus suckers are disposed in about six rows just distal to the
central hook (or enlarged sucker), but these rapidly decrease to
four regular rows which continue out the length of the dactylus to
a circlet of small suckers at the tip. The suckers distal to the
central hook number approximately 110 (full club sucker counts are
not possible, as many of the proximal suckers remain as buds even
in the larger specimens). The dactylus suckers just distal to the
central hook are much larger than in comparably sized individuals
of other _Gonatus_ species. These suckers approach or slightly
exceed the largest medial arm suckers in size; they decrease in
size distally. Tentacle stalk suckers are countable in a 19 mm
individual, they number twenty-five suckers in the ventral row,
twenty-eight in the dorsal row, and fifty-seven on the oral face
between the two rows. In smaller individuals, the stalk suckers
appear to be arranged in roughly six alternating rows.
Measurements of several selected specimens spanning the observed
size range are given in Table 5 (OSUI 695-701).

Twenty-two individuals were collected in 16 midwater hauls
(mostly 0-200 m; two hauls 0-400 m, one 0-2400 m) from the
northern California Current into the Alaska Current as far west as
176°W (Figure 31). Okutani (1982) has seen three similar
individuals in the collections of the University of Alaska. One

Table 5. Measurements (in mm) of selected individuals of Gonatus sp. A (new species). Abbreviations: DML, dorsal mantle length; MW, mantle width; FL, fin length; FW, fin width; HW, head width; AL, arm length; TL, tentacle length; CL, club length; AH, arm hooks (present/absent); CH, central hook (present/absent); OCH, other club hooks (present/absent); ES, enlarged sucker. Sasaki refers to specimen, described by Sasaki (1929), discussed in text.

Haul:	235-46	235-46	849	845	849	837	842	Sasaki
DML	24	20	19	18	17	15	12	14
MW	8	6	8	8	9	6	5	6.5
FL	5	4	4	4	3	3	2	-
FW	11	9	10	10	7	8	7	-
HW	7	7	5	6	5	5	4	-
AL I	7	6	7	8	6	6	5	3.5
AL II	9	9	8	10	8	7	6	4
AL III	10	9	9	10	9	7	6	4
AL IV	8	6	6	8	6	5	3	2.5
TL	19	12	12	-	12	8	8	7
CL	5	5	4	-	3	2	?	?
AH	-	-	-	-	-	-	-	-
CH	+	ES	ES	-	-	-	-	-
OCH	-	-	-	-	-	-	-	-

Figure 31. Location of hauls capturing _Gonatus_ sp. A (crosses) and _Gonatus_ sp. E (triangles).
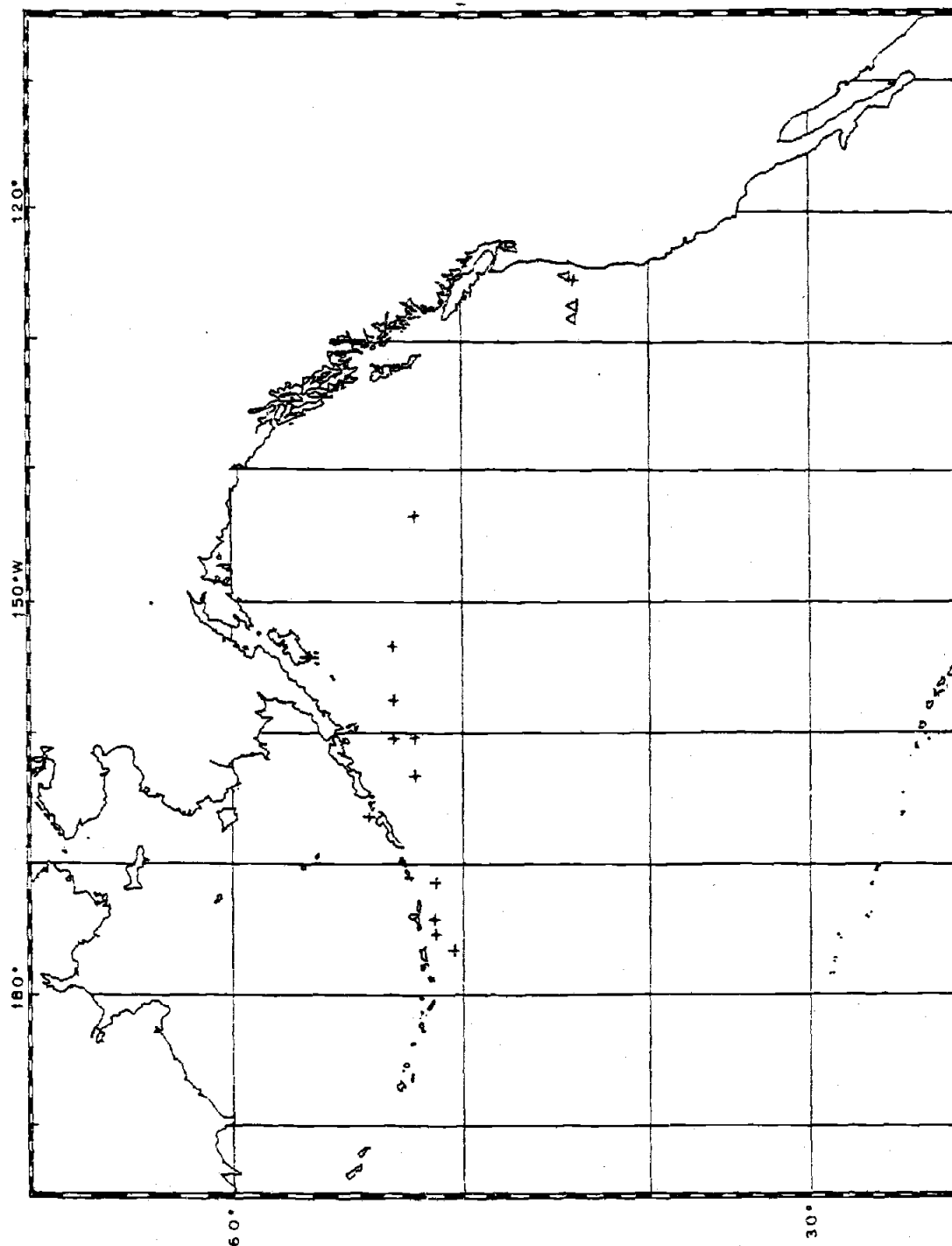
was collected at Seward (60°N, 149°W), and the others in

southeastern Alaska (56°N, 134°W; 58°N, 135°W).

Discussion

This species clearly belongs in the genus _Gonatus_ owing to

the development of a central hook on the tentacular club. It

cannot be placed in _G. pyros_ as it lacks an optic photophore, nor

in _G. berryi_, as no arm hooks are yet evident; neither can it be

placed in _G. tinro_, as it does have a club hook. Comparably sized

individuals are known for _G. onyx_, _G. madokai_, _G. middendorffi_ and

Gonatus sp. E (new species, discussed below); none of these

demonstrates the enlarged brachial and club suckers characteristic

of this species. Bublitz (1981) states that some of his specimens

of _Gonatus_ type A (which was described as _G. middendorffi_,

Kubodera and Okutani, 1981) showed enlarged suckers in the lateral

arm rows. These specimens otherwise agree with the description of

G. middendorffi, which is separable from _Gonatus_ sp. A by its MWI

and the size at which club hooks develop. There are other

differences, especially in club armature, which serve equally well

to differentiate all of these species. _Gonatus_ type C Kubodera

1978 is known from individuals as large as 16 mm DML; there is no

indication of enlarged suckers in these, and this type is further

characterized by a separated epidermis, which does not occur in

Gonatus sp. A. Bublitz's (1981) new species also has no

indication of enlarged suckers in the lateral rows: "each sucker

of the median two rows is about 1.2 times as large as the

corresponding lateral sucker" (Bublitz, 1981, p. 61), and has five rows of sucker buds on the tentacular stalk as opposed to six in larvae of this species. The tentacles of Bublitz's species are shorter (37-49% DML) but have larger clubs (18-49% DML); several other differences in tentacle sucker counts and disposition are evident.

Sasaki (1929) included one larva (Pl. 22, figure 14; Text figure 128C) in the description of _Gonatus fabricii_ which appears to correspond to _Gonatus_ sp. A. Measurements of this individual have been included here, in Table 5. Sasaki (Ibid., p. 269) noted: "The suckers
of the first three pairs of arms, uniform, except in
the largest larva referred to, where the suckers of
the outer two series on these arms are much larger
than those of the inner two series."

He also noted that the proximal suckers on arms IV were also enlarged, and numbered from two to seven, in the larvae of _G. fabricii_ (apparently not only in the larva which corresponds to _Gonatus_ sp. A). No such condition has been noted for _Gonatus_ sp. A. The geographical origin of Sasaki's specimen is unknown; it apparently came from collections of the _Albatross_, and Sasaki listed the following localities in which the _Albatross_ collected _G. fabricii_: "Milne Bay, Simushir I., Kurile group; Bowers Bank, Bering Sea; near Near Is., Aleutians; east of Kamchatka; south of Alaska; and near Commander Is."

Gonatus sp. E (new species)

Body generally plump, widest in the midsection. Head less
wide than mantle; eyes not bearing photophores. Fins broad but
relatively short: FWI = 80-90% for animals over 30 mm DML; FLI =
25-45%.

Arms of moderate length, 59-63% DML in 46 mm DML individual,
43-53% in 30 mm DML individual. Arm formula generally
III≥II>IV≥I. Aboral keels are strong and nearly always evident on
arms IV; they are occasionally discernible on arms I-III.
Trabeculate protective membranes are exceedingly well developed on
arms I-III; the marginal rows of suckers are borne on the
trabeculae. Arms I-III bear hooks in the medial rows; these
develop at a mantle length of 24-30 mm. Arms IV bear four rows of
suckers.

The tentacle is long, 60-105% DML (depending on
preservational state), and bears a fairly large club (21-30% DML).
A swimming keel is present on the dorsal surface of the dactylus,
extending from the level of the distal hook to the tip of the
dactylus. Dorsal and ventral protective membranes are also
present, but are very low. They originate on the stalk and extend
along the club to its tip. The club bears a large central hook, a
distal hook about half the size of the central one, and several
proximal hooks. The central and distal hooks develop at a DML of
about 24-30 mm, but the proximal hooks are not evident until a
length of 35-39 mm is attained. The proximal series consists of
approximately six structures; the suckers next to the central hook

are the first to transform into hooks, so that an animal of 39 mm
may have two hooks proximal to the central, and three to four
suckers, and an animal of 46 mm may have four hooks proximal to
the central, and two suckers.

The locking zone consists of four to five ridges with
accompanying suckers, alternating with five to six knobs. This
series extends onto the stalk. The ventral marginal zone contains
four rows of suckers and the dorsal marginal zone five. The
tentacular stalk bears single rows of suckers on both the ventral
and dorsal margin of its inner face. The space between the rows
is beset with many small suckers. The number of suckers in the
ventral row is at least seventy-four in the 46 mm specimen, in the
dorsal row, at least sixty-three, and on the medial face, at least
seventy. In a 24 mm specimen, the stalk suckers appear to be
arranged in six, somewhat irregular, alternating rows.

The dactylus bears many small but roughly equal sized
suckers. These are disposed in seven or eight rows just distal to
the hooks, and decrease to five or six rows near the tip. A
circlet of small suckers occupies the very tip of the dactylus.
The total number of suckers on the dactylus, ventral marginal
zone, and dorsal marginal zone is 320 in the 46 mm specimen, and
shows a range of 295 to 370 in the other specimens. Ten
individuals were collected in ten midwater hauls (mostly 0-400 m;
one 0-1500 m, one 0-2000+ m) in the northern portion of the
California Current system (Figure 31). Measurements for eight of
these are given in Table 6 (OSUI 687-694).

Table 6. Measurements (in mm) and counts for selected individuals of _Gonatus_ sp. E (new species). Abbreviations as in Table 5, with the following additions: DH, distal hook (present/absent); PH, proximal hooks (number present/absent); CS, number of club suckers.

Haul	1091	1692	1011	1563	2057□4	2107□5	2110□1	2110□5
DML	46	39	35	31	30	30	30	24
MW	16	12	10	13	10	13	10	9
FL	22	17	12	10	12	12	12	8
FW	41	32	28	25	25	25	25	14
HW	10	11	11	9	9	7	9	6
AL I	27	22	16	15	13	13	15	8
AL II	28	25	19	18	15	16	19	10
AL III	29	24	19	17	16	18	20	10
AL IV	28	18	17	14	13	14	18	9
TL	44	27	28	25	19	32	31	18
CL	12	9	9	7	8	9	9	5
AH	+	+	+	+	+	+	+	-
CH	+	+	+	+	+	+	+	-
DH	+	+	+	+	+	+	+	-
PH	4	2	-	-	-	-	-	-
CS	320	347	339	355	370	295	320	300

Discussion

This species is easily separable from all but one of the described species of _Gonatus_. The distribution of hooks on the club separates it from _G. berryi_ (in which the proximal hooks are separated from the central hook by one or two suckers), _G. onyx_ (no proximal hooks), and _G. tinro_ (no club hooks). _Gonatus pyros_ has an optic photophore, and _G. madokai_ has only eight to ten minute suckers on the oral face of the tentacular stalk (several other characters also serve to separate these species). _Gonatus middendorffi_ develops all hooks at a much larger size, and has a much more slender body. _Gonatus_ sp. Bublitz (1981) has fins which are somewhat less broad (43-87% DML, vs. 80-89% in _Gonatus_ sp. E), and shows significant differences in the number and disposition of club suckers (probably fewer than 100 club suckers in _Gonatus_ sp. Bublitz, arranged in four rows on the dactylus).

This species is less easily separable from _G. californiensis_. The distribution of hooks on the club is the same in the two species, and the size at which all hooks develop is similar. There are, however, consistent differences in fin dimensions, in sucker counts on the club, and in distribution of suckers on the dactylus. Young's (1972) specimens of _Gonatus californiensis_ (29-112 mm DML) had fins which consistently measured between 54 and 70% of DML. My specimens 30 mm and over had fin width to DML ratios of 80-89%. The clubs are also somewhat larger in my specimens: 21-30% of DML vs. 17-24% in _G. californiensis_. Club sucker counts show no overlap in the two species: mine range from

295 to 370, and Young's G. _californiensis_ from 217 to 269. In _Gonatus_ sp. E, suckers are arranged in seven to eight rows at the base of the dactylus, and decrease to five to six rows at the tip. In G. _californiensis_, the dactylus suckers are disposed in eight rows basally and "decrease to four rows about halfway out on the dactylus" (Young, 1972, p. 52). The arms are also noticeably longer in my specimens than in G. _californiensis_: at 46 mm, the longest arms (I and II) are 23-24 mm in G. _californiensis_ and 28-29 mm in my specimens. Further comparison supports this difference:

<center>Arm length (II, III)</center>

DML	G. _californiensis_	sp. E
46 mm	23-24 mm	28-29 mm
38-39	18	24-25
34-35	16	19
29-30	12	15-20

This new form thus represents an intermediate condition between G. _tinro_, which has a _Berryteuthis_-like club with no hooks but many (more than 400) suckers, and G. _californiensis_, G. _pyros_, and G. _madokai_, which have central, distal, and proximal hooks, but fewer (less than 270) suckers on the club. I believe that this form represents a distinct species, as several characters show no overlap with G. _californiensis_: fin dimensions, arm length, and sucker number and distribution on the club. My present collection does not appear to contain mature individuals; these differences may be better characterized on examination of larger individuals.

Gonatus type C Kubodera, 1978

Previously described from individuals of 9-15 mm DML only.
Mantle covered by epidermis, but with a broad space between the
two layers. Fins small: FLI, 10-13%; FWI, 35-50%. Arms weakly
muscled, none yet has hooks. Clubs of larger specimens (over
12 mm DML) with one enlarged sucker; five to six longitudinal rows
of small suckers on stalk decreasing to two or three sparse rows
basally. See Kubodera (1978) for further details.

Kubodera (1978) collected this type from the western North
Pacific and the central southern Bering Sea. My samples included
126 individuals (4-16 mm DML) from 54 midwater hauls (mostly
0-225 m, also 0-400 m and 0-1500 m) in the inshore areas of the
California Current system through the Alaska Gyre and Alaska
Current and into the southern reaches of the Bering Sea, and as
far west as 177°E (Figure 32). Two individuals were collected in
a haul at the Subarctic Current - Transition Zone boundary at
47°N, 175°W. My samples thus show an eastern component to the
distribution of this species.

Gonatopsis borealis Sasaki, 1923

Radula with seven teeth in a transverse row (some other
species in this genus have five; this is further discussed in the
final section of this thesis). Tentacles absent in adults. Arm
tips with quadriserial suckers. Larvae with three enlarged
suckers at base of tentacle. See Sasaki (1923, 1929) for further
details.

Figure 32. Location of hauls capturing Gonatus type C Kubodera, 1978. Previous records in hatched area.
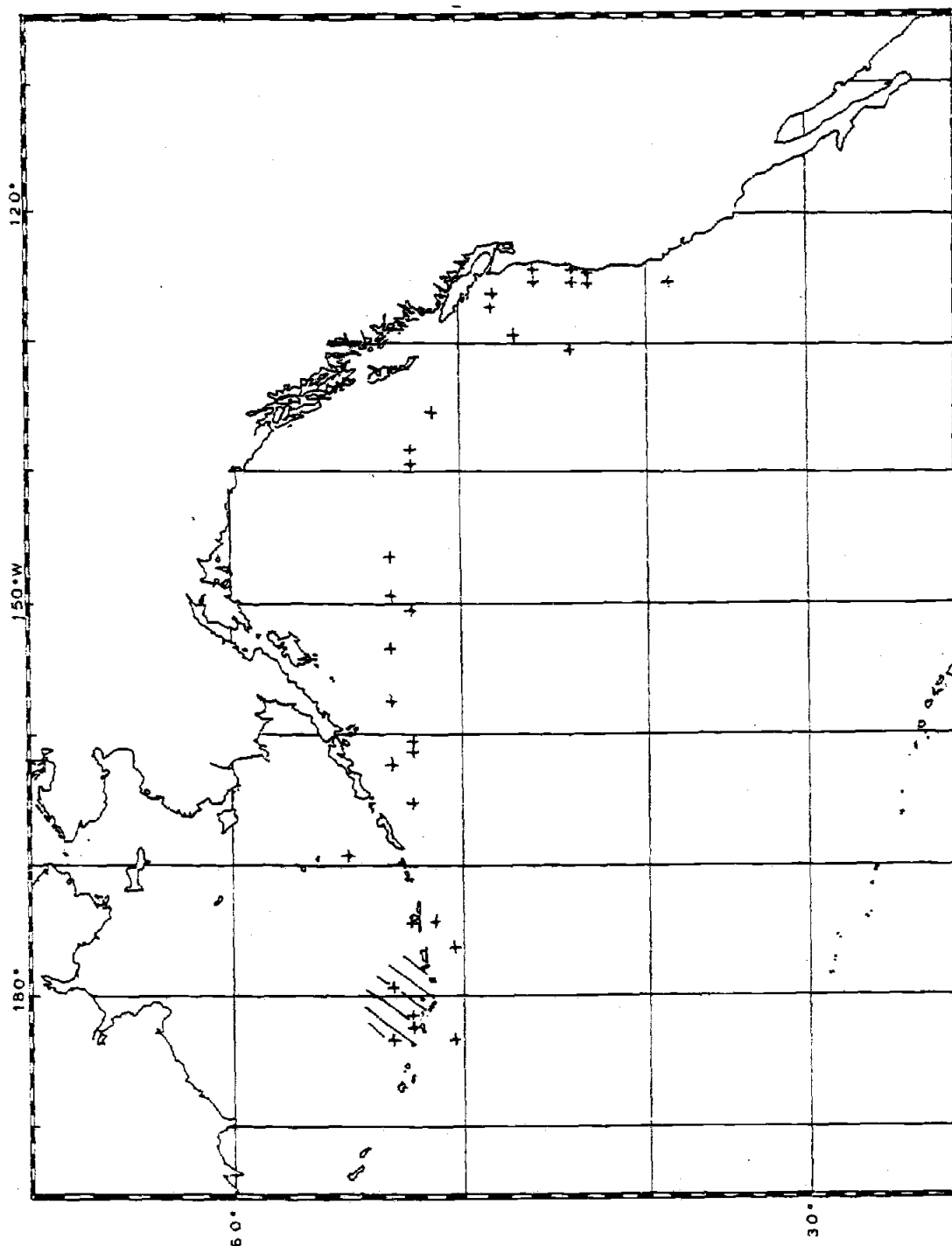
A total of 755 individuals was collected in 401 hauls (14 demersal, 85-650 m, 2600 m maximum; midwater, as deep as 635-720 and 500-1000 m, closed tows; and 0-2600 m, open tows) throughout the California and Alaska Currents, into the southern Bering Sea (Figure 33). There are a few records from transitional waters and even central Pacific waters. Gonatopsis borealis is known from waters across the North Pacific, from southern California (Young, 1972) through Alaskan and Aleutian waters to Japan (Sasaki, 1923, 1929; Akimushkin, 1957; Rice, 1963; Pearcy, 1965; Okutani, 1966; Clarke, 1966; Faculty of Fisheries, Hakodate, 1979, 1980; Fiscus and Mercer, 1982. Also see Figure 9).

This species apparently occurs as two populations - one of small sized individuals with mature gonads, in the Subarctic, and the other, of larger individuals with immature gonads, southeast of the southern and middle Kuriles, and south of the first form in eastern waters (Naito et al., 1977a). Maximum size is 290 mm DML for the female, and 270 mm for the male; longevity is estimated at one year, with growth slowing noticeably after sexual maturity is reached (Naito et al., 1977b).

Okutani (1977) considered this species to be restricted to Subarctic Water. Records from the central and northern Bering Sea (Okutani and Nemoto, 1964; Faculty of Fisheries, Hakodate, 1979, 1980) are probably more accurately referred to Gonatopsis makko, which was not encountered in this study.

Figure 33. Location of hauls which captured Gonatopsis borealis
(crosses; triangles represent captured by T/V Oshoro Maru; circles
represent gill net captures - Fiscus and Mercer, 1982) and
Gonatopsis okutanii (squares; previous record, filled square).
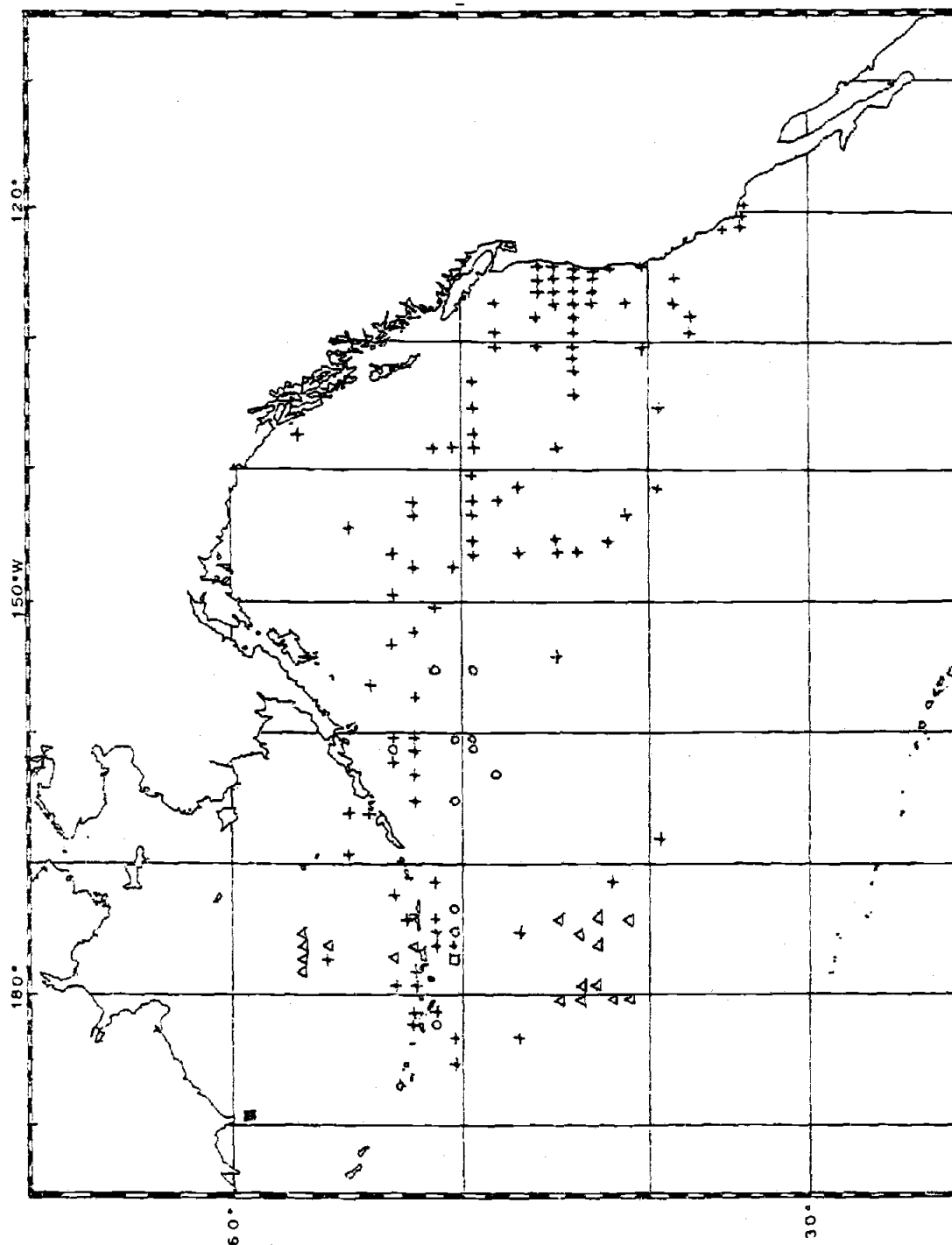
Gonatopsis okutanii Nesis, 1972

Characterized by a very gelatinous, soft body; remnants of tentacles even in adults; and arms at least as long as the mantle. Quadriserial brachial armature may not be immediately evident; the two lateral rows of suckers are frequently lost. Overall colour dark maroon to purple. See Nesis (1972b) for further details.

One individual (OSUI 826) was recovered from the stomach of an Alepisaurus ferox (male, 127 cm) taken in a purse seine (Figure 33). Measurements are given here (all arms were broken):

DML	188 mm	AL I	130+ mm
MW	60	AL II	114+
HW	41	AL III	132+
FL	86	AL IV	115+
FW	117		

This species has been very infrequently recovered; only about ten specimens are described in the literature. Gonatopsis okutanii is known from the western Bering Sea (59°N, 170°E), south and west along the Kuriles to Japan (Okutani, 1967; Okiyama, 1969; Nesis, 1972b). The present specimen is the first to be taken so far east.

Berryteuthis anonychus (Pearcy and Voss, 1963)

Seven teeth in a transverse row on the radula. Tentacle clubs armed only with suckers, all of approximately equal size. Arms with quadriserial armature, but generally without hooks (a few (generally fewer than six) hooks may be present basally on arms I-III in females, but not in males).

A few of the largest females collected (89-99 mm DML) exhibited greatly enlarged suckers in the medial rows of arms I-III. Several hooks were present basally, followed by 12-16 very large suckers, and then by suckers decreasing in size, to equal those of the lateral rows at the arm tip. The enlarged suckers bear about nine very short, widely spaced teeth on their distal borders, which are low and broad, but may be easily damaged to give the impression of pointed teeth. The lateral suckers have six to eight long, thin, blunt teeth on the distal margin. Hooks at the bases of arms I-III are small but well developed and sheathed. All individuals bearing enlarged suckers are females with eggs evident in the ovary. A female of 75 mm does not have enlarged suckers, nor do males of 82 and 88 mm DML. The 82 mm male has many spermatophores within the mantle cavity. Arms I-III in both males lack basal hooks and bear medial suckers which are decidedly globular, with a small opening, and blunt teeth. The medial suckers are slightly larger than, but have dentition similar to, the lateral suckers.

The tentacles of these specimens bear many minute suckers with about four moderately long, narrow, blunt teeth distally, and one low peg-like tooth proximally. The locking zone consists of alternating knobs and suckers beginning on the stalk and extending to about the middle of the manus. Tentacle length is variable, depending on preservation. See Pearcy and Voss (1963) for further details.

A meristic comparison between this group of individuals and the holotype and four paratypes of _B. anonychus_ (61-73 mm DML) yields major differences in arm, tentacle, and club length. The ratios (expressed as percentages) of the longest arm, tentacle, and club to dorsal mantle length for the enlarged sucker forms and the types are, respectively: AL/DML, 41-44%, 30-33%; TL/DML, 53-84%, 36-49%; and CL/DML, 22-33%, 17-23%. The ranges of the values for other ratios (MW, HW, FL, FW to DML) do not differ appreciably; all values overlap. The largest available specimens of _B. anonychus_ measure 76 and 77 mm DML; the ratios for these are: AL/DML, 35-39%; TL/DML, 35-76%; and CL/DML, 19-20%. It appears that the meristic variation in the enlarged sucker forms is simply a matter of their larger size. Measurements of the largest normal specimens, and several of the enlarged sucker specimens are given in Table 7 (OSUI 223, 715-719).

The radula of the enlarged sucker specimens is of the form described for _B. anonychus_: a tricuspid rhachidian flanked by a bicuspid admedian and two unicuspid lateral teeth (see Pearcy and Voss, 1963).

A total of 757 individuals (5 females with enlarged suckers; these came from a haul at 46°10'N, 167°50'E, which also contained the 75 mm female, and the 82 and 88 mm males referred to above) was collected in 169 hauls (midwater, as deep as 930-950 m, closed tows, and 0-1400 m, open tows) from the central California Current, through the Alaska Gyre and Current, into the southern

Table 7. Measurements (in mm) of several individuals of
Berryteuthis anonychus: three females with enlarged suckers, a
male from the same haul, and two large but normal individuals.
Abbreviations as in Table 4, with the following addition: SE,
somewhat enlarged (referring to arm suckers).

Haul	HST-4	HST-4	HST-4	HST-4	OSUI 223	BMT 286
Sex	F	F	F	M	?	F
DML	99	97	93	88	77	76
MW	21	24	27	24	18	27
HW	16	15	17	17	17	13
FL	28	22	28	20	25	20
FW	46	50	51	50	36	45
AL I	38	41	40	32	25	23
AL II	41	43	42	36	27	27
AL III	41	42	44	39	27	30
AL IV	35	38	34	37	26	28
TL	52	81	66	54	27	58
CL	23	32	24	19	15	15+
ES	+	+	+	-	SE	SE
AH	+	+	+	-	-	+

and eastern Bering Sea and Bering Strait (Figure 34). This species has been previously recorded only from an area off western North America between British Columbia and central California (Nesis, 1973b; Anderson, 1978). The present specimens thus represent a major westward and northward range extension. It is notable that the enlarged-sucker individuals were collected to the west of all other individuals, and probably represented reproductively mature animals.

Berryteuthis magister (Berry, 1913)

Radula with seven teeth in a transverse row. Tentacle club with suckers only, the peripheral ones smaller than the medial. Locking apparatus extends along the entire length of the manus. Arms with normal gonatid armature: quadriserial, two medial rows transformed into hooks on arms I-III. See Akimushkin (1963) and Kubodera (1978) for further details.

A total of 478 individuals was taken in 147 hauls (51 demersal, 100-475 m maximum; midwater, one closed tow 200-500 m; and as deep as 0-2400 m in open tows, but most at less than 225 m) from the central California Current, into the Bering Sea (southern, central, eastern, and the Strait - Figure 35). There are a few occurrences in transitional waters. It was also collected by R/V Oshoro Maru at 43°N, 180° in 1979 (Faculty of Fisheries, Hakodate, 1980). This species is known from Japan, the Kuriles, and Aleutians, to Oregon (Berry, 1912b, 1913; Sasaki, 1916, 1920, 1929; Beteshava and Akimushkin, 1955; Akimushkin,

Figure 34. Location of hauls which captured __Berryteuthis__ __anonychus__. Triangle represents haul containing enlarged-sucker forms, and shaded area represents previous records.
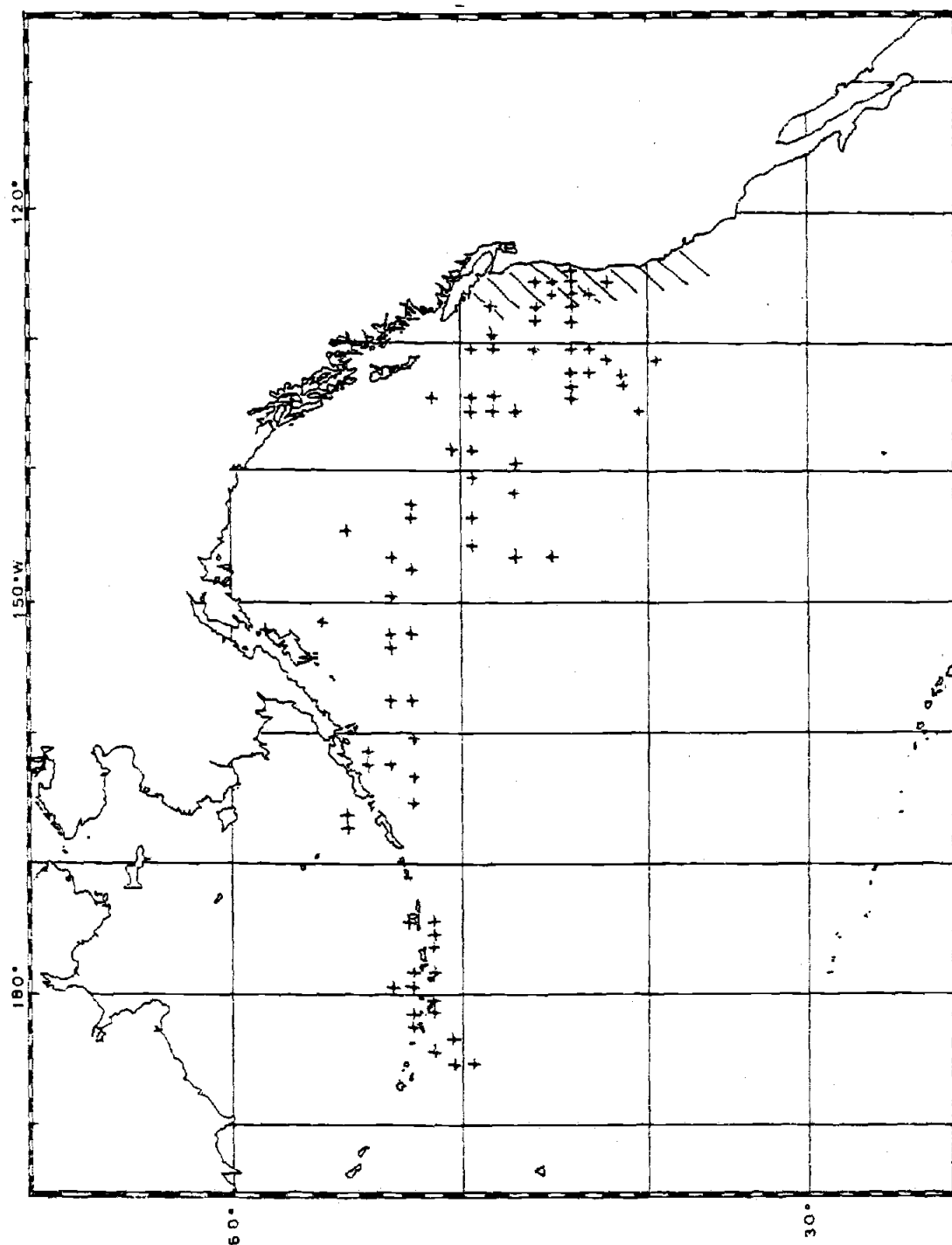
Figure 35. Location of hauls which captured _Berryteuthis_
magister. Triangle represents collection by T/V _Oshoro Maru_.
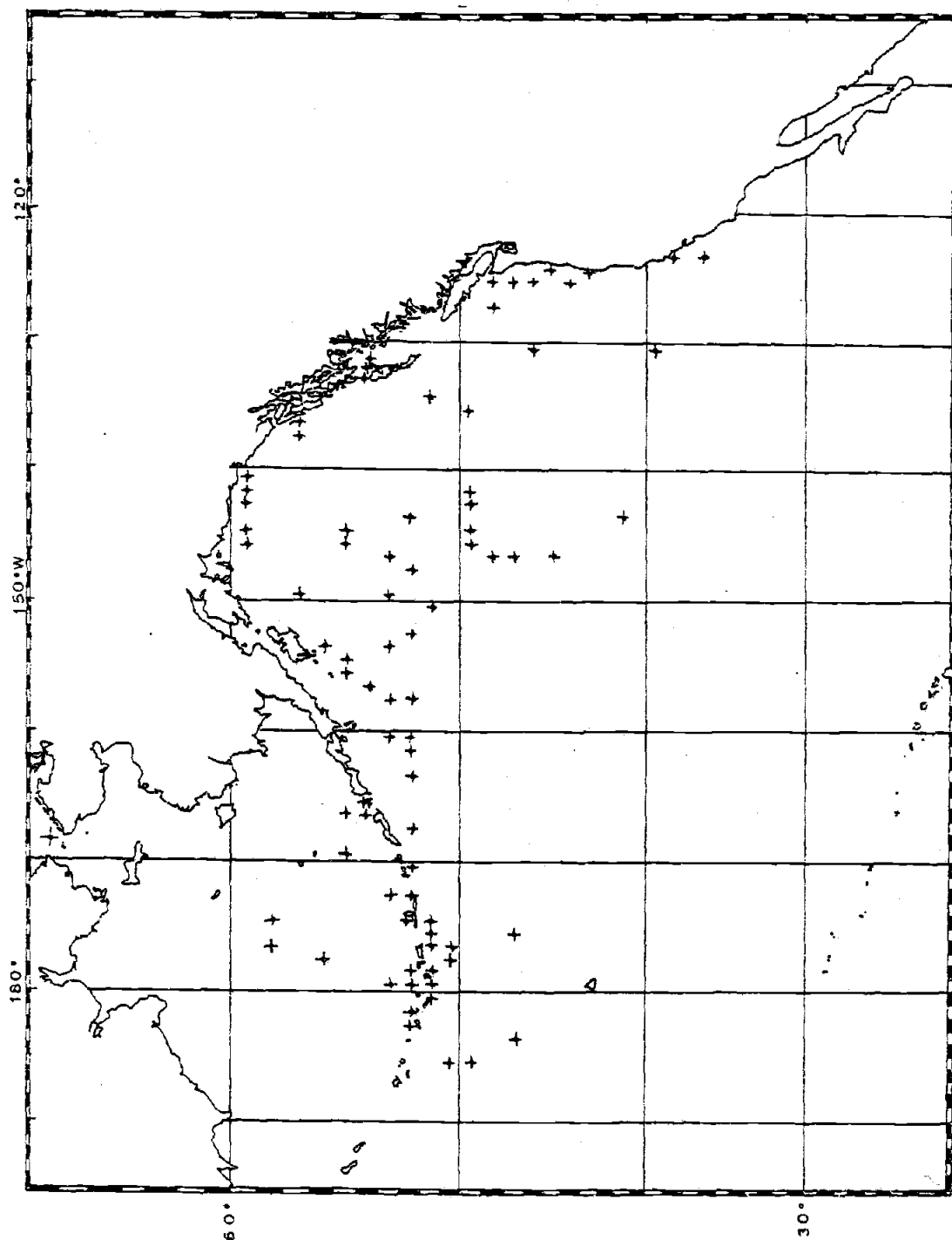
1955, 1963; Okutani and Nemoto, 1964; Pearcy, 1965; Clarke, 1966).
My samples thus represent a slight southern range extension off
the United States, and important occurrences in the Bering Sea and
Strait.

This species is generally considered to be at least partially
demersal or nektobenthic in the adult stage (Roper and Young,
1975). It apparently shifts to a benthic habit before sexual
maturity, and spawns on the continental slope between 200 and
500 m, from June to October, in the Commanders, Attu Island, the
Japan Sea and Tohoku region (Naito et al., 1977a). Naito et al.
(1977b) indicated that the species lives for one year, with growth
habits similar to Gonatopsis borealis, and reaches a maximum size
of 320 mm DML, female, and 250 mm, male. The immature individuals
eat only Crustacea (euphausiids, Parathemisto, calanoids), while
the adults eat only small fish and squid (Naito et al., 1977b).
This species is important in the diets of Physeter macrocephalus
(Akimushkin, 1955; Okutani and Nemoto, 1964), Callorhinus ursinus
(Panina, 1964; Fiscus et al., 1965) and Albatrossia pectoralis
(Sasaki, 1920).

Summary - Family GONATIDAE

The systematics of the Gonatidae remain in a state of flux;
it is clear that several species remain to be named and described.
Generic boundaries are ill-defined, with some species crossing
previously accepted generic boundaries. Gonatus tinro Nesis, 1972
has a radula with five teeth in a transverse row (a long-standing

Gonatus character), and a club totally without hooks (a

Berryteuthis character). There are also variations in the number

of radular teeth in _Gonatopsis_: _Gonatopsis borealis_ and _G. makko_

have seven, while _G. octopedatus_, _G. japonicus_, and _G. okutanii_

all have five. None of the _Gonatopsis_ species so far known has

tentacles in the adult stage, but the larvae do, and the size at

which they are lost varies from about 10 mm DML in _G. borealis_ to

more than 40 mm in _Gonatopsis_ type A Kubodera 1978.

The genus _Gonatus_ is the most polymorphic within the family.

Gonatus pyros possesses the only known luminescent organ within

the family. _Gonatus berryi_ develops arm hooks as a very early

larva, and has a unique club hook arrangement. Club hook

distribution varies from none in _G. tinro_ to central only in _G._

onyx, to central, distal, and several proximal in _G. berryi_,

pyros, _californiensis_, _madokai_, _middendorffi_, and sp. E. There

are additional, as yet undifferentiated, species in the Atlantic

and the Antarctic. Bublitz (1981) has discovered one probable new

species in the eastern Bering Sea, and one of Kubodera's (1978)

types (C) from the northwestern Pacific remains undefined. In the

North Pacific, there are thus at least eleven species of _Gonatus_:

berryi, _californiensis_, _madokai_, _middendorffi_, _onyx_, _pyros_, _tinro_,

sp. A, sp. E, type C Kubodera 1978, and sp. Bublitz (1981). Two

species of _Berryteuthis_ are known: _anonychus_ and _magister_, and

Gonatopsis consists of at least five species: _borealis_,

japonicus, _makko_, _octopedatus_, and _okutanii_. It is not known

whether _Gonatopsis_ type A Kubodera 1978 represents the larval form
of a known or of a new species.

Thirteen species of gonatids were collected during the course
of this study; they can be divided into three broad groups on the
basis of their geographic distributions. The first group includes
two species limited to the California Current system; _Gonatus_
californiensis and _Gonatus_ sp. E are thus far known only from
northern Baja California to Oregon.

The second group includes species whose ranges include the
California and Alaska Currents, but not the Subarctic Current.
Some of these species extend into the Bering Sea and even the
Bering Strait, but none occurs in the northwestern Pacific. This
group includes _Berryteuthis anonychus_, _Gonatus onyx_, _G. pyros_, _G._
berryi, and sp. A. Of these, only _G. pyros_ does not occur in the
Bering Sea; _B. anonychus_ is recorded from Bering Strait in this
study. The three named species of _Gonatus_ occur in quite
southerly waters - _Gonatus pyros_ notably so. There have been
relatively few collections made at the southern limits of the
California Current, so it is difficult to describe the absolute
geographic limits of these species.

The third and last group contains five or six transPacific
species. _Berryteuthis magister_, _Gonatopsis borealis_, _Gonatus_
madokai, and _Gonatus_ type C Kubodera 1978 occur across the
Subarctic Pacific from Japan to Oregon. _Gonatus middendorffi_ is
represented in only one locality in the eastern Aleutians but is
known from the western Pacific. _Gonatopsis okutanii_ is thus far

known only from the northwestern and north central Pacific. All
occur in the Bering Sea, and _Gonatus madokai_ and _Berryteuthis_
magister have been recorded from Bering Strait. Eastward
transport is demonstrable through presence in the southern Bering
Current, just north of the Aleutians, or the Subarctic Current.
However, the lack of samples from all but the easternmost portions
of the Subarctic Current prevents conclusions about that mode of
transport. All these transPacific species do, however, occur in
the southern Bering Current.

Gonatus tinro, although not collected in this study, has a
transPacific distribution as well. It is known from the central
(Nesis, 1972) and eastern (Bublitz, 1981) Bering Sea, the Gulf of
Alaska, and southeast of the Kuriles (Fields and Gauley, 1971;
Nesis, 1972).

In summary, there are three major distributional patterns in
northeastern Pacific Gonatidae: California Current only;
California Current to the Aleutians, and trans-subarctic; and
eastern Pacific, northeastern Pacific, and northern Pacific.

Family HISTIOTEUTHIDAE Verrill, 1881

Characterized by a simple, straight funnel-locking cartilage;
buccal connectives which attach dorsally to arms IV (secondary
connectives may also be developed); biserial brachial armature;
four or more rows of suckers on the clubs; numerous large
photophores; and having the left eye noticeably larger than the
right.

Histioteuthis corona berryi Voss, 1969

Separated from H. corona corona by the pattern of photophores on arms IV. In H. corona berryi, they bear four longitudinal rows of large photophores, versus three in corona corona. The only other members of this genus which possess four rows, reversa and elongata, have a different pattern: three rows of large photophores, and one dorsal marginal row of small photophores. See Voss (1969) for further details.

One individual (OSUI 292) was collected, in a midwater haul (0-2400 m) from transitional waters at 37°10'N, 137°41'W (see Figure 36). The subspecies was described on the basis of two specimens collected at 29°17'N, 125°41'W. As far as I can determine, this is the only specimen reported since the description.

Histioteuthis dofleini (Pfeffer, 1912)

Characterized by three rows of large photophores on arms IV, paired genitalia in the male, 17 photophores in a circlet about the right eye. No enlarged photophores, or concentration of normal photophores, at the arm tips. Distinct flap on the dorsal pad of the funnel organ. Photophores equal sized and widely spaced on anterior third of ventral mantle. See Voss (1969) for further details.

Sixty-seven individuals were collected in 55 hauls (five demersal tows to maximum depths of 100-200 m and 2700-3700 m; midwater tows, as deep as 500-600 m, closed tows, and 0-2500 m,

Figure 36. Location of hauls which captured Histioteuthis corona berryi (circle; square represents capture location of the only previously known specimens) and Histioteuthis dofleini (crosses; triangles represent previous records).
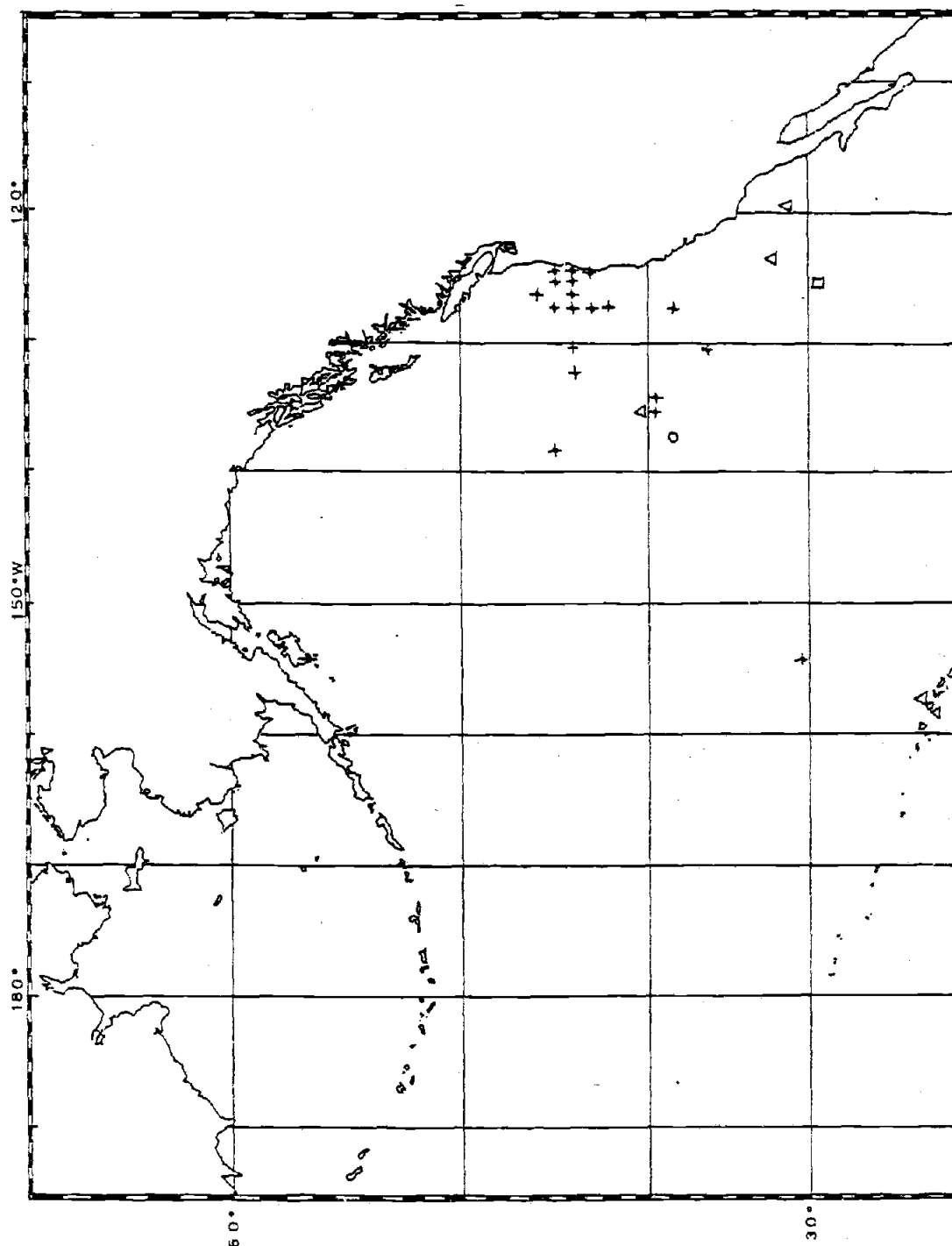
open tows), primarily within the California Current system (Figure 36). One individual was taken in central Pacific waters. This species has a cosmopolitan distribution; it has been recorded from all oceans, between 40°S and about 48°N (Voss, 1969; Young, 1975, 1977, 1978).

Histioteuthis heteropsis (Berry, 1913)

Characterized by eight or nine longitudinal rows of photophores on arms IV; no median tubercular ridge on the dorsal surface of the mantle or at the bases of the arms. See Voss (1969) for further details.

This was the most common histioteuthid in the material examined; 108 individuals were collected in 61 hauls in the California Current region between southern California and central Oregon (Figure 37). It was taken in 19 midwater hauls (mostly 0-500 m or shallower, one haul 0-1000 m) and 42 demersal hauls (mostly 0-500 m maximum). *Histioteuthis heteropsis* has been previously recorded only from waters off central and southern California and northern Baja California in the North Pacific (Young, 1972). There is a single record off Valparaiso, Chile at about 33°S (Voss, 1969); the species may exhibit a biantitropical distribution in the eastern Pacific.

Family NEOTEUTHIDAE Naef, 1921

Characterized by a simple, straight funnel-locking cartilage; buccal connectives which attach dorsally to arms IV; biserial

Figure 37. Location of hauls which captured Histioteuthis heteropsis. Shaded area represents previous records in northern hemisphere (see text).
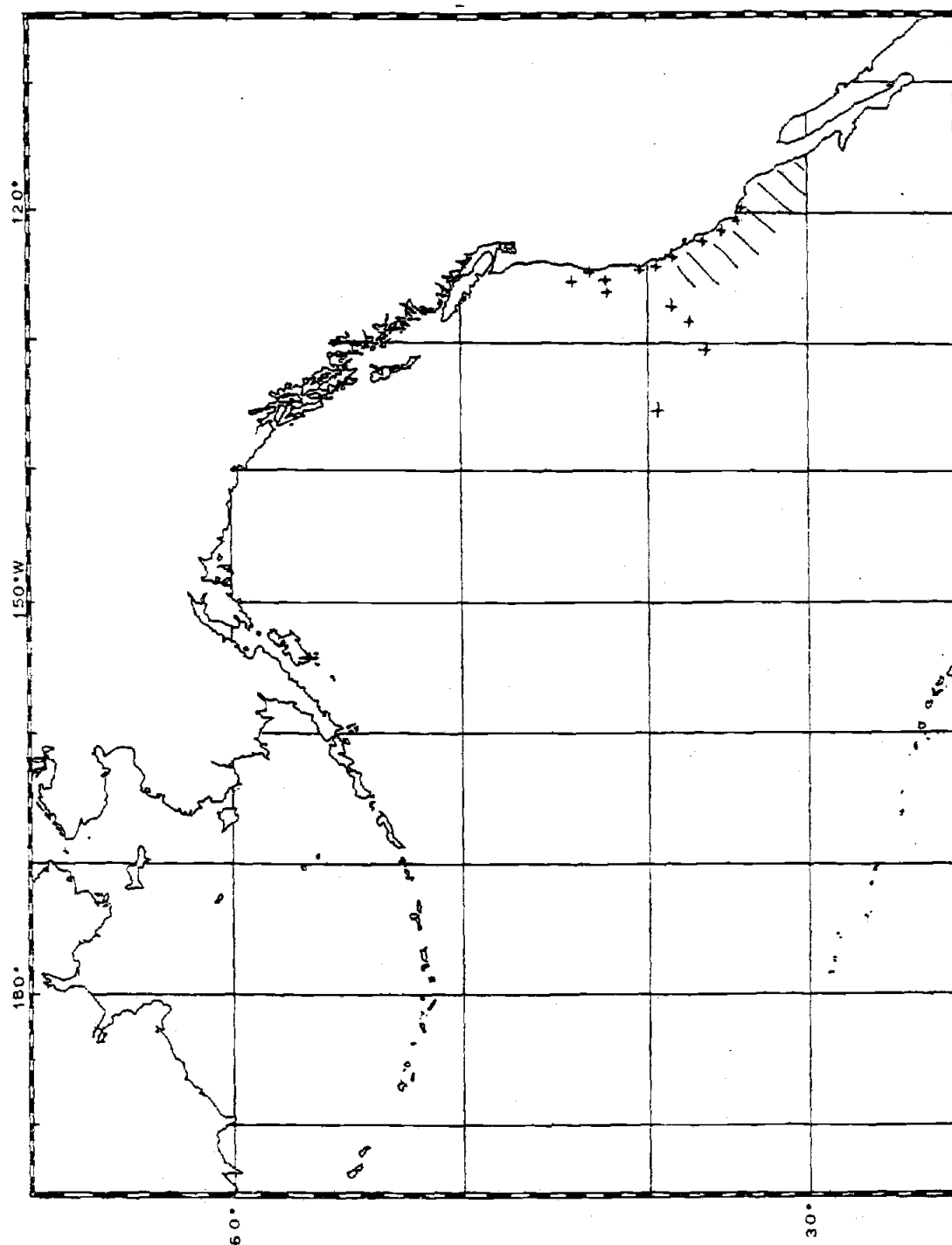
brachial armature; club armature in four rows distally or in young specimens, and in many rows proximally; and the lack of anterior fin lobes.

Genus *Neoteuthis* Naef, 1921

Characterized by having fins longer than 60% of DML; clubs longer than 60% DML, and bearing many hundreds of very small suckers. See Young (1972) for discussion of the genus.

Neoteuthis sp.

Fins long and narrow (more than 60% DML); inserted laterally, broadly separated in the dorsal midline. Clubs long (more than 60% DML), proximal portion of manus bearing many minute suckers. No suckers are present on the protective membrane of the club. The large suckers of the manus appear to bear about eight to ten very short, pointed teeth on their distal borders. The arm suckers have six to eight very low crenulations or broad, truncate teeth on their distal borders. The suckers on arms IV are smaller than those of arms I-III. The mantle is covered with easily damaged silvery tissue. Measurements of the individual collected are given in Table 8 (OSUI 727).

Only one species, *N. thielei*, has been described, but the original description and specimens are inadequate for comparative purposes. The group awaits collection of more specimens and revision.

One individual (21 mm DML) was collected in central Pacific

Table 8. Measurements of the only _Neoteuthis_ collected.
Abbreviations as in Table 4.

DML	21 mm
MW	5
HW	5
FL	15
FW	11
AL I	6
AL II	8
AL III	7
AL IV	7
TL	11
CL	4

Figure 38. Location of the haul which captured _Neoteuthis_ sp.
Previous records shown as triangles.
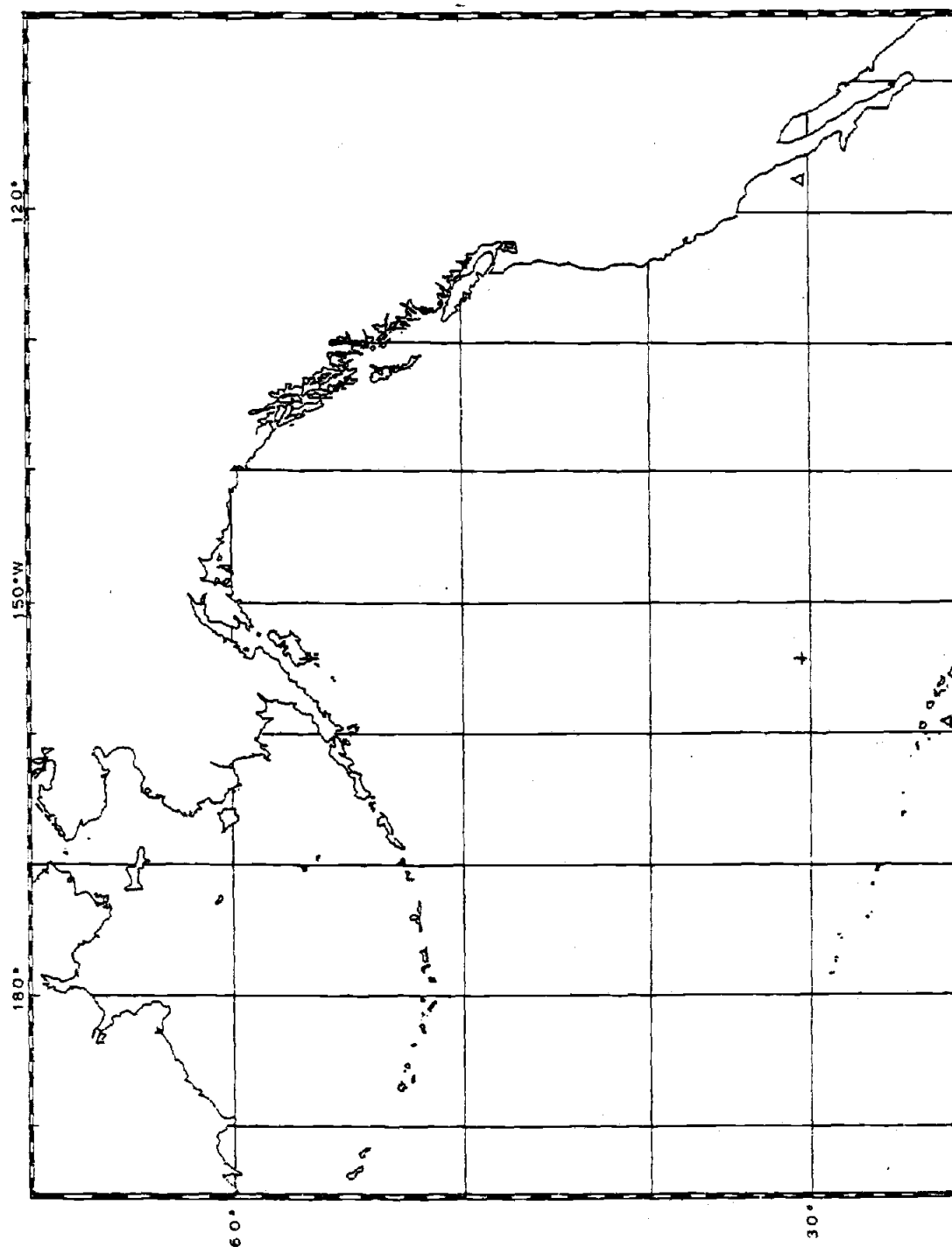
waters (midwater haul, 0-245 m) (Figure 38). Neoteuthis has been recorded from Young's (1972) southern California study area (one individual), off Hawaii (Young, 1978), off New Zealand, and from the Atlantic and Mediterranean (Young, 1972; Lipka, 1975). More than one species is represented; Lipka's (1975) specimen differs from Young's (1972) individual, but it is unknown which, if either, is identical with N. thielei. The genus, at least, is cosmopolitan.

<div align="center">Family BATHYTEUTHIDAE Pfeffer, 1900</div>

Characterized by a simple, straight funnel-locking cartilage; buccal connectives which attach dorsally to arms IV; brachial armature in one or two rows proximally, increasing to three or four rows distally; multiserial club armature; suckers on the buccal lappets, and an embedded photophore at the base of each arm I-III. See Roper (1969) for a thorough discussion of the family.

<div align="center">Bathyteuthis abyssicola Hoyle, 1885</div>

Characterized by the small number of arm suckers (about 100) on each arm I-III; the lack of free trabeculae at the bases of the arms; short blunt arms; and short and narrow gills.

Three individuals (12, 14, 27 mm DML; OSUI 720-722) were collected in three midwater hauls (0-200 m, 0-205 m, 800-1000 m) in central Pacific waters and off the Oregon coast (Figure 39). The species is known from Antarctic waters, the central and North Atlantic, and the Gulf of Panama. Young (1977) collected this

Figure 39. Location of the hauls which captured _Bathyteuthis_
abyssicola (crosses; previous record represented by triangle), _B._
berryi (circles; shaded area represents previous records), and
Bathyteuthis sp. (square).
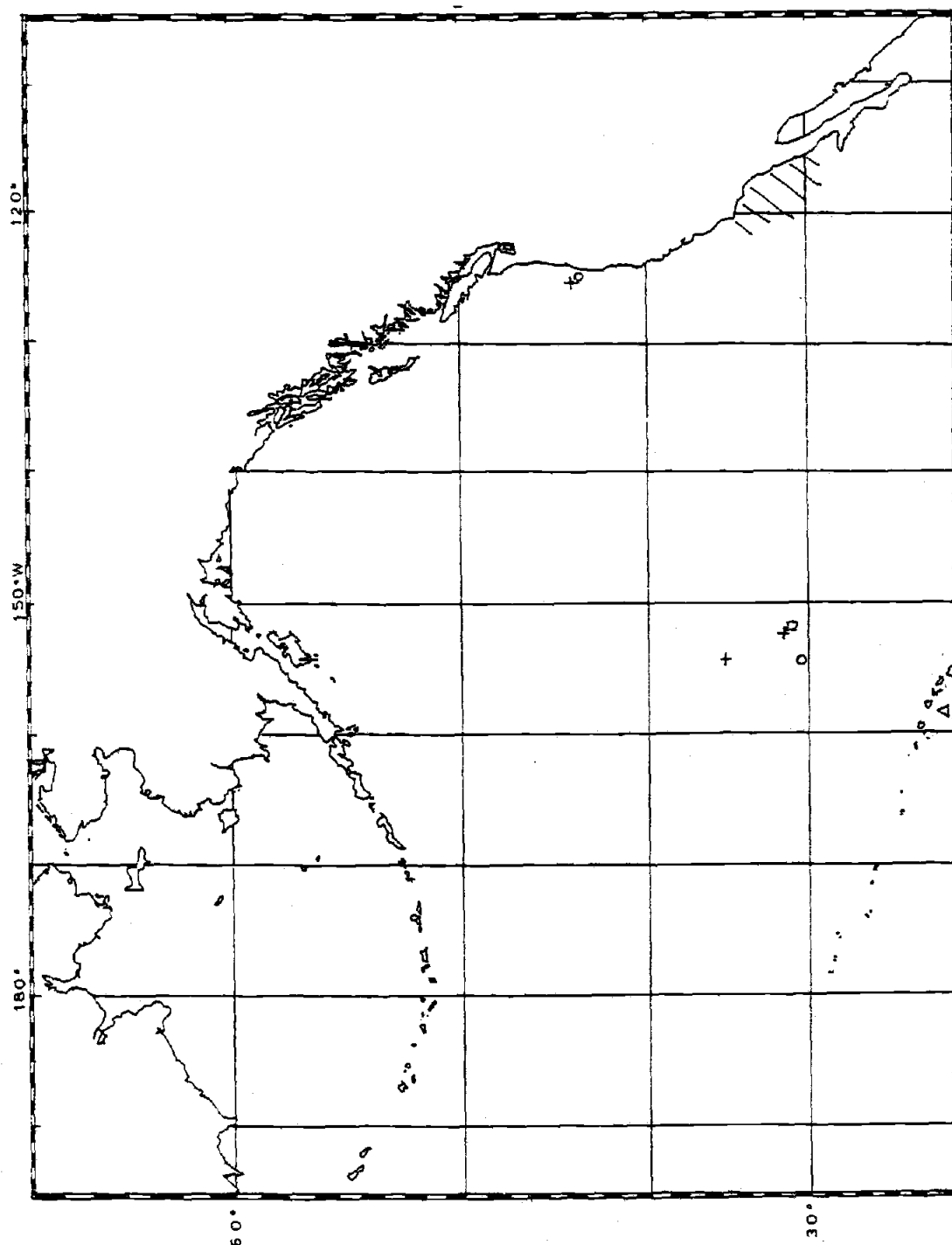
species off Hawaii. My specimens thus represent the first records
in the Pacific north of Hawaii. Roper (1969) expected this
species to be absent from waters of salinity less than 34.5‰.

Bathyteuthis berryi Roper, 1968

Characterized by the large number of suckers on arms I-III
(over 250); the lack of free trabeculae at the bases of the arms;
long, attenuate arms; and long and broad gills.

Two individuals were collected (OSUI 417, 723): one off the
Oregon coast (midwater trawl, 0-20 m), and one from central
Pacific waters north of Hawaii (midwater trawl, 0-252 m) (Figure
39). This species was previously known only from sixteen
specimens taken in Young's (1972) study area off southern
California between 28°30'N and 33°30'N. The present specimens
thus represent a major range extension. An additional specimen of
Bathyteuthis, not specifically identifiable, was collected at
31°N, 153°W (midwater trawl, 0-185 m) (Figure 39). All arms but a
portion of one were missing.

Summary - Family BATHYTEUTHIDAE

Bathyteuthis abyssicola occurs in central Pacific and
Atlantic waters, as well as in Antarctic seas, and thus exhibits a
relatively cosmopolitan distribution. Bathyteuthis berryi is so
far known only from the north central and northeastern Pacific.
The third member of the genus, B. bacidifera, is known from the
eastern equatorial Pacific, and possibly from equatorial waters of

the Indian Ocean (identification in question). The family thus contains one cosmopolitan species, and two species apparently limited to eastern or central Pacific waters.

Family CTENOPTERYGIDAE Grimpe, 1922

Characterized by a simple, straight funnel-locking cartilage; buccal connectives which attach ventrally to arms IV; quadriserial to hexiserial brachial armature on the distal half of arms I-III; eight to fourteen sucker rows on the clubs; the presence of photophores in some instances; ribbed fins; and suckers on the buccal lappets.

Ctenopteryx sicula (Vérany, 1851)

Characters are those of the family. See Rancurel (1970) and Yamamoto and Okutani (1975) for further details.

Six individuals (7, 10, 15, 17, 30, 46 mm DML; (OSUI 365, 741, 792-795) were taken in five midwater hauls (0-250 m maximum) in central Pacific or transitional waters (Figure 40).

The species has been recorded from the Atlantic and Indian Oceans (Clarke, 1966; Nesis, 1973b), and in the Pacific, off Japan (Yamamoto and Okutani, 1975), off northern Baja California (Okutani and McGowan, 1969), in the eastern equatorial Pacific off the Galapagos and as far south as 12°S (Nesis, 1973a), off Hawaii (Young, 1978), and off New South Wales (Allan, 1945). Ctenopteryx sicula probably represents a group of species (Rancurel, 1970); once the systematics of the group have been worked out, the

Figure 40. Location of hauls which captured _Ctenopteryx sicula_. Previous records shown as triangles.
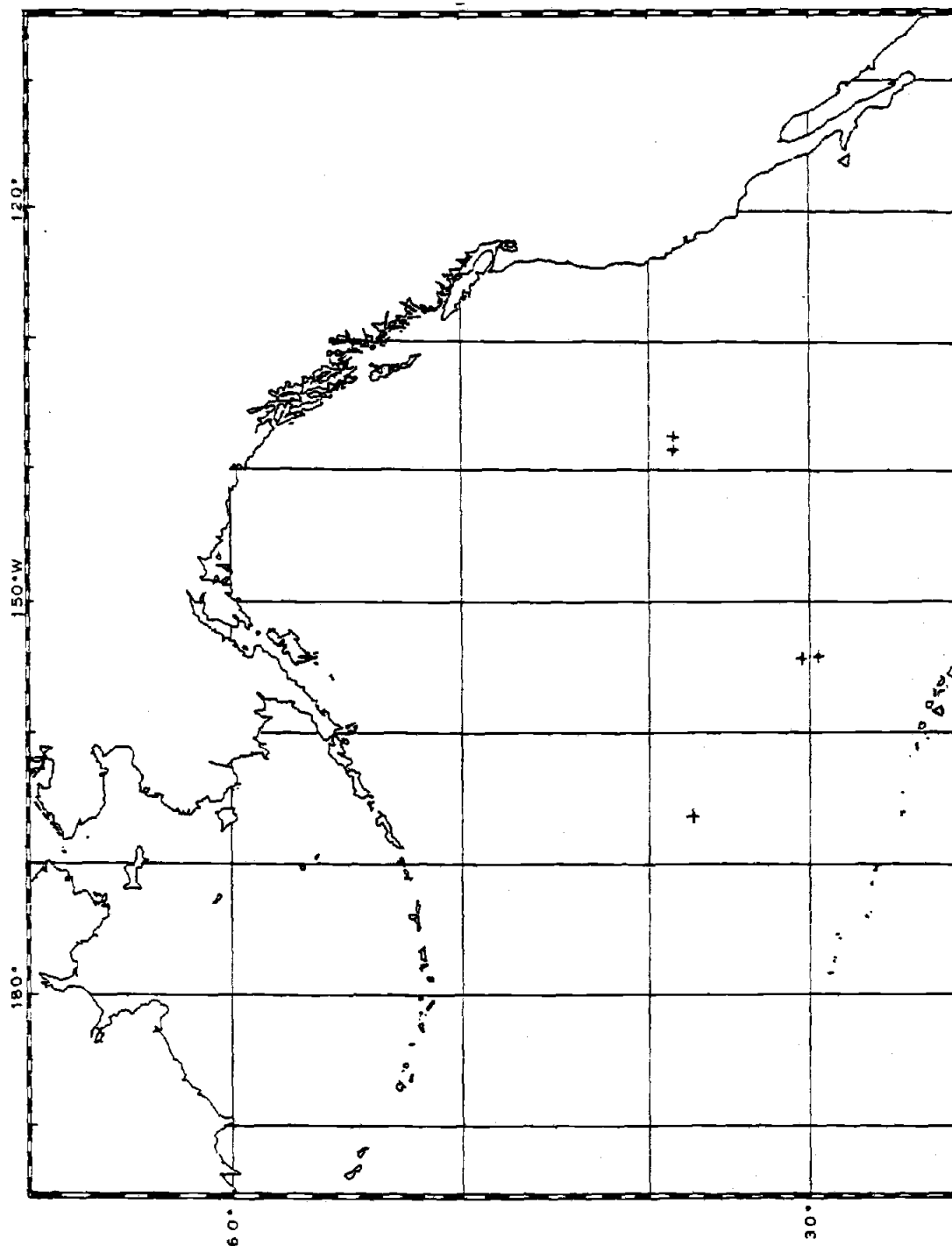
distributions of the individual species may prove to be much less cosmopolitan.

Family BRACHIOTEUTHIDAE Pfeffer, 1908

Characterized by a simple, straight funnel-locking cartilage; buccal connectives which attach ventrally to arms IV; biserial brachial armature; multiserial (more than four rows) proximal club armature; and the absence of photophores.

Genus *Brachioteuthis* Verrill, 1881

Characters are those of the family.

Brachioteuthis sp.

The systematics of the family are confused; I have not attempted to name the individuals collected. Lipka (1975) discusses the described species, and some of the systematic difficulties.

Two small (7,11 mm DML; OSUI 817, 818) individuals were collected in two midwater hauls (0-170 m) in central Pacific waters (Figure 41). A number of specimens of *Brachioteuthis* sp. have been recorded off Hawaii (Roper and Young, 1975; Young, 1978). Six individuals tentatively identified as *B. riisei* are known from the East China Sea and Ryukyu Islands area (Yamamoto and Okutani, 1975). Young (1972) lists *Brachioteuthis* sp. as occurring off Baja California between 30° and 32°N, but no further information is given.

Figure 41. Location of hauls which captured *Brachioteuthis* sp. Previous records of the genus shown as triangle and shaded area.
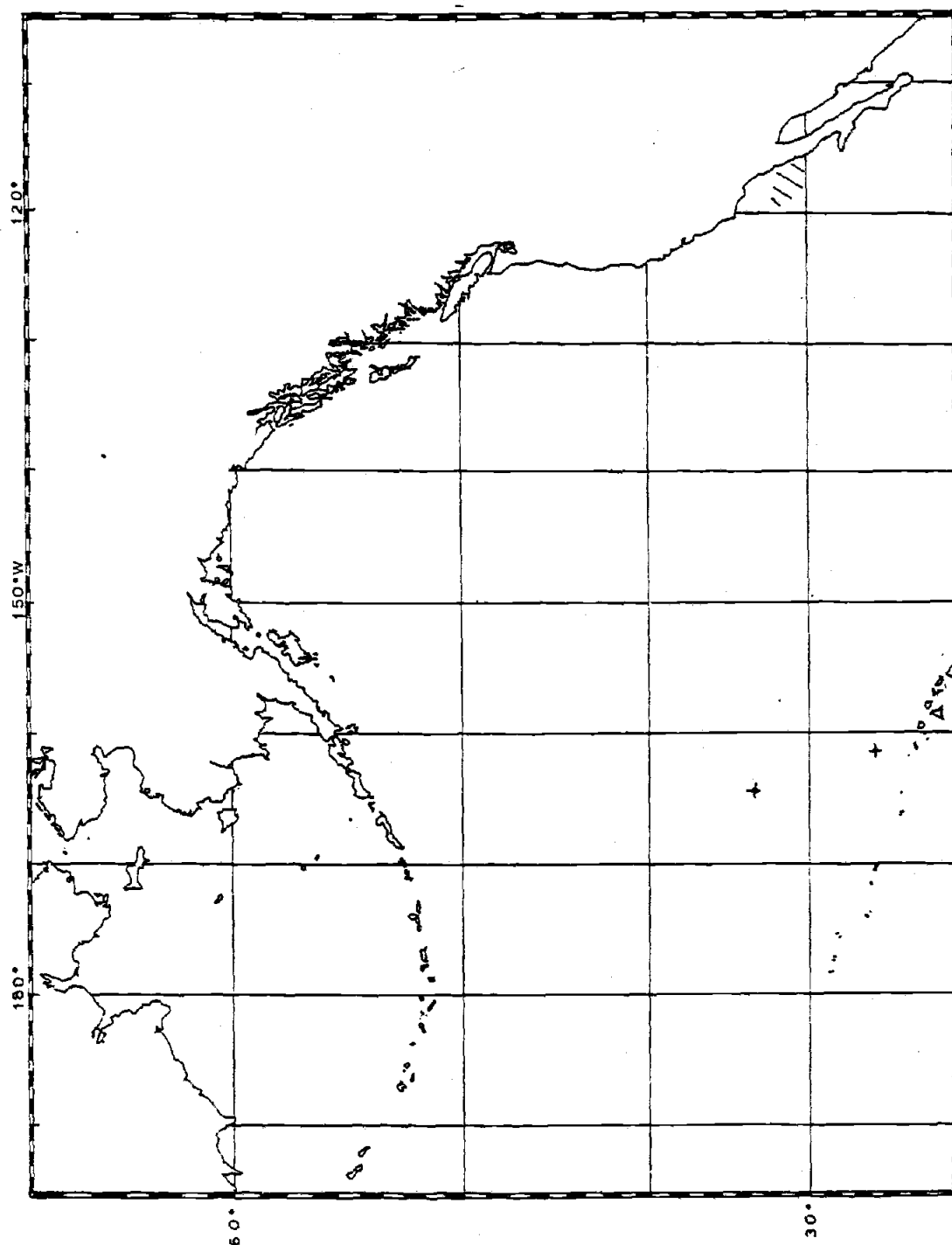
It seems apparent that members of the family occur in the North Pacific (none had been recorded previous to 1966 - Clarke, 1966), but their specific identity (or identities) will have to await the collection of more and larger individuals.

Family OMMASTREPHIDAE Steenstrup, 1857

Characterized by a funnel-locking cartilage in the shape of an inverted T (fused at one point in _Symplectoteuthis_). Buccal connectives attach dorsally to arms IV; brachial armature is biserial; club armature is tetraserial or octoserial. Photophores may be present.

Subfamily OMMASTREPHINAE Steenstrup, 1857

Funnel groove with foveola and several side pockets; photophores present.

Ommastrephes bartramii (LeSueur, 1821)

Four equidistant enlarged teeth in each of the largest tentacular sucker rings. Four to six suckers proximal to the first knob of the fixing apparatus. A broad midventral silvery strip on the mantle. Arm tips not attenuate.

Four individuals (99-230 mm DML; OSUI 402, 763-765) were taken: three by dipnet in central Pacific waters, and one by bow and arrow in the California Current (Figure 42). An additional specimen (146 mm DML) was dipnetted at 11°S, 110°W. This species, which has in the past not always been effectively separated from its congeners, _O. caroli_ and _O. pteropus_, is reported to be a

Figure 42. Location of hauls which captured _Ommastrephes_
bartramii (crosses; triangles represent captures by T/V _Oshoro_
Maru; circles represent gill net captures - Fiscus and Mercer,
1982; one additional specimen was taken at 11°S, 110°W) and
Dosidicus gigas (square; two additional individuals were taken at
9°S, 80°W).
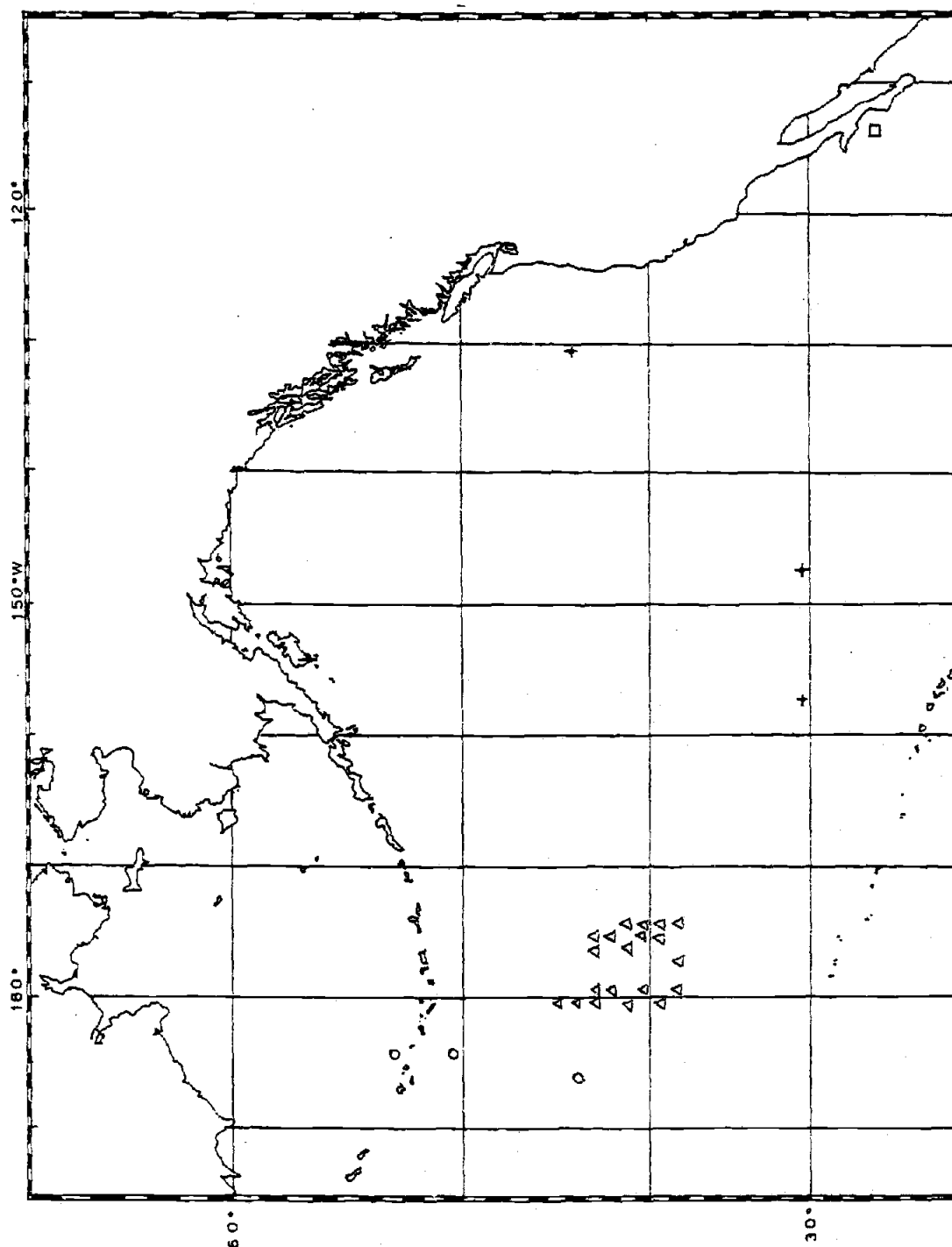
tropical-subtropical cosmopolite. It may, however, especially in the Pacific, more closely approximate an antitropical distribution (Nesis, 1973b; Wormuth, 1976; Okutani, 1977), common between 20° and 40°S, and from 25° to 45°N. It was taken in salmon gillnets by T/V Oshoro Maru between 38° and 45°N, and 174° and 179°E (Faculty of Fisheries, Hakodate, 1979, 1980) and further north (Fiscus and Mercer, 1982) (see Figure 9). Nesis (1973b) considered it to be generally limited to waters of 16°C or higher. Although taken in waters as cool as 10.7°C (one individual) by T/V Oshoro Maru in 1978, and as cool as 12.4°C in 1979, the number of individuals captured was roughly proportional to temperature. Fiscus and Mercer (1982) reported collections at 9.8° to 9.9°C (50-53°N, 175°E) and at 12°C (44°N, 173°E).

Naito et al. (1977a) listed its temperature range as 8-24°C, with abundant captures at 12-18°C. It appears to grow to maturity in one year, reaching a maximum size of 480 mm DML for the females, and 410 mm for the males. The adults eat small fish (Diaphus coeruleus, Engraulis japonica, Sardinops melanosticta, and young Scomber japonicus) and other O. bartramii and Watasenia scintillans, but no Crustacea. Immature individuals eat euphausiids and Parathemisto as well as small fish and squid (Naito et al., 1977b).

This species is an extremely powerful swimmer; adults are seldom captured in standard oceanographic nets. Identification of the larvae remains a problem.

<u>Dosidicus gigas</u> (d'Orbigny, 1835)

Robust arms with very attenuate tips bearing many very small suckers. Trabeculae large, extending beyond protective membranes of arms.

Three individuals (179, 266, 276 mm DML; OSUI 379, 760, 761) were collected in the eastern equatorial Pacific, two by dipnet, and one with hook and line (Figure 42). The species is abundant in the eastern subtropical Pacific (predominantly south of the equator) and occasionally ranges into tropical or northern subtropical waters (Nesis, 1970, 1973a,b; Wormuth, 1976). It has also been reported from the southwestern Pacific: Australia and the Solomon Islands (Clarke, 1966). In the 1930s <u>Dosidicus gigas</u> was exceedingly abundant off the California coast (Phillips, 1961).

<u>Symplectoteuthis luminosa</u> Sasaki, 1915

Funnel-locking cartilage fused at the midpoint to the mantle-locking cartilage. Two broad midventral luminous strips on mantle.

Seven individuals (28-123 mm DML; OSUI 399, 400, 766-770) were recovered: two by dipnet in central Pacific waters, one by squid jig in transitional waters, and four by dipnet at the mouth of the Sea of Cortez (Figure 43). The latter specimens (28-59 mm DML) are notable in that only the largest shows the characteristic

Figure 43. Location of hauls which captured _Symplectoteuthis luminosa_ (crosses). Previous records shown as triangles.
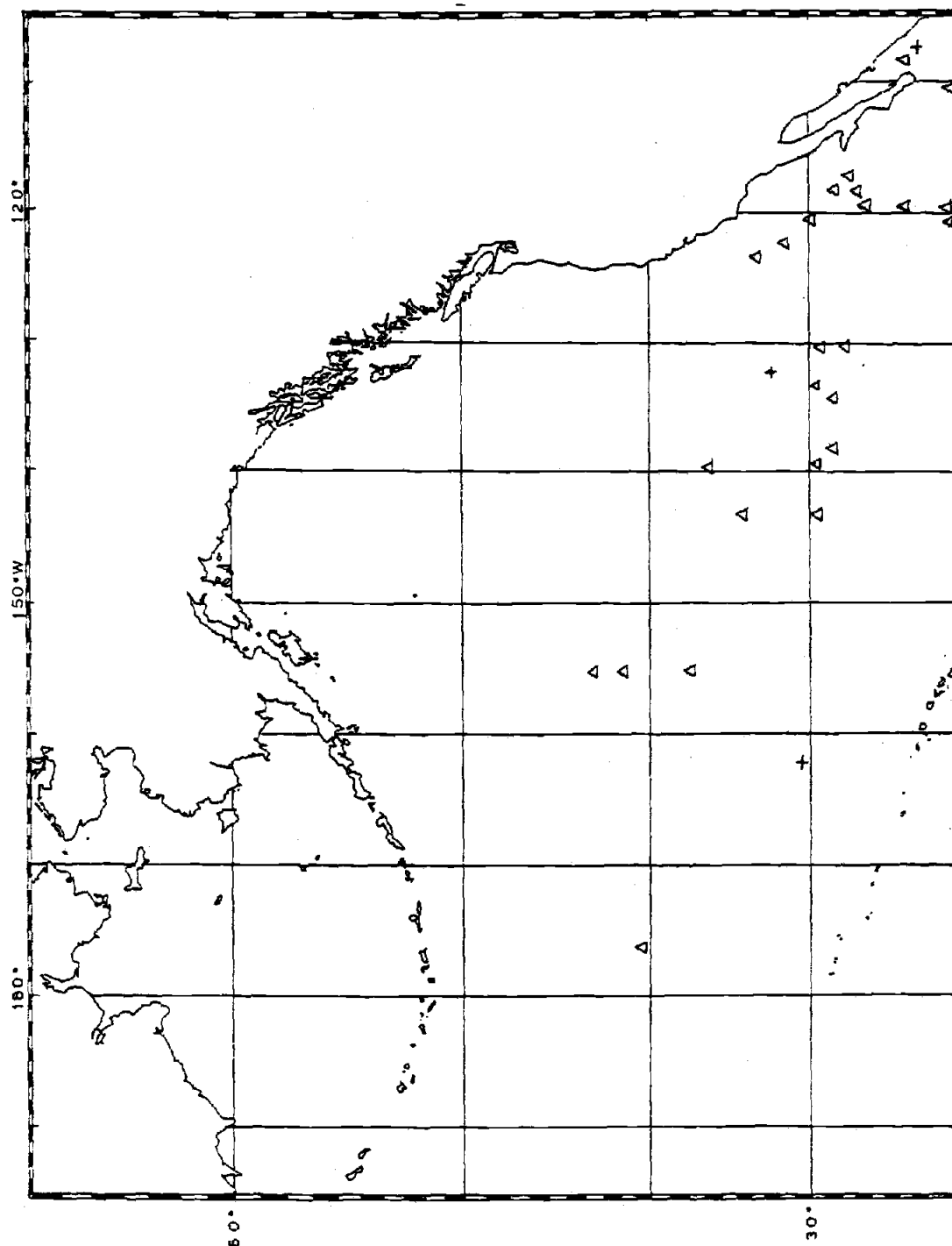
longitudinal luminescent strips, which separate S. luminosa from its congener, S. oualaniensis. This character is apparently only developed at a relatively large size. It might conceivably be important as an intraspecific recognition character for reproductive individuals.

Symplectoteuthis luminosa has been previously recorded off Japan; the Kuriles; along the California coast from 20° to 35°N, north and west in a broad band to 43°N, 155°W and 40°N, 173°W; Australia; the Kermadec Islands; the Indian Ocean; and the South Atlantic (Clarke, 1966; Filippova, 1968; Wormuth, 1976). The central Pacific specimens represent the first records so far into North Pacific Central waters. Symplectoteuthis oualaniensis is known throughout the tropical regions of the Indian and Pacific Oceans. The distributions of the two species are nearly distinct, however, as S. luminosa is generally restricted to peripheral regions of these oceans. Nesis (1973b) termed its distribution "peripheral bicentral"; it appears to be generally antitropical.

Summary - Family OMMASTREPHIDAE

Eighteen individuals, representing three species, were collected. All generally demonstrate an antitropical distribution (Dosidicus gigas, and perhaps Symplectoteuthis luminosa, may occasionally enter tropical waters). The three species are all extremely active animals - Ommastrephes bartramii has often been termed the "flying squid." Their sparse representation in these collections is not indicative of their actual abundance and

considerable ecologic importance. They have been frequently

collected in gillnets in the northern North Pacific.

Family CHIROTEUTHIDAE Gray, 1849

This family is characterized by an oval funnel-locking

cartilage; bearing one or two inwardly directed knobs (tragus,

antitragus). The armature consists of suckers only, and is

biserial on the arms and tetraserial on the tentacular clubs.

Buccal connectives attach to the ventral borders of arms IV.

Photophores are generally present.

Chiroteuthis calyx Young, 1972

This species may be separated from all but two of its

congeners on the basis of its photophore pattern. Distinction

from these two is by fin shape, sucker dentition, relative sucker

size, and the structure of protective membranes on the club (see

Young, 1972 for details).

This genus is notable for the persistence of larval

characteristics to a large body size (50-60 mm DML). This

"doratopsis larva" is an important component of the cephalopod

fauna off Oregon.

A total of 2873 individuals was taken in 1005 hauls (all but

two midwater; no individuals taken in closed hauls below 1000 m).

This species represented 6.6% of all cephalopods captured, and was

present in 36% of all hauls capturing cephalopods. Chiroteuthis

calyx was taken throughout the California Current system and its

northern extensions, as well as occasionally in transitional

waters (Figure 44). It has previously been recorded from waters

off southern California (Berry, 1963; Young, 1972) and Oregon

(Pearcy, 1965). Nesis (1973b) listed two captures south of the

Alaskan Peninsula (see Figure 44). There is one western Pacific

record, from a sperm whale stomach northeast of Honshu (Okutani

and Satake, 1978).

<p align="center"><u>Chiroteuthis joubini</u> Voss, 1967</p>

Characterized by the presence of a single, median visceral

photophore; and ten oval optic photophores, in two rows. See

Young (1972) for discussion of the species.

Four individuals (26, 27, 34, 44 mm DML; OSUI 819-822) which

appear to belong to this species were taken in midwater hauls

(0-170, 0-200 m) in central Pacific and transitional waters

(Figure 45). The species is known only from the central Atlantic

(Joubin, 1933), but it is also the only species in the genus with

a single median visceral photophore. If these specimens prove to

be <u>C</u>. <u>joubini</u>, it will be the first record for the Pacific Ocean.

Fiscus and Mercer (1982) noted the collection of a

fragmentary <u>Chiroteuthis</u> in a salmon gill net at 49 °46'N, 176° 29'W

(Figure 45). It was not specifically identified.

Figure 44. Location of hauls which captured _Chiroteuthis_ _calyx_ (crosses; triangles are records of Nesis, 1973b; other previous records shown as shaded area).
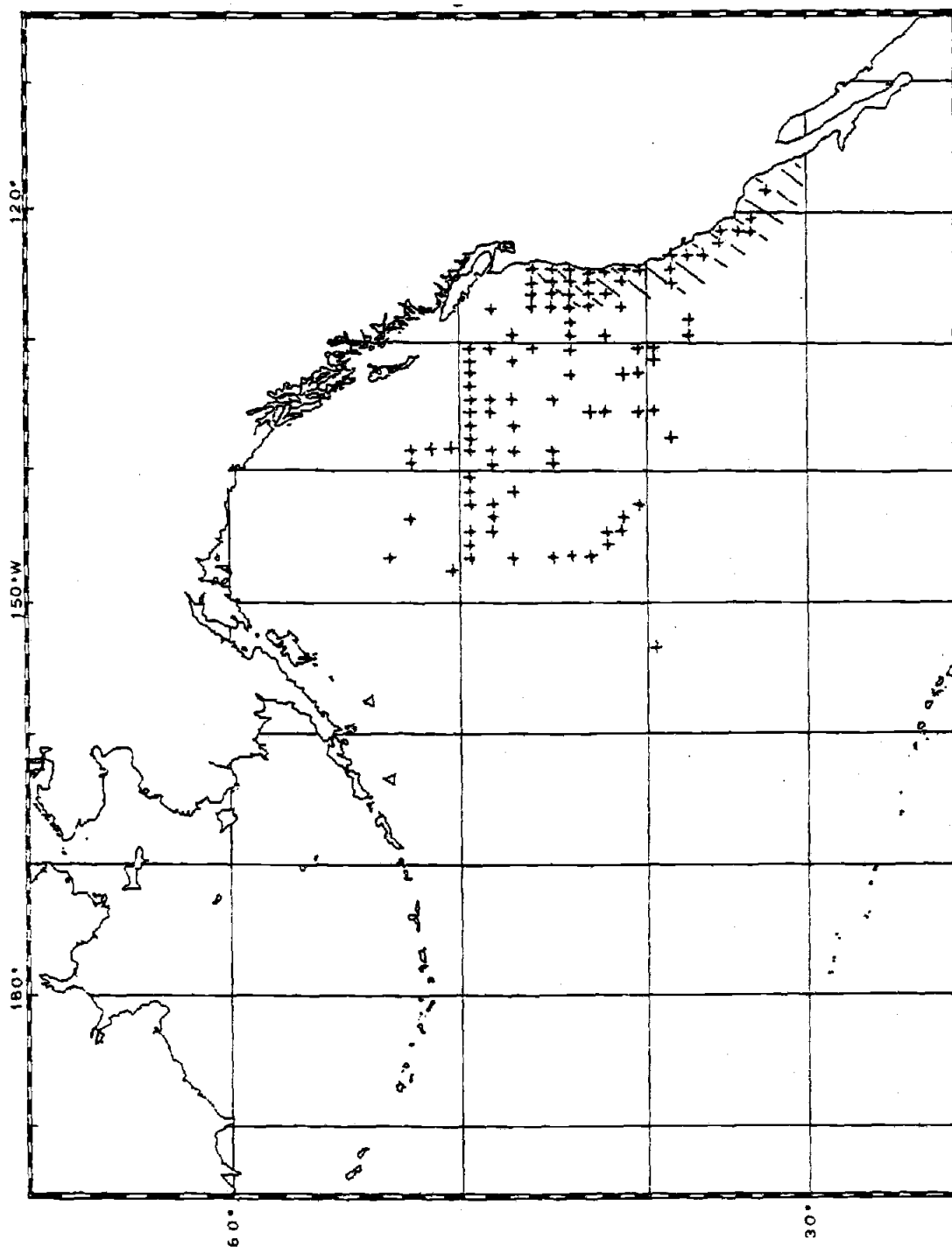
Figure 45. Location of hauls which captured Chiroteuthis joubini
(crosses), Chiroteuthis sp. (triangle - Fiscus and Mercer, 1982),
and Valbyteuthis oligobessa (circles; previous records from shaded
area).
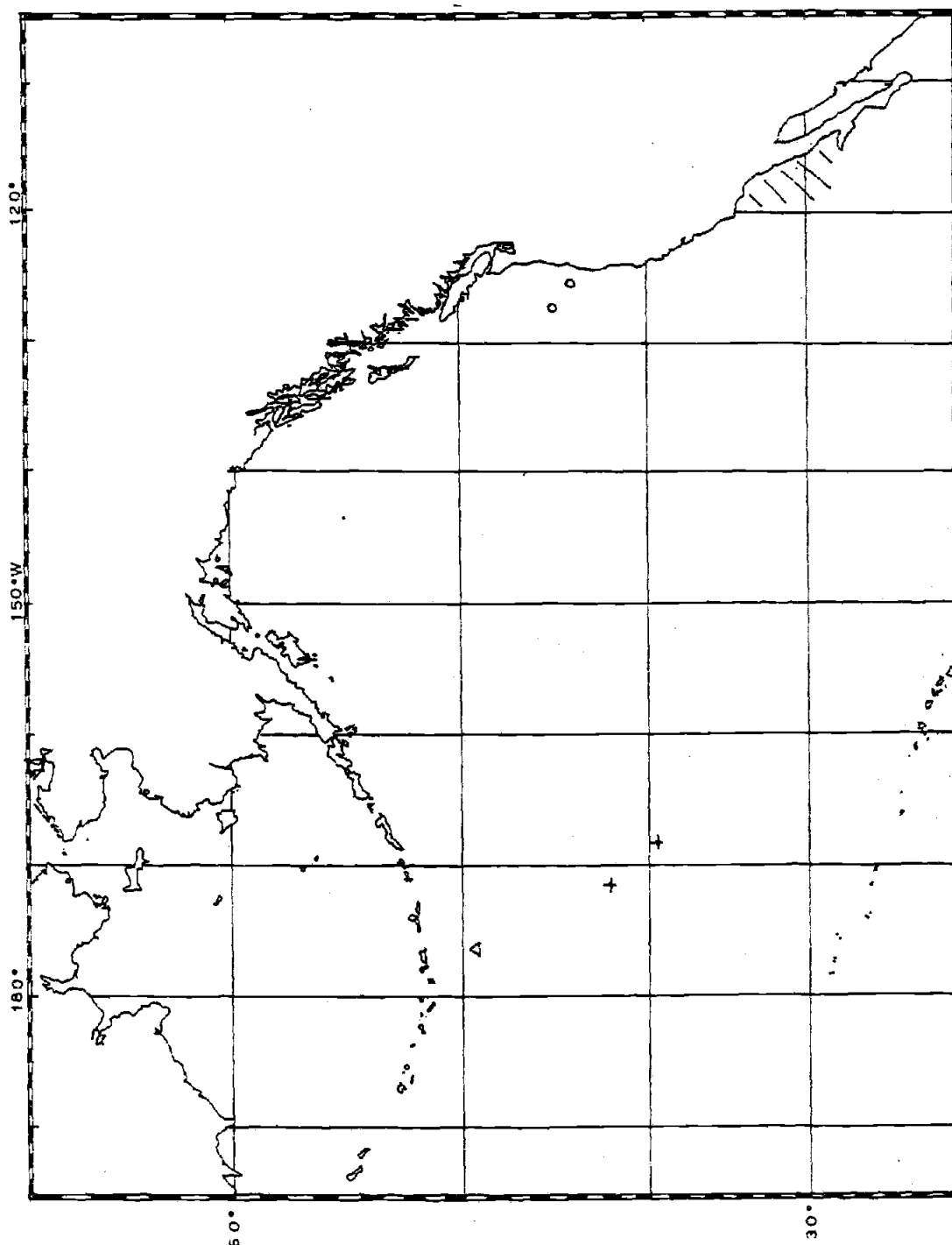
Valbyteuthis oligobessa Young, 1972

Oval funnel-locking cartilage, with antitragus only. Clubs short, compact, with quadriserial stalked suckers. Fins subterminal. No photophores or funnel valve. Two to four suckers on each of arms IV. Twenty-five to 35 narrow teeth on brachial suckers. See Young (1972) for further details.

Three individuals (63, 67, 69 mm DML; representatives: OSUI 565, 773) were collected in three midwater hauls (0-2000 m) off the Oregon coast (Figure 45). The species has been previously described only from Young's (1972) southern California study area. The present specimens thus represent a notable range extension. It is as yet unknown whether the species is limited to the California Current. Nesis (1973b) listed a southern limit as "? Micronesia", but gave no collection data.

Summary - Family CHIROTEUTHIDAE

Three species, including 2886 individuals, were identified in this study. Chiroteuthis calyx and Valbyteuthis oligobessa are absent from central waters; both are essentially limited to the California Current, although C. calyx does extend into transitional waters. Chiroteuthis joubini is limited to central waters of the Pacific and Atlantic. Chiroteuthis calyx and V. oligobessa are known only from the Pacific.

Family MASTIGOTEUTHIDAE Verrill, 1881

Characterized by an oval funnel-locking cartilage, with inwardly-projecting knobs; buccal connectives which attach ventrally to arms IV; biserial brachial and multiserial (more than fifteen rows) club armature; and the presence of photophores.

? *Mastigoteuthis dentata* Hoyle, 1904

Club suckers very small, 0.13-0.16 mm at a DML of 92 mm. Funnel-locking cartilage with a tragus and a weakly developed antitragus. Arm suckers bear 13 teeth on the distal half of the inner ring. Fin length 43-67% DML. Club suckers with a smooth inner ring and 12 to 14 small, inwardly projecting knobs on the outer ring. See Young (1972) for discussion of the genus.

Three individuals (43, 71, 75 mm DML; OSUI 204, 355, 357) were collected in three midwater (0-425, 0-1100, 0-1125 m) California Current hauls (Figure 46). The specimens possess minute club suckers (about 0.1 mm diameter), which precludes identity with *M. pyrodes*. The funnel-locking cartilage has a distinct tragus and a weak antitragus. The arm suckers bear about fifteen more or less pointed teeth. Fin length is 49-72% DML. Arms IV are very long in the larger specimens: 139% DML at 71 mm, 173% at 75 mm. In the smallest specimen, arms IV are 93% DML.

This species is otherwise known only from off the Galapagos Islands and Gulf of Panama (Clarke, 1966).

Figure 46. Location of hauls which captured ? Mastigoteuthis dentata (crosses) and M. pyrodes (circles; previous records from shaded area).
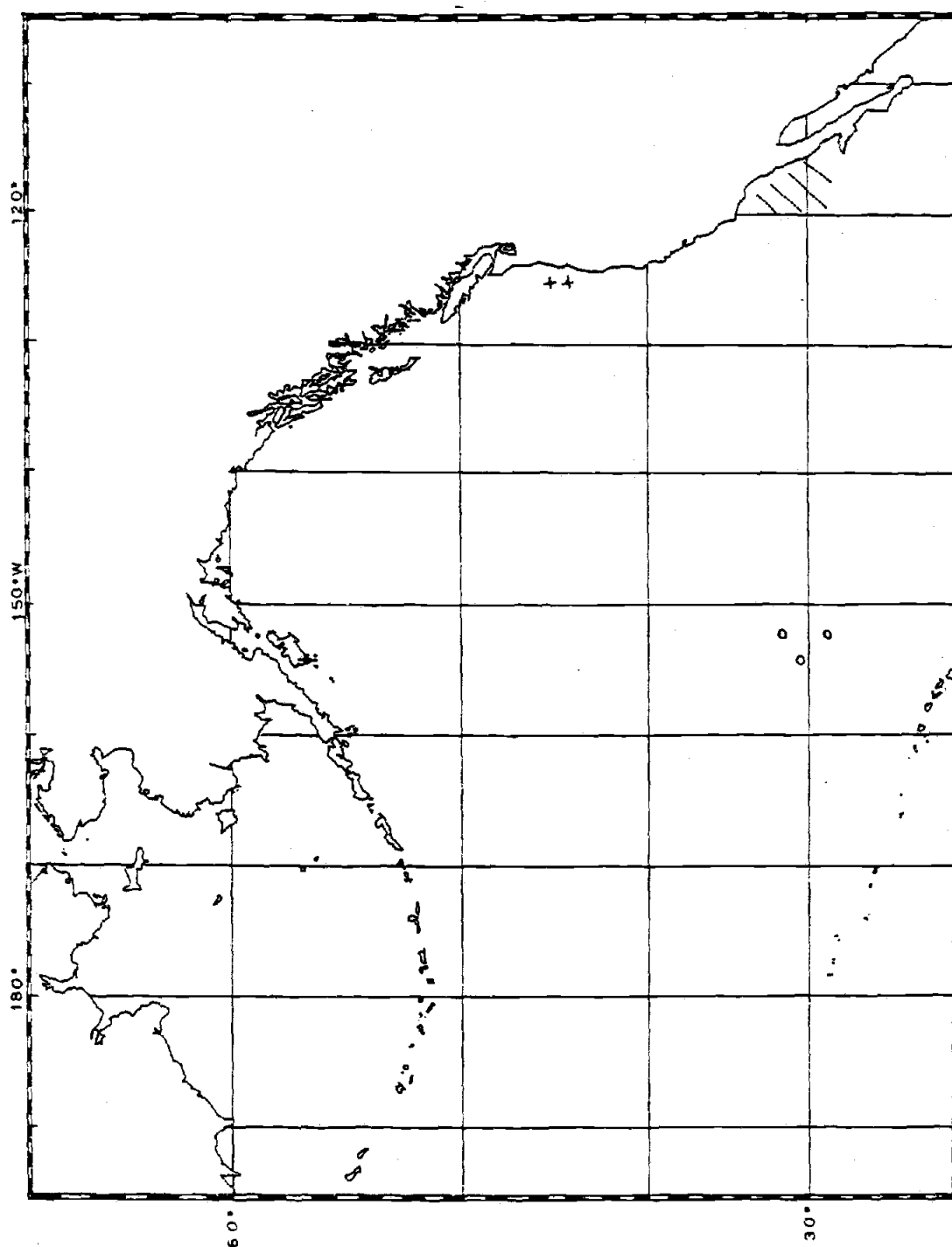
Mastigoteuthis pyrodes Young, 1972

Characterized by the absence of cartilaginous tubercles on external surfaces. Arm suckers bear ten to fifteen teeth; fins are approximately 60% DML, and nearly round. Eyes are not reduced, are of equal size, and do not bear photophores. Ventral arms are greatly enlarged. Club suckers bear three distal knobs on the inner ring, and several inwardly projecting elongate knobs on the outer ring. The largest club suckers are 0.28-0.32 mm in diameter. See Young (1972) for further details.

Four individuals (39, 41, 49, 60 mm DML; OSUI 788-791) were collected in four midwater (0-200, 0-250 m) central Pacific hauls (Figure 46). Clubs are lacking in all individuals, but the fins are very nearly as long as broad, and 55-57% DML. The tragus is very strongly developed, and the antitragus appears to be lacking.

Mastigoteuthis pyrodes was previously known only from Young's (1972) southern California study area. The present specimens thus represent a notable range extension. Three larvae (11, 14, 18 mm DML) which may belong to this species were collected from the same central Pacific area.

Summary - Family MASTIGOTEUTHIDAE

No mastigoteuthids other than *M. pyrodes* and *M. dentata* are known from the eastern Pacific, although *Mastigoteuthis famelica* and *M. inermis* have been recorded off Hawaii (Young, 1978). Thus far, it appear that *M. dentata* is limited to the equatorial

eastern Pacific and the northeastern Pacific, and that _M. pyrodes_ occurs off southern California and north of Hawaii.

Family CRANCHIIDAE Prosch, 1849

In this family, the mantle is fused to the head in the nuchal region and at the lateral corners of the funnel. Buccal connectives attach to the ventral borders of arms IV. The armature is biserial on the arms, generally quadriserial on the clubs. Photophores are present.

Subfamily CRANCHIINAE Pfeffer, 1912

Cartilaginous tubercle-bearing strips on the ventral surface of the mantle, extending caudad from the points of funnel-mantle fusion. The funnel is fused laterally to the ventral surface of the head in the adult. One or more rows of small, round photophores are present on the ventral surface of the eye.

Cranchia scabra Leach, 1817

Mantle and fins covered with stellate cartilaginous tubercles. Fins separate, each nearly circular. Fourteen photophores on each eye. An excellent description is available in Young (1972); the hectocotylus is described in Voss (1980). The genus is monotypic.

Twelve individuals (7-36 mm DML) were taken in nine midwater hauls (0-250 m) in the California Current system, transitional waters, and the central Pacific (Figure 47). The species has been

Figure 47. Location of hauls which captured _Cranchia scabra_
(crosses; previous records from shaded areas, and at triangle).
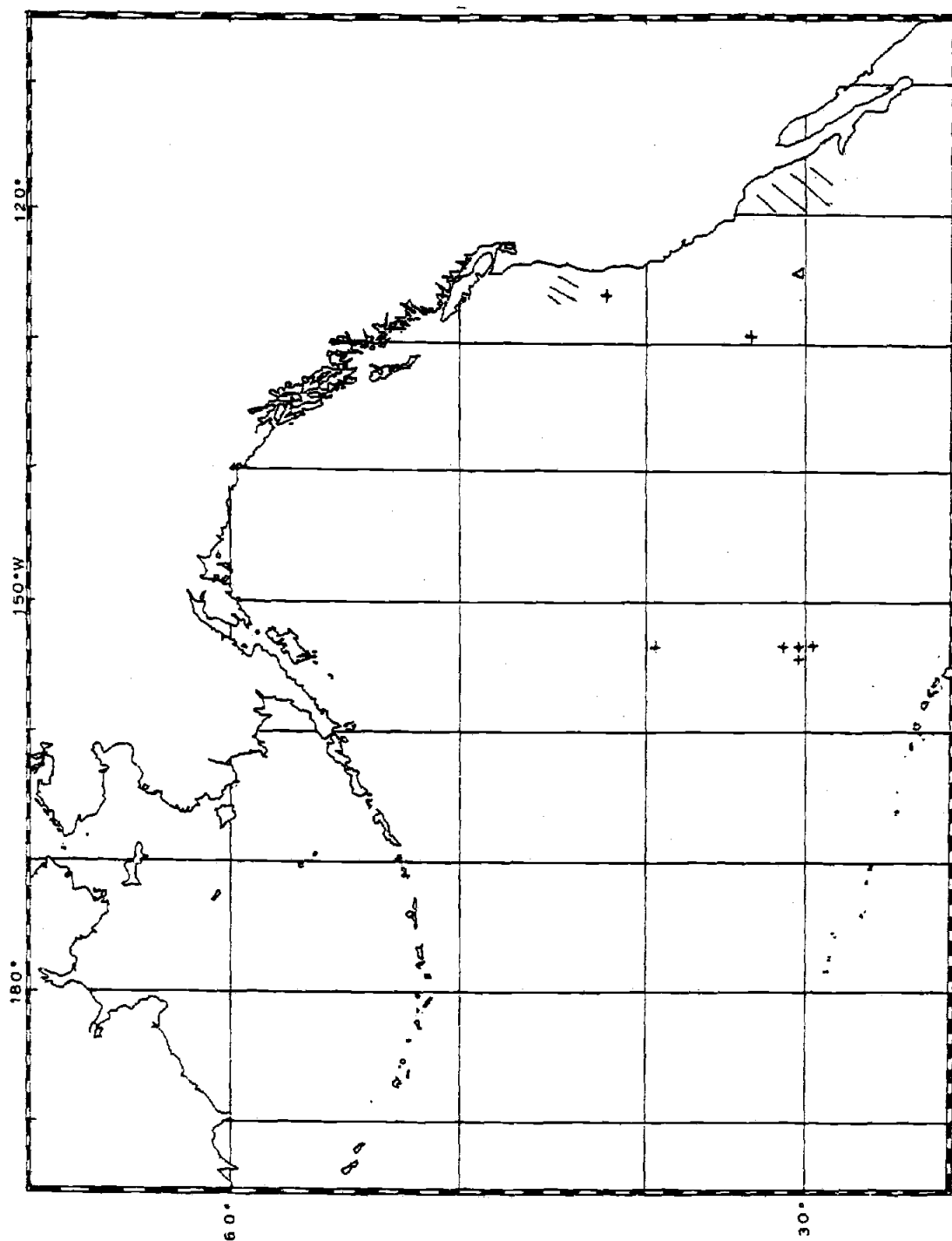
taken circumglobally between 36°N and 38°S (Clarke, 1966; Imber, 1978). In the eastern Pacific, it has been recorded off southern California (Young, 1972) and Oregon (Pearcy, 1965), but not, apparently, off Hawaii. The present specimens are not at variance with a near-surface (upper 200 m) cosmopolitan tropical-subtropical distribution (Voss, 1980).

Leachia dislocata Young, 1972

One cartilaginous tubercle-bearing strip extends posteriorly from each point of funnel-mantle fusion. The second large tubercle in each strip is displaced toward the midline. Arms short and stout. Arms III very large; in adult males, each bearing fewer than 100 suckers. Two rows of optic photophores: the outermost with eight, and the innermost with seven (not all discernible until DML is at least 125 mm).

Ninety-three individuals (5-117 mm DML) were taken in 54 midwater hauls (generally 0-400 m, a few hauls to 1000 m) from the California Current system and northern extensions, transitional waters, and the central Pacific (Figure 48). Young (1972) captured a large number of specimens in his study off southern California, and also noted another record off the Hawaiian Islands at 22°N, 156°W. He considered the species to be largely restricted to eastern North Pacific central waters. The present study has recovered this species much further north.

Imber (1978) considered Leachia dislocata to be a junior synonym of Leachia eschscholtzii (Rathke, 1835). He noted that,

Figure 48. Location of hauls which captured _Leachia dislocata_ (crosses; previous records shown as triangle and shaded area).
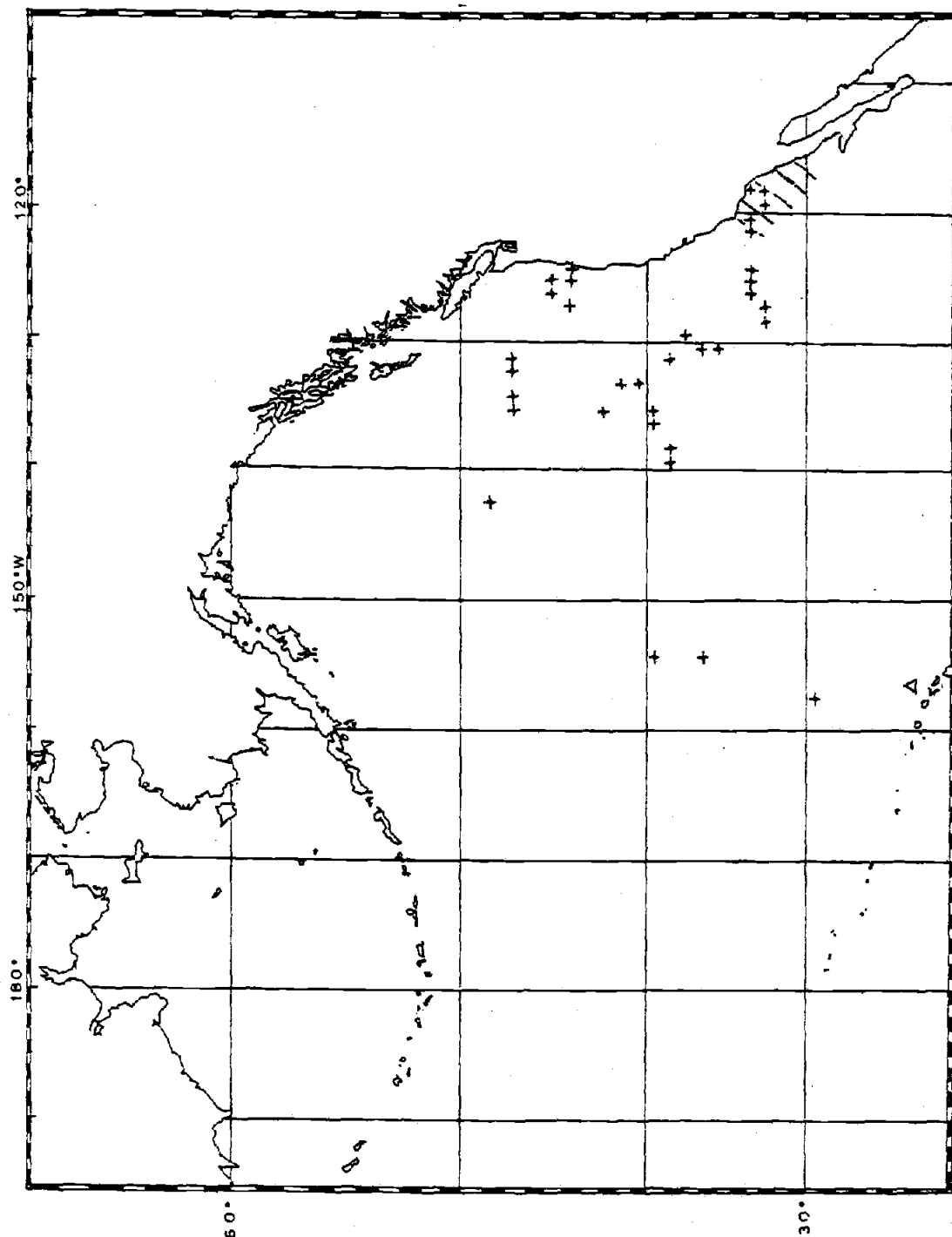
although all six of his specimens basically coincided with Young's (1972) description, only one showed the displaced tubercle characteristic of L. dislocata. Imber (1978) also synonymized a number of other descriptions with this species. The distribution of L. eschscholtzii per Imber (1978) is circumglobal in tropical and temperate latitudes (28 °to 38°S off New Zealand).

Subfamily TAONIINAE Pfeffer, 1912

No cartilaginous strips on ventral surface of mantle; funnel free laterally; one to three crescentic optic photophores.

Taonius pavo (LeSueur, 1821)

Fins long, narrow, about one-third mantle length. Mantle extending slightly beyond posterior margin of fins. Eyes very large, sessile in adult. Largest suckers of the two medial rows of the club modified into bicuspid hooks. No cartilaginous tubercles at funnel-mantle fusion. Tail occupying 30% of gladius; dorsal funnel organ with small central papilla and two posterior mounds. An ontogenetic series is pictured in Voss (1980).

This species was quite abundant, accounting for 2.3% (1005) of all individuals, and occurring in 12.6% of all hauls capturing cephalopods. It was collected in 357 hauls (eight demersal at 2000-4000 m maximum; midwater captures to 500-1000 m in closed hauls) in the California and Alaska Currents, and intervening waters (Figure 49). It has been reported from the eastern and

Figure 49. Location of hauls which captured _Taonius pavo_ (crosses; square is record of Young, 1975) and _Taonius_ sp. larva (triangle).
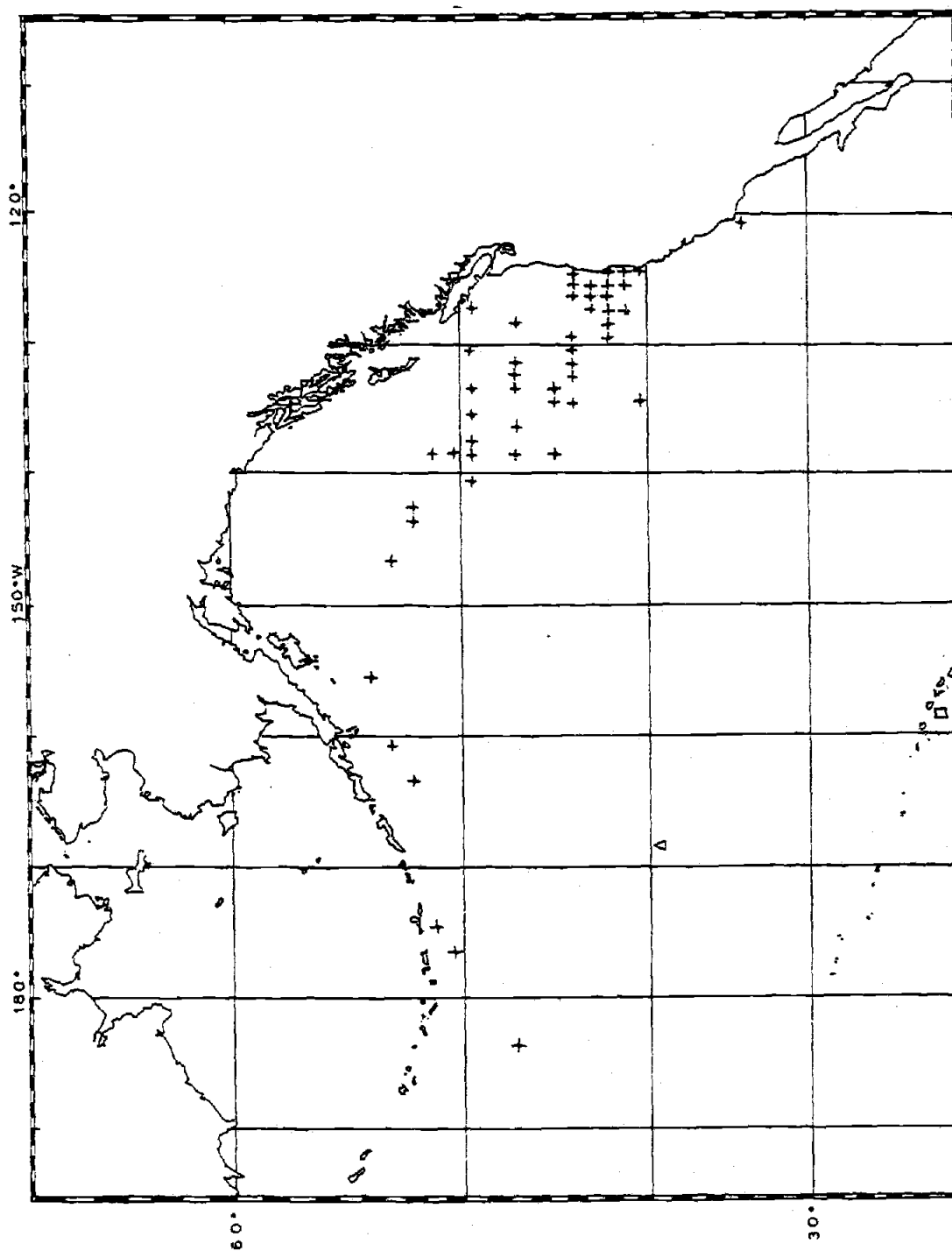
western waters of the North Atlantic and North Pacific, as well as off Antarctica (Clarke, 1966), but it appears to be very rare in central waters. In this study it was restricted to the California and Alaska Current systems and intervening waters, extending as far west as 176°E. Akimushkin (1963) reported the species to be widespread in the Kurile region, on the basis of collections from sperm whales. Iwai (1956) also collected it off Kamchatka.

One larva (17 mm DML; OSUI 753) was identified to the genus Taonius by N.A. Voss; its capture location (39°N, 168°W) is outside the observed distribution of Taonius pavo. Young (1975) collected T. pavo off Hawaii.

Imber (1978) believed T. pavo had been used to include another species, T. belone, in the North Pacific. His conclusion was that T. pavo occurred as far north as 60°N in the Pacific, while T. belone was a warm water form found primarily south of 30°N, and occasionally to 45°N.

Sandalops melancholicus Chun, 1906

Stalked eyes, which are slipper-shaped, with pointed tips. Fins very small. See Voss (1980) for generic description.

One individual (30 mm DML; OSUI 740) was taken in a midwater haul (0-245 m) off Hawaii (Figure 50). The generic identification was confirmed by N.A. Voss. This species has been taken in the Pacific, north of Hawaii (Young, 1975, 1977) and southeast of Japan (Yamamoto and Okutani, 1975). Also known from the Atlantic and Indian Oceans (Nesis, 1973b), it appears to be nearly

Figure 50. Location of the haul which captured Sandalops melancholicus (filled circle; previous record shown as triangle) and Helicocranchia pfefferi (crosses; previous records from shaded area).
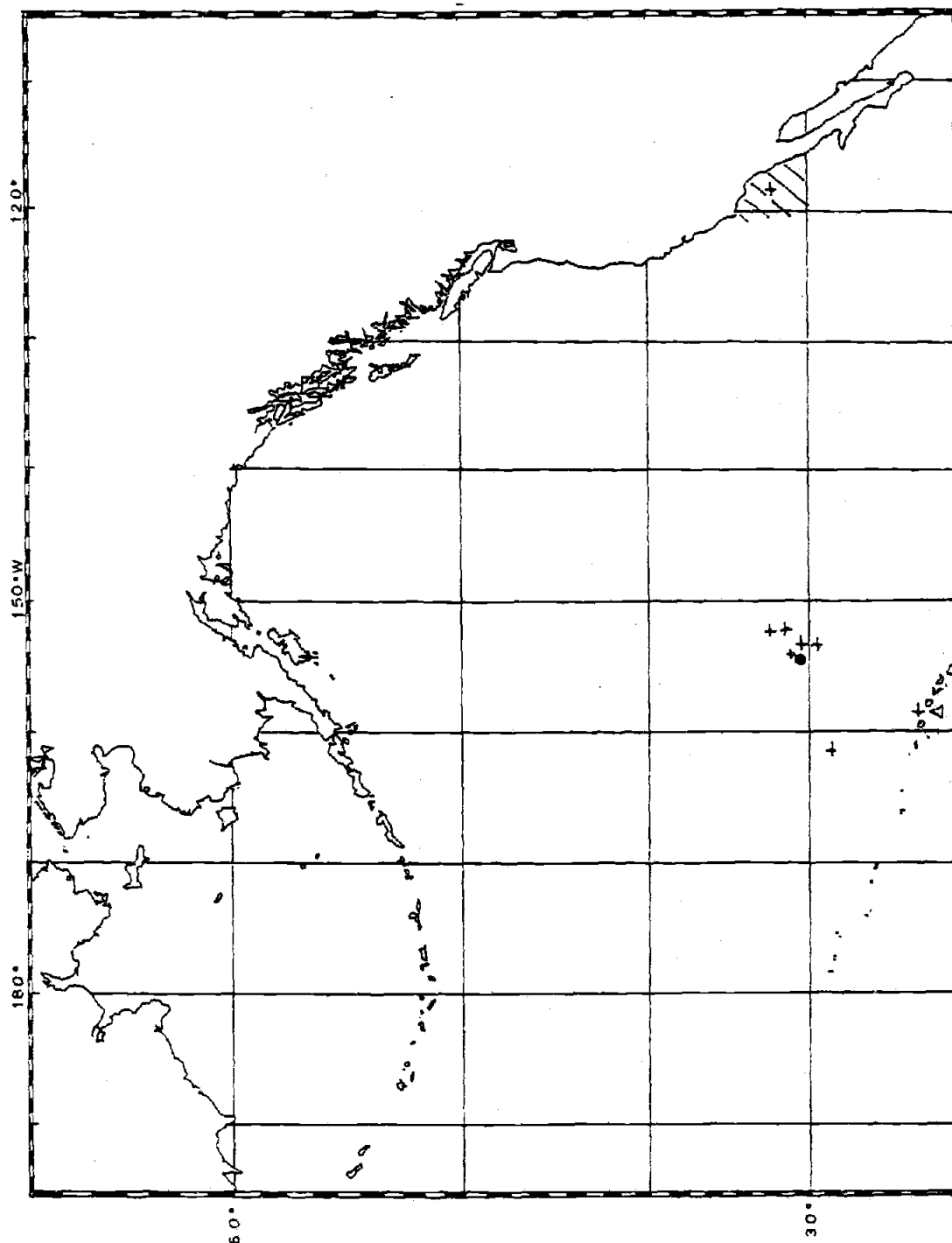
circumglobal in subtropical or tropical waters. It has not been collected in the eastern Pacific, however.

Helicocranchia pfefferi Massy, 1907

Large funnel, the fusion of which with the mantle lacks cartilaginous pads or tubercles. Fins paddle-like, attached to the free tip of the pen, except at the extreme anterior ends. See Young (1972) for a discussion of the genus.

Eleven individuals (5-42 mm DML; representatives: OSUI 735-737, 796-800) were taken in eight midwater hauls (0-255 m) in the California Current and central Pacific waters (Figure 50). This species has been recorded in the Atlantic off Ireland and perhaps from the Bay of Biscay (Clarke, 1966), near the Canary Islands (Clarke, 1969; Clarke and Lu, 1974), in the Straits of Florida (Cairns, 1976), the eastern tropical Pacific (Fields and Gauley, 1972; Nesis, 1973a), and off southern California (Young, 1972). Nesis (1973b) listed collections off central Honshu, Palau Island, and in the central Equatorial Pacific (2°N, 173°W). The central Pacific collections therefore represent new records for this part of the Pacific. The species may be common further south; the present specimens came from the southernmost reaches of the study area.

Imber (1978) considered H. pfefferi and H. beebei Robson, 1948 to be a species pair, evolved from a common ancestor in the eastern tropical Pacific - western tropical Atlantic before the closure of the Panamanian seaway. Much of his argument for the

distinctness of these two species is based on their present
distributions, which he considers as North Atlantic (H. pfefferi)
and eastern central Pacific (H. beebei). He does not mention the
records of Nesis (1973b) in the western North Pacific.

Galiteuthis phyllura Berry, 1911

Characterized by cartilaginous tubercles at the points of
funnel-mantle fusion, and the development of two rows of large
hooks on the clubs of large juvenile and adult animals. See Young
(1972) for a discussion of the genus.

This species accounted for 1.6% of all individuals, or 694
animals, and was collected in 265 hauls (9.3% of hauls capturing
cephalopods; six were demersal to 2500-3500 m maximum; in midwater
tows, the species was consistently taken to 500-1000 m in closed
tows) in the California and Alaska Currents, and occasionally in
transitional waters (Figure 51). The distribution of this species
is much like that of Chiroteuthis calyx, but extends much further
north and west, even into the Aleutian Islands and southern Bering
Sea. Young (1972) described the species as occurring along the
west coast of the United States from 28°N to at least 44°N, and
possibly around Japan. The latter record may result from an
inability to distinguish between G. phyllura and G. armata.
Galiteuthis armata is known from the Atlantic and Pacific Oceans
between 70°S and 60°N (Clarke, 1966). In this study, the
distribution of G. phyllura coincides with the known eastern
Pacific distribution of G. armata. Until a circumglobal review

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Figure 51. Location of hauls which captured *Galiteuthis phyllura* (crosses; previous records from shaded area) and *Megalocranchia* (*Corynomma*) *speculator* (triangles).
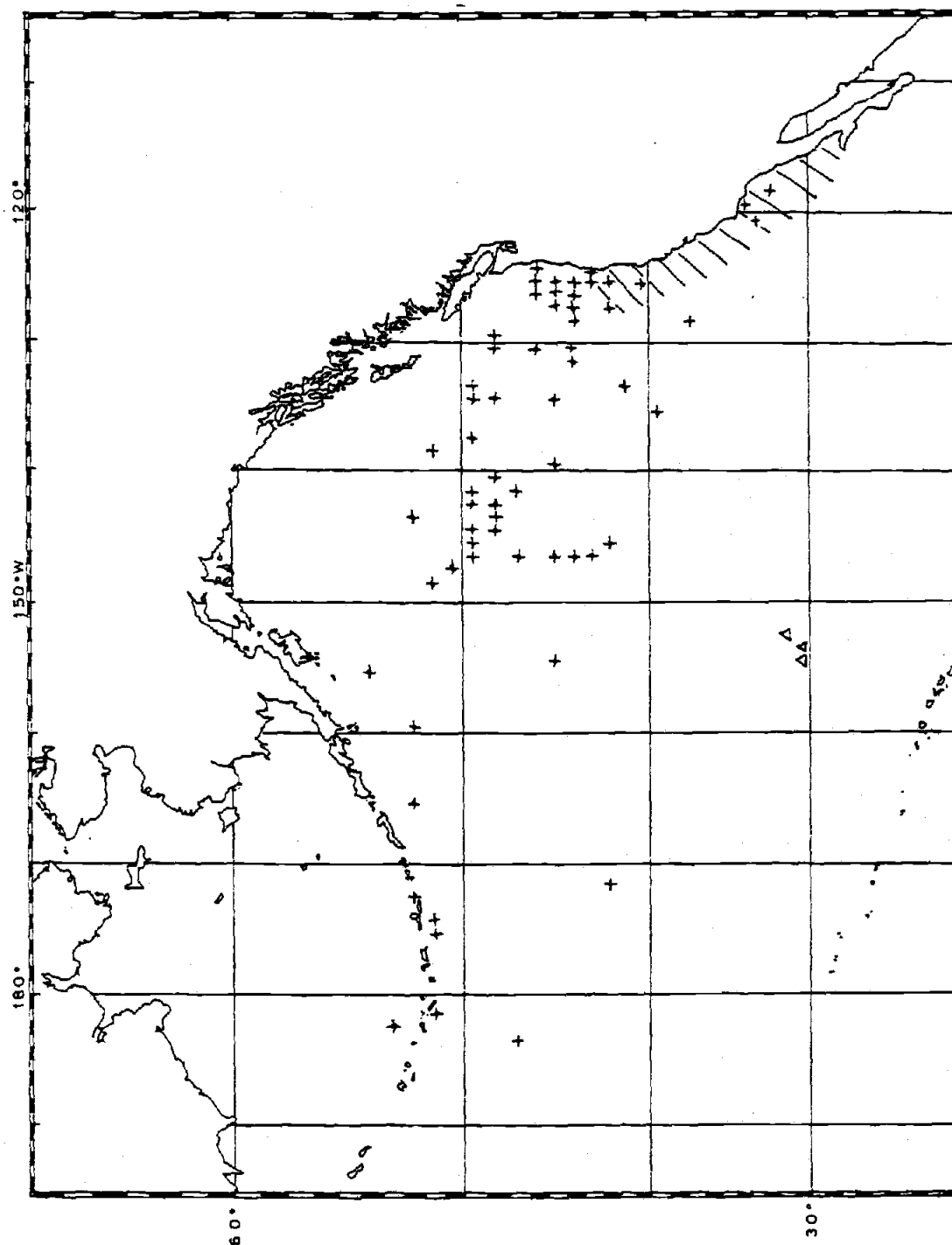
of specimens assigned to both species is made, it seems wiser to
treat them separately. The present study has expanded the known
distribution of G. phyllura to include the eastern and central
Subarctic Pacific; further sampling is needed to confirm its
presence in the western Pacific.

Imber (1978) suppressed Galiteuthis phyllura (and G.
pacifica) in favour of the broader G. armata, attributing Young's
(1972) specimens to developmental and individual variation. Imber
gave the range of G. armata as $55°N$ to $50°S$, but surmised that G.
armata is largely replaced to the south by the Antarctic endemic,
G. glacialis.

Megalocranchia speculator (Chun, 1906)

(Corynomma speculator Chun, 1906)

The genus is undergoing revision by N.A. Voss. It differs
from Sandalops primarily in possessing a large compound hepatic
photophore.

Fourteen individuals (9-38 mm DML; OSUI 684-686, 742-752)
were taken in five midwater (0-260 m maximum) central Pacific
hauls (Figure 51). Identification was confirmed by N.A. Voss.
The species has previously been taken in the Atlantic and Indian
Oceans, and in the Mediterranean Sea (Clarke, 1966). These
specimens represent the first records from the Pacific Ocean.

Imber (1978) synonymized M. speculator (any many others) with
M. maxima Pfeffer 1884. He listed its distribution as

cosmopolitan between 53°N and S, but most abundant within the latitudes 20° to 38° (both north and south).

Summary - Family CRANCHIIDAE

A total of 2990 individuals belonging to this family was collected; seven species were identified.

The geographic distributions of Sandalops and Megalocranchia are quite similar. If a few samples near the west coast of North America are omitted, the distributions of Cranchia scabra and Helicocranchia are comparable to those of Sandalops and Megalocranchia. Leachia dislocata extends quite a bit further north, and is abundant in the area of the California Current. Its extension into transitional waters would tend to separate it, zoogeographically, from these other four species. Its range is more southerly, and extends farther into central waters, than those of G. phyllura and T. pavo.

There are thus three zoogeographic groups represented within the family: one restricted to central waters, perhaps with occasional occurrences in nearshore waters (Sandalops melancholicus, Megalocranchia (Corynomma) speculator, Helicocranchia pfefferi, and Cranchia scabra); a second, in the California Current system, and Subarctic waters (Galiteuthis phyllura and Taonius pavo); and a third, intermediate between the first two, present in central waters, the California Current system, and transitional waters, but not reaching into the Subarctic proper (Leachia dislocata).

Order OCTOPODA Leach, 1818

Characterized by the possession of eight arms; the lack of a shell or gladius; and the lack of horny rings on the suckers.

Suborder CIRRATA Grimpe, 1916

Characterized by the possession of fins and webbed arms, which bear uniserial suckers and cirri; and the lack of a radula, photophores, and an ink sac.

A number of cirrate octopods have been collected by the various benthic sampling programs included in this report. However, most are still on loan and were not available for my inspection. A manuscript on these abyssobenthic octopods from Cascadia and Tufts Abyssal Plains has been submitted for publication by Voss and Pearcy. The following material on cirroteuthid and stauroteuthid octopods may require reconsideration upon comparison with this forthcoming paper.

Family CIRROTEUTHIDAE Keferstein, 1866

Characterized by a broad, saddle-shaped dorsal cartilage, and a broad umbrella. Intermediate web present or absent.

Genus _Cirroteuthis_ Eschricht, 1836

Possessing a large saddle-shaped dorsal cartilage. Eyes present, functional. Suckers not clavate.

Cirroteuthis sp.

Three individuals (39, 60, 90 mm DML; OSUI 403, 780, 781) belonging to this genus were recovered in three demersal hauls (650, 2675, 3655 m maximum) off the Oregon coast (Figure 52). *Cirroteuthis macrope* Berry, 1911 is known to occur off California, and is characterized by a very wide mantle aperture and eyes of unequal size (the left much the larger). No difference in eye size was noted in these specimens.

Cirrothauma murrayi Chun, 1911

Characterized by the great reduction of the eyes, which are embedded in and covered over by gelatinous tissue. Suckers greatly elongated, clavate, with a rudimentary cup at the tip.

Three specimens (28, 38, 110 mm DML; OSUI 397, 778, 779) which probably belong to this species, were recovered in demersal hauls (2700-3700 m maximum) off the Oregon coast (Figure 52). The species is known only from a handful of specimens collected in the Atlantic and Arctic (Chun, 1914; Voss, 1967b).

Family STAUROTEUTHIDAE Robson, 1932

Characterized by having a very narrow pallial aperture, semispheroidal gills, and a narrow, horseshoe, or V shaped dorsal cartilage, with the ends directed cephalad. Umbrella present or absent; intermediate web present or absent.

Genus *Stauroteuthis* Verrill, 1879

Dorsal cartilage posterior in position, and horseshoe shaped.

Figure 52. Location of hauls which captured _Cirroteuthis_ sp.
(crosses), _Cirrothauma murrayi_ (triangles), and _Stauroteuthis_ sp.
(circles).
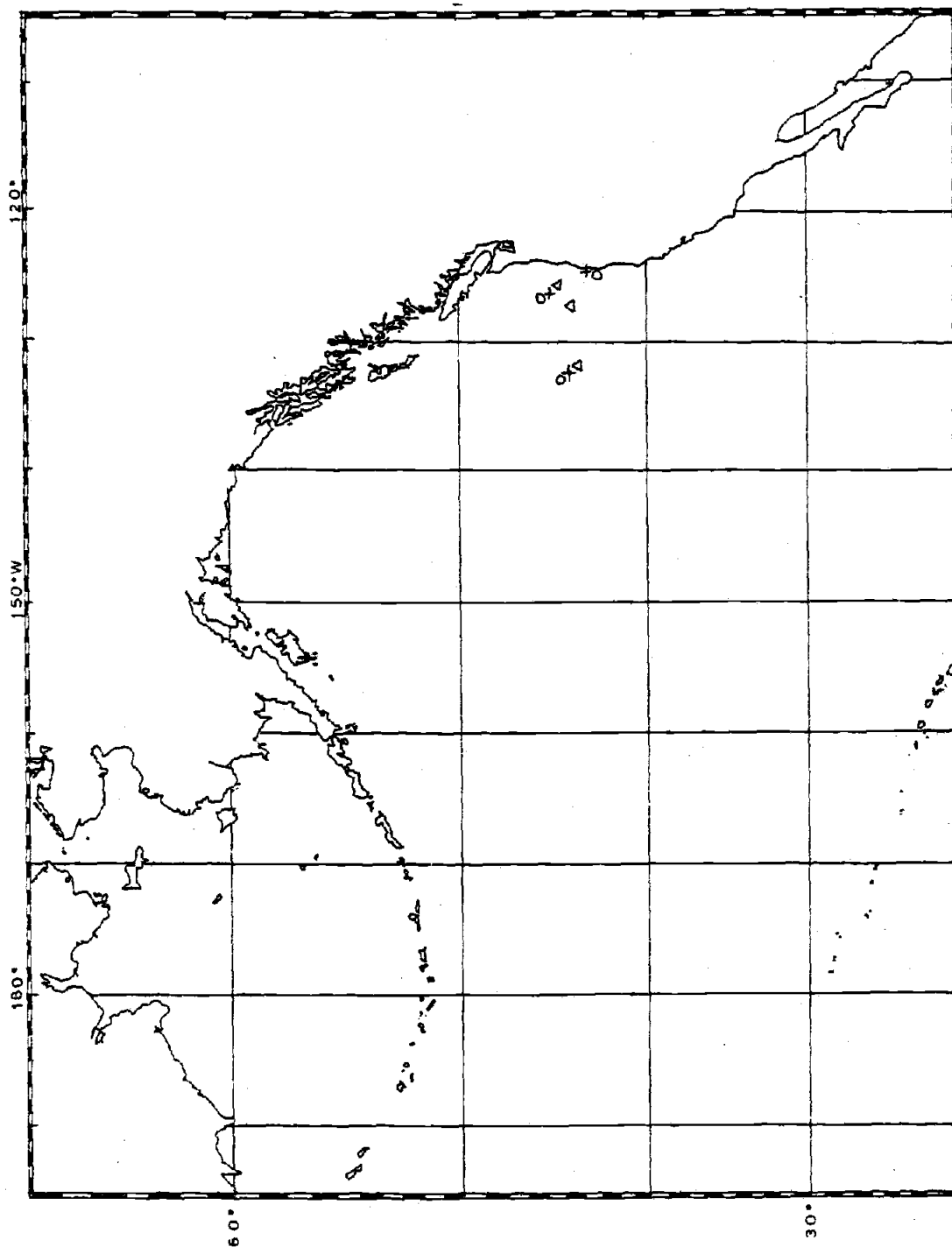
Umbrella present. Intermediate web present in some species.

Stauroteuthis sp.

Three specimens (33, 46, 80 mm DML; OSUI 775-777) referable
to this genus were recovered in three demersal hauls (810,
2700-3700 m maximum) in the California Current region (Figure 52).
Berry (1912b) recorded a juvenile of this genus from off southern
California.

Family OPISTHOTEUTHIDAE Verrill, 1883

Characterized by an anterior-posteriorly flattened body; a
straight or slightly crescentic dorsal cartilage, with the ends
turning outward; semispheroidal gills; a well developed median
septum; and a narrow mantle aperture.

Opisthoteuthis californiana Berry, 1949

Characterized by smaller suckers, more posteriorly placed
fins, and a wider pallial aperture than its congeners, O. depressa
Ijima and Ikeda, 1895 and O. pluto Berry, 1918. No radially
arranged areolar spots on the aboral surface. Male with eight to
ten greatly enlarged suckers on all arms, beginning with the third
sucker on the basal portion of the arm. Dorsal arms have a second
series of such enlarged suckers, separated from the basal series
by eleven to thirteen small suckers.

Forty-nine individuals were collected in 27 relatively
shallow demersal hauls (280-800 m) in the Aleutians and off the

western coast of the United States (Figure 53). The species was described from northern California waters, and has subsequently been recorded from waters off Oregon, Washington, the eastern Aleutians, Prince William Sound, and central California (Berry, 1949, 1952; Pereyra, 1965; Anderson, 1978). The present specimens thus represent first records for the western and central Aleutians, and extend the range to southern California.

Suborder INCIRRATA Grimpe, 1916

Characterized by the lack of fins or cirri and the presence of an ink sac. Suckers may be biserial or uniserial, and the web is small or absent.

Family BOLITAENIDAE Chun, 1911

Pelagic octopods characterized by uniserial suckers; broad mantle aperture; stomach and liver in "normal" position. Ctenoglossan radula (radula having multicuspid rhachidian and lateral teeth; as opposed to heteroglossan radula with multicuspid rhachidian, and simple lateral teeth). See Chun (1911), Young, 1972, and Lipka (1975) for further details.

Eledonella pygmaea Verrill, 1884

Characterized by small eyes, long optic nerve, and having the third left arm hectocotylized in males. See Lipka (1975) for further details.

Two individuals (38, 77 mm DML; OSUI 412, 823) were

Figure 53. Location of hauls which captured Opisthoteuthis
californiana (crosses; previous records shown as triangles) and
Eledonella pygmaea (circle; previous record shown as square).
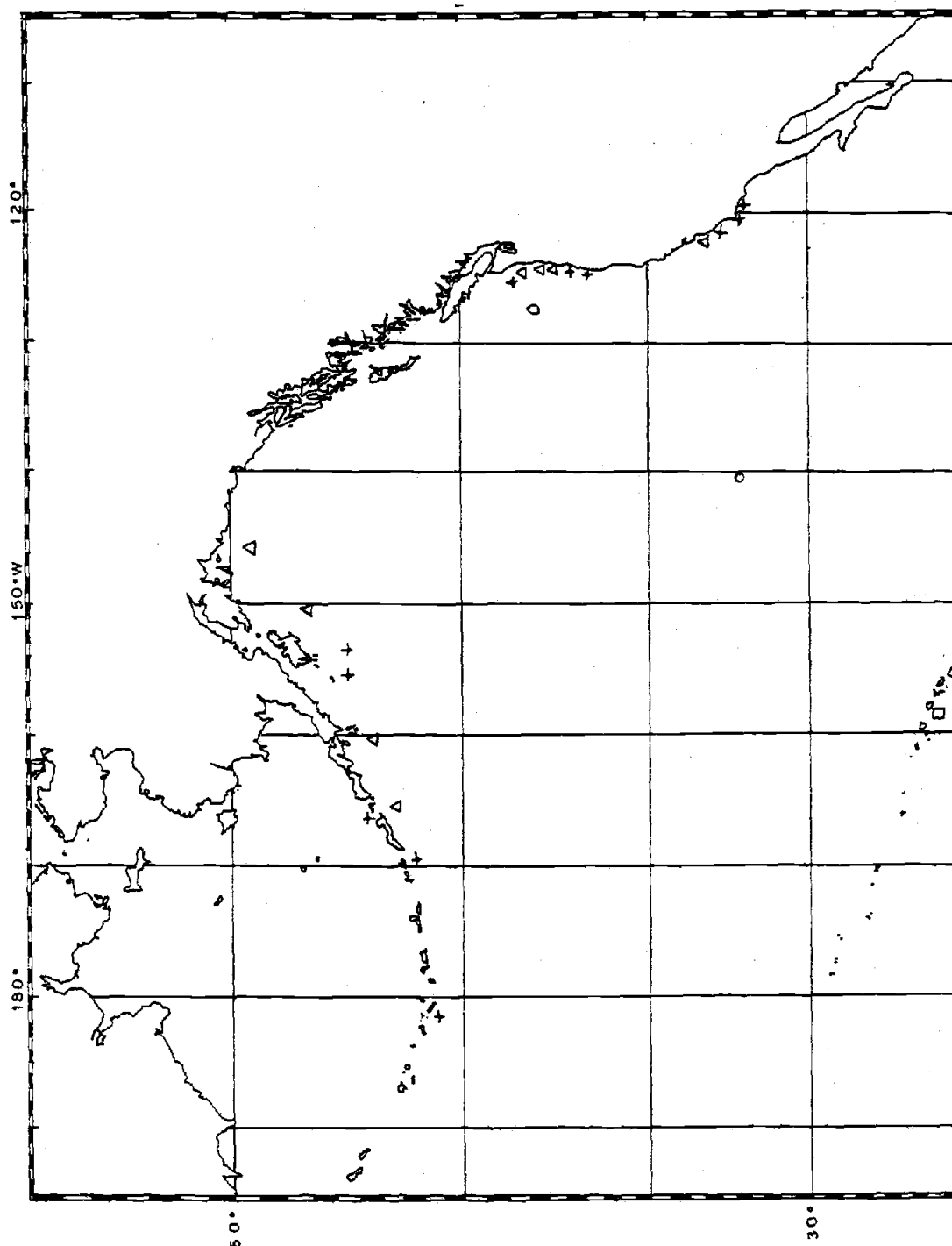
collected: one off the Washington coast (dipnet) and the other at the transitional/central Pacific boundary (midwater trawl, 0-2450 m) (Figure 53). This species has been recorded from the Atlantic, Indian, and western Pacific Oceans between approximately 40°N and S. It has been recorded from the eastern tropical Pacific (Thore, 1949; Nesis, 1973a) and off Hawaii (Young, 1978). One individual, identified only as _Eledonella_ sp., was recorded from Young's (1972) southern California study area. The present specimens thus represent a northward range extension. _Eledonella pygmaea_ is not known from north of 40°N even in the Atlantic (Thore, 1949).

Japetella _heathi_ (Berry, 1911)

Characterized by large eyes, short optic nerve, and having the third right arm hectocotylized (enlarged suckers) in the male. See Young (1972) for a discussion of the genus.

This species was exceedingly abundant in the present study, comprising 2664 individuals taken in 834 hauls (ten demersal, 245, 2700-3900 m maximum; midwater, as deep as 900-1000 m and 500-1500 m in closed tows, and 0-3000 m in open tows) from all water masses and current systems sampled south of the Aleutians (Figure 54). It represented over 6% of all cephalopods collected and occurred in 29% of hauls capturing cephalopods.

Japetella _heathi_ is known from the coasts of Oregon and California (Young, 1972), the Kuriles (Akimushkin, 1963), and the Gulf of Alaska south to eastern Australia and Chile (Nesis,

Figure 54. Location of hauls which captured <u>Japetella heathi</u>
(crosses; square, record of Fiscus and Mercer, 1982; see text for
other previous records) and <u>Japetella</u> sp. Young 1972 (triangle,
previous records in shaded area).
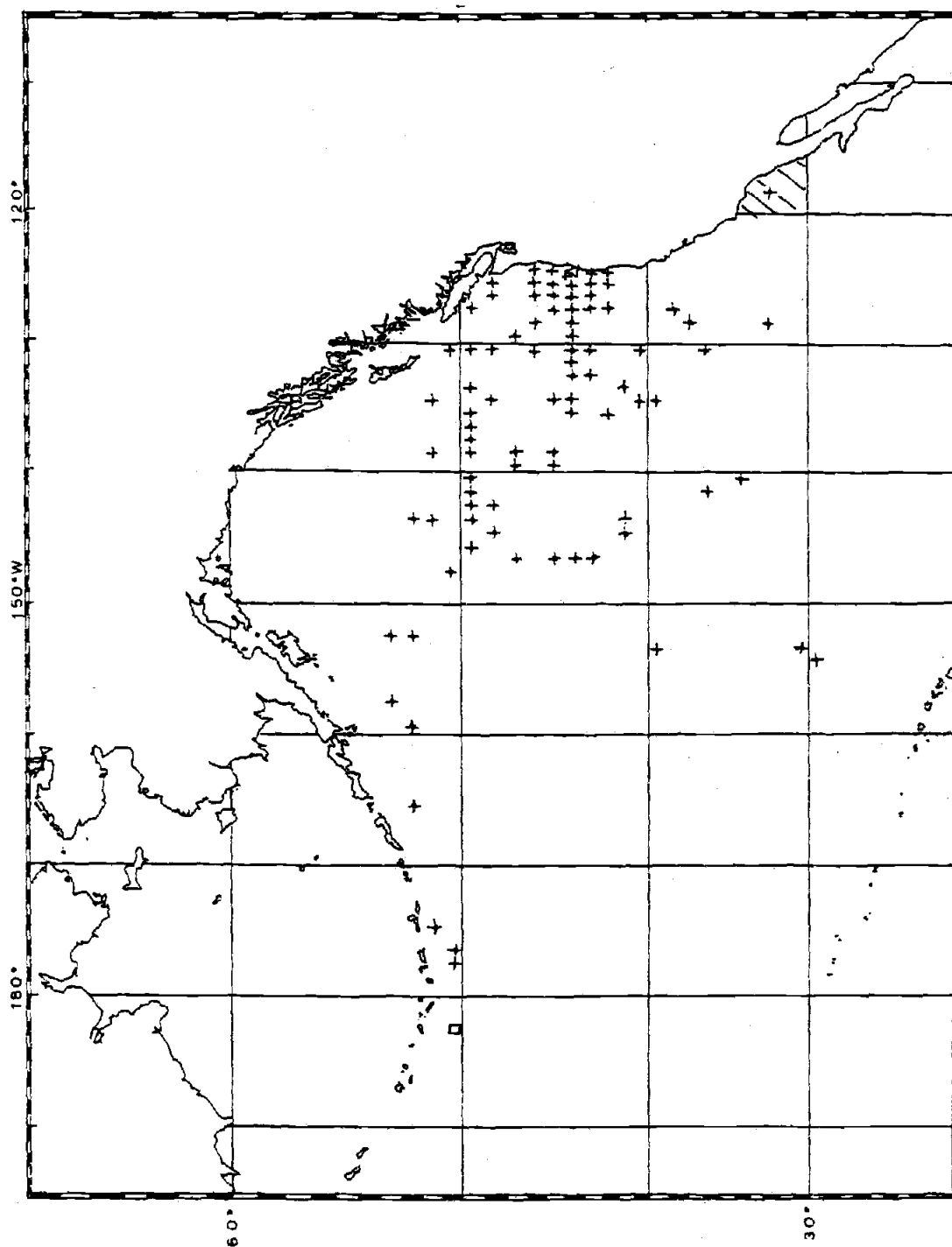
1973b). According to Nesis (1973b), it is absent from the Bering Sea, the western Subarctic circulation, and the Sea of Okhotsk. In areas of the Pacific other than those recorded by Young (1972), *J. heathi* is imperfectly separated from *J. diaphana* Hoyle 1885. This remains an impediment to discussion of the zoogeography of the species. It appears, however, that at least the genus has a cosmopolitan distribution. Thore (1949) discusses the Atlantic, Indian, and equatorial and South Pacific distribution of *J. diaphana*.

Japetella sp. Young, 1972

Differs from *J. heathi* in the lack of iridescent tissue on the eyes and liver, and in the much larger size of the male reproductive system. Smaller viscera compared to *J. heathi* of equivalent size. See Young (1972) for further details.

Two individuals (73, 85 mm DML; OSUI 783, 784) probably belonging to this species or type were collected in two midwater hauls (closed tows, 500-520, 515-555 m) off Oregon (Figure 54). The species is known only from Young's (1972) southern California study area (where it was imperfectly separated from *J. heathi*) and the present specimens. Thus, little can be said concerning the zoogeography of this species.

Summary - Family BOLITAENIDAE

Eledonella pygmaea and *Japetella* (*heathi* + *diaphana*) are

cosmopolitan in distribution; <u>Japetella</u> sp. Young, 1972 is thus far known only from off the west coast of the United States.

Family OCTOPODIDAE d'Orbigny, 1845

Benthic heteroglossan octopods with biserial or uniserial brachial suckers. Simple lateral radular teeth. Hectocotylus either right or left third arm, not detachable. Stomach and caecum posterior to liver. For further details see Young (1972), Lipka (1975), and Green (1973).

Genus <u>Octopus</u> Lamarck, 1798

Characterized by biserial brachial armature; wide mantle aperture; and hectocotylized third right arm.

No attempt was made to identify the members of this genus to species. It was felt that the confused state of the systematics in the genus, as well as the frequent immature state of the specimens, would render such an undertaking unproductive. A total of 636 individuals was collected in 368 demersal and midwater hauls. The midwater collections included primarily pelagic juveniles, and the demersal hauls comprised mostly post-settling individuals. Specimens were taken in waters of the California, Alaska, and Bering Current systems (Figure 55).

<u>Octopus</u> sp. A

A distinct group of juvenile octopods was recovered from ten midwater hauls (0-200, 0-2400, 0-3000 m maximum) in northern

Figure 55. Location of the hauls which captured Octopus.
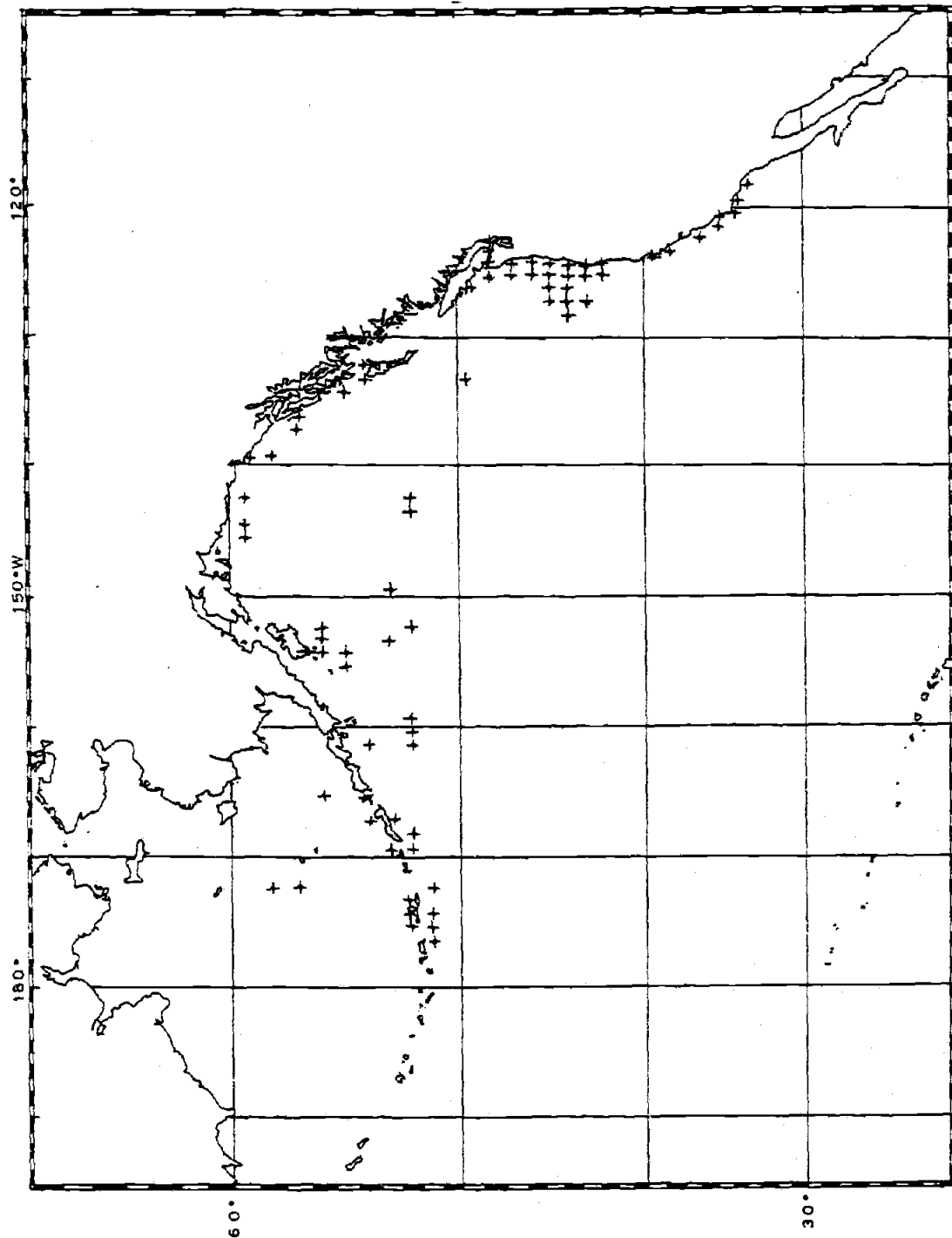
waters (Figure 56). Twenty-seven individuals (2-11 mm DML; representatives: OSUI 728-734) were collected; their primary distinguishing characteristic was their relatively long arms. Measurements of a larger individual:

DML	10	AL I	15
MW	7	AL II	13.5
TTL	27	AL III	13
ED	2	AL IV	12

(Abbreviations as in Table 4, with the following additions: TTL, total length; ED, eye diameter).

The funnel organ is in the form of a broad W. Brachial armature is biserial except for the basal two or three suckers, which are nearly aligned with the longitudinal axis of the arm. The web is deepest (5 mm) between the dorsal arms and between arms I and II. The identity of this group remains unknown, but it has a subarctic distribution.

Octopus sp. B

Three juvenile octopods (5, 5, 6 mm DML; OSUI 785-787) were recovered from midwater hauls in northern waters (Figure 56). They were distinguished by a very deep web, extending to about half the length of the arms. Their specific identity is unknown.

Family TREMOCTOPODIDAE Tryon, 1879

Radula heteroglossan. Biserial brachial armature. Right third arm hectocotylized; detachable, coiled in pouch. Male much smaller than female. Two pairs of aquiferous pores on the head: one pair at the bases of the ventral arms, and one pair at the

Figure 56. Location of the hauls which captured Octopus sp. A
(crosses) and Octopus sp. B (triangles).
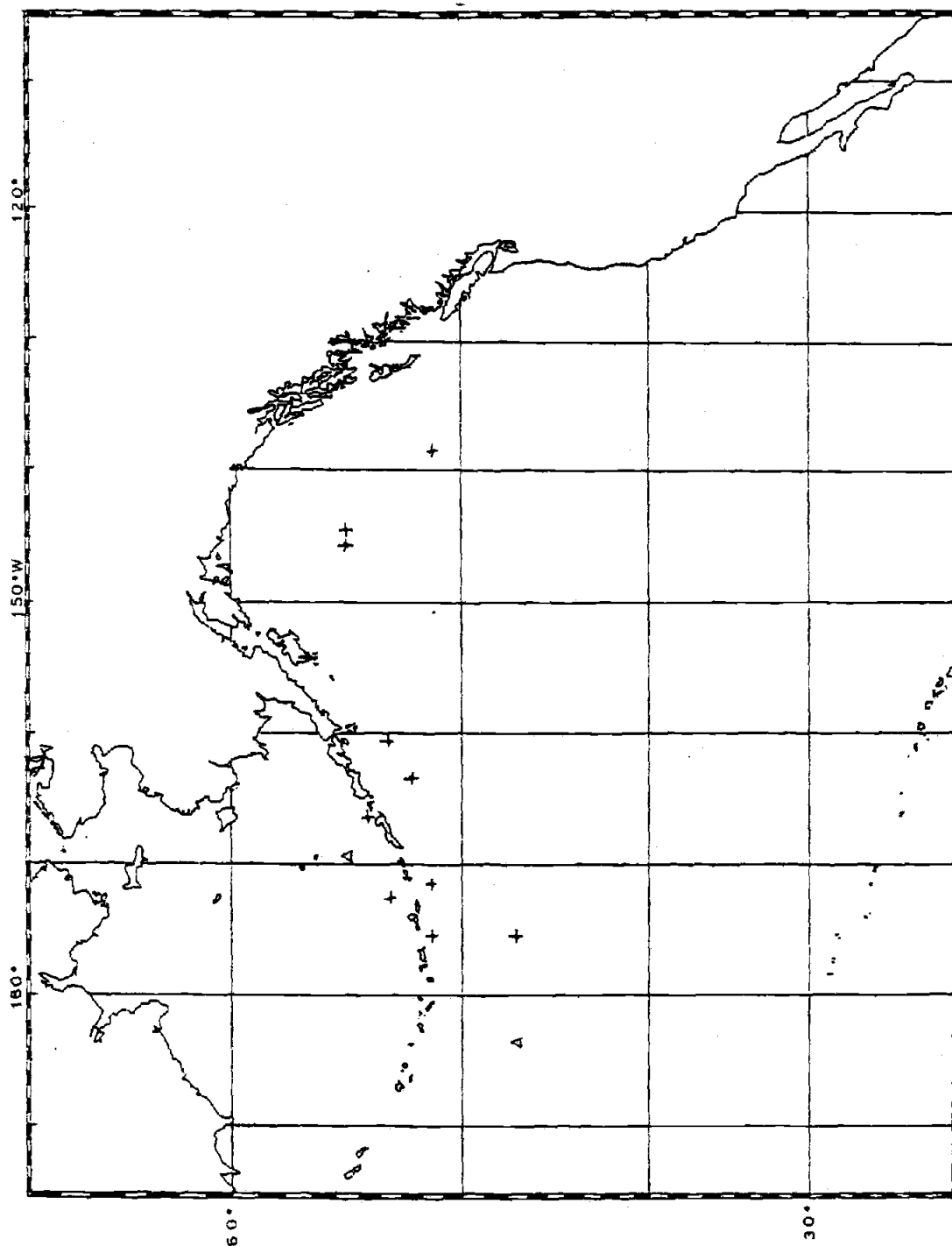
bases of the dorsal arms. Monotypic. See Lipka (1975) for
further details.

Tremoctopus violaceus Delle Chiaje, 1830

Characters are those of the family.

One individual (9 mm DML; OSUI 825) was collected in North
Pacific Central waters (midwater, 0-170 m) (Figure 57). The
species is cosmopolitan in tropical and temperate latitudes
(Lipka, 1975). In the Pacific, it has been recorded off Peru
(Nesis, 1973a), south of the Kuriles (Akimushkin, 1963), off
Hawaii and in the western tropical Pacific (Berry, 1912c).

Family OCYTHOIDAE Gray, 1849

Characterized by a hectocotylized third right arm coiled in a
sac; arms II and III much shorter than I and IV, all with biserial
armature. Ventral surface of mantle bearing tubercles and
anastamosing ridges. Monotypic. See Young (1972) for further
details.

Ocythoe tuberculata Rafinesque, 1814

Characters are those of the family.

Two very young individuals (6, 8 mm DML; OSUI 738, 739) were
collected from the California Current (midwater tows, 0-120,
0-400 m) (Figure 57). The species occurs in tropical waters of
all the oceans (Rees and Maul, 1956); fewer than twenty specimens

Figure 57. Location of the hauls which captured _Tremoctopus violaceus_ (cross; previous records shown as triangles) and _Ocythoe tuberculata_ (squares).

are known from the waters off central and southern California

(Berry, 1955; Young, 1972).

Order VAMPYROMORPHA Pickford, 1936

Characterized by the presence of eight arms bearing

uniserial, achitinate suckers, and cirri; two slender, retractile

sensory filaments; fins; an internal chitinous pen; photophores; a

web; and by having the mantle fused to the head. Monotypic. See

Pickford (1936, 1939, 1946, 1949) for further details.

Family VAMPYROTEUTHIDAE Thiele, 1915

Characters are those of the order.

Vampyroteuthis infernalis Chun, 1903

Characters are those of the family.

Ninety individuals (8-135 mm DML) were collected in 53 hauls

(five demersal, 2500-3700 m maximum; midwater, as deep as

930-950 m and 500-1000 m in closed tows, and 0-2500 m in open

tows) in the California Current system (Figure 58). The species

is cosmopolitan in distribution, primarily in deep water, between

$40°$ N and $40°$ S (Pickford, 1946, 1959). In the eastern Pacific, it

has been recorded from southern California (Young, 1972), Hawaii

(Young, 1978), and off Oregon (Pearcy, 1965). The present

specimens thus represent only a slight northward range extension.

Figure 58. Location of the hauls which captured Vampyroteuthis
infernalis (crosses; previous records in shaded areas and at
triangle).
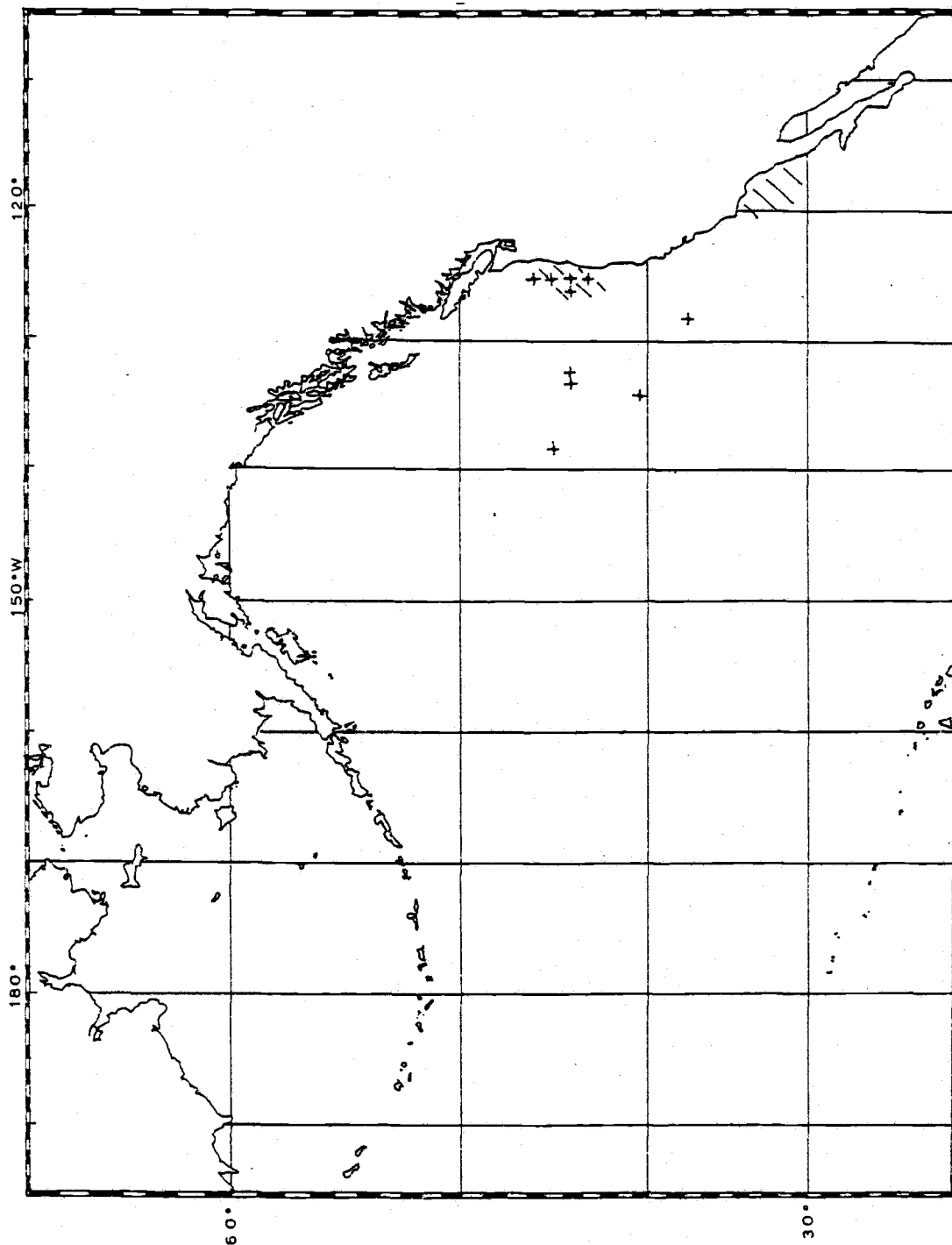
ZOOGEOGRAPHY

Introduction

The data on which the following zoogeographic scheme is based
include all the collections which I examined, as well as
literature records of other authhours, for those species included
in the systematic section. The records of others are noted on the
figures as "previous records" and are specifically identified in
the systematic section, as are wide-ranging records of others too
numerous to show in the figures. Only personally examined
collections are included in the quantitative section. Sampling
intensity is discussed in the Results section.

Quantitative considerations of these data are hampered by the
diversity of collection methods. Sampling devices ranged from
single organism samplers to nets with mouth openings of 0.7 m2 to
124 m2 (Table 1). The collections spanned 23 years, all seasons,
and most depth intervals from 0 to 3900 m. The majority of
collections were made in Subarctic, Transition Zone, and
California Current waters. For these reasons, species-group
analyses or clustering algorithms (e.g., Fager and McGowan, 1963)
were not appropriate or useful. Valid quantitative comparisons
can be made, but only on relatively small and geographically
restricted subsets of the data. Quantitative considerations were
therefore restricted to community statistic analyses of the IKMT
samples.

The zoogeography of cephalopods in the northeastern Pacific
is discussed in this section as it relates to water masses.
Brinton (1962) and Fager and McGowan (1963), among others,
attempted to relate the distributions of other taxa to water
masses in the North Pacific. The following water masses or
oceanographic areas are included: Subarctic Water, Transition
Zone, California Current, North Pacific Central Water, and the
eastern tropical Pacific (Sverdrup et al., 1942; see Figure 59).
These have been defined in the Introduction.

Cephalopod Distributional Types

The epipelagic and mesopelagic cephalopods discussed here
fall into three broad distributional classes (cold water, warm
water, and eurythermal), and into twelve distributional patterns,
which are given in Table 9.

The cold water group includes four distributional types:
Arctic-Subarctic forms; endemics of the Subarctic Water Mass, here
termed northern endemics; holosubarctic forms, occurring in the
Subarctic Water Mass as well as Transition Zone and California
Current waters; and transitional endemics limited to the
Transition Zone of the eastern Pacific and the California Current.

A group of cephalopods is limited to the central gyre, at
least in the North Pacific; a characteristic group inhabits the
eastern tropical Pacific; and a third ranges from central to
equatorial waters. These comprise the warm water groups.

Figure 59. Broad zoogeographic divisions discussed in the text, and their approximate boundaries.
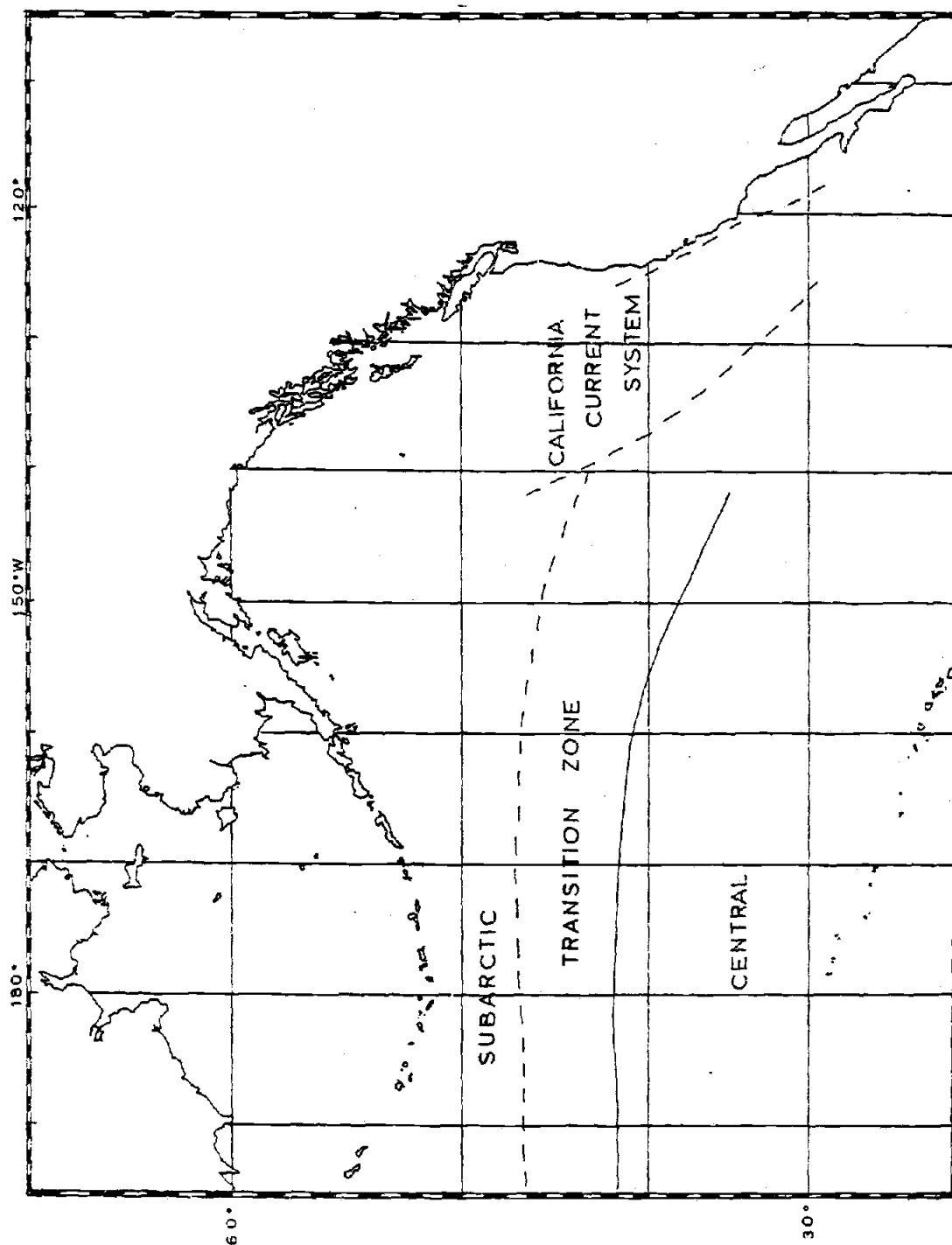
Table 9. Cephalopod distributional types and their species composition.

1) Arctic-Boreal
  Cirrothauma murrayi
	7) Central-equatorial
	  Thelidioteuthis alessandrinii
	  Onychoteuthis banksii
	  Tremoctopus violaceus

2) Northern endemics
  Gonatus madokai
  Gonatus sp. A*
  Gonatus type C
  Gonatopsis okutanii
  *Berryteuthis anonychus**
  Octopus sp. A*
  Octopus sp. B*
	8) Subarctic-central or equatorial
	  Onychoteuthis borealijaponicus
	  Taonius pavo

3) Holosubarctic
  *Gonatus berryi**
  Gonatus middendorffi
  Gonatus onyx
  *Gonatus pyros**
  Gonatopsis borealis
  Berryteuthis magister
  Moroteuthis robusta
  Chiroteuthis calyx
  *Galiteuthis phyllura**
  Japetella heathi
	9) Transitional-central
	  *Abraliopsis falco**
	  *Pyroteuthis addolux**
	  Pterygioteuthis gemmata
	  Onykia carribaea
	  Ommastrephes bartramii
	  Symplectoteuthis luminosa
	  Histioteuthis dofleini
	  *Bathyteuthis berryi**
	  *Mastigoteuthis pyrodes**
	  Neoteuthis sp.*
	  Chiroteuthis joubini
	  Cranchia scabra
	  *Leachia dislocata**

4) Transitional endemics
  *Gonatus californiensis**
  Gonatus sp. E*
  *Histioteuthis corona berryi**
  *Histioteuthis heteropsis**
  *Octopoteuthis deletron**
  *Abraliopsis felis**
  *Valbyteuthis oligobessa**
  *Loligo opalescens**
  Japetella sp.*
  Cirroteuthis sp.*
  Stauroteuthis sp.*
	10) Transitional-equatorial
	  Mastigoteuthis dentata
	  Crenopteryx sicula
	  Helicocranchia pfefferi
	  Ocythoe tuberculata
	  Eledonella pygmaea
	  Vampyroteuthis infernalis

5) Central
  Abraliopsis hoylei
  Abraliopsis pfeffari
  Megalocranchia speculator
  Sandalops melancholicus
  Brachioteuthis sp.
  Bathyteuthis sp.
	11) Bathypelagic
	  Bathyteuthis abyssicola
	  Valbyteuthis oligobessa
	  Vampyroteuthis infernalis

6) Eastern tropical Pacific
  *Dosidicus gigas**
	12) Nektobenthic/Benthic
	  Rossia pacifica
	  Loligo opalescens
	  Moroteuthis robusta
	  Berryteuthis magister
	  Cirroteuthis sp.
	  Cirrothauma murrayi
	  Stauroteuthis sp.
	  Opisthoteuthis californiana
	  Octopus sp.

*Limited to eastern Pacific

Four eurythermal groups have distributions which include transitional and warmer waters: one ranges from Subarctic to central or equatorial waters; two from the Transition Zone and California Current to North Pacific central waters (one of which is limited to the eastern Pacific); and a final group extends from the Transition Zone to equatorial waters.

A group of nektobenthic or benthic cephalopods is included, as is a group of bathypelagic cephalopods. Members of these groups have distributions which do not necessarily correlate with surface water masses.

Arctic-Subarctic

One cephalopod captured in this study, *Cirrothauma murrayi* (Figure 52), is known to occur in the Atlantic, Arctic, and Subarctic Pacific. In this study, it was collected only in deep hauls off Oregon, in the northern reaches of the California Current system.

Northern endemics

The Subarctic Water Mass holds a characteristic group of cephalopods, primarily members of the Gonatidae: *Gonatus madokai*, *Gonatus* sp. A, *Gonatus* type C Kubodera, *Gonatopsis okutanii*, and *Berryteuthis anonychus* (their distributions are shown in Figures 27, 31, 32, 33, and 34, respectively). *Gonatus* sp. A, *Berryteuthis anonychus*, and *Octopus* spp. A and B (Figure 56) are

limited to the eastern Pacific. These have been collectively plotted in Figure 60 to show the character of the distribution.

All collections which sampled these species were made at or north of the Transition Zone - Subarctic boundary. Two species were collected in the northern reaches of the California Current region: _Gonatus_ type C, north of 38°N, and _Berryteuthis_ _anonychus_, north of 36°N. Point Conception, at 34°N, is generally recognized as an important zoogeographic boundary between northern and southern (or warm and cold water) forms, both littoral and neritic (Briggs, 1974). All these cephalopods were absent from the Transition Zone, southern portions of the California Current, and central waters.

Figure 60. Northern endemics. Zoogeographic boundaries as in
Figure 59. Symbols as follows: Gonatus madokai (O, previous
records, ⊙), Gonatus sp. A (□), Gonatus type C (△, previous
records, \\\\), Gonatopsis okutanii (G), Berryteuthis anonychus (+,
previous records, ////), Octopus sp. A (A), and Octopus sp. B (B).
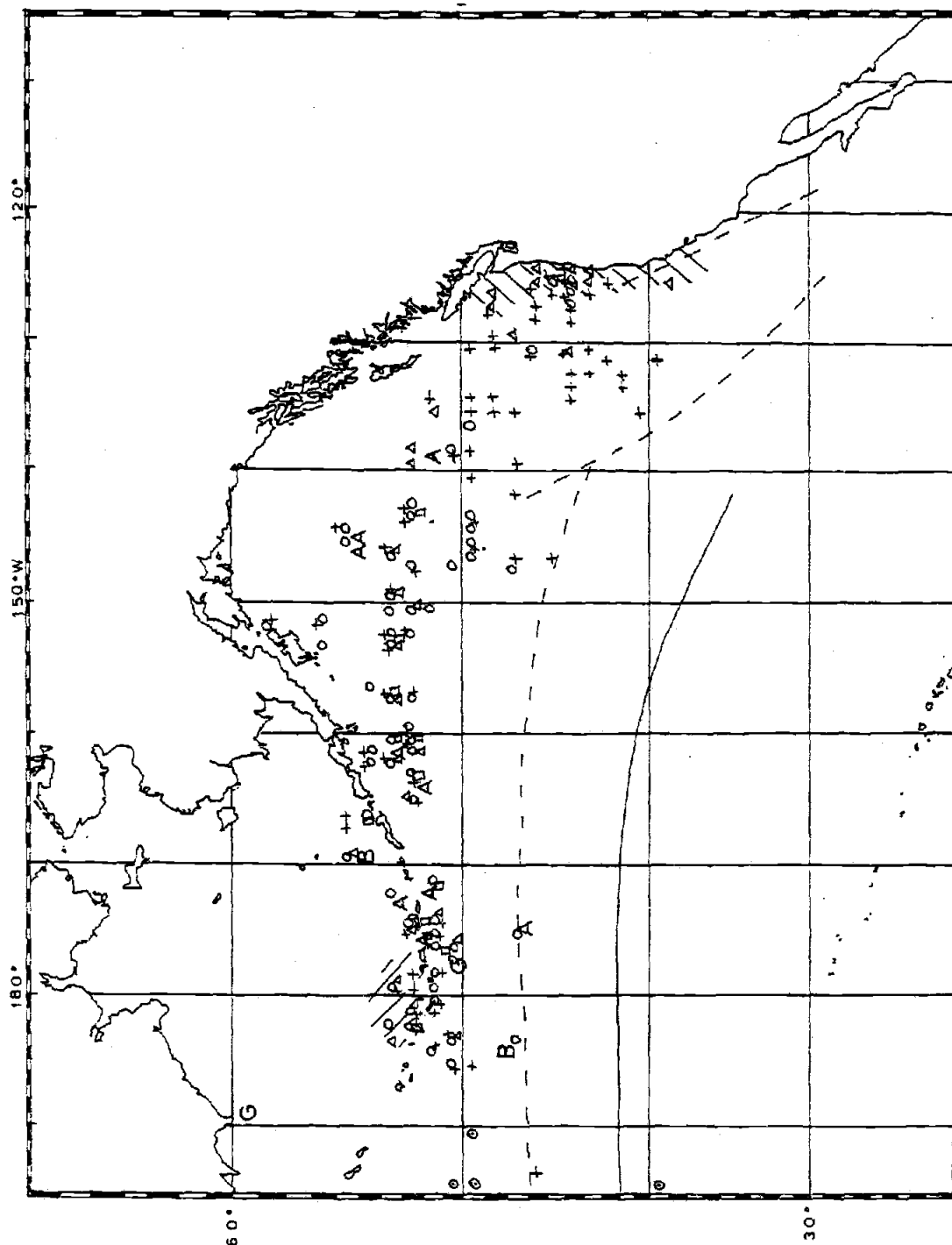
Holosubarctic

This distributional type encompasses occurrences from the California Current and Transition Zone through the Subarctic Water Mass. Cephalopods with this distribution include the eastern Pacific *Gonatus berryi*, *G. pyros*, and *Galiteuthis phyllura*[2] (Figures 25, 30, and 51), and the panPacific *Gonatus middendorffi*, *G. onyx*, *Gonatopsis borealis*, *Berryteuthis magister*, *Moroteuthis robusta*, *Chiroteuthis calyx*, and perhaps *Japetella heathi*[3] (Figures 28, 29, 33, 35, 24, 44, and 54).

All of these subarctic species appear to be limited to the California Current system and the Subarctic proper (Figure 61). Most occur only in the northern portions of the Transition Zone, only *Gonatopsis borealis* and *Japetella heathi* occurring consistently as far south as the central Pacific - Transition Zone boundary. The central water occurrences of *J. heathi* may be the result of the *heathi* - *diaphana* identification problem, while the southernmost captures of *Gonatopsis borealis* probably represent seasonal oscillation of the polar front with southward incursions

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[2]*Galiteuthis phyllura* seems to be inadequately separated from *G. armata* in the western Pacific; the presence of the former species in that area requires confirmation. Imber (1978) tentatively identified several cephalopod beaks from New Zealand waters as *Gonatus berryi*, but the confirmed presence of this species in the southwestern Pacific awaits better evidence.

[3]*Japetella heathi* is imperfectly separated from the cosmopolitan *J. diaphana*, and its distribution is well understood only in the northeastern Pacific. It is apparently absent from the Bering Sea, Sea of Okhotsk, and western Subarctic circulation (Nesis, 1973b).

Figure 61. Holosubarctic distributions. Zoogeographic boundaries
as in Figure 59. Symbols as follows: Gonatus berryi (▲), G.
pyros (P), G. middendorffi (□), G. onyx (.), Moroteuthis robusta (◐
). Gonatopsis borealis (○;⊘ previous records), Berryteuthis
magister (+), Chiroteuthis calyx (C), Galiteuthis phyllura (△),
and Japetella heathi (H).
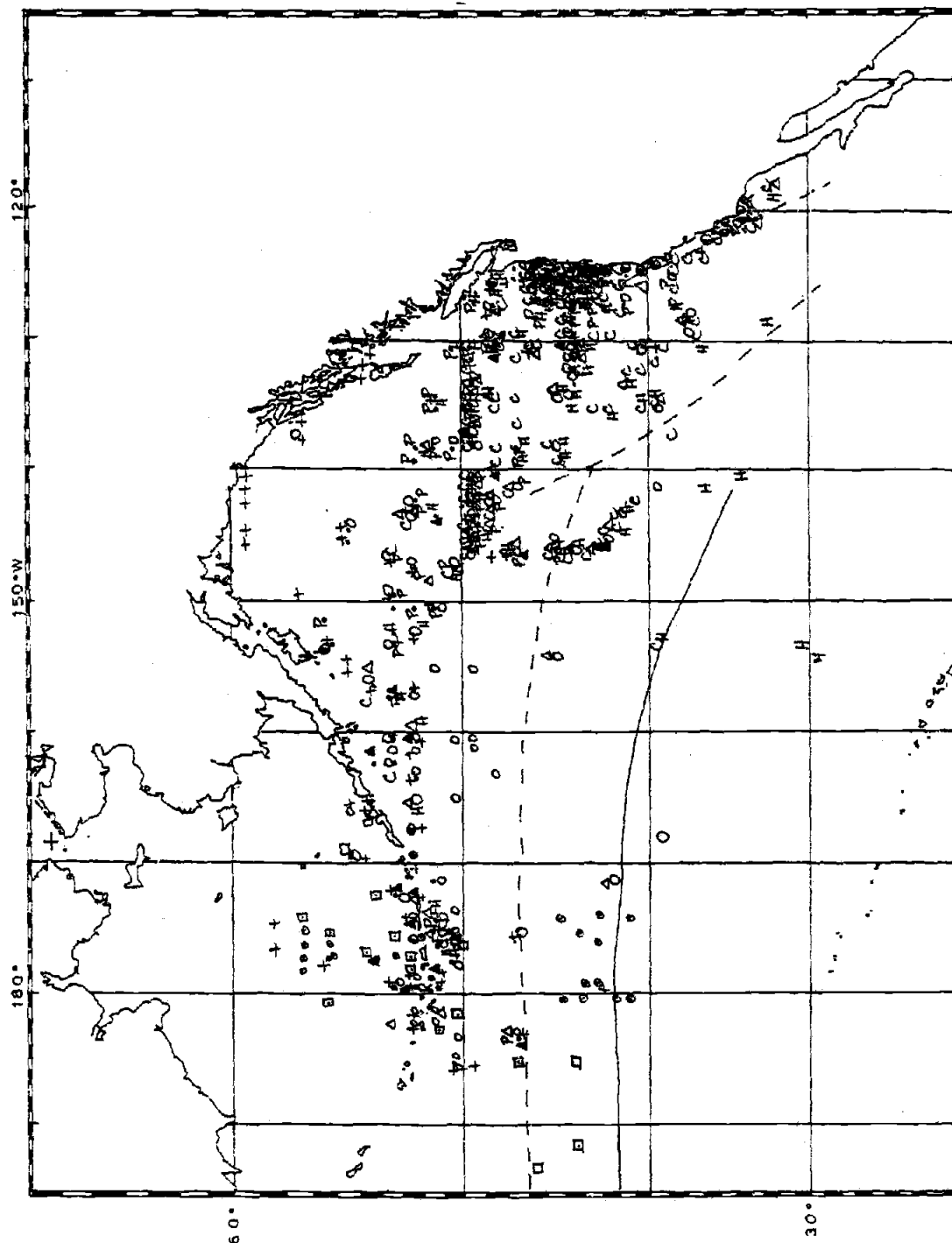
of Subarctic water. The observed distributions of all the other
"Subarctic" species stop well short of areas where data are
lacking; this supports the idea that these distributions represent
reality, and not simply sampling intensity.

Transition endemics

The fourth distributional type includes a number of
cephalopods limited to the California Current and eastern portion
of the Transition Zone: _Gonatus californiensis_ [4], _Gonatus_ sp. E,
Histioteuthis corona berryi, _H. heteropsis_, _Octopoteuthis
deletron_, _Abraliopsis felis_, _Valbyteuthis oligobessa_, _Loligo
opalescens_, _Japetella_ sp. Young [5], and perhaps _Cirroteuthis_ sp. and
Stauroteuthis sp. (Figures 26, 31, 36, 37, 22, 18, 45, 16, 54, 52,
and 52). All of these transitional endemics are fairly well
limited to California Current waters (see Figure 62). _Abraliopsis
felis_ has the widest distribution; in this study it was taken
quite far west in the Transition Zone, and Young (1972) reported
it in central waters.

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[4] Imber (1978) believed _G. californiensis_ to represent the same
species as _G. antarcticus_. If this is indeed the case, the
species has an intermittent distribution through the eastern
tropical Pacific to the Peru Current and the Subantarctic. This
may be a similar phenomenon to that seen for _Eukrohnia hamata_, a
cold water chaetognath which shows subtropical submergence and
equatorial emergence (Bieri, 1959).

[5] This species is imperfectly separated from _Japetella heathi_.

Figure 62. Transitional endemics. Zoogeographic boundaries as in
Figure 59. Hatched area is area where _Abraliopsis felis_ has been
reported by Young (1972). See text for other previous records.
Symbols as follows: _Loligo opalescens_ (L), _Abraliopsis felis_ (A),
Octopoteuthis deletron (O), _Gonatus californiensis_ (+), _Gonatus_
sp. E (E), _Histioteuthis corona berryi_ (CB; previous records, x),
H. heteropsis (H), _Valbyteuthis oligobessa_ (V), _Cirroteuthis_ sp. (Δ
), _Stauroteuthis_ sp. (S), and _Japetella_ sp. (J).
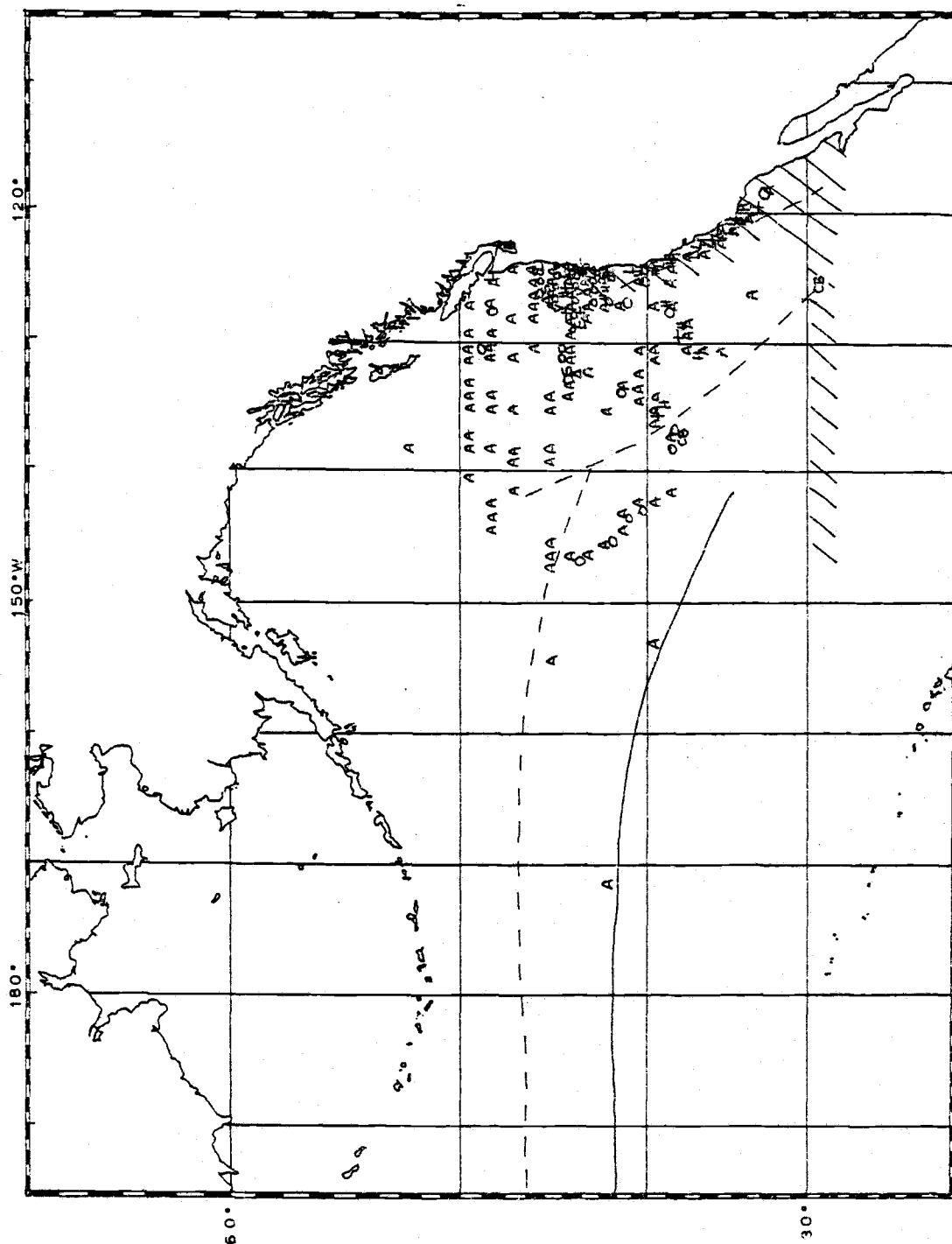
Central

A number of cephalopods have distributions which correspond to the central gyre, at least in the North Pacific: _Abraliopsis hoylei_, _A. pfefferi_, _Megalocranchia speculator_, _Sandalops melancholicus_, _Brachioteuthis_ sp., and _Bathyteuthis_ sp. (Figures 19, 19, 51, 50, 41, and 39). Their collective distribution is shown in Figure 63.

All these species, and at least some species of _Brachioteuthis_ and _Bathyteuthis_, occur in warm waters of other oceans, but are absent from the equatorial Pacific. It should be noted that my data do not contain records for many species known to occur in this region. This is further discussed in a later section.

Eastern tropical Pacific

Dosidicus gigas is the only cephalopod in my collections which is commonly taken in this region (see Figure 42).

Central to equatorial

Cephalopods occurring in subtropical and tropical waters of the North Pacific include _Thelidioteuthis alessandrinii_, _Onychoteuthis banksii_, and _Tremoctopus violaceus_ (Figures 19, 23, and 57). The collective distribution is shown in Figure 64. Although none was taken in equatorial waters in this study, all are known from equatorial waters in the Pacific, but not necessarily within the area of the map.

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Figure 63. Central distributions. Zoogeographic boundaries as in
Figure 59. Symbols as follows: Abraliopsis pfefferi (P), A.
hoylei (A), Bathyteuthis sp. (O), Brachioteuthis sp. (+),
Sandalops melancholicus (S, previous records, Ø), and
Megalocranchia speculator (M).
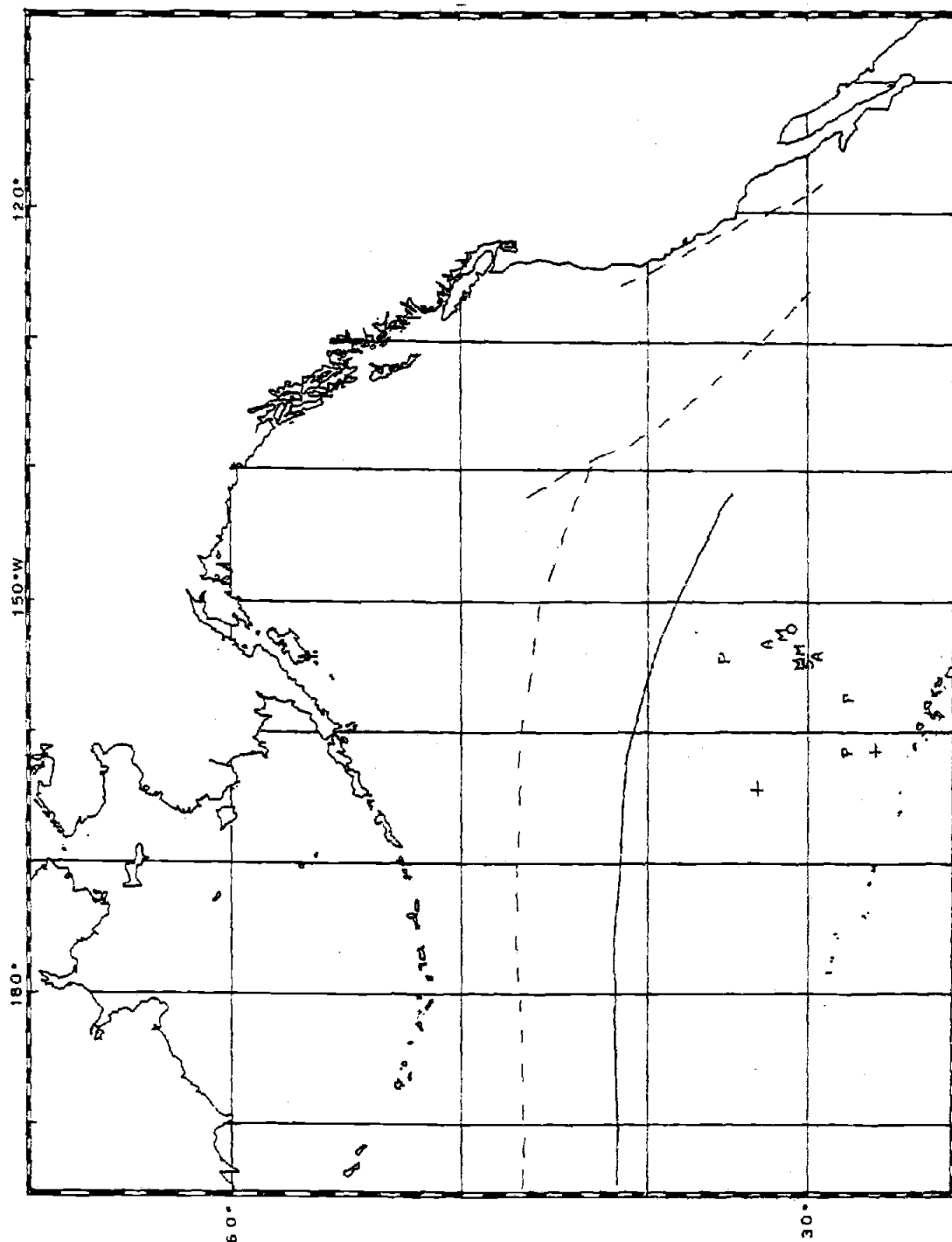
Figure 64. Central-equatorial distributions. Zoogeographic
boundaries as in Figure 59. Records from equatorial Pacific
waters are outside the area of this map. Symbols as follows:
Thelidioteuthis _alessandrinii_ (x, previous records, T),
Onychoteuthis _banksii_ (0), and _Tremoctopus_ _violaceus_ (V, previous
records, △).
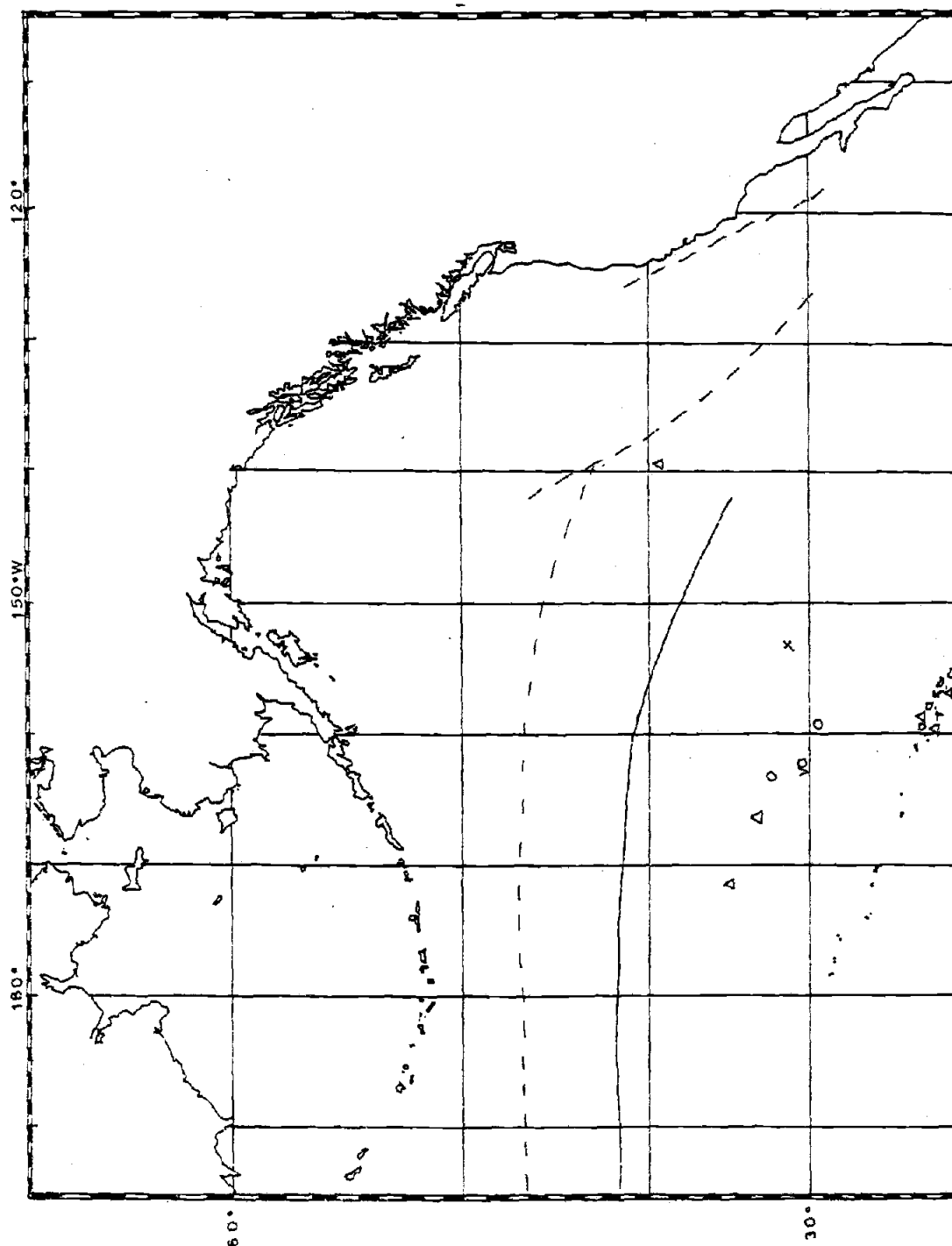
Subarctic to central or equatorial

One eurythermic cephalopod (_Taonius pavo_, Figure 49) occurs from tropical to boreal latitudes in the Pacific and Atlantic. In the Pacific, it ranges between 60°N and Antarctica (Clarke, 1966; Nesis, 1972). _Onychoteuthis borealijaponicus_ (Figure 23) ranges from 28°N to 58°N in the North Pacific, encompassing central, transitional, and Subarctic waters.

Transitional to central

Many cephalopods occur in Transition Zone and California Current waters as well as in the central gyre: _Abraliopsis falco_, _Pyroteuthis addolux_, _Pterygioteuthis gemmata_, _Onykia carribaea_, _Ommastrephes bartramii_, _Symplectoteuthis luminosa_, _Histioteuthis dofleini_, _Bathyteuthis berryi_, _Mastigoteuthis pyrodes_, _Neoteuthis_ sp., _Chiroteuthis joubini_, _Cranchia scabra_, and _Leachia dislocata_ (Figures 17, 20, 21, 24, 42, 43, 36, 39, 46, 38, 45, 47, and 48).

Pyroteuthis addolux, _Leachia dislocata_, _Mastigoteuthis pyrodes_, _Neoteuthis_ sp., and _Bathyteuthis berryi_ seem to be primarily eastern central North Pacific species (Figure 65). All of these apparently eastern Pacific forms were described from material taken off the Californias. They have all been recovered in the vicinity of the Hawaiian Islands, and some occur further north, to Transition Zone or northern California Current waters. None has yet been reported west of 170°W. This could be a result of their relatively recent description, or could reflect a separation between eastern and western central Pacific faunas.

Figure 65. Transitional-central distributions. Eastern Pacific
forms. Zoogeographic boundaries as in Figure 59. Symbols as
follows: Puroteuthis addolux (P, previous records, P and ////).
Neoteuthis sp. (N, previous records, Ⓝ). Bathyteuthis berryi (B,
previous records, \\\\), Mastigoteuthis pyrodes (+, previous
records, ≡), and Leachia dislocata (△, previous records, L
and \\\\).
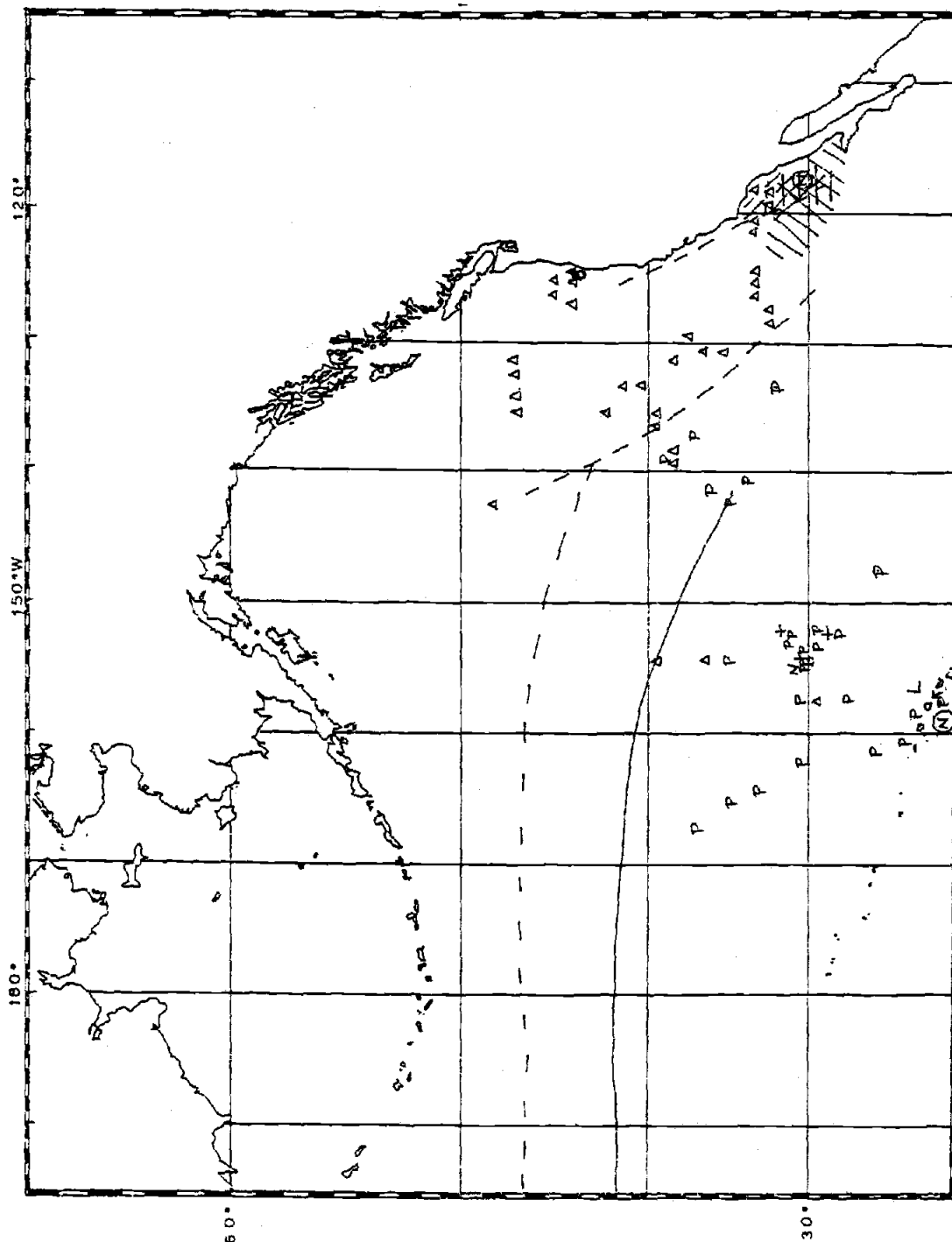
The remaining transitional-central species (Figure 66) are nearly all known to occur on both sides of the dateline. _Abraliopsis falco_, however, is not known to occur in the western Pacific, but does occur off central and South America. All of the others appear to be biantitropical central species, at least in the Pacific.

Transitional to equatorial

A few eurythermic species occur from the Transition Zone and California Current into equatorial waters: _Mastigoteuthis dentata_[6], _Ctenopteryx sicula_, _Helicocranchia pfefferi_, _Ocythoe tuberculata_, _Eledonella pygmaea_, and _Vampyroteuthis infernalis_ (Figures 46, 40, 50, 57, 53, and 58). All are cosmopolitan in low latitudes (Figure 67), although _Vampyroteuthis_ is limited to deeper water.

Bathypelagic

Bathyteuthis abyssicola is widely distributed in depths of 500 to 2500 m (Roper, 1969); _Valbyteuthis oligobessa_ is known only from hauls to 2000 m in this study and 1000 m or deeper in Young's

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[6] _Mastigoteuthis dentata_ is unusual in occurring in deep waters off Oregon, and also in the Gulf of Panama and off the Galapagos Islands. Its presence off Oregon could represent northward transport of a basically tropical species (in the northward countercurrent below the California Current).

Figure 66. Transitional-central distributions. PanPacific forms.
Zoogeographic boundaries as in Figure 59. Symbols as follows:
Abraliopsis falco (A, previous records, A and ////),
Pterygioteuthis gemmata (P, previous records, P and \\\\), Onykia
carribaea (x, previous records, (x)), Histioteuthis dofleini (+,
previous records, ⊕), Ommastrephes bartramii (O, previous
records ⊙), Symplectoteuthis luminosa (S, previous records, $),
Chiroteuthis joubini (J), and Cranchia scabra (△, previous
records ▲).
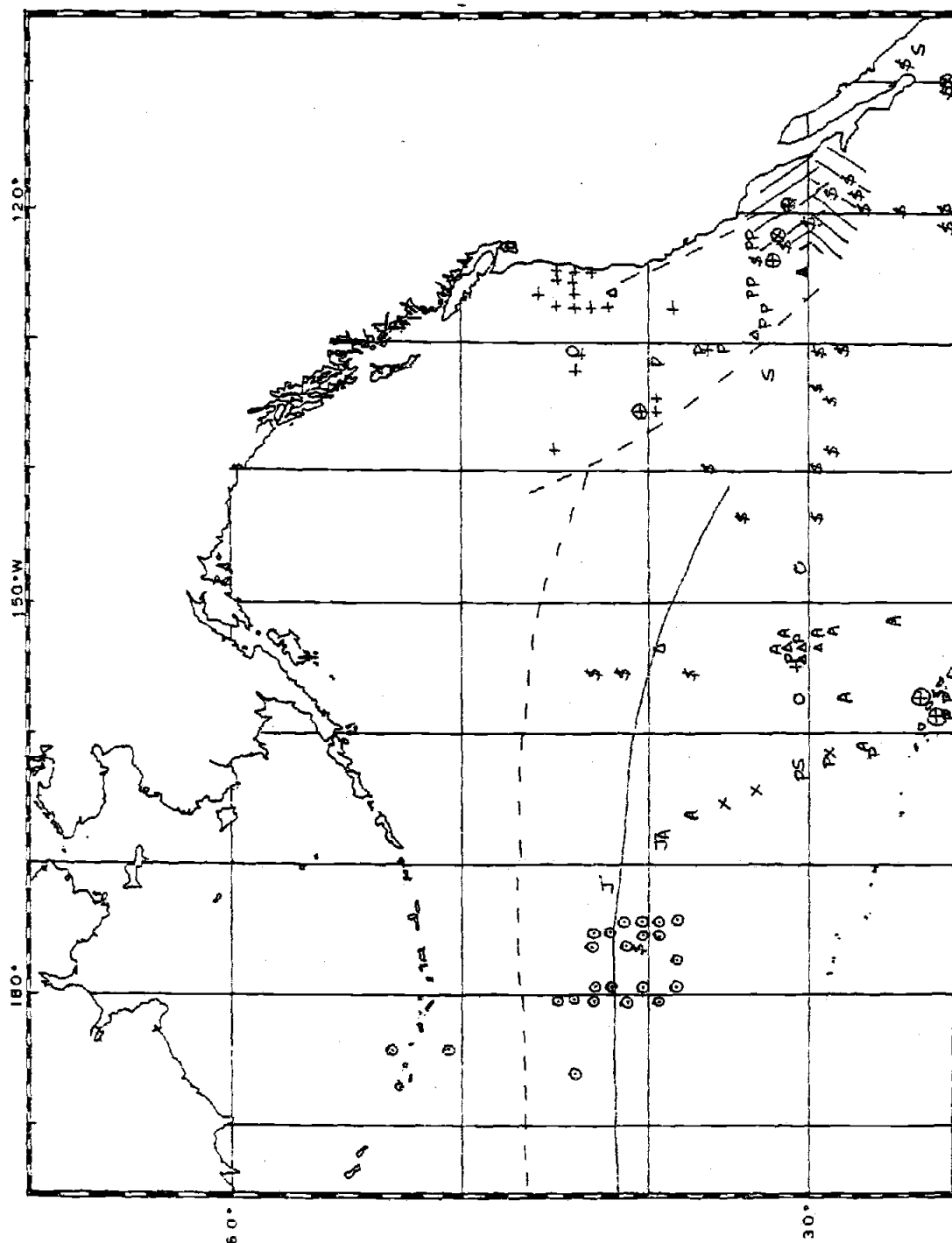
Figure 67. Transitional-equatorial distributions. Zoogeographic
boundaries as in Figure 59. Other equatorial Pacific records are
outside the limits of this map. Symbols as follows: _Ctenopteryx
sicula_ (C, previous records, ∅), _Mastigoteuthis dentata_ (M),
Helicocranchia pfefferi (H, previous records,////), _Eledonella
pygmaea_ (E, previous records,△), _Ocythoe tuberculata_ (O), and
Vampyroteuthis infernalis (+, previous records △ and \\\\).
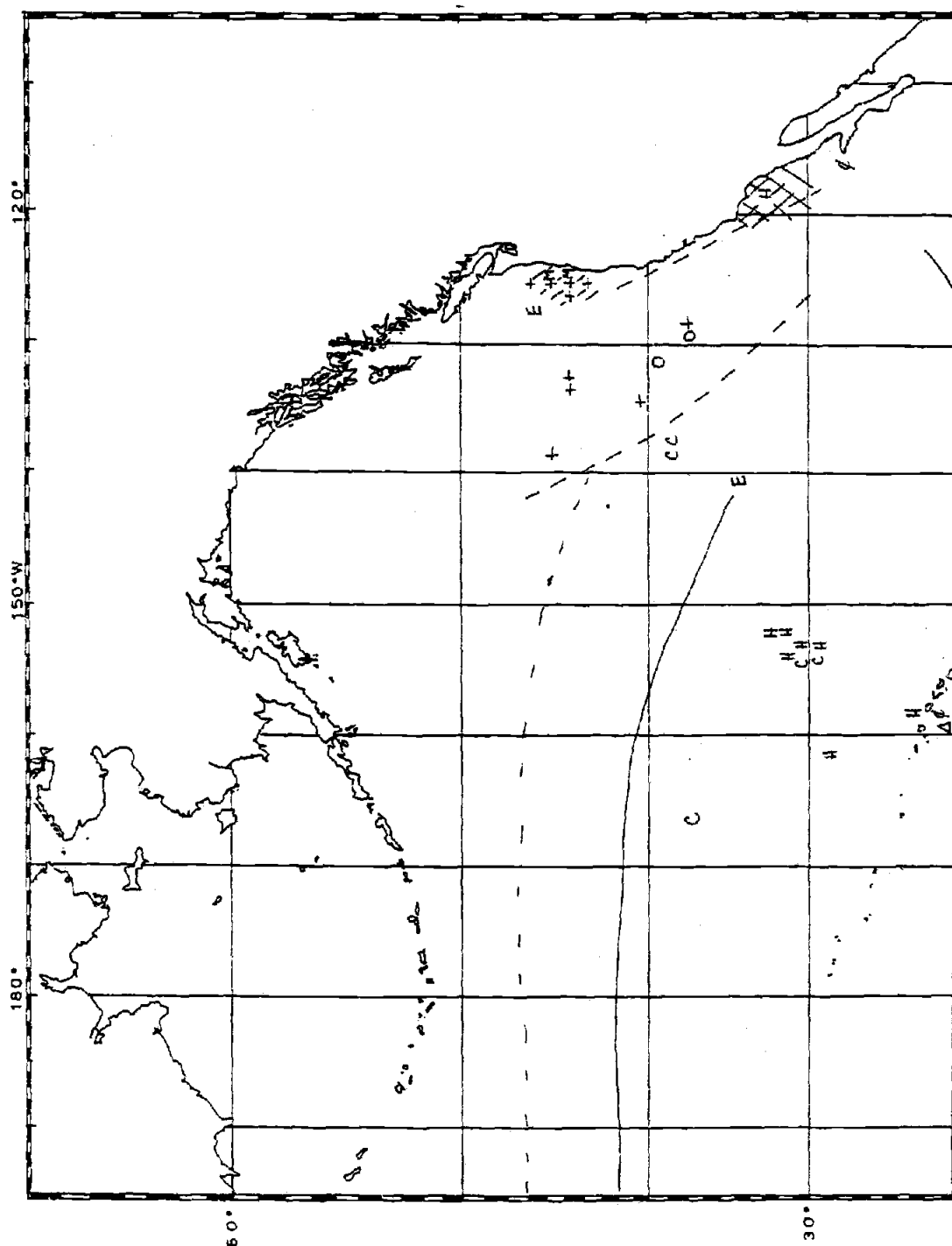
(1972) report, and only in the California Current. *Vampyroteuthis infernalis* is cosmopolitan in tropical and subtropical latitudes and most abundant at 1000 to 2500 m (Pickford, 1946). It occurred primarily below 500 m, in the California Current, in this study. The distributions of these three species are shown in Figures 39, 45, and 58.

Nektobenthic or benthic

Several species discussed in this report are associated, to a greater or lesser degree, with the bottom, and were captured primarily in demersal sampling gear: *Rossia pacifica*, *Loligo opalescens*, *Moroteuthis robusta*, *Berryteuthis magister*, *Cirroteuthis* sp., *Cirrothauma murrayi*, *Stauroteuthis* sp., *Opisthoteuthis californiana*, and the Octopodidae (except *Octopus* spp. A and B) (see Figures 15, 16, 24, 35, 52, 52, 52, 53, and 55). These forms may or may not show a distributional correspondence to overlying, surface water masses. *Rossia pacifica* occurs around the Pacific Rim from Japan to California, and in the Bering Sea, at shelf depths, in a latitudinal expanse equivalent to the general Subarctic region (Subarctic Water Mass plus Transition Zone and California Current). *Loligo opalescens* is an endemic species of the California Current. It occurs in shelf depths and has demersal eggs, although other stages of the life cycle may not be strictly associated with the bottom. *Moroteuthis robusta* and *Berryteuthis magister* occur in the

Subarctic and transitional regions at shelf and upper slope
depths, from the Aleutians to southern California and Japan.

Cirroteuthis sp., *Stauroteuthis* sp., and *Cirrothauma murrayi*
are bathyal forms taken, in this study, only in bottom trawls in
the California Current region. *Cirrothauma* occurs at least in the
cold waters of the Atlantic and the Arctic, and the other two
forms may occur elsewhere as well.

Opisthoteuthis californiana has a latitudinal and depth
distribution similar to *Moroteuthis robusta* in the eastern
Pacific, but is replaced by *O. depressa* in the western Pacific.

The Octopodidae taken in this study (except *Octopus* spp. A
and B, which occurred only as pelagic larvae) occurred at shelf,
slope, and even bathyal depths. Only larvae or very early
juveniles were taken in pelagic hauls.

These benthic or nektobenthic animals, in most cases, have
distributions which correspond with the latitudinal expanses of
pelagic forms. Those species with holosubarctic distributions (at
least where appropriate depths occur) include *Rossia pacifica*,
Moroteuthis robusta, *Berryteuthis magister*, Octopodidae (except
Octopus spp. A and B), and *Opisthoteuthis californiana*, although
the latter is restricted to waters east of about 180° longitude.
Several transitional endemics occur: *Loligo opalescens*, and
possibly *Cirroteuthis* sp. and *Stauroteuthis* sp. One Arctic-Boreal
species is represented: *Cirrothauma murrayi*.

These basic distributional patterns for cephalopods in the northeastern Pacific can be considered in a broader context as combinations of the various water mass patterns. For example, type 8, Subarctic to central or equatorial (Table 9), is a broadly eurythermal distribution crossing most water mass boundaries; type 2 (northern endemics) is a water mass endemic; and type 9 (transitional-central) crosses only one water mass boundary.

PACIFIC CEPHALOPOD DISTRIBUTIONS RECORDED BY OTHER WORKERS

My data are at significant variance with those of Young
(1972) in only one regard. Onychoteuthis borealijaponicus, which
he listed as Subarctic-Transitional, is here thought to be better
described as Subarctic-Central.

Nesis (1973b) concluded that five zoogeographic regions or
subregions exist for cephalopods in the North Pacific; these are
detailed in the Introduction. I have listed narrower latitudinal
distributions than did he for fourteen species and broader
distributions for four. Two species which Nesis considered
broadly boreal in the North Pacific are here considered to be
limited to the eastern Pacific (Gonatus berryi and Galiteuthis
phyllura).

Many Hawaiian cephalopods were not collected in this study,
as a result of the limited sampling effort in that region (see
Table 10). Several of these species are known to occur in areas
which were reasonably well sampled, primarily southern California.
These species and their known northern extents are: Valbyteuthis
danae, Monterey Bay (Anderson, 1978); Pterygioteuthis giardi,
southern California (McGowan, 1967); Grimalditeuthis bomplandii,
Galiteuthis pacifica, and Liocranchia sp., southern California
(Young, 1972); Argonauta pacifica, Monterey Bay (Berry, 1912b);
and Histioteuthis meleagroteuthis, Oregon (Pearcy, 1965; Voss,
1969). Their absence in the present study may be due to their
rarity in their environment or to their primarily southern (i.e.,
equatorial) distributions. Probably none is a good net avoider,

Table 10. Cephalopods known to occur off Hawaii, but not
collected in this study. If no reference is listed, datum is from
Young (1978).

Heteroteuthis hawaiiensis 1,3
Stoloteuthis iris 3,4
Euprymna scolopes 4
Sepioteuthis arctipinnis 3,4
Enoploteuthis spp. nov.
Abralia andamanica 2,11
Abralia astrosticta 1-4
Abralia trigonura 1,4
Abraliopsis spp. nov.
Pterygioteuthis giardi
Pterygioteuthis microlampas 1,2,4
Octopoteuthis nielseni
Taningia danae 12
Onychoteuthis compacta 1,4
Onykia sp.
Cycloteuthis serventyi
Discoteuthis laciniosa
Histioteuthis celetaria pacifica
Histioteuthis meleagroteuthis 12
Nototodarus hawaiiensis 1,4
Symplectoteuthis oualaniensis 1,4
Hyaloteuthis pelagicus
Thysanoteuthis rhombus

Chiroteuthis picteti
Chiroteuthis sp. nov.
Valbyteuthis danae 5-10
Planktoteuthis lippula
Chiroteuthidae gen.n., sp.n.
Mastigoteuthis famelica 1-4
Mastigoteuthis inermis
Grimalditeuthis bomplandii
Joubiniteuthis portieri
Leachia pacifica
Liocranchia reinhardti 1,4
Liocranchia valdiviae
Phasmatopsis fisheri 1,4
Helicocranchia beebei
Galiteuthis pacifica
Bathothauma lyromma
Japetella diaphana
Amphitretus pelagicus
Vitreledonella richardi
Argonauta boettgeri 3,12
Argonauta hians 12
Alloposus mollis 14

1, Young, 1978. 2, Clarke, 1966. 3, Berry, 1909. 4, Berry,
1914. 5, Joubin, 1931. 6, Nesis, 1973a. 7, Young, 1972. 8,
Clarke and Lu, 1974. 9, Anderson, 1978. 10, Roper and Young,
1967. 11, Voss, 1963. 12, Nesis, 1973b. 13, Roper and Young,
1975. 14, Thore, 1949.

in the way that an ommastrephid or onychoteuthid would be expected
to be.

Cephalopods occurring in the eastern tropical Pacific have
been described by Okutani (1974, larvae) and Fields and Gauley
(1972). At least three species occurring there also have been
taken rarely off southern California: _Galiteuthis pacifica_,
Valbyteuthis danae, and _Argonauta pacifica_ (see Berry, 1912b;
Young, 1972).

Aside from a large number of species occurring in Hawaiian
waters, many of which are probably equatorial, and were not taken
in this study, my data basically agree with what was previously
known of cephalopod distributions in the northeastern Pacific.
New species have been found in this region, as well as new
distributional records for species occurring elsewhere.

PATTERNS IN OTHER TAXA

The next important question concerns the way in which the
observed patterns of cephalopod distribution relate to those seen
for other planktonic and nektonic taxa. Examples of patterns
which correspond to the cephalopod distribution patterns seen here
occur in many other taxonomic groups (Table 11). As far as I am
aware, no authour has attempted to collect all data on
zoogeographic distributions of plankton and/or nekton for the
North Pacific. This information remains widely scattered,
generally in the taxonomic literature. A few authours have
described distribution patterns for one or a few higher taxa in
this region; among them are Fager and McGowan (1963),
chaetognaths, euphausiids, and pelagic molluscs; Tebble (1962),
polychaetes; Brinton (1962, 1967) and Boden et al. (1955),
euphausiids; Alvariño (1965a,b) and Bieri (1959), chaetognaths;
Alvariño (1971), siphonophores; Bradshaw (1959), Foraminifera; and
Johnson (1982), evermannellid and scopelarchid fishes. Reid et
al. (1978) treated the zoogeographic problem in broad terms,
noting that many species were restricted to one gyral system,
particularly the high latitude cyclones, mid-latitude
anticyclones, and the equatorial zonal current systems, with
extensions occurring in the eastern and western boundary currents.
The cephalopods of the northeastern Pacific in many cases have
distributions spanning more than one gyre, current system, or
water mass, perhaps the result of their often more nektonic habit.

Table 11. Taxa other than cephalopods with members whose
distributions correspond to the cephalopod distribution patterns
described here. Numbers correspond to references at end of table.

ARCTIC - BOREAL

Aglantha digitalis 2
Sagitta elegans 1.3.4.5.55
Copepods 2,6
Euphausiids 2,6,7,8
Fish 9,10

NORTHERN ENDEMICS

Sagitta maxima 4
Copepods 6,11,12,13
Epipelagic fish 9
Mesopelagic fish 14,15
Phytoplankton 16
Pelagic Foraminifera 17

HOLOSUBARCTIC

Poeobius meseres 18,19,20
Polychaetes 21
Limacina helicina 1
Heteropod 22
Euphausiids 1,6,7
Fish 9,14,20,24,25,26,56
Pelagic tunicate 23

TRANSITIONAL ENDEMICS

Chaetognaths 1,3,5,27,29
Euphausiids 1,7,28,29
Heteropod 22
Copepod 13,20
Fish 14,20,56

CENTRAL

Polychaetes 21,31
Chaetognaths 4,6
Pelagic molluscs 1,8
Copepods 6,8,32
Euphausiids 1,6,7,8,29,33
Foraminifera 6
Fish 14,20,24,34-39,56

EASTERN TROPICAL PACIFIC

Euphausiids 6,7,8
Pteropod 8
Chaetognaths 4
Fish 10,20,26,35,42,43,56

CENTRAL - EQUATORIAL

Siphonophore 2
Ctenophore 2
Chaetognaths 1,3,4,5
Pelagic molluscs 1,8
Copepods 2
Euphausiids 1,7,8
Pelagic tunicate 23
Foraminifera 17
Fish 10,20,24,26,44-47,56

SUBARCTIC-CENTRAL/EQUATORIAL

Polychaetes 21,31
Siphonophore 2
Chaetognaths 4
Euphausiids 1,6,7
Copepod 2
Amphipods 2
Fish 9,20,24,48,49

TRANSITIONAL - CENTRAL

Euphausiids 1,7,29
Polychaetes 21
Foraminifera 17
Fish 9,20,24,35,51

TRANSITIONAL - EQUATORIAL

Polychaetes 21
Chaetognaths 5
Euphausiids 7
Copepod 52
Fish 20,24,48,53,54,56
Pteropod 3,22

1. Fager and McGowan (1963). 2. Ekman (1953). 3. Hida (1957).
4. Bieri (1959). 5. Alvariño (1965b). 6. Johnson and Brinton
(1963). 7. Brinton (1962). 8. Reid et al. (1978). 9. Larkins
(1964). 10. Briggs (1974). 11. Brodsky (1957). 12. Johnson
(1941). 13. Fleminger and Hulsemann (1973). 14. Parin (1961a).
15. Wisner (1959). 16. Beklemishev and Semina (1956). 17.
Bradshaw (1959). 18. Heath (1930). 19. McGowan (1960). 20.
Ebeling (1962). 21. Tebble (1962). 22. McGowan (1971). 23.
Berner (1960). 24. Hart (1973). 25. Haffner (1952). 26. Morrow
(1961). 27. Alvarino (1962). 28. Brinton (1975). 29. Boden et
al. (1955). 30. Lang (1965). 31. Day (1967). 32. Bowman
(1955b). 33. Baker (1965). 34. Parin (1959). 35. Parin (1960b).
36. Parin (1961b). 37. Mukhacheva (1964). 38. Becker (1964).
39. Bussing (1965). 42. Wisner (1963). 43. Ebeling (1967). 44.
Rass (1967). 45. Parin (1968). 46. Ebeling and Weed (1963). 47.
Rofen (1966). 48. Strasburg (1958). 49. Paxton (1967). 50. Grey
(1955). 51. Mead and Haedrich (1965). 52. Frost and Fleminger
(1968). 53. Otsu and Uchida (1963). 54. Gibbs and Collette
(1967). 55. Marumo (1966). 56. Johnson (1982).

Fager and McGowan (1963) found several groups with distributions corresponding to those seen here for the cephalopods. Their Group II is essentially equivalent to my distributional type 3 (holosubarctic). Groups I and VII are basically central-equatorial groups of the western Pacific, and Group IV is equatorial; they generally occurred outside the main area of my study. Groups III and VI are basically central, and correspond, at least generally, to my distributional type 5. Group V is transitional and occurs across the Pacific, while my distributional type 4 is limited to transitional waters of the eastern Pacific.

Johnson (1982), in a study of the fish families Evermannellidae and Scopelarchidae, found distributional types which correspond very well with those seen here for the cephalopods. He found species with distributions of the following types (my terminology): Holosubarctic; Transitional endemics; Central; Eastern Tropical Pacific; Central-Equatorial; and Transitional-Equatorial. He noted a significant zoogeographic difference in the eastern boundary currents and the offshore Transition Zones in both the North and South Pacific. He listed five species with distributions ranging from transitional (in this case, California Current between $30°$ and $35°N$) waters to central and equatorial waters. He further noted that many records from the Hawaiian Islands region are of basically equatorial species, which probably occur there due to locally increased productivity (Clarke, 1974; Barnett, 1975).

QUANTITATIVE ZOOGEOGRAPHY

I shall now consider the relative abundance of cephalopods
found in each of the main water mass types (SA, TZ, CC, NPC)[7].
Data were obtained with 0.9, 1.8, and 3.0 m IKMTs. All areas but
central Pacific waters were sampled with the 0.9 m IKMT, and the
California Current region was also much sampled with a 2.4 m IKMT
and a large (50 m2 mouth area) midwater trawl (MT). The mesh size
in the various IKMTs was roughly comparable, but the large
midwater trawl had a somewhat larger mesh size in the body and cod
end than did the IKMTs:

Net (User)[8]	Mesh size in body (at least aft portion)	Mesh size in cod end
0.9 m IKMT (UW)	13 mm	3.2 mm
1.8 "	13	3.2
0.9 m IKMT (OSU)	0.571	0.571
1.8 "	5.	0.571
2.4 "	5.	0.571
3.0 "	5	0.571
50 m2 MT (OSU)	19.	9.

Statistics

The following community statistics were computed for each
zoogeographic area: S, number of species; N, number of
individuals; He", Shannon's diversity index; Hmax", theoretical

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[7] SA, Subarctic Water Mass; TZ, Transition Zone; CC, California
Current; NPC, North Pacific Central Water Mass.

[8] User: UW, University of Washington, R/V Brown Bear; OSU, Oregon
State University.

maximum of $He^{''}$; E, evenness; and E(Sn), the expected number of species in a sample of size n. The Shannon index of diversity is computed as

$$He^{''} = -\sum_{I}^{S} pi \ln pi$$

where pi represents the proportion of the total number of individuals belonging to species i (Shannon and Weaver, 1949). It varies from zero to the theoretical maximum, which is computed as

$$Hmax^{''} = \ln S$$

The evenness measure, E, is computed as the ratio of $He^{''}$ to its theoretical maximum. Heip (1974) has shown that E remains constant when the number of individuals is incremented by a common multiple, and Sheldon (1969) has demonstrated that this evenness index is essentially independent of the number of species. This is illustrated in Jefferts (1977).

The expected number of species, E(Sn), is computed as

$$E(Sn) = \sum_{i=1}^{S} \left[1 - \frac{\left(\begin{array}{c} N-Ni \\ n \end{array} \right)}{\left(\begin{array}{c} N \\ n \end{array} \right)} \right]$$

where n in the number of individuals in the sample and Ni is the number of individuals belonging to species i in a collection of N individuals (Hurlbert, 1971; Rex, 1973). This parameter is designed to allow intercomparison of species richness among samples of varying size (N), since species richness (S) generally increases with increasing sample size.

The computed indices are as follows, for all the 0.9, 1.8, and 3.0 m IKMT data:

Area	H[9]	S	N	He¨	Hmax¨	E	E(Sn)
SA	223	17	2931	2.063	2.773	0.74	12.16
TZ	43	14	198	1.842	2.639	0.70	10.74
CC	1366	31	9617	1.981	3.434	0.58	12.67
NPC	30	26	259	2.429	3.258	0.75	19.88

When a compilation of all the data is made for each of the zoogeographic regions, several interesting trends become evident. Despite the 45-fold difference in number of total hauls, nearly the same number of species was taken in the California Current area and in the central Pacific area. The Transition Zone, with half again as many hauls as the central Pacific area, yielded only slightly more than half as many species. The Subarctic area produced only a few more species than the Transition Zone, even with five times as many hauls. Diversity, evenness, and E(Sn) are highest in the central Pacific region; in addition, many species are known to occur there which were not collected in this study. The Subarctic region has the next highest diversity and evenness, although E(Sn) is slightly lower than for the California Current area, which has the next highest diversity, but by far the lowest evenness.

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[9] H, number of hauls; S, number of species; N, number of individuals. Octopodidae other than *Octopus* spp. A and B not included in statistics. For expected number of species, n=100.

Central North Pacific

The central Pacific area evidences both high diversity and evenness measures; there are relatively few dominant species, and many species of lesser importance (see Table 12 and Figure 68).

The central North Pacific has by far the highest expected number of species; twenty species are expected in a sample of 100 individuals. The other areas have expected numbers of species of eleven to thirteen.

The dominant species (in the aggregate of 1.8 and 3.0 m IKMT hauls) is *Pyroteuthis addolux*, representing 32% of the individuals. *Abraliopsis falco* (14%) and *A. felis* (13%) are the only other species accounting for over 5% of the total. Roughly half of the species collected here are shared with the other areas: *Abraliopsis felis* (CC - abbreviations as in previous table), *Pyroteuthis addolux* (TZ), *Pterygioteuthis gemmata* (CC), *Onychoteuthis borealijaponicus* (CC, SA), *Gonatopsis borealis* (CC, SA, TZ), *Histioteuthis dofleini* (TZ, CC), *Bathyteuthis berryi* (CC), *Chiroteuthis calyx* (CC, TZ, SA), *C. joubini* (TZ), *Cranchia scabra* (CC), *Leachia dislocata* (CC, TZ), *Helicocranchia pfefferi* (CC), and *Japetella heathi* (CC, TA, SA).

The central Pacific samples in this study are dominated by members of the family Enoploteuthidae; five of the six most abundant species belong to this family, and the seven species represented comprise nearly 70% of the individuals. The Cranchiidae is the second most important family; its five members represent 14% of the individuals. Two onychoteuthids yield an

Table 12. Numbers of individuals of each species captured with
1.8 and 3.0 m IKMTs in the central Pacific region. Fifteen hauls
were made with each type of IKMT.

	1.8 m	3.0 m	TOTAL
Abraliopsis falco	30	5	35
Abraliopsis felis	33		33
Abraliopsis hoylei		5	5
Thelidioteuthis alessandrinii	1		1
Pyroteuthis addolux	70	13	83
Pterygioteuthis gemmata	6	5	11
Onychoteuthis borealijaponicus	11	2	13
Onykia carribaea	4		4
Gonatopsis borealis	1		1
Histioteuthis dofleini		1	1
Neoteuthis sp.		1	1
Bathyteuthis abyssicola	1	1	2
Bathyteuthis berryi		1	1
Ctenopteryx sicula	1	3	4
Brachioteuthis sp.	2		2
Chiroteuthis calyx	3	1	4
Chiroteuthis joubini	3		3
Mastigoteuthis pyrodes		4	4
Cranchia scabra	4	6	10
Leachia dislocata	2		2
Sandalops melancholicus		5	5
Helicocranchia pfefferi	3	5	8
Megalocranchia speculator	1	10	11
Japetella heathi	1	2	3
Tremoctopus violaceus	1		1
TOTAL	188	71	259

Figure 68. Per cent of individuals belonging to each species in the central Pacific area, based on collections with 1.8 and 3.0 IKMTs.

the California Current area, based on collections with 0.9, 1.8, and 3.0 m IKMTs.

Figure 70. Per cent of individuals belonging to each species in the Transition Zone, based on collections with 0.9, 1.8, and 3.0 m IKMTs.

Figure 71. Per cent of individuals belonging to each species in the Subarctic Water Mass, based on collections with 0.9, 1.8, and 3.0 m IKMTs.
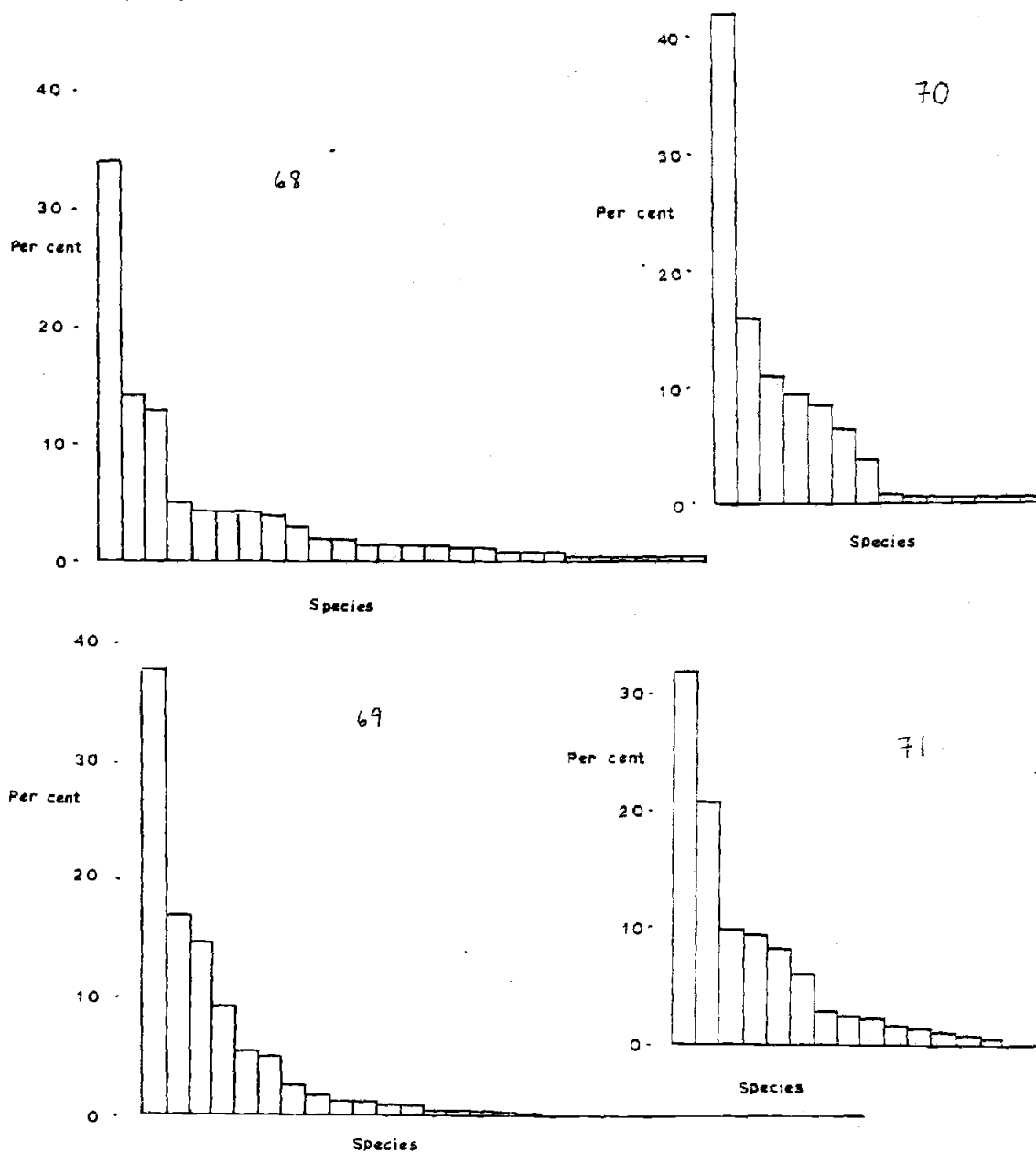
additional 6.5%, and the remaining individuals belong to twelve
species in nine families.

California Current

The California Current harbours a large number of species of
cephalopods (Table 13), but it is dominated by a few very abundant
species. Note that the expected number of species is nearly the
same as for the Subarctic. In the aggregate of 0.9, 1.8, and
3.0 m IKMT samples, the most important species are _Gonatus onyx_
(38% of the individuals), _Chiroteuthis calyx_ (17%), _Abraliopsis
felis_ (15%), and _Japetella heathi_ (9.2%). Figure 69 shows the
distribution of individuals among the species. This curve has a
much flatter tail than that for the central Pacific area, probably
due to the much larger number of hauls in the California Current
area. In addition, the first four species account for over 79% of
the individuals in the California Current area versus 64% in the
central Pacific area. These differences are reflected in the
diversity and evenness statistics, which are quite a bit lower for
the California Current data.

Like the Transition Zone fauna, and unlike that of the other
two areas, the California Current cephalopod community is not
overwhelmingly dominated by a single family. The Gonatidae
comprise less than 48% of the individuals, in eleven species. One
chiroteuthid yields 17%, the two enoploteuthids about 15%, the
Bolitaenidae 9%, the Cranchiidae (five species) nearly 7%, and the
eleven remaining species in nine families but 1 or 2% each.

Table 13. Numbers of individuals of each species captured with 0.9 m.(67 hauls), 1.8 m (1184 hauls), and 3.0 m IKMT (115 hauls), and 50 m2 MT (125 hauls) in the California Current region.

	0.9 m	1.8 m	3.0 m	50 m2	TOTAL
Loligo opalescens		7	1		8
Rossia pacifica		7			7
Abraliopsis felis	137	1079	236	78	1530
Pterygioteuthis gemmata	1	26			27
Octopoteuthis deletron	3	120	37	164	324
Onychoteuthis borealijaponicus	1	121	17	1	140
Gonatus berryi	1	38	13	56	101
Gonatus californiensis		3	1	2	6
Gonatus madokai		13			13
Gonatus onyx	31	3507	145	9296	12,979
Gonatus pyros	3	390	48	504	945
Gonatus sp. A		1	1		2
Gonatus sp. E		5			5
Gonatus type C	1	29	11		41
Gonatopsis borealis	5	209	49	188	451
Berryteuthis anonychus	2	81	7	4	94
Berryteuthis magister	5	12	1		18
Histioteuthis dofleini		23	7	5	35
Histioteuthis heteropsis		11	4	4	19
Bathyteuthis abyssicola		1			1
Bathyteuthis berryi			1		1
Chiroteuthis calyx	81	1320	214	440	1992
Mastigoteuthis dentata		3			3
Cranchia scabra		3			3
Helicocranchia pfefferi		3			3
Leachia dislocata	4	76	5		85
Galiteuthis phyllura	2	92	24	301	419
Taonius pavo	1	340	91	342	774
Ocythoe tuberculata		2			2
Japetella heathi	13	726	144	1165	2048
Japetella sp.				2	2
Vampyroteuthis infernalis	1	12	8	55	76
TOTAL	292	8260	1065	12605	22161

species; the Bolitaenidae, 9%; the Cranchiidae, 5% in two species; the Chiroteuthidae, 3.5%; five families and six species comprise the remainder.

The extreme dominance of <u>Gonatus onyx</u> is related at least in part to the patchiness of its distribution. Aside from being present in most hauls in the California Current area, it is occasionally present in great abundance - usually as many similar sized individuals, perhaps representing a "school". This phenomenon was most apparent in several of the 50 m2 MT samples, in one series of which the following catches of <u>G. onyx</u> occurred: 39, 81, 593, 1904, 4024, 108, 63, 180, 894, 23 (numbers of individuals). In the total collection of MT samples, <u>G. onyx</u> accounted for 74% of the individuals.

The statistics for the MT samples are noticeably different from those for the IKMT samples; relatively few species were taken (the same number as in about half as many 0.9 m IKMT hauls) despite the very large mouth opening. None of the warmer water species was taken, which suggests that the relatively limited geographic coverage with this gear may be at least a partial explanation. After <u>G. onyx</u>, the remaining important species are <u>Japetella heathi</u> (9.2%), <u>Gonatus pyros</u> (4.0%), <u>Chiroteuthis calyx</u> (3.5%), <u>Taonius pavo</u> (2.7%), <u>Galiteuthis phyllura</u> (2.4%). Over 90% of the individuals belong to the four most abundant species; this is well reflected by the diversity and evenness indices. The Gonatidae account for about 80% of the individuals, in six species; the Bolitaenidae, 9%; the Cranchiidae, 5% in two species; the Chiroteuthidae, 3.5%; five families and six species comprise the remainder.

Transition Zone

The offshore Transition Zone harbours relatively few species; however, it has not been extensively sampled (43 hauls of 0.9, 1.8, and 3.0 m IKMTs). *Abraliopsis felis* is the dominant member of the cephalopod community (41% of all individuals), followed by *Chiroteuthis calyx* (16%), *Pyroteuthis addolux* (11%), *Galiteuthis phyllura* (9.6%), *Gonatopsis borealis* (8.6%), and *Japetella heathi* (6.7%). Table 14 shows the species composition and frequency of occurrence, and Figure 70 shows the proportion of the total in each species. The first four species comprise 76.8% of the total, comparable to the California Current area (cf. diversity and evenness statistics). The Enoploteuthidae (two species) represent 52% of the individuals; Chiroteuthidae, 16.2%; Cranchiidae, 10%; Gonatidae, 9.6%; Bolitaenidae, 7%; Octopoteuthidae, 4%; and the remaining two families and three species, less than one per cent.

The true transitional nature of this region is evident in the species composition; *Abraliopsis felis* and *Chiroteuthis calyx* are abundant in the California Current area, and *Pyroteuthis addolux* is the dominant species in eastern central Pacific waters, while *Galiteuthis phyllura* and *Gonatopsis borealis* are characteristic of Subarctic and California Current waters. The remaining species are a mixture of representatives of all three areas.

Subarctic

The Subarctic harbours sixteen species, dominated by *Berryteuthis anonychus* (32%) and *Gonatus onyx* (21%), followed by

Table 14. Numbers of individuals of each species captured with 0.9 m (2 hauls), 1.8 m (39 hauls), and 3.0 m (2 hauls) IKMTs in the Transition Zone.

	0.9 m	1.8 m	3.0 m	TOTAL
Abraliopsis felis	2	79		81
Pyroteuthis addolux		13	8	21
Ctenopteryx sicula		2		2
Octopoteuthis deletron	1	7		8
Gonatus berryi		1		1
Gonatopsis borealis		17		17
Berryteuthis magister		1		1
Histioteuthis corona berryi			1	1
Galiteuthis phyllura		19		19
Leachia dislocata		1		1
Chiroteuthis joubini		1		1
Chiroteuthis calyx	5	26		31
Japetella heathi		12	1	13
Eledonella pygmaea			1	1
TOTAL	8	179	11	198

Gonatopsis borealis (10%), Berryteuthis magister (9.5%), Gonatus madokai (8.3%), and Gonatus pyros (6.2%) (See Table 15). Figure 71 shows percentage composition by species. The first four species account for 72% of the individuals, somewhat lower than the California Current and Transition Zone samples. The community statistics are higher than in those two areas, and the evenness approaches that for the central Pacific samples. The seven most abundant species, comprising 89% of the individuals, belong to the family Gonatidae. Three more species of this family bring the total to 90.7%. Two cranchiid species total 4.3% of the individuals; each of the remaining species holds fewer than three per cent of the individuals. The great numerical dominance of the family Gonatidae seems to be a primary feature of the cephalopod community in the Subarctic Pacific.

In summary, the central North Pacific is dominated by enoploteuthids and the Subarctic Pacific by gonatids. In the Transition Zone and California Current, the most abundant families comprise only about 50% of the individuals. It is noteworthy that the Enoploteuthidae and the Gonatidae share a number of morphological characteristics indicative of an active, predatory autecology. Most members of both families, including the abundant species treated here, have muscular mantles and bear hooks both on arms and tentacles. The enoploteuthids tend to be much smaller than the gonatids, probably the result of reduced food supplies in central waters (Bogorov, 1958; Reid et al., 1978), although the species of gonatids in the California Current are generally

Table 15. Numbers of individuals of each species captured with 0.9 m (10 hauls), 1.8 m (203 hauls), and 3.0 m (10 hauls) IKMTs in the Subarctic Water Mass.

	0.9 m	1.8 m	3.0 m	TOTAL
Abraliopsis felis	1	44		45
Onychoteuthis borealijaponicus		2		2
Gonatus berryi	1	11	2	14
Gonatus madokai	3	227	12	242
Gonatus middendorffi		3		3
Gonatus onyx	1	552	54	607
Gonatus pyros	3	177	1	181
Gonatus sp. A	1	19	2	22
Gonatus type C		82	3	85
Gonatopsis borealis	8	264	21	293
Berryteuthis anonychus	1	932		933
Berryteuthis magister	7	245	26	278
Taonius pavo		33	16	49
Galiteuthis phyllura		72	5	77
Chiroteuthis calyx	7	62		69
Japetella heathi		28	3	31
TOTAL	33	2753	145	2931

smaller than those of the Subarctic. The only other family which has members with both club and arm hooks is the Cranchiidae, although no species represented here has brachial hooks. It is the second most abundant family in both areas. The cranchiids represented here are not well muscled forms, and presumably not strong swimmers. Most have thin walled or gelatinous mantles. The Subarctic forms are again significantly larger than the central Pacific species.

Hooks are present in only two other families, the Octopoteuthidae, which have brachial hooks but lack tentacles, and in the Onychoteuthidae, which have club hooks, but not arm hooks. The former is represented by one fairly large (to 182 mm DML), heavy bodied species in California Current and Transition Zone waters; the latter has one representative (large, muscular) present in all areas, and two more (smaller, muscular) which are found only in central waters (*Onychoteuthis banksii* and *Onykia carribaea*). One may infer that, although all of these families are carnivorous, the lack of tentacles and/or well developed musculature probably militates against active, pursuivant carnivory in the Cranchiidae and Octopoteuthidae.

MAINTENANCE OF DISTRIBUTION PATTERNS

The aim of the section is to detail possible mechanisms for maintaining the patterns of cephalopod distribution seen here, in terms of assuring both reproductive success and genetic continuity within the species. This summary must of necessity rely on mechanisms shown to be important in other taxa.

Planktonic organisms require environmental or behavioural mechanisms to maintain distributional "closure," but the distribution of nektonic organisms, which are able to stem currents, is less subject to oceanic circulation patterns. Both ecological types are represented among the cephalopods discussed here. The more planktonic types include the larvae and juveniles of many species, as well as most of the Cranchiidae, the Bathyteuthidae, _Brachioteuthis_, the Chiroteuthidae, Mastigoteuthidae, and most of the pelagic octopods. The truly nektonic forms are represented by adults of _Onychoteuthis_, _Gonatopsis borealis_, and the Ommastrephidae.

Population or species maintenance within a single gyre (i.e., North Pacific Central gyre, Subarctic gyre) is readily understandable. One revolution of the gyre requires a few years, which would seem to be sufficiently short to prevent reproductive isolation. However, there are indications that smaller, partially closed circulations may occur within these gyres. Examples are the gyrals in the Gulf of Alaska, in the western Bering Sea, and in the northwestern Pacific (Wisner, 1959), and perhaps one in the

eastern portion of the North Pacific central gyre (Venrick, 1979;

Shulenberger, 1982)[10].

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[10]The latter is discussed in the section on transitional-central
distribution maintenance, as only species with this (TZ-CNP)
distribution exhibit limitation to the eastern Pacific central
gyre.

<u>Subarctic</u>

The Subarctic water mass can be divided into eastern (Gulf of Alaska) and western (Bering Sea - Sea of Okhotsk - Oyashio) gyres; some biological data lend support to this distinction. Three species of pelagic Subarctic gonatids, all with primary distributions in the northwestern Pacific, were not collected in this study: <u>Gonatus tinro</u>, <u>Gonatopsis makko</u>, and <u>Gonatopsis octopedatus</u>. They have also been reported from the Bering Sea. As their larval and juvenile forms are not well defined, they may have gone unnoticed in the Gulf of Alaska[11]. These northwestern Pacific distributions might also be an artifact of low abundances and consequent lack of captures in the northeast.

Further evidence of distinct populations in the eastern and western Subarctic may be seen in the distributions of two other species. <u>Tarletonbeania taylori</u> has two distinct populations in the Subarctic, one in the Alaskan gyral, and one in the northwestern Pacific. Wisner (1959) believed the two populations to be reproductively isolated, and the Alaska gyre form to have arisen from the other. Notably, <u>Tarletonbeania</u> is represented in the California Current by a different species, <u>T. crenularis</u>. The planktonic gastropod <u>Limacina helicina</u>, whose distribution also includes the California Current and Transition Zone, also exhibits two morphs: a high spired, striated form (Type A) which occurs in

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[11]Bublitz (1981) has recently described the larval stages of <u>G. tinro</u>. They appear to be very similar to those of <u>B. magister</u>.

the western Pacific and Aleutians east to about 145°W; and a low spired, unstriated form (Type B) limited to the California Current and Alaskan Gyral west to Kodiak, and the Transition Zone (McGowan, 1963). The distribution of the two forms and of their intergrades indicates that Type B is derived from Type A. Spined and unspined forms of the euphausiid _Thysanoessa longipes_ also occur within the Subarctic (Brinton, 1962); these latter examples represent incomplete (genetic) separation of populations, and perhaps incipient speciation.

The many species of closely related gonatids in the North Pacific may represent a further stage in this process. This concept is discussed more fully in the final section.

Central

A number of species, in varying taxa, are endemic to the North Pacific central gyre. Others have biantitropical distributions in the North and South Pacific, or occur in all central gyres (Indian, North and South Atlantic, North and South Pacific).

Population or species maintenance in the central gyre of the North Pacific is readily understandable; what is less clear is how disjunct distributions of some species are maintained in four or five central gyres. For example, the euphausiids _Euphausia brevis_ and _Stylocheiron suhmii_, and the copepod _Clausocalanus lividus_ occur in all subtropical gyres, but not in equatorial waters. Has it simply not been long enough since these gyres were last

connected for speciation to have taken place, or is some leakage
(gene flow) occurring now? A further piece in this puzzle is the
Euphausia hemigibba - gibba species pair; E. gibba occurs in the
South Pacific while E. hemigibba occurs in the other four
subtropical anticyclones.

Transition Zone and California Current

Population maintenance within the Transition Zone is not well
understood. Eurybathic species could return westward at depth
(Reid et al., 1978). Vertical migration, either seasonal,
diurnal, or ontogenetic, can prevent constant unidirectional
transport (Damas, 1905; Damas and Kofoed, 1907; Sømme, 1933, 1934;
Mackintosh, 1937; Ostvedt, 1955; Vervoort, 1965; Voronina, 1968).
For example, Nematoscelis difficilis undergoes diurnal vertical
migration, but ascends only to the thermocline, thus avoiding the
intense easterly and/or southerly transport at the surface (Reid
et al., 1978). McGowan (1971) postulated seasonal and meridional
variation in the zonal component of Ekman transport as a mechanism
for population maintenance of planktonic organisms in the
Transition Zone. Some such mechanism seems required for
non-migratory species, such as Thysanoessa gregaria.

Species with populations in the California Current system can
be maintained there by seasonal, diurnal, or ontogenetic migration
between depths at which the current directions vary, i.e.
southerly at the surface, and northerly deeper, or by seasonal

onshore-offshore migration between the California and Davidson (surface) Currents.

Maintenance of species integrity in the biantitropical forms is also an enigma. The cephalopod species which are common to the California and Peru Currents are replaced by congeners in the eastern tropical Pacific: *Octopoteuthis nielseni* replaces *O. deletron* off Mexico and Central America; *Histioteuthis meleagroteuthis* and possibly *H. miranda* replace *H. heteropsis*; and *Abraliopsis falco* is supplanted by *A. affinis*. *Dosidicus gigas* apparently displaces two other ommastrephids, *Symplectoteuthis luminosa* and *S. oualaniensis*, in the eastern tropical Pacific. It is conceivable that the northern and southern hemisphere populations are reproductively isolated, but no morphological differences of taxonomic importance have arisen.

Eastern tropical Pacific

Population maintenance in the eastern tropical Pacific appears to be more the result of the high residence time of the water than of a clearly closed circulation (see Wyrtki, 1965). However, some closure is possible, in that return of individuals to this region may occur through ontogenetic migration (e.g., to the Cromwell Current from the South Equatorial Current) (Bruun, 1958).

Distributions in more than one water mass

Holosubarctic

Distributions here termed "holosubarctic" are confined to the
Subarctic Water Mass and its derivatives, the Transition Zone and
California Current. Ecological supporting data for the validity
and distinctiveness of this distributional type are available in
the distributions of at least two polychaetes. *Tomopteris
planktonis* is absent from the Subarctic Pacific, although it
occurs in all other oceans and latitudes. *Typhloscolex mulleri*,
another otherwise cosmopolitan polychaete, is present in the
Subarctic Pacific as a distinct morphological variant, although
such variation occurs nowhere else, including the Antarctic
(Tebble, 1962). Population maintenance for this distributional
type, and most which include more than one water mass type, is
probably best considered as the aggregate of the subsumed water
masses or gyres (e.g., holosubarctic distributions could be
maintained separately in the California Current, Transition Zone,
and Subarctic Water Mass). Presumably gene flow across the water
mass boundary(s) is adequate to maintain species integrity.

Subarctic - Central/Equatorial

Species of two types may have this broad kind of
distribution: eurythermic, stenobathic forms; and stenothermic
forms which inhabit progressively deeper waters toward the equator
(cold water cosmopolites). Cosmopolitan epipelagics in other taxa

which submerge in lower latitudes include _Calanus finmarchicus_, _Limacina balea_, and several amphipods (Ekman, 1953). Several chaetognaths show an interesting variation on this distribution; _Eukrohnia fowleri_ and three species of _Sagitta_ are cold water, often deep, forms which may be relatively more abundant in near-surface equatorial waters of the eastern Pacific (Bieri, 1959), as the result of equatorial upwelling (e.g., Neumann and Pierson, 1966). Depth of distribution data may thus be important to an understanding of geographic distribution.

Transitional - Central

Two types of cephalopod distributions are included here: those limited to the eastern Pacific, and those which are cosmopolitan in the subtropics. Many of the joint central Pacific - California Current distributions probably result from seasonal migration of central waters into the California Current area. An example is the distribution of _Pyroteuthis addolux_ (see Figure 66). Its primary distribution seems to be the eastern central Pacific, but it also occurs in the Transition Zone west of the central California Current, and off southern California and northern Baja. It is absent, however, from the California Current system north of Point Conception. _Helicocranchia pfefferi_ and _Ctenopteryx sicula_ have similar distributions. The situation is not ambiguous if one recalls that the southern portion of the California Current system is an area of significant mixing.

Population maintenance for this group as a whole may be understood as a combination of the processes operating in the Transition Zone, California Current system, and central gyre. Population maintenance for the eastern central North Pacific group (*Pyroteuthis* etc.) could be effected by seasonal migration of the subtropical convergence. Some recirculation does occur from the North Equatorial Current to the North Pacific Current in the region northeast of the Hawaiian archipelago, forming an eastern gyral in the North Pacific (Sverdrup et al., 1942; Neumann and Pierson, 1966). Venrick (1979) distinguished an eastern environment from a western one in the North Pacific central gyre, and noted that it was significantly more oligotrophic than other areas along a California - Japan transect. Among other taxa, the polychaete *Pedinosoma curtum* is limited to the eastern Pacific (east of 164°W), but also occurs in warm North Atlantic water (Tebble, 1962; Day, 1967). Shulenberger (1982) noted a consistent and significant change in the hyperiid community structure at about 180° on a latitudinal transect along 28°N. His results were consistent with those of Barnett (1975) for mesopelagic fishes.

Three of the cephalopods show antitropical distributions with apparently disjunct populations in the North and South Pacific, although they have contiguous distributions in the North and South Atlantic (*Symplectoteuthis luminosa*, *Ommastrephes bartramii*, *Pterygioteuthis gemmata*). Why should these otherwise cosmopolitan species be absent from the equatorial Pacific? It could be a result of the much greater expanse of the equatorial Pacific,

which allows development of a much more structured equatorial current system than in the Atlantic. The Equatorial Countercurrent in the Atlantic deteriorates during the northern winter, when it is restricted to the easternmost portions of the tropical Atlantic (Neumann and Pierson, 1966). During that season the general flow is from east to west over most of the Atlantic between 30°N and 30°S. No hydrographic feature exists to separate northern and southern hemisphere subtropical populations in the Atlantic, or to allow development of a distinct equatorial fauna, except perhaps seasonally. The situation in the Pacific is markedly different: the Equatorial Countercurrent persists during all seasons across most of the Pacific, providing a possible barrier to communication between northern and southern subtropical populations. However, at least _Symplectoteuthis_ and _Ommastrephes_ are properly classified as nektonic; it may be that the equatorial region supports a less preferred food source, or that they are displaced by another species.

Arctic-Subarctic

The mechanism for population or species maintenance for species (e.g., _Cirrothauma murrayi_) with this type of distribution is unclear. Present circulation patterns are almost exclusively Pacific→Arctic→Atlantic. The flow through Bering Strait is almost always northerly, amounting to about 1.4 Sv (Coachman and Aagaard, 1966; Coachman et al., 1975). Occasional current reversals may occur, but they are probably insignificant (Coachman

and Aagaard, 1966). One can imagine, however, that even occasional flow from the Arctic to the Pacific would contribute to gene flow and prevent reproductive isolation of the Pacific and Atlantic-Arctic stocks.

Benthic-Nektobenthic

Population and species maintenance for these animals may depend to a greater degree on ontogenetic depth variation than is the case for pelagic species. Benthic or nektobenthic animals may also remain in a fairly localized area for most of their lives; some have demersal and/or brooded eggs. The problem in such cases may be in ensuring adequate dispersal, rather than in maintaining adequately high population densities (or preventing over-dispersal).

IMPLICATIONS FOR SPECIATION

The variety of distributional types encountered in the North Pacific shows clearly that the type of barrier required for reproductive isolation varies widely among cephalopod species (see Simpson, 1944; Ebeling, 1962; Day, 1963, for a general discussion of isolating mechanisms). Reproductive isolation may be maintained in a number of ways - as ecological or geographic isolation, or through the development of dissimilarities in reproductive structures or behavioural characteristics (e.g., vertical migration patterns) (David, 1961, 1963). Current patterns apparently separate the two populations of _Tarletonbeania taylori_ in the Subarctic Water Mass. Temperature and salinity influence distributions both directly, as in the distributions of estuarine animals, and indirectly or subtly, as in distributions confined to a single water mass. Gradients of oxygen or nutrient concentration may also correlate with distributional patterns - several species seem to avoid or prefer areas of low oxygen tension in the eastern tropical Pacific, and some have distributions closely correlated with neritic areas of high productivity. Food supply has likely been an important factor in the development of dwarf species of fish in the oligotrophic areas of the western equatorial region and the central water masses (Ebeling, 1962).

The distribution of pelagic organisms is in best agreement with water mass distributions in eastern tropical regions and in boreal regions (Bary, 1959; Bieri, 1959; Ebeling, 1962). This,

and the occurrence of the largest (body size) species in these regions, is generally interpreted as evidence that food supply is, or can be, an important factor governing the distribution or abundance of bathyal and abyssal organisms (Bruun, 1956), the polychaete _Poeobius_ (McGowan, 1960), chaetognaths (Bieri, 1959), and pelagic fishes (Sette, 1958; Brandhorst, 1958; Ebeling, 1962). Bieri (1959; also David, 1961) offered other possible explanations for the good agreement in eastern tropical regions: high sampling intensity; and slower currents, allowing development of more significant temperature and salinity discontinuities, and also preventing long-distance transport of organisms before they succumb to unfavourable environmental conditions.

The northeastern Pacific cephalopods show a distribution pattern correlated with food supply; the largest species, _Moroteuthis robusta_, _Berryteuthis magister_, _Gonatopsis_ spp., _Gonatus madokai_, and _Dosidicus gigas_, are found in areas of high productivity, while all of the central species (with the exception of _Ommastrephes bartramii_) are small.

Apparently one of the most important groups of isolating factors in the North Pacific includes convergences and the currents which bound water masses. David (1963) noted several possibilities why such barriers might be effective, such as an organism's ability to breed, survive, or compete on the opposite side of such a boundary or in the fluctuating conditions of the boundary. The results of such processes can be seen in a number of geminate species groups: the spined and unspined forms of

<u>Thysanoessa</u> <u>longipes</u>; Type A and Type B of <u>Limacina</u> <u>helicina</u>; the two forms of <u>Tarletonbeania</u> <u>taylori</u>; the Rassenkreis of <u>Stylocheiron</u> <u>affine</u>; and the several species of <u>Gonatus</u>. Many of these closely related forms live on opposite sides of convergences or water mass boundaries and are incompletely isolated from each other (Brinton, 1962; and others).

On the other hand, water mass boundaries provide little or no restriction to cosmopolitan forms. Within the sixty-four cephalopod taxa examined (the Octopodidae other than <u>Octopus</u> spp. A and B have been omitted from the following discussion, due to taxonomic confusion), 37 are confined to specific water masses of the Pacific Ocean. A plurality of these Pacific endemics consists of the thirteen Subarctic and California Current gonatids. Twelve more are species which are also limited to colder waters of the Pacific (Subarctic and/or California Current and/or Peru Current). Only eleven species are warm-water Pacific endemics. One species, <u>Japetella</u> <u>heathi</u>, occurs in warm and cold waters of the Pacific. Twenty-one of the 26 cosmopolites have warm-water distributions in the Pacific. The exceptions are <u>Taonius</u> <u>pavo</u>, <u>Vampyroteuthis</u> <u>infernalis</u>, <u>Cirroteuthis</u> sp., <u>Cirrothauma</u> <u>murrayi</u>, and <u>Stauroteuthis</u> sp. The Cranchiidae are currently undergoing major revision (by N.A. Voss); the Atlantic and Pacific forms of <u>T</u>. <u>pavo</u> could prove to be distinct species. The three octopods and <u>Vampyroteuthis</u> were taken only in the California Current. All are deep water or nektobenthic forms whose distribution may bear little relation to surface water mass distribution. The only

pelagic cephalopods known from the high Arctic are _Gonatus_
fabricii (sensu lato), _Cirroteuthis_ sp., and _Cirrothauma murrayi_.
With a lack of continuous distribution through the Arctic, it is
not surprising that most cold-water North Pacific forms should be
absent from the Atlantic. Conversely, many South Pacific cold
water forms are circumaustral in extent: Psychroteuthidae,
Batoteuthidae, _Alluroteuthis antarcticus_, _Oregoniateuthis_
lorigera, _Crystalloteuthis glacialis_, _Teuthowenia antarctica_,
Mesonychoteuthis hamiltoni, and _Gonatus antarcticus_. The North
Pacific cephalopod fauna is thus characterized by a large number
of cold-water endemics, a few warm-water endemics, and a large
number of warm-water cosmopolites.

SUMMARY - ZOOGEOGRAPHY

There are three primary distribution types in the North Pacific, and a number of secondary types, which are combinations or subsets of the three zoogeographic centres: Subarctic (and derivatives), Central, and Equatorial. The eastern tropical Pacific is a special case. Each of the zoogeographic centres has endemic elements; other species are more or less widely distributed. Population and species maintenance can be fairly clearly understood for each of the zoogeographic centres, but problems arise in explaining distributions limited to a portion of one centre, for example, the Transition Zone, or the eastern portion of the North Pacific Central gyre. Species may be maintained there by local reproduction, or by constant immigration from a more favourable environment.

ORIGIN OF DISTRIBUTION PATTERNS

A brief summary of the evolutionary history of the recent Cephalopoda is in order here; the following discussion is drawn primarily from Donovan (1964) and Teichert (1967). Aside from the Nautilida, of which *Nautilus* is the only living example, modern cephalopods are believed to have arisen from the Belemnoidea, which first appeared in the Carboniferous. Ancestors of the Vampyromorpha were the first group to diverge from this stock, probably in the Permian. Sepioids and Teuthoidea are first represented as fossils in the lower Jurassic. The earliest octopods did not appear until the Upper Cretaceous, and *Spirula* is post-Eocene.

The final breakup of Gondwana occurred during the latest Cretaceous and earliest Tertiary (van Andel, 1979; Zinsmeister and Camacho, 1980; Zinsmeister, 1982). The North Atlantic opened in the early Cretaceous, and the South Atlantic by about 75 MYBP (late Cretaceous). A psychrospheric ocean did not apparently exist before about forty million years ago, at the Eocene-Oligocene boundary. Glacial ice first existed to sea level, and the deepwater circulation developed at that point (Zinsmeister, 1982). Circulation in the Pacific probably took on a modern character in the middle Tertiary, with the exception that a broad equatorial current (at least 200 m deep) flowed from west to east through the Panamanian seaway (Ramsay, 1973; Zinsmeister, 1982). The opening of the Drake passage about 23.5 MYBP first provided a continuous deep water passage around Antarctica (Barker

and Burrell, 1977; van Andel, 1979; Zinsmeister, 1982). No deep
water connection between the tropical Atlantic and Pacific has
existed since the Cretaceous demise of the Tethys Seaway
(Zinsmeister, 1982). During much of the Tertiary, the Panamanian
seaway was more restricted in geographic extent than the Tethys
had been. The Panamanian seaway finally closed completely early
in the Pliocene (Durham and Allison, 1960; Johnson and Brinton,
1963; Woodring, 1966; van Andel, 1979).

During the Tertiary, the North Pacific had everywhere a
temperate climate, which was apparently more suited to the
development of a cold-temperate fauna than was the North Atlantic
(Ekman, 1953). Late Cenozoic glaciation appears to have had
relatively little broad effect on marine faunas; the primary
results have been range extension and contraction (Valentine,
1973). The circulation of the North Pacific 18,000 years ago was
much like that of the present, with the following differences:
there was an intensification of the subarctic front and a general
southward extension of subarctic waters, especially in the west;
and a greater seasonal temperature variation was evident
(Sancetta, 1977). It should be noted that the Bering Seaway has
been very shallow at all times during recent interglacials
(Hopkins, 1967; Dunbar, 1968).

Three significant radiation centres, or immigration sites,
from which the North Pacific faunas are derived, are: the
Indo-West Pacific; the North Atlantic (via the Arctic and Bering
Strait); and the western tropical Atlantic and Caribbean (via the

Panamanian seaway). I have made the assumption in the following discussion that a modern centre of diversity is equivalent to an historic centre of origin. The question of whether or not this assumption is valid cannot be decided without the aid of fossil evidence. Examples are available in other taxa (eg., Good, 1974) which exhibit both situations (i.e., that a modern centre of diversity equals an historic centre of origin and that a modern centre of diversity is not at the historic centre of origin).

The Indo-West Pacific has probably been the centre of origin for many higher taxa, including several zooplankton groups (Alvarino, 1968) and several families of bathypelagic fishes (Ebeling, 1962). That area has been said to hold the "great mother fish-fauna" (Myers, 1940). Many families of fish probably originated in shallow, productive waters, and successively colonized colder and deeper waters (Marshall, 1963). The cephalopods may well have followed a similar pattern (Teichert, 1967). In any case, a comparison of eastern and western North Pacific cephalopod faunas shows several interesting phenomena. Species pairs exist in many families, with one representative confined to the eastern Pacific and the other to the western Pacific. In some instances species of different, but closely related, genera within a family form these pairs. Several variations on this basic pattern are notable (see Table 16). There are groups in which one member is endemic to the northeastern Pacific and the other(s) to the northwestern Pacific

Table 16. A comparison of selected species pairs or groups of the eastern and western North Pacific. Central refers only to longitudinal distribution, not only to the central gyre.

western Pacific[1]	central Pacific	eastern Pacific
Rossia mollicella	Rossia pacifica[2]	
Loligo aspera, budo, chinensis, gotoi, japonica, tagoi, uyii, yokovae		Loligo opalescens
Watasenia scintillans	Abraliopsis falco[3]	Abraliopsis felis
Octopoteuthis sp. nov.[4]	Taningia danae	Octopoteuthis deletron
Moroteuthis lonnbergi	Moroteuthis robusta[2]	
	Gonatus madokai[2]	Gonatus berryi
	middendorffi[2]	californiensis
	onyx	pyros
	tinro[2]	sp. A
	type C Kubodera[2]	sp. B
Gonatopsis japonicus	Gonatopsis borealis[2]	
maikko	okutanii[2]	
octopedatus		
	Berryteuthis magister[2]	Berryteuthis anonychus
Histioteuthis corona inermis	Histioteuthis celetaria pacifica[5] meleagroteuthis[6]	Histioteuthis corona berryi
Mastigoteuthis laticinna	Mastigoteuthis famelica[7] inermis[8]	Mastigoteuthis pyrodes
	Leachia pacifica[9]	Leachia dislocata
	Helicocranchia beebei[10]	Helicocranchia pfefferi
Opisthoteuthis depressa		Opisthoteuthis californiana

1, Distributional information for western Pacific from Nesis (1973b) unless otherwise specified. 2, PanPacific - see systematic section. 3, central and eastern Pacific (Voss, 1969). 4, Okutani and Satake (1978). 5, central and western Pacific (Voss, 1969). 6, Atlantic, Indian, and Pacific Oceans (Voss, 1969). 7, central only (Berry, 1909; Young, 1978). 8, Atlantic and Pacific (Rancurel, 1972; Young, 1978). 9, Atlantic and Pacific (Clarke, 1966; Young, 1978). 10, central and eastern Pacific, (Robson, 1948; Young, 1978).

(*Loligo* spp.; *Opisthoteuthis* spp.); groups where a member is
endemic to the northeastern or northwestern Pacific and another is
relatively cosmopolitan (*Leachia* spp.; *Mastigoteuthis* spp.;
Histioteuthis spp.); and groups where one or more members are
confined to the northeastern or northwestern Pacific, and the
"central" Pacific members have a distribution which extends to the
eastern or western Pacific, overlapping that of the endemic form
(Gonatidae; Enoploteuthidae; *Moroteuthis* spp.; *Rossia* spp.;
Helicocranchia spp.).

The endemic species of the northwestern Pacific are
nektobenthic or neritic (pelagic) forms, while those of the
northeastern Pacific are all pelagic, except perhaps *Loligo*
opalescens, which spawns on the bottom, and *Opisthoteuthis*
californiana, which is nektobenthic. This may be a reflection of
the difference in habitat types available on the two sides of the
North Pacific. The northwestern Pacific has a much more extensive
shelf, and several inland seas, allowing development of a resident
fauna, which includes two endemic genera (*Watasenia*, *Sasakinella*).
The circulation of warm water from the south is such that there is
limited possibility for development of an endemic cold water
fauna. Even periods of global cooling would allow the retention
of northerly warm water currents in the northwestern Pacific, and
an environmental refuge for these tropical-temperate forms. The
far greater number of species in the west represents the radiation
of warm water forms from the Indo-Pacific tropical fauna,

isolation,[13] exist for Subarctic forms, owing to the more or less continuous habitat available across the North Pacific; there are many more species widely distributed across the Subarctic than endemic to a portion thereof (e.g., Bering or Okhotsk Seas). However, warm water neritic and nektobenthic forms encounter an environmental hiatus in the North Pacific Drift and the North Equatorial Current, and thus, presumably, an obstruction to gene flow. The existing greater number of families, genera, and species in lower latitudes in itself contributes to a greater absolute number of endemics.

Atlantic-Arctic

In general, the Pacific Subarctic shallow water fauna varies considerably from that of the Atlantic, although much of the North Atlantic fauna is derived from the Pacific, through trans-Arctic migration during interglacials (Durham and MacNeil, 1967). The North Pacific holds by far the greater number of endemic taxa, especially those of higher order (Schmidt, 1904; Jordan, 1905; Djakonov, 1945; Ekman, 1953; Nesis, 1963). Many species have distributions which point to an Arctic connection between the Atlantic and Pacific (see Ekman, 1953). Durham and MacNeil's (1967) consideration of a number of benthic invertebrate groups showed that Pacific → Atlantic trans-Arctic migrations after

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[13]But see discussion of eastern and western Subarctic forms, pp 230-231.

the Eocene probably occurred about ten times as frequently as the reverse.

The distribution of the Gonatidae also indicates a trans-Arctic connection, probably via a North American Arctic migration route during the post-glacial Wurm Period (Nesis, 1963; Mercer, 1969). The distribution of the family is not now continuous, there being an hiatus between the Barents Sea and Hudson Strait (Nesis, 1965; Mercer, 1969). The existence of *Gonatus antarcticus* in notalian (austral) waters is either the result of trans-tropical migration during a period of Pleistocene cooling (Berg, 1933; Hubbs, 1952; there has likely been no such opportunity since the Pleistocene - Johnson and Brinton, 1963), or the genus is much older and has existed in the southern hemisphere since much earlier in geologic history. Another possibility is migration from the North to South Atlantic in cold, deep water.

It is curious that the Atlantic and Antarctic Gonatidae have not undergone the same explosive radiation as have the North Pacific forms. It is perhaps premature to speculate on reasons for this apparent dichotomy, as the Atlantic and Antarctic forms have certainly not been as well studied as the Pacific species, but it could be a function of elapsed time since the group arose and invaded the Arctic and Antarctic.

Western tropical Atlantic

The shallow eastern tropical Pacific shares a number of common elements with the Caribbean and western tropical Atlantic,

and indeed there a number of geminate or sibling species pairs in
these two areas (e.g., Rosenblatt, 1963). Among the cephalopods,
Valbyteuthis danae may be represented by different races (perhaps
subspecies or species) in the two regions (Young, 1972; Lipka,
1975), and *Helicocranchia pfefferi* and *H. beebei* may each be
restricted to one side of the isthmus (see discussion in
systematic section).

PHYLOGENY OF THE GONATIDAE

It seems appropriate to conclude with a discussion of
phylogeny in the Gonatidae, especially as it relates to
zoogeography. The Gonatidae is by far the most important
cephalopod group in the Subarctic Pacific; it likely arose here
and only twice have representatives successfully emigrated. The
systematics of the Atlantic and Antarctic species is neither
complete nor well understood; these forms have been omitted from
the following discussion.

The only fossil Gonatidae known are members of the genus
Berryteuthis, which occur in late Pliocene deposits of southern
California (Clarke and Fitch, 1979).

Primitive characters

The ancestral gonatid is here postulated to have had a radula
with seven rows of teeth, brachial hooks, a muscular mantle, and a
simple, hookless club. Brachial and tentacular hooks occur fairly
rarely among the Cephalopoda (see discussion, pp 227-228). Club
hooks are often present in only one or a few members of a family,
indicating that this character is a derived one (probable
exception, the Onychoteuthidae). On the other hand, when brachial
hooks occur, they usually occur in all or nearly all members of a
family (exceptions - Cranchiidae, where only Mesonychoteuthis has
arm hooks, and Gonatidae, where in Berryteuthis anonychus only a
few hooks are present in females, and males lack them altogether).
Several Belemnoidea, which are thought to be ancestral to all

modern cephalopods except Nautilus, are known to have had hooks (e.g., Pollard, 1968; Donovan, 1977). Whether the existence of arm hooks in the Gonatidae represents a direct link with hook bearing belemnoids or a secondary appearance is moot. The existence of arm hooks in the Gonatidae is a primitive character for the family, as hooks appear in all species. Donovan (1977) noted that the Onychoteuthidae, Ommastrephidae, and Gonatidae all have gladii similar to those of the Jurassic Plesioteuthidae, but only the Gonatidae and Plesioteuthidae have arm hooks. He begs the question of whether or not hooks are primitive features.

If one subscribes to the view that ancestral cephalopods were shallow water in habit (e.g., Teichert, 1967), one may also make a case for the primitive nature of a muscular mantle. Among the families with generally muscular mantles, all live in the upper portions of the water column. Most of the less well muscled families are believed to inhabit deeper water (e.g., Voss, 1967b).

Support for the postulated primitive nature of a septemdentate radula lies in the fact that nearly all described modern cephalopod radulae are of this type. Nautilus has thirteen radular rows, but is believed to have diverged from the ancestral stock much earlier than the ancestors of the modern Teuthoidea. The only other known exceptions are in the Gonatidae; in Thaumeledone (Octopodidae), with only a vestigial radula; and in some cirromorph octopods, which lack radulae (Aldrich et al., 1971; Solem and Roper, 1975).

Relationships

The genus *Berryteuthis* thus represents the primitive type within the family (Figure 72). I consider *Berryteuthis magister* the exemplar; *B. anonychus* represents a derived condition, having lost most arm hooks. *Gonatopsis* is the next most primitive genus; its only unifying characteristic is the absence of functional tentacles in the adult. I believe Nesis' (1972b) division of the genus *Gonatopsis* into the subgenus *Boreoteuthis*, with a septemdentate radula, and the subgenus *Gonatopsis*, with a quinquedentate radula, is valid, and these subgenera should be elevated to generic status. The radular change (loss of two rows of teeth) is much less likely to have arisen twice (in *Gonatopsis* and *Gonatus*) than the secondary loss of tentacles (in *Gonatopsis* and *Boreoteuthis*). Various degrees of tentacle degeneration are seen in *Gonatopsis* (s.l.): from loss at a very small size (about 15 mm DML in *borealis*) to persistence at a size of at least 40 mm DML (*okutanii*). Within *Boreoteuthis*, *B. makko* has a variant nuchal cartilage, and probably represents a derivative of *B. borealis*.

Gonatopsis (s.str.) holds three species: *G. japonicus*, *G. octopedatus*, and *G. okutanii*. *Gonatopsis octopedatus* is probably the most derived, with eight to twelve rows of suckers at the arm tips (vs. four in all other Gonatidae), reniform fins, and a tentacle remnant (tubercle) remaining in the adult. *Gonatopsis japonicus* loses its tentacles at an early stage, and has a

Figure 72. Postulated relationships among the Gonatidae.
Vertical separation between species of one genus, and between
genera, implies primitive - derived differences.
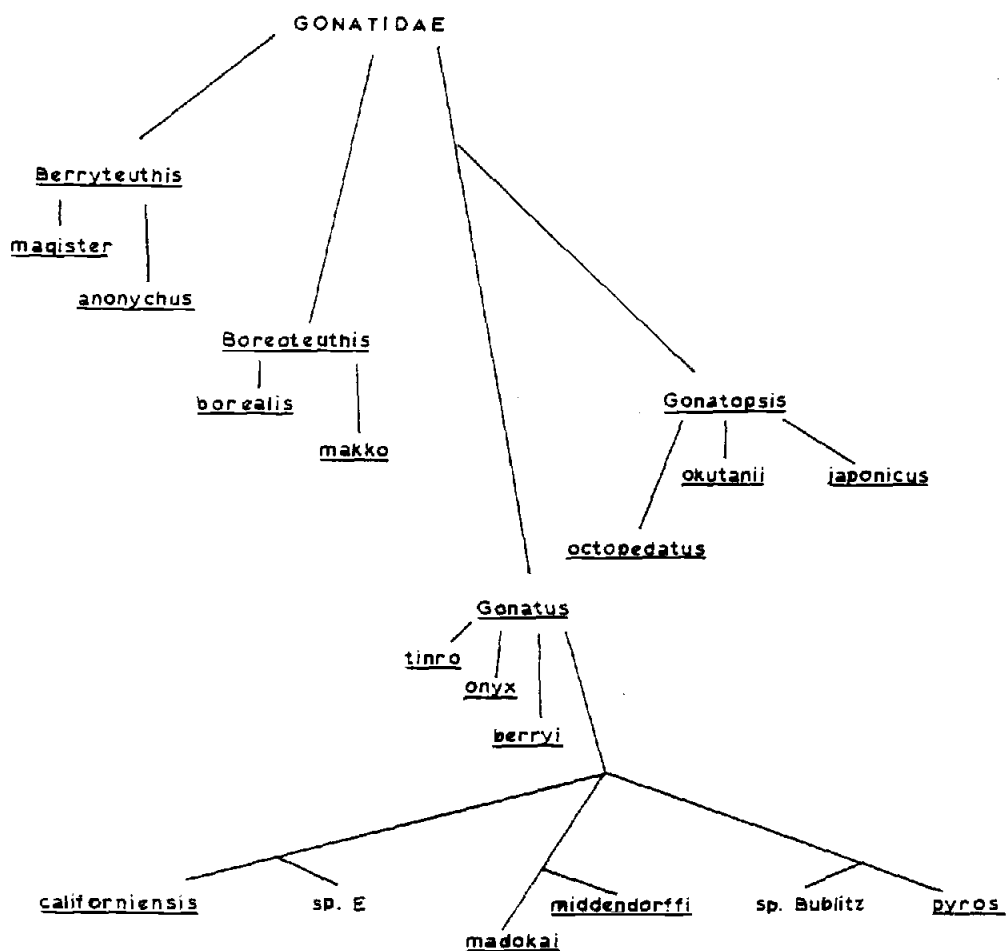
cardiform fin, while in G. okutanii a tentacle remnant persists,
and the fins are also cardiform (although elongate). Notably,
Clarke et al. (1980) have concluded that Gonatopsis is more
closely related to Gonatus than to Berryteuthis, on the basis of
discriminant analysis of statolith structure.

Nesis (1972b) placed Gonatus tinro in the subgenus Eogonatus,
on the basis of lack of tentacle hooks. There is as yet no
evidence to suggest a diphyletic origin for Gonatus (s.l.);
therefore, I believe that a subgeneric distinction between G.
tinro and all the other species is adequate. The ancestral
Gonatus is believed to have been something like G. tinro, with all
derivative species developing tentacular hooks. Gonatus onyx,
with one club hook, represents the first derivative. Gonatus
berryi, with club armature of the type hHsshh (h, hook; H, central
hook; s, sucker), and very early development of brachial hooks,
represents a second derivative. All of the remaining species
(except perhaps sp. A and type C, for which the tentacle armature
is as yet unknown) belong to a third derivative type, here termed
the "californiensis group." These species possess club armatures
of the type hHhhhs (with more or fewer proximal hooks, but no
suckers intervening between the central hook and the first
proximal hook). The common ancestor of the californiensis group
gave rise, in turn, to three other groups. The first contains G.
californiensis and Gonatus sp. E, both of which have very many
club suckers (more than 250). The second holds two forms which do
not develop hooks until very late, G. middendorffi and G. madokai.

The third holds G. pyros and Gonatus sp. Bublitz, which are distinguished from the other members of the californiensis group by having four rows of suckers on the dactylus just distal to the hooks, having a lower total number of club suckers (less than 200), and by developing arm and club hooks at a size of 20 to 30 mm DML.

Distributions

The genus Berryteuthis arose in the North Pacific; B. magister retains a panPacific distribution in the Subarctic, while B. anonychus is limited to the eastern Pacific. Boreoteuthis borealis is holosubarctic, while B. makko is limited to the northwestern Pacific. Gonatopsis (s.str.) is strictly northwestern Pacific, with G. japonicus apparently limited to the Sea of Japan. Gonatus tinro is limited to the northwestern Pacific, G. onyx is holosubarctic, but apparently more abundant in the northeast, and G. berryi is northeastern Pacific. Both G. californiensis and Gonatus sp. E are limited to the California Current. Gonatus madokai is a northern form, perhaps more abundant in the northwest, and G. middendorffi is limited to the northwest. Gonatus pyros is a northeastern Pacific form, and Bublitz's species is so far known only from the eastern Bering Sea (Table 17).

The putative primitive forms in the Gonatidae have broadly Subarctic distributions (Berryteuthis magister, Boreoteuthis borealis), while the derivative forms have distributions limited

Table 17. Zoogeographic distribution of the Gonatidae. West, occurring only in the northwestern Pacific; East, only in the northeastern Pacific; Both, pansubarctic. Latitudinal information not included.

	West	Both	East
Berryteuthis magister		x	
anonychus			x
Boreoteuthis borealis		x	
makko	x		
Gonatopsis japonicus	x		
octopedatus	x		
okutanii	x		
Gonatus tinro	x	?	
onyx		x	?
berryi			x
californiensis			x
sp. E KJ			x
madokai	?	x	
middendorffi	x		
pyros			x
sp. Bublitz		?	
sp. A KJ			x
type C Kubodera		x	

to the eastern or western Pacific (_Berryteuthis anonychus_,
Boreoteuthis makko and _Gonatopsis_ (s.str.), many _Gonatus_). In the
genus _Gonatus_, only primitive forms (_G. tinro_; _G. middendorffi_,
relative to _madokai_) have western Pacific distributions, which
suggests a northwestern Pacific origin for the Gonatidae. Most of
the _Gonatus_ speciation has occurred in the eastern Pacific (only
one other non-_Gonatus_ gonatid is restricted to the northeastern
Pacific - _Berryteuthis anonychus_). _Gonatus_ is the only genus to
have successfully migrated outside the North Pacific - into the
North Atlantic (_G. fabricii_ (s.str.) et al.) and the Antarctic (_G. antarcticus_ et al.). It appears that the northeastern Pacific has
become an important radiation centre for, at least, _Gonatus_.

Gonatus has been extremely successful at colonizing new
environments and producing new species in those environments. The
Atlantic and Antarctic populations have apparently produced more
than one species in each ocean. In the North Pacific, where the
taxonomy is somewhat better understood, a large number of similar
species occur within a restricted geographic area. What has
provided genetic isolation for speciation in _Gonatus_?
Possibilities include depth segregation, differences in season of
reproduction, and isolation by smaller scale current patterns than
discussed here, but the question remains open.

SUMMARY

1. A total of 43,742 individual cephalopods was examined, from 2890 collections in the northeastern Pacific. These represent sixty-four species.

2. Three species are recorded from the Pacific for the first time; six from the central Pacific for the first time; and range extensions for twenty-seven species are noted.

3. Descriptions are given for Neoteuthis sp.; unusual specimens of Berryteuthis anonychus; Gonatus middendorffi; Gonatopsis okutanii; two new species of Gonatus; and two unidentified species of Octopus larvae.

4. In relation to water masses, the zoogeography of cephalopods in the northeastern Pacific shows twelve distributional types. These show good correlation with the results of others for cephalopods and other taxa. Good correlation is seen with the work of Johnson (1982) for evermannellid and scopelarchid fishes.

5. Diversity and evenness statistics were computed for each zoogeographic region. Central Pacific samples are dominated by Enoploteuthidae (70%) and Subarctic samples by Gonatidae (90%); these two areas are the most diverse, and have the highest evenness. California Current and Transition Zone samples are less diverse and show lower evenness; the most abundant families represent about 50% of the individuals.

6. The northeastern Pacific cephalopod fauna is characterized by a large number of cold water endemics, a few warm water endemics, and a large number of warm water cosmopolites. A number of

cephalopods have distributions limited to the eastern or western North Pacific.

7. _Berryteuthis_ _magister_ is postulated to be the ancestral type of the Gonatidae. _Gonatopsis_ (s.l.) is a first order derivative of that type, and _Gonatus_ represents the most derived genus within the family. Within the genus _Gonatus_, it is postulated that _G. tinro_ represents the most primitive form, as all the other species show greater degrees of complexity in the club armature.

8. It is proposed that _Boreoteuthis_ be elevated to generic status.

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APPENDICES

APPENDIX A

The National Marine Fisheries Service sponsored my
participation in this research to examine the cephalopods
collected during a rockfish survey of the coastal waters of the
western United States and Alaska (see Figure 2 for survey
location). Gear descriptions and methodology may be found in
earlier sections of this paper and in Jefferts and Pearcy (1978,
1979, 1980, 1981). Cephalopods numbering 10,252 were collected
from 326 demersal hauls and 23 midwater tows. Twenty-one taxa
were represented, and most of them were collected only or
primarily off the western United States in 1977 (see Table A-1).
Nine species were recovered in each of 1978 and 1979, and six in
1980. Nearly 97% of the individuals were collected in the 1977
survey, although most belong to two species, Loligo opalescens and
Gonatus onyx, neither of which was collected in reasonable numbers
in later years. The rarity of oceanic species is not unexpected,
as the sampling program was limited to water depths of 90 to
450 m.

The species which occur consistently in three or four years'
samples are those which can be considered characteristic of the
shelf and upper slope environment in the northeastern Pacific:
Rossia pacifica, Moroteuthis robusta, Gonatopsis borealis,
Berryteuthis magister, Opisthoteuthis californiana, and the
species of Octopus. These are subarctic, nektobenthic species
which occur around the North Pacific rim. Some are replaced in
the northwestern Pacific by congeners: Rossia pacifica by R.

Table A-1. Numbers of individuals of each species sampled in the four years of the rockfish survey.

TAXON	1977	1978	1979	1980	TOTAL
Rossia pacifica	14	2	3	3	22
Loligo opalescens	8076				8076
Abraliopsis felis	4				4
Octopoteuthis deletron	11				11
Onychoteuthis borealijaponicus	25				25
Moroteuthis robusta	26	1		3	30
Gonatus berryi	2	2			4
Gonatus californiensis	1				1
Gonatus madokai		1	1		2
Gonatus onyx	1424		4		1428
Gonatus pyros	4				4
Gonatus spp./Gonatidae	43		2		45
Gonatopsis borealis	6	2	16	4	28
Berryteuthis magister	48	55	83	38	224
Histioteuthis dofleini	1				1
Histioteuthis heteropsis	87				87
Chiroteuthis calyx	15				15
Taonius pavo	1				1
Galiteuthis phyllura			1		1
Opisthoteuthis californiana	30	4	4	3	41
? Japetella sp.			1		1
Octopus spp.	104	30	36	29	199
Unidentified squid	2				2
TOTAL	9924	97	151	80	10,252

mollicella; Moroteuthis robusta by M. lonnbergi; Gonatopsis
borealis by several others; and Opisthoteuthis californiana by O.
depressa. The northwestern Pacific also harbours a number of
other species of Octopus. These species, with the addition of the
neritic Loligo opalescens, which occurs primarily in the central
and southern California Current region, are those likely to
provide fisheries opportunities. They occur close to shore and in
such a manner that bottom or near bottom trawls can exploit them.

The pelagic species have only a few representatives which
have any fisheries potential. Gonatus onyx, although relatively
small, often occurs in fairly large concentrations - it might be a
candidate for a trawl fishery. The other possibilities are large
organisms which would probably be best exploited by jigging:
Onychoteuthis borealijaponicus, Ommastrephes bartramii, and
Symplectoteuthis luminosa. These three occur farther offshore,
but are used, at least to some extent, by the Japanese (Okutani,
1977). None of the other cephalopods which occur in the
northeastern Pacific is likely to become the basis of a fishery,
either because of rarity, small size, ammoniacal tissues, or
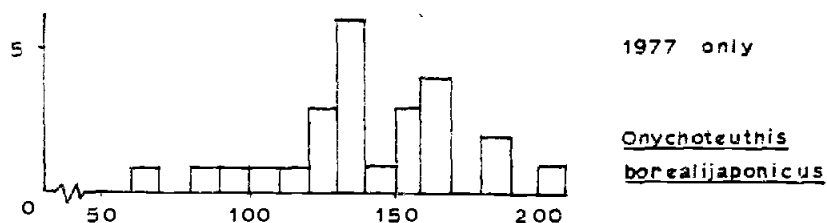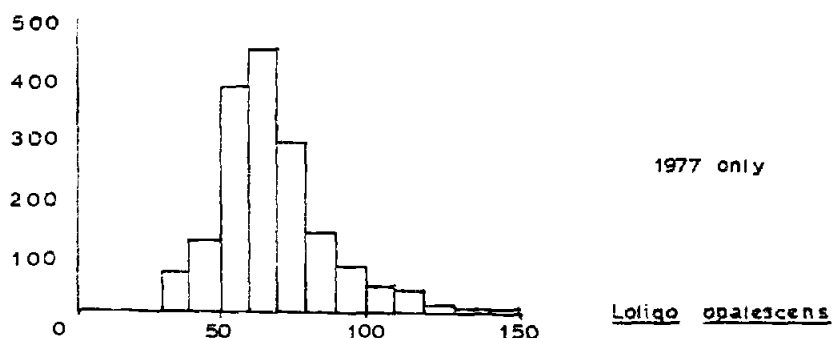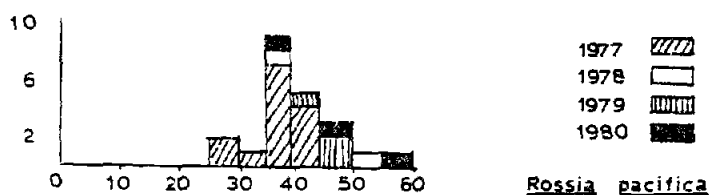gelatinous consistency.

An examination of length-frequency distributions of the
abundant species taken during the rockfish survey (Figures A-1
through A-9) shows only a few trends. Two species seem to occur
as larger individuals in the northern survey areas: Rossia
pacifica, and Opisthoteuthis californiana, and one as smaller
individuals (Berryteuthis magister). None of these represents a

major trend; a firm conclusion would require more data. In partial support of this, however, W. Summers has noted a similar size-latitude trend in _Rossia_ _pacifica_ (Summers, 1981).
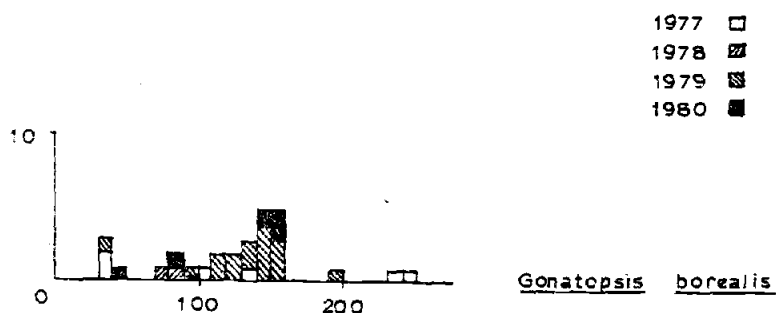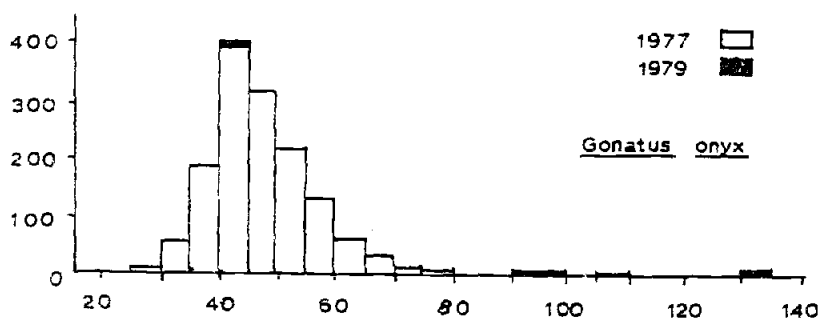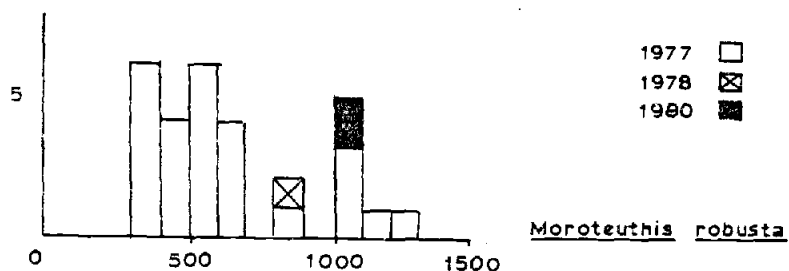
No trends in latitudinal depth distribution were observed for these species. Summaries for each year's samples are given in Jefferts and Pearcy (1978, 1979, 1980, 1981).

The reader is referred to the preceding sections for a discussion of geographic distribution of these species.

Figures A-1 through A-3.   Length-frequency distributions for three abundant cephalopods from the rockfish survey.   Abscissa is DML (mm); ordinate, number of individuals.

Rossia pacifica

1977 / 1978 / 1979 / 1980

1977 only

Loligo opalescens

1977 only

Onychoteuthis borealijaponicus

Figures A-4 through A-6. Length-frequency distributions for three abundant cephalopods from the rockfish survey. Axes as in previous figures.

Moroteuthis robusta

1977 ☐
1978 ☒
1980 ▨

Gonatus onyx

1977 ☐
1979 ▨

Gonatopsis borealis

1977 ☐
1978 ▨
1979 ▨
1980 ■
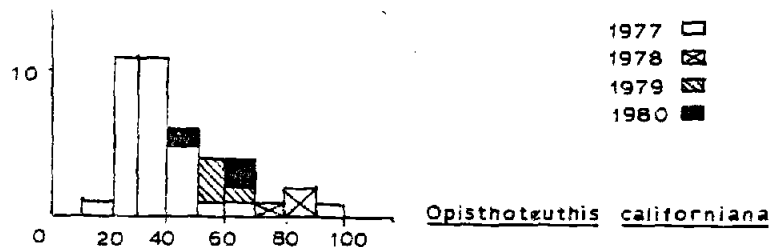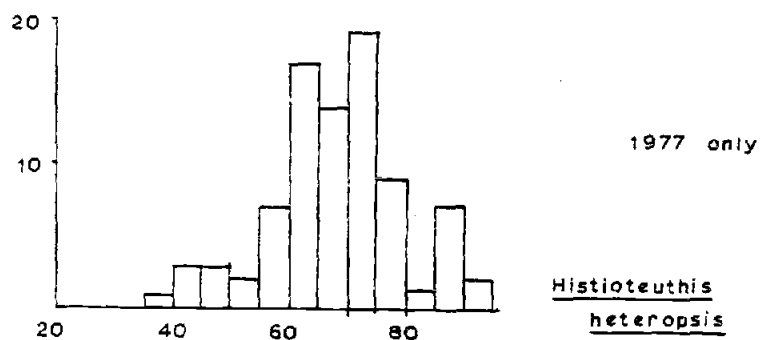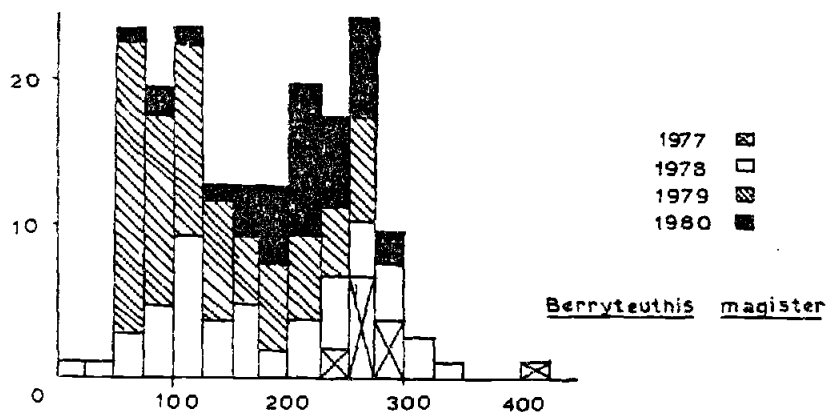
Figures A-7 through A-9. Length-frequency distributions for three abundant cephalopods from the rockfish survey. Axes as in previous figures.

Berryteuthis magister

1977
1978
1979
1980

Histioteuthis heteropsis

1977 only

Opisthoteuthis californiana

1977
1978
1979
1980

APPENDIX B

A listing of all specimens referred to by OSUI number (Oregon

State University Invertebrate reference collection number) and

pertinent collection data (in this order: OSUI #; species; DML;

type of collection gear; station and/or cruise; date; latitude;

longitude; time; and depth).

204 Mastigoteuthis dentata (71 mm DML). 1.8 m IKMT; NH-50; 8
January 1963; 44°31.3'N, 125°17.7'W; 1536-1651; 0-500 m.

223 Berryteuthis anonychus (77 mm DML). dipnet; NH-145; 1 July
1969; 44°N, 127°W; surface.

292 Histioteuthis corona berryi (24 mm DML). 3.0 m IKMT;
SICSPAC; 6-7 March 1965; 37°35.0'N, 137°14.0'W; 2020-0305;
0-2400 m.

322, 323 Onychoteuthis banksii (74, 76 mm DML). dipnet; HAH-25,
YALOC66; 9 June 1966; about 29°N, 159°W (N of Oahu); surface.

330 Onychoteuthis banksii (70 mm DML). dipnet; HAH-32, YALOC66;
32°40.0'N, 163°55.0'W; 1930-2100; surface.

355 Mastigoteuthis dentata (75 mm DML). 1.8 m IKMT; AH-65; 31
July 1965; 45°31.5'N, 125°38.0'W; 1024-1207; 0-1000 m.

357 Mastigoteuthis dentata (43 mm DML). 1.8 m IKMT; NH-50; 7
January 1963; 44°21.4'N, 125°15.7'W; 2358-0412; 0-1125 m.

365 Ctenopteryx sicula (46 mm DML). 1.8 m IKMT; SICSPAC; 27
February 1965; 38°34.0'N, 138°26.9'W; 2345-0035; 0-190 m.

379 Dosidicus gigas (179 mm DML). hook and line; SP-65; 7 March
1970; 25°20'N, 113°12.6'W.

397 Cirrothauma murrayi (110 mm DML). beam trawl; TP-3; 3 June
1970; 44°39.8'N, 133°37.2'W; 1758-2025; 3724 m.

398 Onychoteuthis banksii (88 mm DML). dipnet; HAH-30, YALOC66;
10 June 1966; 30°55.4'N, 162°37.4'W; 2100; surface.

399, 400 Symplectoteuthis luminosa (106, 116 mm DML). dipnet;
HAH-30, YALOC66; 10 June 1966; 30°55.4'N, 162°37.4'W; 2100;
surface.

402 Ommastrephes bartramii (230 mm DML). bow and arrow; NH-268; 24 August 1965; 44°N, 130°W; 0400; surface.

403 Cirroteuthis sp. (60 mm DML). beam trawl; TP-2; 1 June 1970; 44°27'N, 132°14'W; 0125-0945; 3655 m.

412 Eledonella pygmaea. dipnet; 10 July 1967; 46°30'N, 127°00'W; 0400; surface.

417 Bathyteuthis berryi (44 mm DML). 3.0 m IKMT; NH-65; 29 July 1965; 44°21.0'N, 125°41.5'W; 1308-1423; 20-30 m.

565 Valbyteuthis oligobessa (69 mm DML). 2.4 m IKMT+MPS; NH-65; 24 July 1973; 44°46.5'N, 125°46.5'W; 0205-0435; 0-2200 m.

680 Gonatus californiensis. 50 m2 midwater trawl; NH-65; 21 July 1976; 44°N, 125°W; 1355-1455; 440 m.

681 Gonatus californiensis. 1.8 m IKMT; Brown Bear cruise 254, haul 5; 17-18 March 1960; 37°45'N, 129°19'W; 2243-0002; 0-400 m.

682 Gonatus californiensis. 1.8 m IKMT; Brown Bear cruise 254, hauls 1; 12 March 1960; 33°42'N, 49°27'W; 2144-2309; 0-400 m.

684-686 Megalocranchia cf. speculator. 3.0 m IKMT; FRONTS; 24 January 1980; 30°32.0'N, 153°07.8'W; 1933-2044; 0-260 m.

687 Gonatus sp. E. 1.8 m IKMT; NH-65; 13 February 1967; 44°46.2'N, 125°52.0'W; 1347-1728; 0-1500 m.

688 Gonatus sp. E. 1.8 m IKMT; NH-65; 3 June 1967; 44°40.9'N, 127°56.2'W; 2300-2343; 0-185 m.

689 Gonatus sp. E. 1.8 m IKMT; NH-165; 30June-1July 1969; 44°40.2'N, 127°49.1'W; 2330-0020; 0-220 m.

690 Gonatus sp. E. 2.4 m IKMT+MPS; NH-65; 21July 1971; 44°35.1'N, 125°32.5'W; 0314-0348; 400-300 m.

691 Gonatus sp. E. 2.4 m IKMT+MPS; NH-65; 29 November 1972; 44°33.9'N, 125°39.2'W; 0105-0216; 0-200-150 m.

692 Gonatus sp. E. 2.4 m IKMT+MPS; NH-65; 29 November 1972; 44°37.4'N, 125°41.3'W; 0327-0335; surface.

693 Gonatus sp. E. 2.4 m IKMT+MPS; NH-65; 28 November 1972; 44°37.2'N, 125°42.3'W; 0641-0715; 300-200 m.

694 Gonatus sp. E. 1.8 m IKMT; NH-185; 21 August 1969; 44°39.1'N, 128°21.8'W; 0327-0414; 0-240 m.

695 _Gonatus_ sp. A. 1.8 m IKMT; YALOC66; 1 July 1966; 51°43.8'N, 175°20'W; 0309-0347; 0-200 m.

696 _Gonatus_ sp. A. 1.8 m IKMT; YALOC66; 4 July 1966; 54°58.2'N, 166°02'W; 0240-0321; 0-200 m.

697 _Gonatus_ sp. A. 1.8 m IKMT; YALOC66; 22 June 1966; 50°32.3'N, 176°04.5'W; 0031-0107; 0-160 m.

698, 699 _Gonatus_ sp. A. 3.0 m IKMT+MPS; YALOC66; 6 July 1966; 52°58.5'N, 162°48'W; 0707-1330; 0-2400 m.

700, 701 _Gonatus_ sp. A. 1.8 m IKMT; _Brown Bear_ cruise 235, haul 46; 25 July 1959; 53°57'N, 157°39'W; 0129-0222; 0-225 m.

702 _Gonatus madokai_. 1.8 m IKMT+MPS; NH-65; 13 June 1973; 44°42.7'N, 125°33.0'W; 0205-0245; 450 m.

703, 704 _Gonatus madokai_. 3.0 m IKMT+MPS; YALOC66; 23 June 1966; 50°21.0'N, 176°54.8'W; 1330-1605; 0-2400 m.

705 _Gonatus madokai_. 1.8 m IKMT+MPS; NH-65; 3 June 1969; 44°55.5'N, 125°37.9'W; 1333-1445; 800-0 m.

706 _Gonatus madokai_. 3.0 m IKMT; YALOC66; 23 July 1966; 50°29'N, 138°32'W; 0225-0310; 0-150 m.

707, 708 _Gonatus middendorffi_. 1.8 m IKMT; YALOC66; 4 July 1966; 54°58.2'N, 166°02'W; 0240-0321; 0-200 m.

709-711 _Gonatus middendorffi_. purse seine (set C-10); High Seas Tagging □2; 8 July 1977; 50°57'N, 176°25'W.

712, 713 _Gonatus middendorffi_. purse seine (set C-19); High Seas Tagging □3; 27 July 1977; 50°58'N, 176°24'W.

714 _Gonatus middendorffi_. purse seine (set G-33); High Seas Tagging □5; 26 June 1980; 44°18'N, 174°12'E.

715-718 _Berryteuthis anonychus_. purse seine (set G-3); High Seas Tagging □4; 18 June 1980; 46°10'N, 167°50'E.

719 _Berryteuthis anonychus_. beam trawl; NH-65; 8 March 1972; 44°49.6'N, 125°33.0'W; 0850-1050; c. 2800 m.

720 _Bathyteuthis abyssicola_. 1.8 m IKMT; WELOC76; 21-22 August 1976; 35°26.0'N, 154°01.2'W; 2306-0140; 0-200 m.

721 _Bathyteuthis abyssicola_. 3.0 m IKMT; FRONTS; 6 February 1980; 31°18.1'N, 152°56.5'W; 2050-2155; 0-205 m.

722 Bathyteuthis abyssicola. 1.8 m IKMT+MPS; NH-65; 3 June 1969; 44°52.8'N, 125°36.1'W; 1241-1319; 1000-800 m.

723 Bathyteuthis berryi. 3.0 m IKMT; FRONTS; 28 January 1980; 30°39.2'N, 154°00.2'W; 2000-2128; 0-250 m.

724 Onykia carribaea. 1.8 m IKMT; YALOC66; 3 June 1966; 28°22'N, 161°30'W; 0235-0321; 0-150 m.

725 Onykia carribaea. 1.8 m IKMT; YALOC66; 12 June 1966; 33°33.6'N, 164°24.5'W; 0034-0120; 0-170 m.

726 Onykia carribaea. 1.8 m IKMT; YALOC66; 13 June 1966; 35°26.4'N, 165°52.4' ; 0630-0712; 0-160 m.

727 Neoteuthis sp. 3.0 m IKMT; FRONTS; 3 February 1980; 30°43.3'N, 154°01.0'W; 1955-2103; 0-245 m.

728-731 Octopus sp. A. 1.8 m IKMT; YALOC66; 1 July 1966; 51°43.8'N, 175°20'W; 0309-0347; 0-200 m.

732-734 Octopus sp. A. 1.8 m IKMT; YALOC66; 7 July 1966; 53°35'N, 160°01'W; 0125-0205; 0-160 m.

735-737 Helicocranchia pfefferi. 1.8 m IKMT; Brown Bear cruise 199, hauls 207; 31 July-1 August 1958; 32°49'N, 118°49'W; 2338-0034; 0-225 m.

738 Ocythoe tuberculata. 1.8 m IKMT; Brown Bear cruise 254, haul 9; 18 March 1960; 37°56'N, 129°36'W; 0237-0347; 0-400 m.

739 Ocythoe tuberculata. 1.8 m IKMT; Brown Bear cruise 254, haul 14; 19 March 1960; 39°56'N, 131°36'W; 0200-0240; 0-120 m.

740 Sandalops sp. 3.0 m IKMT; FRONTS; 3 February 1980; 30°43.3'N, 154°01.0'W; 1955-2103; 0-245 m.

741 Ctenopteryx sicula. 1.8 m IKMT; YALOC66; 13-14 June 1966; 37°11.7'N, 167°00.0'W; 2345-0025; 0-150 m.

742-744 Megalocranchia cf. speculator. 3.0 m IKMT; FRONTS; 26 January 1980; 30°34.7'N, 153°18.3'W; 2049-2158; 0-230 m.

745 Megalocranchia cf. speculator. 3.0 m IKMT; FRONTS; 29 January 1980; 30°03.4'N, 154°19.3'W; 2034-2142; 0-225 m.

746-749 Megalocranchia cf. speculator. 3.0 m IKMT; FRONTS; 3 February 1980; 30°43.3'N, 154°01.0'W; 1955-2103; 0-245 m.

750-752 Megalocranchia cf. speculator. 3.0 m IKMT; FRONTS; 6 February 1980; 31°18.1'N, 152°56.5'W; 2050-2155; 0-205 m.

753 Taonius sp. 1.8 m IKMT; YALOC66; 15 June 1966; 39°30'N, 168°40'W; 0021-0105; 0-170 m.

757 Thelidioteuthis alessandrinii. 1.8 m IKMT; WELOC76; 22-23 August 1976; 31°58.8'N, 153°07.1'W; 2214-0005; 0-70 m.

760, 761 Dosidicus gigas. dipnet; 3 March 1972; 9°21.0'S, 80°43.9'W; 1940; surface.

763 Ommastrephes bartramii. dipnet; Alpha Helix; 16 November 1971; 30°N, 147°W; night; surface.

764, 765 Ommastrephes bartramii. dipnet; WELOC76; 24 August 1976; 30°16.5'N, 157°59.2'W; 0215; surface.

766 Symplectoteuthis luminosa. squid jig; Alpha Helix; 20 November 1971; 32°09.1'N, 132°32.5'W; 2015; surface.

767-770 Symplectoteuthis luminosa. dipnet; SP-77; 10 March 1970; 22°16'N, 107°31.8'W (probable location); 2220; surface.

773 Valbyteuthis oligobessa. 2.4 m IKMT+MPS; NH-130-165; 22July 1973; 45°20.3'N, 127°07.5'W; 0320-0420; 2000-0 m.

775 Stauroteuthis sp. beam trawl; TP-3; 4 May 1970; 44°40.8'N, 133°26.3'W; 3717 m.

776 Stauroteuthis sp. otter trawl; CBT-38-Y; 7 August 1973; 43°30.6'N, 124°56.5'N; 0802-0830' 810 m.

777 Stauroteuthis sp. 3 m beam trawl; CP-2-C; 18 February 1971; 45°20.8'N, 126°37.7'W; 0130-0330; 2750 m.

778 Cirrothauma murrayi. beam trawl; 4 November 1973; 44°53.5'N, 127°27.5'W; 2826 m.

779 Cirrothauma murrayi. beam trawl; 18 February 1971; 45°1705'N, 126°28.4'W; 2710 m.

780 Cirroteuthis sp. beam trawl; 16 January 1970; 45°45.5'N, 126°42.4'W; 2675 m.

781 Cirroteuthis sp. otter trawl; CBT-38; 7 August 1973; 43°28.1'N, 124°52.8'W; 2342-0012; 650 m.

782 Chiroteuthis sp. 1.8 m IKMT; YALOC66; 16 June 1966; 42°36.9'N, 171°04.5'W; 2201-2248; 0-200 m.

783 Japetella sp. Young, 1972. 50 m2 midwater trawl; NH-80; 2 September 1978; 44°30.2'N, 125°32.0'W; 1536-1736; 500-520 m.

784 _Japetella_ sp. Young, 1972.   50 m2 midwater trawl; NH-80; 5 September 1978; 44°35.0'N, 125°37.4'W; 2158-2358; 515-555 m.

785 _Octopus_ sp. B. 3.0 m IKMT; stn. 35, Nemoto; 29 July 1978; 55°00.7'N, 169°57.5'W; 2145-2307; 0-500 m.

786, 787   _Octopus_ sp. B. 3.0 m IKMT; stn. 41, Nemoto; 14 August 1978; 47°54.9'N, 176°14.5'E; 2040-2220; 0-520 m.

788 _Mastigoteuthis pyrodes_. 3.0 m IKMT; FRONTS; 3 February 1980; 30°43.3'N, 154°01.0'W; 1955-2103; 0-245 m.

789 _Mastigoteuthis pyrodes_. 3.0 m IKMT; FRONTS; 6 February 1980; 31°18.1'N, 152°56.5'W; 2050-2155; 0-205 m.

790 _Mastigoteuthis pyrodes_. 3.0 m IKMT; FRONTS; 7 February 1980; 28°58.7'N, 152°55.3'W; 2045-2203; 0-215 m.

791 _Mastigoteuthis pyrodes_. 3.0 m IKMT; FRONTS; 8 February 1980; 31°04.9'N, 152°40.0'W; 2055-2210; 0-185 m.

792, 793 _Ctenopteryx sicula_. 3.0 m IKMT; FRONTS; 2 February 1980; 29°19.4'N, 154°21.2'W; 1945-2055; 0-220 m.

794 _Ctenopteryx sicula_. 3.0 m IKMT; FRONTS; 3 February 1980; 30°43.3'N, 154°01.0'W; 1955-2103; 0-245 m.

795 _Ctenopteryx sicula_. 1.8 m IKMT; _Brown Bear_ cruise 199, haul 146; 18 July 1958; 38°50'N, 137°56'W; 0045-0120; 0-30 m.

796 _Helicocranchia pfefferi_. 3.0 m IKMT; FRONTS; 23 January 1980; 32°14.8'N, 152°38.1'W; 2107-2205; 0-250 m.

797 _Helicocranchia pfefferi_. 3.0 m IKMT; FRONTS; 25 January 1980; 30°06.1'N, 153°02.4'W; 2145-2253; 0-255 m.

798 _Helicocranchia pfefferi_. 3.0 m IKMT; FRONTS; 28 January 1980; 30°39.2'N, 154°00.2'W; 2000-2128; 0-250 m.

799 _Helicocranchia pfefferi_. 3.0 m IKMT; FRONTS; 5 February 1980; 29°42.3'N, 153°17.7'W; 2137-2252; 0-195 m.

800 _Helicocranchia pfefferi_. 3.0 m IKMT; FRONTS; 8 February 1980; 31°04.9'N, 152°40.0'W; 2055-2210; 0-185 m.

801, 802 _Abraliopsis hoylei_. 3.0 m IKMT; FRONTS; 23 January 1980; 32°14.8'N, 152°38.1'W; 2107-2205; 0-250 m.

803-805 _Abraliopsis hoylei_. 3.0 m IKMT; FRONTS; 5 February 1980; 29°42.3'N, 153°17.7'W; 2137-2252; 0-195 m.

806　Abraliopsis pfefferi.　3.0 m IKMT; YALOC66; 2 June 1966; 28°05.0'N, 161°30.4'W; 1910-2155; 0-2400 m.

807-814　Abraliopsis pfefferi.　1.8 m IKMT; WELOC76; 21-22August 1976; 35°26.0'N, 154°01.2'W; 2306-0140; 0-200 m.

815, 816　Abraliopsis pfefferi.　1.8 m IKMT; WELOC76; 24 August 1976; 27°04.1'N, 157°59.0'W; 2225(+9)-2331(+10); 0-70 m.

817　Brachioteuthis sp.　1.8 m IKMT; YALOC66; 2 June 1966; 26°01.5'N, 161°26.0'W; 0016-0058; 0-170 m.

818　Brachioteuthis sp.　1.8 m IKMT; YALOC66; 12 June 1966; 33°33.6'N, 164°24.5'W; 0034-0120; 0-170 m.

819-821　Chiroteuthis joubini.　1.8 m IKMT; YALOC66; 15 June 1966; 39 30'N, 168°40'W; 0021-0105; 0-170 m.

822　Chiroteuthis joubini.　1.8 m IKMT; YALOC66; 16 June 1966; 42°36.9'N, 171°04.5'W; 2201-2248; 0-200 m.

823　Eledonella pygmaea.　3.0 m IKMT; SICSPAC; 5 March 1965; 34°50.0'N, 140°19.1'W; 1645-2245; 0-2450 m.

825　Tremoctopus violaceus.　1.8 m IKMT; YALOC66; 11 June 1966; 31°00.0'N, 162°42.6'W; 0100-0144; 0-170 m.

826　Gonatopsis okutanii.　purse seine (stomach contents of 127 cm male Alepisaurus ferox); High Seas Tagging □6; 3 July 1980; 50°03'N, 177°32'W.