

AN ABSTRACT OF THE THESIS OF

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(Name of student) (Degree)

in Zoology presented on May 5, 1972
(Major) (Date)

Title: ZOOGEOGRAPHY OF PELAGIC SHRIMPS (NATANTIA:
PENAEIDEA AND CARIDEA) IN THE NORTH PACIFIC
OCEAN

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Abstract approved: _____
Dr. Ivan Pratt

A study was done on the zoogeography of species of oceanic shrimp in the North Pacific from 22°N to 56°N and from 124°W to 145°E, using samples of shrimp collected from 1954 to 1969. These collections were made during the following cruises: John R. Manning Cruise 22, and the Hugh M. Smith Cruises 27 and 30 of the Pacific Oceanic Fisheries Investigations (POFI), the SICS-PAC and YALOC 66 cruises of the R/V Yaquina of the Department of Oceanography, Oregon State University, and the first trans-Pacific cruise of the C.N.A.V. Endeavour of the Pacific Oceanographic Group, Fisheries Research Board of Canada.

Taxonomic keys were constructed to the sections, families, genera and species of shrimps taken in the samples. A restricted synonymy, a brief diagnosis, and a short note on general distribution

of each shrimp was also given.

Forty-one species of pelagic shrimps representing thirteen genera and five families were identified. There were 25 species of Penaeidea and 16 Caridea. The Sergestidae were most numerous, both in numbers of species (16) and in number of specimens (7017); the Oplophoridae were next in abundance with 11 species and 1111 specimens. Sergestes similis, Hymenodora frontalis, and H. glacialis together contributed over 90% of the total catch, with Sergestes similis making up the bulk. Thirty-five species each made up less than 1% of the total. Sixteen species were either recorded from the Pacific for the first time or had their Pacific ranges further extended as a result of this study.

The zoogeography of the shrimps was discussed in relation to the physico-chemically defined water masses of the study area and the biological factors associated with water masses. It was concluded that the distributions of oceanic shrimps were in general agreement with previous studies of this sort done in the Pacific with other groups of animals. Most of the species do not follow the boundaries of the physico-chemically defined water masses, but tend to either overlap boundaries or to localize within one water mass.

Four groups of species were distinguished: a Subarctic-Transitional group of 12 species inhabiting waters having a fairly high level of primary productivity, a Transitional group of three

species inhabiting mixed waters between the Subarctic and Central water masses, a Central-Transitional group of nine species inhabiting the relatively unproductive Central waters, but also extending into the somewhat richer Transitional waters marginal to the Central waters, and a Central group consisting of 16 species whose ranges follow closely the more barren mid-parts of the Central water masses.

Lastly, a brief discussion of the supposed importance of water mass boundaries to speciation of oceanic animals was presented.

Zoogeography of Pelagic Shrimps (Natantia: Penaeidea and
Caridea) in the North Pacific Ocean

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

June 1972

APPROVED:

Redacted for privacy

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Date thesis is presented May 5, 1912

Typed by Ilene Anderton for Robert Allen Wasmer

ACKNOWLEDGEMENTS

A study of this type is only made possible through the work of many individuals, from unnamed but not unappreciated crew members of the research ships, to others who had a more direct part in its completion.

First, I want to acknowledge my major Professor, Dr. Ivan Pratt, who was gracious enough to allow me to work on a problem in a field outside of that in which most of his students work, and who provided facilities and advice.

A special thanks goes to Dr. William G. Pearcy of the Department of Oceanography, who gave me access to the shrimp collections of the Department and who had a major part in making arrangements for me to examine the other collections used in this study. He provided financial support and travel expenses for a portion of this work through U. S. Atomic Energy Commission Contract AT(45-1) 1750. He also supplied ideas and advice.

I wish to thank Mr. R. J. LeBrasseur of the Fisheries Research Board of Canada, Nanaimo, B. C., for providing me with the shrimp specimens collected on the 1969 Canadian trans-Pacific cruise, and for the kindness and helpfulness shown me on my visit to Nanaimo. A thanks is also due Mr. E. C. Jones of the Hawaii Area Fishery Research Center in Honolulu for his help in obtaining the shrimp

samples collected by the vessels of the POFI, and for making my visit to Hawaii more enjoyable.

I also acknowledge the help of the following individuals: Dr. G. Hartwich of the Zoologisches Museum, East Berlin; Dr. J. Forest of the Museum National D'Histoire Naturelle, Paris; Mr. S. Pinkster, of the Zoologische Museum, Amsterdam; and Dr. L. B. Holthuis, of the Rijksmuseum van Natuurlijke Historie, Leiden. They provided specimens of Parapandalus on loan to me from their respective institutions.

And, lastly, it is a pleasure to acknowledge the help and understanding, in more ways than I can list, of my wife, Glennis. This work was made that much easier by her constant encouragement.

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ZOOGEOGRAPHY OF PELAGIC SHRIMPS (NATANTIA: PENAEIDEA AND CARIDEA) IN THE NORTH PACIFIC OCEAN

INTRODUCTION

Among the many distributional patterns of organisms in the ocean, those associated with the shore and shallow seas (the littoral and neritic regions) are best known. Temperature has long been regarded as the most important single external factor responsible for maintaining distributional patterns in the sea. Salinity is of less importance than temperature in influencing distributions of organisms, except for those organisms in estuaries and nearshore regions where large amounts of runoff occur, and in the intracontinental seas (the Baltic, Black, and Caspian Seas) with their reduced salinities.

Patterns of distribution in the littoral and neritic regions generally conform to the temperature conditions, so that one can refer to arctic, temperate and tropical faunas and floras, each associated with certain temperature ranges. These major temperature realms are typically divided further into biogeographical regions or provinces. Hedgpeth (1957) discussed ideas and works pertinent to the biogeography of the littoral and neritic regions of the seas.

Early work on the distribution of oceanic pelagic organisms continued to focus largely on temperature as a factor limiting the range of species (Bieri, 1966). However, because pelagic organisms

have a three-dimensional distribution, it is often hard to relate the entire horizontal distributions of species solely to the horizontal distributions of temperature and salinity of the layer in which they are found. As pointed out by McGowan (1960), the development of the concept of water masses has made it possible to relate the distributions of oceanic species to that of bodies of water having distinct physico-chemical (and often biological) characteristics.

Water Masses

Water masses are identified on the basis of their temperature-salinity characteristics (Sverdrup et al. 1942). A volume of water is called a water mass because within its boundaries there exists a certain consistency of the temperature-salinity relationships. Plots of temperature vs. salinity throughout the depth of a water column results in a particular temperature-salinity (T-S) curve. Below 100-200 meters T-S curves constructed from hydrographic data taken from a particular water mass fall within certain limits; these limits enclose the water mass envelope, which has a characteristic shape and is used to identify the water mass. Non-conservative properties such as oxygen, phosphate, nitrate, and silicate concentrations may also be used to characterize water masses.

Zoogeography of Pelagic Animals

Recent work dealing with the zoogeography of pelagic animals has stressed the relationship between the distribution of species and physico-chemically defined water masses. Pickford (1946) was the first to use this concept in her study of the distribution of the bathypelagic cephalopod Vampyroteuthis infernalis Chun. Haffner (1952) utilized the method to study the zoogeography of the bathypelagic fish genus Chauliodus. The method has grown mostly as a result of studies in the Pacific Ocean, where it has been demonstrated that frequent, but not invariable, associations occur between the geographical distributions of certain pelagic species and the water masses as defined on the basis of their temperature-salinity relationships. While a species may be localized within a part of a water mass, may be distributed throughout a single such water mass, or overlap two or more water masses, there is often marked conformance of the boundaries of the range of species with the boundaries of the water masses.

In the Pacific there appear to be specific faunas and floras associated with each water mass as well as for the transitional regions between the water masses. Thus, chaetognaths (Bieri, 1959; Sund, 1959), Poeobius meseres, a planktonic worm (McGowan, 1960), euphausiids (Brinton, 1962), bathypelagic fishes of the genus

Melamphaes (Ebeling, 1962), euphausiids, chaetognaths and pteropod molluscs (Fager and McGowan, 1963), bathypelagic fishes of the genus Scopelogadus (Ebeling and Weed, 1963), midwater fishes of the family Myctophidae (Paxton, 1967), the bathypelagic squid Bathyteuthis (Roper, 1969), and pelagic diatoms (Venrick, 1971) each include species limited to subarctic, subtropical and tropical zones. These ecological zones have been designated by Brinton (1962) as subarctic, central, and equatorial faunal zones after the role played by the water masses in the physical zonation of the open ocean. In addition, a fourth faunal zone, the transition zone, is recognized between the central and subarctic water masses; in the South Pacific the zone occurs between the central and subantarctic water masses.

Other studies on distributions of organisms in the northern and northeastern Pacific generally agree with the above patterns: polychaetous annelids by Dales (1957) and Tebble (1962); pelagic tunicates by Berner (1960); and copepods by Johnson (1938). Hida (1957) discussed the use of chaetognaths and pteropods as biological indicators useful in distinguishing types of water in the central North Pacific. Aron (1959, 1960) found myctophid fishes to be particularly useful as indicators of water masses in the northeastern Pacific.

Biological Characteristics of Water Masses

Although water masses are identified by their T-S

relationships, it is unlikely that temperature and salinity alone are the only factors limiting organisms to specific water masses. Thus, McGowan (1960) showed that while Poeobius meseres is found only in Subarctic Water or in waters which may have subarctic components, water having temperatures and salinities characteristic of points of the Subarctic Water Mass are found in many other parts of the world.

Each water mass not only has its unique temperature-salinity relationships, each has diagnostic biological characteristics, such as dissolved metabolites and organic production. These biological characteristics depend ultimately on physico-chemical phenomena of the water mass, such as its temperature, salinity, oxygen content, transparency of water, horizontal current systems, and amount of vertical mixing and enrichment of surface waters with nutrient salts (Ebeling, 1962).

Although Ebeling (1962) found that distributions of species of Melamphaes generally coincide with water masses, when they do depart from this it is to follow the contours of productivity. Roper (1969) found that the distribution of BathYTEUTHIS is governed in part by water mass characteristics, but that the primary limiting factor in the distribution of the species is high organic production.

Previous Work on Oceanic Shrimps in North Pacific

Nektonic shrimps often make up a significant portion of the

biomass of the pelagic community of animals in the open ocean and the deep-sea. Surprisingly little has been published about the species of pelagic shrimp and their distributions in the North Pacific Ocean. The Challenger Expedition took samples of pelagic shrimps from the western North Pacific (Bate, 1888; Hansen, 1903; Kemp, 1909). The cruises of the Albatross provided material for several reports on shrimps from the North Pacific (Faxon, 1895; Rathbun, 1904; Schmitt, 1921). Since most of the Albatross collections were made with bottom trawls on the continental shelf, few species of oceanic shrimps are included in these reports.

Pearcy and Forss (1966) discussed the depth distributions of 16 species of oceanic shrimps collected mainly from a single station located just beyond the continental shelf off the central Oregon coast. The systematic relationships of many of these species were discussed by Forss (1966). Sergestes similis Hansen is the most abundant pelagic shrimp in the northern North Pacific. Several reports have dealt with aspects of the biology and ecology of Sergestes similis in the North Pacific (Pearcy and Forss, 1966; Renfro and Pearcy, 1966; Milne, 1968; Genthe, 1969; Pearcy and Forss, 1969). The vertical distribution and migration of meso- and bathypelagic shrimps in the northwestern Pacific off Japan has been discussed by Aizawa (1969).

Other scattered reports dealing with pelagic shrimp in the North Pacific are to be found in the literature. These are mostly

descriptions and redescriptions of species and are mainly of taxonomic interest.

That the pelagic shrimps in the North Pacific have in the past been poorly known is reflected in the many new distributional records and range extensions (Forss, 1966; Wasmer, 1972c) and new species (Milne, 1968; Wasmer, 1972a) which continue to be reported from the area.

Scope of Study

The purpose of this thesis is to investigate the zoogeography of oceanic shrimps in the North Pacific Ocean, specifically in that part of the Pacific from 22° N to 56° N and from 124° W to 145° E. In addition to investigating which species of pelagic shrimps are present and where they are in this area of the Pacific, other questions to be examined include: What makes up the species boundaries in the North Pacific Ocean and where are they located? Are the distributions of different pelagic shrimps limited by these boundaries into distinct faunal regions? And lastly, is it possible to say anything of the isolating mechanisms which may be of importance in the speciation of pelagic shrimps in this region? The study emphasizes the importance and influence of water masses, as defined both physico-chemically and biologically, in answering these questions.

Abundant samples from a number of stations made across the

major water masses and their boundaries, plus concurrent oceanographic and capture data are essential for such a study. These requirements are met in the collections examined in the course of this work, with the exception of the samples taken on the John R. Manning Cruise 22; the shrimps collected on this cruise have been included only to further indicate the presence or absence of species of shrimp in the area of this cruise.

The work presented here is divided into two major parts. The first part is a taxonomic study of the shrimps involved in the thesis. In this section is found a discussion of the expeditions and trawling gear, preservation of specimens, explanations of counts and determinations of sex. Keys are provided to the sections, families, genera and species of shrimp which are present in the samples. Synonyms, materials examined, a brief diagnosis, and a short note on general distribution of each species are also given.

The second part is a discussion of the zoogeography of the species in the North Pacific. The physical oceanography of the North Pacific, as it relates to the formation and distribution of the water masses in the area of study, is discussed. Descriptions of the methods used in the water mass analysis and in establishing ranges of species relative to the water masses are given. The geographic ranges of the species in the North Pacific are established, and the physico-chemical and biological factors which influence these

distributions are discussed. Lastly, there is a discussion of the influence and importance of the water masses and their boundaries and associated biological factors in the speciation of shrimps in the open ocean.

SYSTEMATICS

Methods and Materials

The shrimps discussed here were collected in the North Pacific from about 22° N to 56° N and from 124° W to 145° E, during six cruises made over a fifteen year period. Figures 1 and 2 show cruise tracks and sample stations for the cruises from which the material was taken. These cruises and the responsible institutions and agencies are: John R. Manning Cruise 22, September and October 1954, Hugh M. Smith Cruise 27, January and February 1955, and the Hugh M. Smith Cruise 30, July and August 1955, Pacific Oceanic Fishery Investigations (POFI), now the Hawaii Area Fishery Research Center of the National Marine Fisheries Service; SICS-PAC (Selected Interval Cast Study - Pacific) cruise during March 1965, and YALOC 66 (Yaquina Long Cruise - 1966) from 20 April to 29 July 1966, Department of Oceanography, OSU; and the first trans-Pacific cruise of the Canadian research vessel Endeavour, 17 March to 1 May 1969, Pacific Oceanographic Group, Fisheries Research Board of Canada, Nanaimo, British Columbia.

The John R. Manning Cruise 22 and the Hugh M. Smith Cruise 27 were undertaken by the POFI laboratories as part of a long range program from 1951 to 1956 to sample quantitatively the forage

organisms which form the basis of fishery stocks in general, and in particular those organisms utilized by tunas (King and Iversen, 1962).

From August to September, 1955, Canada, the United States and Japan undertook a joint program called NORPAC, which provided extensive synoptic coverage of the Pacific north of 20° N. Hugh M. Smith Cruise 30 was the POFI contribution to this program.

The SICS-PAC cruise of the R/V Yaquina into central Pacific waters to the southwest of Oregon was undertaken to permit a comparison of the fauna from two water masses which occur off the west coast of the U.S. Wasmer (1967) discussed the systematic relationships of many of the species of shrimp taken on this cruise. The first long cruise of the R/V Yaquina (YALOC 66) was undertaken with several objectives in mind (Borden, 1966). The biological studies on this cruise included, in addition to the midwater trawling studies, in situ measurements of primary productivity, and sampling of benthic epifauna and infauna.

The first trans-Pacific cruise of the Canadian research vessel Endeavour was made to study production processes in a transect of the subarctic North Pacific and a small part of the Kuroshio Current (Parsons and Anderson, 1970). The cruise track followed an approximate great circle route from Esquimalt, British Columbia, to Tokyo, and back from Hakodate to Esquimalt.

The samples used were taken with either a 6-ft or a 10-ft

Isaacs-Kidd midwater trawl. Most samples were taken within 320 meters of the surface. Some tows on the SICS-PAC were made to depths of 2400 m. Seven tows on the YALOC 66 cruise were made with an Isaacs-Kidd midwater trawl modified to capture animals within three depth strata during one oblique tow. For these the 10-ft trawl was adapted with an opening and closing codend unit (Pearcy and Hubbard, 1964) to sample at intervals of 1000-2600 m, 500-1000 m, and 200-500 m; a 6-ft trawl sampled the 0-200 m interval. Unfortunately, some collections made with the multiple sampler were thru 2600 to 0 m. Further details of sampling methods on specific cruises are given in the following references: POFI cruises, King and Iversen (1962); OSU cruises, Percy (1964); Canadian trans-Pacific cruise, F.R.B.C. (MS.1970).

Samples were preserved at sea. Later, all shrimps and other nekton were sorted, identified, and measured in laboratories ashore. Copies of the original data sheets on which are recorded the species of shrimp and the number of males and females of each and their size are on file in the Departments of Zoology and Oceanography at OSU. Shrimps were identified to species by comparison with either the original species description or a subsequent redescription.

The measurement used as an indication of size was the carapace length, measured from the postorbital margin to the median posterior edge of the carapace. Measurements were made to the

nearest millimeter. Although this measure of size has the disadvantage that it does not give a clear indication of the total length of the organism, it can be more precisely determined than the total length. In most shrimps, particularly the Caridea, it is difficult to extend the abdomen to its greatest length after the shrimp has been preserved.

Determination of sex in the Penaeidea was done by examining the first pleopod for the presence of the petasma, a copulatory structure in the males. The Caridea, with the exception of the Oplophoridae, were sexed by looking for the appendix masculina on the inner margin of the second pleopods in the males. The endopod of the first pleopods is usually sexually modified in the Oplophoridae (Chace, 1940); this character was used to sex members of this family.

Keys to the sections, families, genera and species found in this study were constructed to assist subsequent workers in identifying the shrimps from this region of the Pacific since no single key to their determination is currently available. The keys in most cases have been modified from existing keys; such modifications are acknowledged in the keys. Several species known to be found in the study area, but which were not taken in the course of this study have been included in the keys; these species are enclosed in square brackets.

In the species accounts which follow, complete synonymies

usually are not given; instead only the original citation and the most recent works giving a complete synonymy and/or figures are listed. The collection records for each species are listed by stations under the cruise designations. The total number of specimens taken at any particular station is given in parentheses following the station number. Station locations, dates, times and depth of trawls for each of the cruises are on file in the Zoology and Oceanography Departments.

General Considerations

The Order Decapoda is divided into the Suborders Natantia and Reptantia. The former includes all shrimps and the latter the lobster, crayfish and crabs. The Natantia can be characterized as follows: Body more or less compressed laterally; antennal scale large; the first two or three pairs of legs chelate; abdominal appendages (pleopods) well-developed and used for swimming.

The schematic drawing of a caridean shrimp in lateral view (Figure 3) with appropriate structures labeled will explain most, but not all, of the terms used in the keys. The following terms are used in some of the keys; since their meanings may not be apparent to the user of the key, short definitions are given.

Arthrobranch. A type of gill attached to the articular membrane between the body wall and the coxa.

Petasma. The paired copulatory structure of male penaeids;

attached medially to first pair of pleopods. The two halves are interlocked by many hooks on their median margins. The distal margins are variously divided into lobes which also may bear hooks. An important taxonomic character.

Pleurobranch. Type of gill attached to the lateral wall of the thoracic somite.

Podobranch. Type of gill attached to epipod of appendage.

Thelycum. Genital structure of female penaeids formed by modifications of the last three thoracic sternites; it consists of depressions and tubercles, plates, and ridges of various dimensions. An important taxonomic character.

The Suborder Natantia is divided into three sections, the Caridea, the Stenopodidea, and Penaeidea. The three sections may be distinguished by means of the following key (Modified from Holthuis, 1955):

Key to the Sections of Natantia

1. Pleurae of second abdominal somite overlapping those of first and third segments; no chelae on the third pereopods, abdomen usually with sharp bend or hump.... Caridea
- Pleurae of second abdominal somite not overlapping those of the first segment; third legs with a chelae; abdomen without a sharp bend or hump..... 2

2. Third leg distinctly stronger than the preceding; males without petasma..... [Stenopodidea]^{1/}
- Third pereiopod never stronger than preceding, generally all chelipeds of equal strength; males with petasma Penaeidea

Section Penaeidea

Abdomen not flexed sharply. Pleurae of second abdominal segment not overlapping those of first and third segments. Third pair of legs never stronger than first and second. First pleopods of male with a petasma; appendix masculina present on second pleopods. Eggs not carried by females.

Key to the Families of Penaeidea (from Barnard, 1955).

1. Gills numerous; first three pairs of pereiopods chelate; fourth and fifth pairs of pereiopods well developed Penaeidae
- Gills few or absent..... 2
2. Gills few, not over eight; first pereiopods not chelate; fourth and fifth pairs of pereiopods reduced or absent..... Sergestidae
- Gills absent; first two pairs of pereiopods not chelate; third pereiopods chelate (imperfectly); fourth and fifth pairs of pereiopods absent..... [Luciferidae]^{2/}

^{1/} Not represented in these collections.

^{2/} Not represented in these collections.

Family Penaeidae

Rostrum laterally compressed, usually well developed. Gills numerous. All pereopods well developed; first three pairs chelate. Petasma sometimes asymmetrical. Thelycum usually well developed. Principally marine, both pelagic and benthonic habit. The family includes four subfamilies, two of which are represented in the present material; nine species in three genera were taken. Martin D. Burkenroad, in a series of papers (1934a, 1934b, 1936 and on), did much to straighten out the confusion existing in the classification of the Penaeidae. The keys which follow are modified from keys constructed by others, but based largely on data derived from Burkenroad's publications.

Key to Subfamilies of the Penaeidae (adapted from Anderson and Lindner, 1945).

1. Distinct median tubercle on ocular peduncle; epipodites on all coxae from 2nd maxillipeds through 4th leg
..... Aristaeinae
- No median tubercle on ocular peduncle; epipodites absent behind 3rd legs..... Penaeinae

Subfamily Aristaeinae Alcock

According to Burkenroad (1936), this subfamily is without exception oceanic. The subfamily is divided into two series,

Aristeae and Benthescymae. The Benthescymae are distinguished from the Aristeae by having the distal, filamentous portion of the superior antennular ramus extensively developed. No specimens belonging to the series Aristeae were taken in the study material, although specimens belonging to two genera in the series have been reported from off the Oregon coast (Wasmer, 1972c). The series Benthescymae consists of four genera, two of which are found in the present material.

Burkenroad (1936) discussed in detail the diagnostic characters of the species of Benthescymae. He regarded Amalopenaeus Smith as a synonym of Gennadas Bate, which was restricted to include only the species without podobranchs on the first three pairs of pereopods and with only a single pair of mobile lateral spines on the telson; he gave a new name Bentheogennema to the species with podobranchs on the first three pereopods and more than a single pair of mobile spines on the truncate telson. The two genera resemble each other closely in other details.

A new species of shrimp belonging to the Benthescymae from waters off the west coast of North America resembles species of Gennadas in having only one pair of mobile lateral spines on the telson but which resembles Bentheogennema in gill number and arrangement. This shrimp necessitates an assessment of the relative importance of the number of pairs of spines on the telson and of the number and

arrangement of gills as characters of importance in separating the two genera.

Kemp (1909, p. 719) considered this problem when he wrote,

Podobranchs are rarely found on the thoracic limbs of Decapoda, Natantia; they are most frequently present in the Penaeidea, and in such a tribe, which abounds in primitive characters, the absence of these gills is rightly regarded as a feature of great importance, for it indicates in no uncertain way the degree of specialization to which the species has attained.

If the number of pairs of spines on the telson can be considered to be of less taxonomic value than the number and arrangement of the gills in this group, then the new species should be assigned to Bentheogennema on the basis of its gills.

The keys to the genera and species of Benthescymae which follow are adaptations of keys in Burkenroad (1936), Anderson and Lindner (1945), and Tirmizi (1959).

Key to Genera of Subfamily Aristeinae

1. Podobranch present on each appendage from 2nd maxilliped to 3rd pereopod; arthrobranch of 1st maxilliped richly plumose..... Bentheogennema
- No podobranch behind 2nd maxilliped; arthrobranch of 1st maxilliped reduced to a vestige..... Gennadas

Genus Bentheogennema Burkenroad, 1936

The genus contains four species in addition to the new one

briefly diagnosed here; little recent work has been done on the genus.

Key to the Species of *Bentheogennema* Burkenroad

1. Cervical and postcervical sulci on carapace not closely approximating each other dorsally and not interrupting postrostral carina; two pairs of mobile spines on telson B. borealis
- Cervical and postcervical sulci closely approximating each other dorsally and interrupting postrostral carina; only one pair of mobile spines on telson. . . . Bentheogennema n. sp.^{3/}

Bentheogennema borealis (Rathbun)

Gennadas borealis Rathbun, 1902, p. 887; Rathbun, 1904, p. 147, figs. 88a, 88b, 89a, 89b.

Gennadas calmani, Kemp, 1909, p. 724, pl. 74, figs. 5-11, pl. 75, figs. 4 and 5.

Bentheogennema borealis, Burkenroad, 1936.

Collection Records: SICS-PAC: 610(3); 611(1); 613(7).

YALOC 66: 840(6); 849(56); 854(3);

857(7); 866(5).

Trans-PAC: 08(1); 10(5).

Diagnosis: Cervical and postcervical sulci not closely approximating each other dorsally and not interrupting postrostral carina. Strong pterygostomian spine followed by a perceptible carina. Telson

^{3/} This species will be described separately at a later time.

bears one pair of lateral spines at its posterior fourth, two spines at the tip. Median lobe of petasma somewhat truncated; accessory lobe weakly developed. Thelycum with pair of triangular projections on the anterior part of the sternite between fourth pereopods, the median angles of which extend into a space between sternites of fourth and third pereopods.

Distribution: Bentheogennema borealis is limited to the North Pacific, from Japan (Kemp, 1909) through the Aleutians and down the Pacific coast of North America to Southern California (Rathbun, 1902, 1904; Schmitt, 1921). Bentheogennema, like Gennadas, probably leads an exclusively pelagic life. Since all earlier records for B. borealis are from bottom trawls, it is probable that the shrimp were taken during the ascent of the trawl. Pearcy and Forss (1966) reported the species from 200-1000 m. Aizawa (1969) concluded that off Japan the species (as G. calmani) is non-migrating, with its center of distribution from 500-1300 m. In the present study, specimens were taken in open midwater trawls to 3000 m; specimens were also taken in one opening-closing trawl which sampled the interval 1000-2000 m.

Bentheogennema New Species

Collection Records: SICS-PAC 605(8); 606(4); 607(6);

608(3); 610 (6); 611(6); 612(18); 613(8).

YALOC 66: 857(2); 866(3).

Trans-PAC: 01(1).

Diagnosis: Cervical and postcervical sulci closely approximating each other dorsally and interrupting postrostral carina. Pterygostomian spine present. Telson with only one pair of mobile lateral spines distally. Podobranchs on each appendage from second maxilliped to third pereopod. Internal lobe of petasma extends beyond other lobes on distal margin; external lobe with spines; accessory lobe greatly developed, extending beyond medial edge of internal lobe and with subterminal hook or tooth in adult. Thelycum with anterior part of seventh thoracic sternite between fourth pereopods produced into a shield which is deeply concave in the center; seventh thoracic sternite between fifth pereopods in form of a large plate with strong spines on its free anterior margin.

Distribution: This species is only known from the northeastern Pacific from about 52° N to 32° N, east of 142° W. Percy and Forss (1966) reported it mainly from depths of 200-1000 m. In the present study, specimens were taken in tows made from as deep as 3000 m.

Genus Gennadas Bate, 1881

The genus Gennadas contains 18 species and is very homogenous,

with considerable similarity of the species in most features other than genital structures. The result of this is that features of the petasma and thelycum are used almost entirely in construction of keys to the species. The keys, based on genital structures, devised by Burkenroad (1936) brought some order to the chaos which had existed previously, when not only males and females of the same species had been placed under different names, but sexes of distinct species were coupled under the same name. Tirmizi (1959) pointed out that the appendix masculina could be a useful taxonomic character in the males of seven species examined by her.

Key to Species of *Gennadas*, Based on Petasma and Thelycum

A. Male (Petasma).

1. Median lobe undivided 2
- Median lobe divided 3
2. External lobe undivided G. capensis
- External lobe weakly divided, armed with
hooks G. tinayrei
3. Median lobe tripartite, accessory lobe a long narrow
flap G. parvus
- Median lobe bifurcate, accessory lobe more prominent
..... 4
4. Inner lobule of median lobe wider than the outer lobule
..... 5
- Lobules of median lobe of about same width. G. bouvieri

5. External lobe much longer than median lobe, deeply cleft G. incertus
 - External lobe shorter than median lobe ... G. propinquus
- B. Female (Thelycum).
1. A narrow tongue-like projection directed backward from the posterior margin of the fifth thoracic sternite G. tinayrei
 - No projection from the fifth thoracic sternite 2
 2. Transverse elevation of hind margin of sixth thoracic sternite **W**-shaped G. capensis
 - Transverse elevation of hind margin of sixth thoracic sternite not **W**-shaped 3
 3. Plate on eighth thoracic sternite with long narrow anterolateral process G. bouvieri
 - Plate on eighth thoracic sternite without long narrow anterolateral process 4
 4. Elevation of seventh thoracic sternite **^**-shaped G. parvus
 - No **^**-shaped elevation on seventh thoracic sternite ... 5
 5. Anterior edge of plate on eighth thoracic sternite raised from body surface G. incertus
 - Anterior edge of plate on eighth thoracic sternite not raised from body surface G. propinquus

Gennadas capensis Calman

Gennadas capensis Calman, 1925, p. 5, pl. 1, fig. 1 and 2;
 Roberts and Pequegnat, 1970, p. 34, fig. 3-2A.

Collection Records: YALOC 66: 823(1).

Diagnosis: Median lobe of petasma undivided, much wider than the internal lobe; internal lobe with stout tooth-like projection in middle of its median margin; accessory lobe a slender, distally directed clavate rod, inserted mediad the lateral margin of the internal lobe.

Distribution: Gennadas capensis was originally described from two males taken in the South Atlantic off the Cape of Good Hope, but it also occurs abundantly in the Bahamas, Caribbean, and the Gulf of Mexico (Burkenroad, 1936; Roberts and Pequegnat, 1970). The one specimen taken in this study is the first record of the species in the Pacific, but it agrees very well with published figures and descriptions regarding features of the petasma. It was taken in a modified opening-closing midwater trawl which failed to operate correctly, sampling the depth range 0-2700 m.

Gennadas tinayrei Bouvier

Gennadas tinayrei Bouviere, 1906, p. 10, fig. 2-4 and 14;
Tirmizi, 1959, p. 367, figs. 40f and 81-83.

Collection Records: HMS-27: 21(1)

HMS-30: 3(2); 6(1).

SICS-PAC: 606(1); 607(2); 609(16);

610(27); 612(2).

YALOC 66: 826(1); 830(3); 831(1);

834(1).

Trans-PAC: 25(1).

Diagnosis: Median lobe of petasma broader than external lobe; external lobe weakly divided, armed with hooks; accessory lobe triangular. Thelycum with narrow tongue-like projection directed backward from the posterior margin of fifth thoracic sternite. Outer scale of appendix masculina with straight inner margin and rounded apex,

Distribution: Gennadas tinayrei has previously been taken only in the Atlantic (chiefly in the North) and Indian Oceans (Tirmizi, 1959). This is the first record of the species from the Pacific. Tirmizi (1959) reported the species from 0-2500 m. Specimens in the present study were taken in tows made in the depth range 0-320 m and in a non-closing trawl towed through the depth range 0-2480 m.

Gennadas parvus Bate

Gennadas parvus Bate, 1881, p. 192; Tirmizi, 1959, figs. 40a, 48a, 49-51.

Collection Records: HMS-30: 30(1).

Trans-PAC: 24(2); 25(1).

Diagnosis: Median lobe of petasma divided into three lobules, the narrow middle lobule is largest and directed upward and forward;

the internal lobule expanded and cup-like in appearance. Elevation of seventh thoracic sternite of thelycum \wedge -shaped, with its base depressed and the anterior part somewhat higher; plate on eighth thoracic sternite with two prominent depressions on its surface separated by a low carina which runs in an anterior-posterior direction; small, medially directed leaf-like structures with spiny apices originate posterior to bases of third pereopods.

Distribution: Gennadas parvus was originally described from a specimen taken in the North Pacific south of Japan (Bate, 1881; Kemp, 1909), and has been reported from the Indo-Pacific region by many workers (Tirmizi, 1959). Aizawa (1969) concluded that off Japan the species migrates vertically, with a daytime distribution of 400-1000 m, while at night the maximum distribution moved up to 200-600 m. The specimens in the present study were taken in tows made in the upper 320 m.

Gennadas bouvieri Kemp

Gennadas bouvieri Kemp, 1909, p. 726, pl. 74, figs. 1-4; pl. 75 figs. 6 and 7; Tirmizi, 1959, p. 360, figs. 40d, 48e, and 70-75; Roberts and Pequegnat, 1970, p. 36, fig. 3-2B, C.

Collection Records: YALOC 66: 823(2); 826(2).

Diagnosis: External lobe of petasma divided into two lobules, tips of both acuminate; median lobe divided into two lobules of about equal width, their pointed tips directed toward each other; internal

lobe much smaller than other lobes, armed with long hooks; accessory lobe extends beyond median lobe. Thelycum with a large flap extending from posterior margin of sixth thoracic sternite to the anterior margin of eighth sternite, kept in position by lateral projection of the seventh sternite; anterolateral processes of plate on eighth sternite about one-third length of plate, with setose tips.

Distribution: Previous to Burkenroad's (1936) work, the male and female of Gennadas bouvieri were described as two different species, the males as G. alcocki and the females as G. bouvieri. Males had been taken from the Indian Ocean and the South Atlantic; females had been taken in the eastern Pacific and the Indian Ocean. It was not until 1927 that the two sexes were taken together for the first time (Burkenroad, 1936, p. 81) in Bahaman and Bermudan waters. Roberts and Pequegnat (1970) reported the species from the Gulf of Mexico. Males and females were taken together in the present study. Two specimens were taken in an opening-closing trawl which sampled the depth interval of 500-1000 m, and two additional specimens were taken from a depth range of 0-2400 m.

Gennadas incertus (Balss)

Amalopenaeus incertus Balss, 1927, p. 265, figs. 24-29.

Gennadas incertus, Tirmizi, 1959, p. 364, figs. 40e, 48f, and 76-80.

Collection Records: HMS-30: 12(1); 15(1); 18(2); 21(10);
57(1); 63(1); 69(2); 101(1); 107(1).

SICS-PAC: 609(5); 610(2).

YALOC 66: 830(1).

Trans-PAC: 14(1); 16(6); 24(4); 25(9).

Diagnosis: External lobe of petasma much longer than median lobe, deeply cleft. Thelycum with a large plate on eighth thoracic sternite, raised anteriorly; shield on sixth thoracic sternite concave in center and markedly concave laterally, where it bears small spines.

Distribution: Gennadas incertus has been taken from the Indian Ocean (Tirmizi, 1959) and in the North Pacific Ocean (Pearcy and Forss, 1966; Aizawa, 1969). Percy and Forss (1966) reported it from 500-1000 m off Oregon. Aizawa (1966) concluded that off Japan the species migrates vertically, with a daytime depth range of 400-900 m and a nighttime depth range of 100-300 m. The specimens in the present study were most often taken within the upper 320 m.

Gennadas propinquus Rathbun

Gennadas propinquus Rathbun, 1906, p. 907, figs. 61a, 61b.

Collection Records: HMS-30: 15(9); 23(1); 27(3); 60(4);
107(1); 110(1).

SICS-PAC: 607(9); 609(7); 610(12);
611(2); 612(1).

YALOC 66: 823(1); 830(2); 831(2).

Trans-PAC: 14(1); 16(2); 24(1).

Diagnosis: External lobe of petasma shorter than median lobe, divided into two lobules, the outer lobule narrow, longer than inner lobule, its tip recurved; median lobe divided into a distally narrow and pointed outer lobule and a larger and broader, apically truncate inner lobule; accessory lobe long, triangular, reaching towards median margin of internal lobe. Inner scale of appendix masculina armed medially with spines, the proximal seven of which are extremely elongated, two rows of smaller spines distally; outer scale about same length as inner scale, somewhat truncate distally. Thelycum with an oval median plate on eighth thoracic sternite; seventh thoracic sternite has narrow posterior plate which has six or eight lateral spines; anterior plate longer than posterior plate, but narrower, laterally armed with spines, anterior margin tridentate; sixth sternite with a triangular shield, the apex smoothly rounded, usually with a pair of small spines three-quarters distance to apex; seminal orifices located between shield on sixth sternite and trident margin of anterior plate on seventh sternite.

Distribution: Reported only from the North Pacific (Rathbun, 1906; Percy and Forss, 1966). Burkenroad (1936) considered

G. clavicarpus de Man and G. propinquus to be identical and used the latter name since it had priority. Tirmizi (1959) redescribed G. clavicarpus and pointed out differences between the genital features of it, G. propinquus and G. scutatus Bouvier. The appendix masculina of specimens of G. propinquus from the present study differ from the figure and description of the same structure for G. clavicarpus given by Tirmizi (1959). This species is in need of redescription.

Pearcy and Forss (1966) reported the species from 200-1000 m. Specimens in the present study were taken in tows made in the depth range of 0-300 m, as well as from deeper tows (0-2700 m).

Subfamily Penaeinae Burkenroad

No median ocular tubercle on ocular peduncle. A foliaceous flexible appendage (the prosartema) on inner margin of basal joint of first antenna. No podobranchs on legs. Exopods usually present on second and third maxillipeds. Pleopods with two rami. Cervical groove not reaching dorsum. First joint of mandibular palp smaller than second.

The Penaeinae for the most part are littoral in habit, except for Funchalia, which is pelagic and oceanic (Burkenroad, 1936).

Genus Funchalia Johnson, 1867

Penaeinae with pleurobranch on last thoracic somite. Third maxilliped with epipod. Rostrum with or without ventral teeth. Antero-inferior angle of carapace dentiform. Telson armed with three pairs of fixed spines. Telson, carapace and abdomen covered by dense pubescence. External margin of uropodal exopods with strong tooth proximad the tip. Incisor process of mandible elongate, scimitar-like, lying transversely behind labrum. Petasma simple, open, often asymmetrical. Thelycum simple, with deep seminal receptacle, open or closed by paired flaps. Only one species was represented in the study material. Dall (1957) presented a key to the known species of Funchalia.

Funchalia taaningi Burkenroad

Funchalia taaningi Burkenroad, 1940: 36.

<u>Collection Records:</u>	JRM-22:	8(2).
	HMS-27:	25(1); 40(1); 65(2).
	HMS-30:	12(1); 60(1); 63(1); 65(1).
	YALOC 66:	823(2).

Diagnosis: Rostrum without ventral teeth. Antennal spine present. Hepatic spine absent in adults. Rostrum with 5+1 to 6+1 dorsal teeth. Frontal margin of carapace sloping posteriorly ventral

to pterygostomian spine. Petasma without projection on ventral surface of free distal part of larger endopod. Thelycum with large median tooth-like tubercle behind seminal receptacle.

Distribution: Funchalia taaningi is known from the Indian Ocean (Dana Station 3920 III), from which it was described in a preliminary fashion by Burkenroad (1940); the species has not been fully described nor illustrated. Little is known of the bathymetric range, development or habits of Funchalia (Gordon and Ingle, 1956). All Funchalia spp. have to date been collected in the open ocean. Foxton (1970b) considered F. villosa (Bouvier) to be a shallow mesopelagic species which undergoes a marked diurnal migration. Specimens of F. taaningi in the present material were taken from tows in the upper 200 m, and in one tow from the depth range 0-2700 m.

Family Sergestidae

Carapace moderately compressed, rostrum shorter than eye-stalks, small, sometimes rudimentary. Lower flagellum of first antenna in male modified as prehensile organ. First maxilliped with well-developed epipod and exopod. Third maxilliped and all pereopods without exopods. Gills few. Fourth and fifth pereopods reduced or absent. Petasma always symmetrical. No thelycum, but sternite between third pereopods, sometimes also fourth pereopods, and the coxa of third pereopods in females modified.

Only two genera, Sergestes and Petalidium, were taken; these are morphologically similar in many respects (Hansen, 1922, p. 189; Wasmer, 1972b).

Key to the Genera of Sergestidae

1. Arthrobranchs of up to 13 rami, with as many as 12 lamellae per rami; lamellae relatively large and independent in appearance; petasma with processus ventralis forked Petalidium
- Arthrobranchs with more than 13 rami, with more than 12 lamellae per rami; lamellae small and closely spaced; petasma with processus ventralis not forked.....
..... Sergestes

Genus Sergestes H. Milne-Edwards, 1830

Sergestidae with first three pairs of pereopods elongate; first pereopod with reduced chela; second and third pereopods nearly always with very small chelae; fifth pereopod much shorter than fourth, both natatory. Branchial lamellae as well as arthrobranchs present; lamellae on rami closely spaced, more than 13 lamellae per rami; always two arthrobranchs above fourth pereopod, none above fifth. Processus ventralis of petasma not forked. (Adapted from Yaldwyn, 1957).

Yaldwyn (1957) discussed the past history of this rather unwieldy genus, gave formal definitions of the two subgenera, and presented keys to the major groups of species within each subgenus.

At least 58 species are currently accepted. The systematics of the genus is complicated by the fact that in 1940 Burkenroad described 18 new species of Sergestes in a preliminary fashion, without illustrations, by comparing them to one another and to previously described species. The result of this is that it is now very difficult to identify many of the species he has dealt with in such a manner since most of these have yet to be fully described and illustrated. Two of the species thus described by Burkenroad were taken in this study.

Three types of luminous organs occur in the genus, although no species has more than one type and some have none at all (Yaldwyn, 1957). The two subgenera are defined partly on the basis of the type of luminous organs present. Characters useful in distinguishing the species include the following: the petasma; features of the third maxillipeds; and the pattern of dermal photophores in those species which have them.

In addition to the species of Sergestes discussed here, specimens representing five apparently undescribed species were also taken. These all belong to Yaldwyn's (1957) "S. robustus" group of the subgenus Sergia (with photophores of the lens-less "opaque spot" type); since these are each represented by only one specimen, and all are somewhat damaged, they have not been included in this discussion, but perhaps will be described at a later date.

Key to the Subgenera of Sergestes

1. Specialized luminescent modifications of gastrohepatic gland (organs of Pesta) present and without dermal photophores; color in life due to red subcuticular chromatophores mainly concentrated on the anterior part of the body.....
..... subgenus Sergestes s. s.
- Without specialized luminescent modifications of the gastrohepatic gland (organs of Pesta); with or without dermal photophores, which when present may or may not have cuticular lenses; adults with red cuticular pigment distributed over entire body and appendages in life.....
..... subgenus Sergia

Key to the Species of Subgenus Sergestes s. s.

1. Third maxillipeds subequal with third pereopods..... 2
.....
- Third maxillipeds greatly enlarged, considerably longer than third pereopods 3
2. Third segment of antennular peduncle shorter than first; petasma with processus uncifer terminally hooked
..... S. similis
- Third segment of antennular peduncle subequal or longer than first; petasma with processus uncifer not terminally hooked S. atlanticus
3. Two distal segments of the fifth pereopods setose on both margins; petasma with processus uncifer well-developed and with long pars media 4
- Two distal segments of the fifth pereopods setose on only one margin; petasma with rudimentary processus uncifer and with short pars media 5
4. Fifth and sixth segments of third maxillipeds with comb-like row of short spines S. pectinatus

- Fifth and sixth segments of third maxillipeds without comb-like row of short spines; spines variable in size S. sargassi
- 5. Dactyl of third maxilliped with four subsegments; outer margin of uropodal exopodite not setose proximally 6
- Dactyl of third maxilliped with six subsegments; outer margin of uropodal exopodite setose for entire length 7
- 6. Uropodal exopodite setose for about five-sixths length of outer margin; dactyl of third maxilliped with 20-25 spines S. vigilax
- Uropodal exopodite setose for about two-thirds length of outer margin; dactyl of third maxilliped with 13-15 spines S. armatus
- 7. Inner margin of dactyl of the third maxilliped with 37 spines, excluding the two terminal spines S. orientalis
- Inner margin of the dactyl of the third maxilliped with 47-50 spines, excluding the two terminal spines S. consobrinus

Sergestes (Sergestes) similis Hansen

Sergestes atlanticus Bate, 1888: 390 (in part).

Sergestes similis Hansen, 1903; 60, pl. 11, figs. 6a-6b; Milne, 1968; 22, figs. 1-4.

nec Sergestes arcticus, Cecchini, 1928: 33.

Collection Records: JRM-22: 20(95).

HMS-30: 30(25); 33(47); 36(10);

38(9); 40(18); 42(14); 45(14); 75(10); 78(53); 80(74); 82(38); 85(59);

88(210); 91(2); 95(11); 98(14).

SICS -PAC: 601(816); 602(769);
603(5); 604(10); 605(58); 606(2); 607(2); 611(3); 613(4); 614(2); 615(7).

YALOC 66: 835(20); 836(25); 837(11);
843(33); 849(21); 850(19); 854(5); 855(9); 856(15); 857(66); 860(41);
861(37); 865(408); 866(3165); 867(70); 868(151).

Trans-PAC: 1(71); 2(34); 4(7); 6(78);
7(73); 8(44); 10(11); 12(12); 14(9); 16(1); 24(21); 25(11); 27(2); 28(7);
30(13); 32(10); 33(54); 34(25); 36(12); 37(13); 38(33).

Diagnosis: Posterior arthrobranch above third pereopod not quite half as long as anterior arthrobranch above fourth pereopod, and semi-rudimentary. Petasma with lobus terminalis longer than processus ventralis and not armed distomedially; lobus armatus not armed with crochets along entire length of its median margin. Coxa of third pereopod in female with two pronounced, curved teeth on posteromedian margin; proximal tooth shorter, less pointed than anteriorly directed tooth.

Distribution: Sergestes similis is restricted to the northern North Pacific, where it occurs off Japan in the western Pacific and from the Bering Sea to the Gulf of California. It is apparently the only oceanic sergestid found in the mid-Pacific north of about 40°N. The species is an upper mesopelagic vertical migrator; it is often found in large numbers in near-surface waters at night off Oregon (Pearcy and Forss, 1966). In the present study, specimens were

taken in tows made from as shallow as 95 m.

More is known about the biology and ecology of Sergestes similis than any other oceanic shrimp in the North Pacific (see list of references on p. 6),

Sergestes (Sergestes) atlanticus H. Milne-Edwards

Sergestes atlanticus H. Milne-Edwards, 1830: 346, pl. 10;
Hansen, 1922: 41, pl. 2, figs. 1-2.

Collection Records: HMS-30 3(1); 6(2); 9(1).

Diagnosis: Organs of Pesta present. Rostrum rather short, directed a little ahead and upwards, triangular in side view, pointed, with the superior margin a little convex. Petasma with processus ventralis in form of large triangular plate.

Distribution: Sergestes (Sergestes) atlanticus has been reported from warmer parts of all the oceans (Sund, 1920). It has been taken in the uppermost water layers, though the adults seem to descend to intermediate depths. The specimens taken in this study were all taken within 215 m of the surface.

Sergestes (Sergestes) pectinatus Sund

Sergestes henseni, Hansen, 1896: 959 (part not S. henseni Ortm.)

Sergestes pectinatus Sund, 1920: 24, fig. 42-43; Hansen, 1922: 142 pl. 8 fig. 4.

Collection Records: HMS-30: 3(1); 15(1).

SICS-PAC: 610(2).

YALOC 66: 820(9); 830(4).

Diagnosis: Organs of Pesta present. Dactyl of third maxilliped subdivided into five subsegments, terminating in one large spine; dactyl and propodus armed on inferior border with series of closely placed small spines, interspersed with six larger spines, the entire series appearing comb-like. Processus ventralis of petasma fairly long, slim, and unarmed; lobus armatus almost cylindrical, shorter than processus ventralis and processus terminalis, armed distally with two crochets; processus uncifer hooked, not reaching base of lobus armatus. Sternite between third pereopods in female with a transverse ridge or raised area at posterior border, interrupted in the midline; median surface of coxa of third pereopod with a single anteriorly curved tooth.

Distribution: Sergestes pectinatus has previously been reported from the Atlantic and Indian Oceans; the specimens taken in the present study extend the geographical range of the species into the Pacific for the first time. Foxton (1970b) concluded that the species is a shallow mesopelagic species which migrates vertically at night; it had a day range of 580-700 m, migrating at night to the upper 100 or so meters. The specimens recorded here were most often taken in tows made in the upper 228 m, except for the two

from the SICS-PAC which were taken in a trawl towed through a depth range of 0-2450 m.

Sergestes (Sergestes) sargassi Ortmann

Sergestes sargassi Ortmann, 1893: 34, pl. 3, fig. 1; Hansen, 1922: 148, pl. 9, figs. 2-3.

Collection Records: HMS-30: 23(1).

SICS-PAC: 608(1); 610(1).

YALOC 66: 826(1); 830(4); 831(3);

833(1).

Diagnosis: Organs of Pesta present. Dactyl of third maxilliped subdivided into five segments, terminating in three spines, two large and one small; first and second subsegments have large spine at distal end of segment, near superior border; inferior border of dactyl has large number of spines of various sizes. Lobus armatus of petasma two-thirds or more the length of processus ventralis, the latter of which bears five or more large stellate spinules and row of simple spines; lobus terminalis armed only with a single crochet at tip; lobus connectens represented by large crochet on external surface of lobus terminalis. Postero-medial edge of coxa of third pereopod in female with two curved, pointed teeth, the distal of the two teeth smaller; margin of the coxa between the two teeth often appears -shaped.

Distribution: Sergestes sargassi previously has been recorded only from the Atlantic and the western Mediterranean Sea; the specimens taken in the present study extend the geographical range of the species into the Pacific for the first time. Foxton (1970b) concluded that the species is a shallow mesopelagic species, with a daytime distribution between 300 and 950 m; at night, the distribution was shifted by migration to between 110 and 435 m, with the maximum at 150 to 200 m. The specimens recorded here were taken in tows made in the upper 280 m, as well as in two deeper tows to 2400 m.

Sergestes (Sergestes) vigilax Stimpson

Sergestes vigilax Stimpson, 1860: 114; Hansen, 1922: 159, pl. 1, fig. 8, pl. 9, fig. 4, pl. 10, figs. 1-3.

<u>Collection Records:</u>	JRM-22:	2(1)
	HMS-30:	3(2)
	SICS-PAC:	610(2).
	YALOC 66:	820(1); 830(1).

Diagnosis: Organs of Pesta present. Uropodal exopodite setose for about five-sixths length of outer margin. Inferior border of dactyl armed with 21-27 spines of varying lengths, terminal spines well-developed. Processus ventralis of petasma small, slender, with pointed end; lobus terminalis long, thick, with several large crochets distally on anterior face; lobus inermis shorter and thicker

than lobus terminalis, expanded distally, unarmed. Genital area of female with operculum covering most of sternite between third pereopods, its posterior margin concave in middle; coxa of third pereopod with single postero-medial projection.

Distribution: The species has been reported previously from the central Atlantic, Indian, and Pacific Oceans. The Pacific record (Bate, 1888) was that of a mastigopus stage, S. parvidens, taken north of the Hawaiian Islands and off Sydney and Wellington, Australia (see Hansen, 1922, p. 172). The specimens from the present study are apparently the first adult S. vigilax recorded from the Pacific. Foxton (1970b) concluded that the species is a shallow mesopelagic species that undergoes diurnal vertical migration; during the day it was taken between 575 and 950 m with a maximum of 650 m, while at night the upper limit and maximum moved upward to 110 m. The specimens recorded here were taken in tows made in the upper 200 meters, with the exception of one tow from 0-2450 m.

Sergestes (Sergestes) armatus Kröyer

Sergestes armatus Kröyer, 1855: 10; Hansen, 1922: 174, pl. 10, fig. 6; Barnard, 1950: 643, fig. 120.

Collection Records: HMS-30: 23(1); 27(1); 54(1); 67(2); 69(3).

SICS-PAC: 609(3); 610(6); 611(4);

612(1).

YALOC 66: 820(2); 830(3); 831(1).

Diagnosis: Organs of Pesta present. Uropodal exopodite setose for about one-third length of outer margin. Inferior border of dactyl armed with 13-15 spines of varying lengths, terminal spine well-developed. Processus ventralis of petasma small, slender, with blunt end; lobus terminalis rather long, finger-shaped, with four crochets on medio-distal edge; lobus inermis shorter than lobus terminalis, not expanded distally, unarmed. Genital area of female with operculum covering most of sternite between third pereopods, evenly rounded posteriorly; coxa of third pereopod with single distally expanded postero-medial projection.

Distribution: This species has previously been identified with certainty only in the North and South Atlantic. Bate's specimens (1888) from the Pacific and from Australian waters are not referable to S. armatus (see Hansen, 1903, p. 63). The specimens recorded here thus are the first from the Pacific. Foxton (1970b) considered the species to be a shallow mesopelagic vertical migrator, with a restricted day time range with an upper limit at 480 m and a possible lower limit at 600 m; the shallowest night occurrence was at 110 m. The specimens recorded here were generally taken within the upper 250 meters, except for several tows through a range of 0-2000 m.

Sergestes (Sergestes) orientalis Hansen

Sergestes orientalis Hansen, 1919: 22, pl. 2, figs. 2a-2q.

Collection Records: YALOC 66: 824(2).

Diagnosis: Organs of Pesta present. Rostrum rather short, directed forwards and somewhat upwards, obliquely triangular, acute. Inner margin of dactyl of third maxilliped with 37 spines and two terminal spines. Petasma with processus ventralis minute, oblong-triangular, with distal part very narrow; lobus connectens moderately short, very thick, with end broadly rounded; lobus armatus short, broad, divided into two diverging branches; lobus inermis longer than other lobes, very thick to the broad, obtuse end, without hooks; middle of three projections along lateral margin of pars media low and rounded.

Distribution: The species has only definitely been reported previously from the China Sea and southeast of South Africa (Hansen, 1919). Milne (1968) was of the opinion that the specimens reported as S. edwardsi by Rathbun (1906) from the Pacific and by Illig (1927) from the Indian Ocean are probably S. orientalis. Hansen (1919) recorded the species from tows made in the depth range of 0-2000 m. The specimens reported here were taken in a tow made through a depth range of 0-2000 m.

Sergestes (Sergestes) consobrinus Milne

Sergestes (Sergestes) consobrinus Milne, 1968: 26, figs. 5-9.

Collection Records: YALOC 66: 820(6); 825(1).

Diagnosis: Inner margin of dactyl of third maxilliped with from 47-50 spines and two terminal spines of unequal lengths. Petasma with processus ventralis rudimentary, very small, conical; lobus connectens large and strongly bilobed; lobus armatus anteriorly coiled, with many large crochets; lobus inermis very long, slender, without hooks; middle of three projections along lateral margin of pars media about same height or higher than other two, with blunt or squared distal edge.

Distribution: The species has been recorded only from the Pacific; Milne (1968) recorded it from off the coast of California from south of 41° 10' N to 32° 06' N. It has been taken from depths of 20 m to about 40 m, with the greatest numbers taken at about 120 m. The specimens recorded here were taken in tows made through a depth range of 0-200 m.

Key to the Species of Subgenus Sergia

1. Dermal photophores (lens-bearing or lens-less) present on body and appendages; integument not membraneous..... 2

- No dermal photophores present on body or appendages;
integument membranous 6
- 2. Photophores of the lens-bearing type 3
- Photophores of the lens-less "opaque spot" type 5
- 3. Antennal scale with row of four photophores; lobus armatus
of petasma biramous; genital area of female with two
subparallel longitudinal ridges on sternite between coxae
of third pereopods, their posterior portions strongly
curved S. (Sergia) talismani
- Antennal scale with more than four photophores; lobus
armatus of petasma not biramous; genital area of female
without two longitudinal ridges between coxae of third
pereopods 4
- 4. Antennal scale with row of seven photophores; processus
ventralis of petasma small, not two-fifths as long as lobus
armatus; posteromedian tooth-like projection of coxa of
third pereopod of female curved and elongate, reaching
more than halfway to midline of sternite
..... S. (Sergia) scintillans
- Antennal scale with row of 9-13 photophores; processus
ventralis of petasma longer than lobus armatus; postero-
medial tooth-like projection of coxa of third pereopod of
female reaching less than halfway to midline of sternite
..... S. (Sergia) prehensilis
- 5. Rostrum high, projecting obliquely upwards and forwards;
apex slender and acutely pointed; ventro-distal margin
concave; a prominent tooth in middle of dorsal edge
..... S. (Sergia) gardineri
- Rostrum very short and deep with a marked ventro-distal
angle, nearly square; with a short point and no more than
a rudiment of a dorsal tooth S. (Sergia) bigemmeus
- 6. Cornea of eyes much broader than distal part of ocular
peduncle; peduncle with elongate ocular tubercle
..... S. (Sergia) tenuiremis

- Cornea of eyes barely wider than distal part of ocular peduncle; no ocular tubercle on peduncle S. (Sergia) japonicus

Sergestes (Sergia) talismani Barnard

Sergestes splendens Hansen, 1920: 480; 1922: 121, pl. 7, figs. 2a-2o.

Sergestes talismani Barnard, 1947: 384 (nov. nom. for S. splendens Hansen)

Collection Records: HMS-30: 3(11).

Diagnosis: Organs of Pesta absent; numerous dermal photophores with well-developed cuticular lenses present. Antennal scale with row of four photophores; five to six photophores in horizontal line on inner surface of carapace above gills; two photophores on uropodal exopodite; others as listed by Hansen, 1922, p. 123. Processus ventralis of petasma slender, extending as far as lobus terminalis, extremity pointed, curved to exterior; lobus armatus biramous, external branch about twice as long as internal branch; lobus terminalis shorter than lobus connectens, bilobed; lobus inermis moderately long, extending beyond lobus terminalis, curved to exterior distally. Operculum on genital area of female rather short, its anterior border very convex, its posterior border slightly convex, anterior border somewhat raised above sternite of preceding somite; sternite between coxae of third pereopods with two

subparallel longitudinal ridges which are strongly curved to exterior posteriorly.

Distribution: The species has previously been reported only from the North Atlantic Ocean, from the west of the Cape Verde Islands, and from 16° 52' N-27° 32' W (Hansen, 1922), from depths of 550-760 m. The specimens of the species from the present study agree with Hansen's (1922) description and figures of the species, and thus extend the known geographical range of the species into the Pacific; they were taken in a tow made in the depth range of 0-192 m.

Sergestes (Sergia) scintillans Burkenroad

Sergestes (Sergia) scintillans Burkenroad, 1940: 43.

Collection Records: HMS-27: 15(8); 43(2); 68(2).

HMS-30: 3(2); 6(1); 9(3); 12(2);

15(2); 63(1); 113(1).

YALOC 66: 826(1).

Diagnosis: Organs of Pesta absent; numerous dermal photophores present with well-developed cuticular lenses. Row of seven photophores in antennal scale; 12 very minute photophores in branchiostegite, parallel with lower border of carapace; four in midline of sixth pleonic sternite; two or three in exopodite of uropod; and others. Petasma with small processus ventralis, less than two-fifth as long as the short, stout lobus armatus; lobus terminalis small, closely

applied to anterior base of lobus connectens; lobus inermis large, lamellar, oblong, and widely separated from lobus connectens. Postero-medial tooth-like projection of coxa of third pereopod in female curved and elongate, reaching more than halfway to midline of sternite.

Distribution: The only previous record of the species is that of the holotype from 25° 54' S 172° 36.9' E in the South Pacific ("Dana" Station 3622I). The specimens collected in the present study were generally taken in tows made in the upper 250 m. This is one of the species described in a preliminary fashion by Burkenroad (1940); it has yet to be fully described and illustrated.

Sergestes (Sergia) prehensilis Bate

Sergestes prehensilis Bate, 1888: 385, pl. 71; Gordon, 1935: 314, figs. 1a-1b, 3b-3c, 6c-6d, 8, 9.

Sergestes gloriosus Stebbing, 1905: 84, pls. 22, 23; Hansen, (p. 24, in Calman, 1925).

Nec. Sergestes prehensilis of Japanese authors (= S. lucens Hansen, 1922).

Collection Records: Trans-PAC: 16(7).

Diagnosis: Organs of Pesta absent; numerous dermal photophores with well-developed cuticular lenses present. Antennal scale with row of 9-13 photophores; 4 or 5 minute photophores in horizontal line above gills inside carapace; a series of 12-20 minute photophores

in branchiostegite parallel with lower border of carapace; see list and diagrams of others in Gordon (1935). Processus ventralis of petasma longer than lobus armatus; lobus terminalis small, closely applied to base of lobus connectens. Postero-medial tooth-like projection of coxa of third pereopod in female reaching less than halfway to midline of sternite.

Distribution: The species was described from the North Pacific off Japan, where the type was taken by the "Challenger" (Bate, 1888). It has been reported only once since from this region of the Pacific (Aizawa, 1969); the S. prehensilis of previous Japanese workers is in reality S. lucens Hansen (see Gordon, 1935 and Omori, 1969). S. prehensilis has also been recorded from off the east and west coasts of South Africa.

Aizawa (1969) concluded that the species migrates vertically, since it had a daytime range of distribution from 400-800 m and a nighttime distribution from 0-300 m. The specimens in the present study were taken in a trawl which was towed through a depth range of 0-350 m.

Sergestes (Sergia) gardineri Kemp

Sergestes gardineri Kemp, 1913: 55, pl. 7, figs. 2-5; Hansen, 1919: 9, pl. 1, figs. 2a-2c.

Collection Records: HMS-27: 15(2); 18(1).

HMS-30: 6(1); 113(1).

Diagnosis: Organs of Pesta absent; with numerous minute lens-less dermal photophores. Rostrum high, projecting obliquely upwards and forwards; apex slender and acutely pointed; ventrodorsal margin concave; a prominent tooth in middle of dorsal edge. Uropodal exopodite with row of about 9-12 very minute photophores close to median margin along nearly its entire length; antennal scale with similar row of 16-17 photophores placed farther from margin; sixth pleonic sternite without median photophores, but with row of minute ones along its lateral margins; and others. Petasma without lobus accessorius; lobus armatus curved, shorter than processus ventralis; lobus terminalis about one-half as long as lobus connectens; processus ventralis longer than lobus inermis, both armed with crochets.

Distribution: The species has previously been recorded only from the Indian Ocean, where it has been taken in tows made between 2000 meters and the surface. The specimens taken in this study extend the range of the species into the Pacific; they were taken in tows made within 224 meters of the surface.

Sergestes (Sergia) bigemmeus Burkenroad

Sergestes (Sergia) bigemmeus Burkenroad, 1940: 49.

Collection Records: SICS-PAC: 609(2).

YALOC 66: 830(1).

Diagnosis: Organs of Pesta absent; with numerous minute lens-less dermal photophores. Rostrum very short and deep with a marked ventro-distal angle, nearly square; with a short point and no more than a rudiment of a dorsal tooth. Uropodal exopodite with row of about 12-14 very minute photophores placed close to median margin along nearly its entire length; antennal scale with a similar row placed farther from the margin; sixth pleonic sternite without median photophores, but with row of minute ones along its lateral margins; and others. Petasma with well-developed lobus accessorius and lobus inermis; lobus armatus straight, longer than processus ventralis, reaching almost as far as lobus connectens; lobus terminalis less than a third as long as lobus inermis and directed laterally. Postero-medial projection of coxa of third pereopod in female broad and subrectangular.

Distribution: The only previous record of the species is that of the holotype from 14°01'S 147°51.5'W in the South Pacific ("Dana" Station 3570VI). The specimens taken in the present study were taken in tows made through the depth ranges of 0-250 m and 0-2000 m. This one of the species described in a preliminary fashion by Burkenroad (1940); it has yet to be fully described and illustrated.

Sergestes (Sergia) tenuiremis Kröyer

Sergestes tenuiremis Kröyer, 1855: 30; 1859: 255, 278, 285, pl. 4, fig. 11a-11b; Hansen, 1922: 81, pl. 4, figs. 4a-4o.

Collection Records: SICS-PAC: 610(2).

YALOC 66: 857(2).

Diagnosis: Organs of Pesta absent; no dermal photophores present; integument membranous. Rostrum short, low and obtuse, hardly projecting beyond anterolateral margin of carapace. Cornea of eyes much broader than ocular peduncle; a rather small, sub-cylindrical, distally rounded ocular tubercle present on peduncle. Two arthrobranchs above third pereopod. Lobus armatus of petasma rather long, thick at base, strongly curved distally; lobus accessorius at base of lobus armatus about as thick as long; lobus connectens long, exceeding processus ventralis in length, thick basally, quite slender distally; lobus inermis long, curved a little toward median, exceeding all other lobes in length. Operculum of genital area of female short, with its middle posterior border angular. Coxa of third pereopod in female with two medial projections, the anterior one small, the posterior one average in size, curved a little, acute.

Distribution: The species has been recorded from the Atlantic, Indian and Pacific Oceans; it appears to be most common in the

northeastern Atlantic. The only previous records of the species from the Pacific are those cited by Bate (1881, 1888), as S. kroyeri, from northeast of New Zealand, and by Rathbun (1906) from the Hawaiian Islands. Foxton (1970b) concluded that it appears to be a deep mesopelagic species that migrates to mid-depths at night. The specimens reported from the present study were taken in trawls towed through depth ranges of 0-2450 m and 0-3000 m.

Sergestes (Sergia) japonicus Bate

Sergestes japonicus Bate, 1881: 194.

Sergestes mollis Smith, 1884: 419; 1886: 93, pl. 20, figs. 3-5;
Hansen, 1922: 75, pl. 4, fig. 3.

Sergestes (Sergia) japonicus, Yaldwyn, 1957: 22, figs. 6-9.

Collection Records: YALOC 66: 857(3).

Diagnosis: Organs of Pesta absent; no dermal photophores present; integument membraneous. Rostrum small and obtuse, hardly projecting beyond anterolateral margin of carapace and little raised above dorsal surface of carapace. Eyes small, cornea barely wider than distal part of ocular peduncle; no ocular tubercle on peduncle. An arthrobranch and branchial lamella above third pereopod. Lobus connectens of petasma very long; processus ventralis shorter, with distinct distal neck; lobus armatus curved, shorter than processus ventralis; lobus terminalis a simple armed

projection between unarmed lobus inermis and base of lobus connectens. Operculum of genital area of female quite long, its posterior border strongly convex. Coxa of third pereopod in female with single blunt postero-medial projection.

Distribution: Sergestes (Sergia) japonicus was originally described from specimens taken from off Japan and the Philippines by the "Challenger" (Bate, 1881, 1888). Sergestes mollis was described from specimens taken from the western Atlantic off the east coast of the U.S.A.; this species has been shown to be synonymous with S. japonicus Bate (see Hansen, 1896; Burkenroad, 1940, p. 53). It is a well-known deep mesopelagic species in the North Atlantic, where it has been recorded by many workers. The only other record for the species from the Indo-Pacific region is that of Yaldwyn (1957), who recorded it from Cook Strait, New Zealand. The three specimens recorded here are the first records from the northeastern Pacific; I have recently seen another specimen of the species, on deposit in OSU Oceanographic collections, which was taken on 31 May, 1970 at 44° 46.3'N 131° 25.6'W by a one-half meter net attached to the beam of a beam trawl which was towed through a depth range of 0-3354 m.

Specimens taken on the SOND Cruise (Foxton, 1970b) had a daytime upper limit at 800 m with a possible maximum at 950 m, while the nighttime upper limit occurred at 580 m with a maximum at 920 m; presumably, migration upward at night of a part of the

population occurring below 950 m by day was responsible for this small vertical displacement of the population. The specimens taken in the present study were taken in a trawl towed through the depth range of 0-3000 m.

Genus *Petalidium* Bate, 1881

Sergestidae with first three pairs of pereopods elongate; first pereopod with reduced chela; second and third pereopods with very small chelae; fifth pereopod much shorter than fourth pereopod, both natatory. Branchial lamellae as well as arthrobranchs present; arthrobranchs of up to 13 rami, with as many as 12 lamellae per rami; lamellae relatively large and independent. Number of arthrobranchs above fourth pereopods variable: none, a single rudimentary, or two may be present; none above fifth. Processus ventralis of petasma forked.

Only one species, *Petalidium suspiriosum*, has been reported from the North Pacific; previously known only from two females, it has recently been redescribed (Wasmer, 1972b).

Petalidium suspiriosum Burkenroad

Petalidium suspiriosum Burkenroad, 1937: 325, figs. 8-12;
Wasmer, 1972b.

Collection Records: SICS-PAC: 610(33); 611(21); 613(39).

YALOC 66: 857(4); 866(4).

Diagnosis: A well-developed anterior arthrobranch of nine rami, with up to six lamellae per rami, and a small posterior arthrobranch of three rami bearing several lamellae each above fourth pereopod. An anterior arthrobranch, which may have up to thirteen rami, with up to twelve lamellae per rami, and a posterior arthrobranchial lamella above third maxilliped and first three pereopods. Posterior, secondary branch of lobus armatus of petasma reaching beyond middle of primary branch, armed with up to six crochets; external branch of processus ventralis reaching beyond external branch, and almost as far as internal branch, of lobus terminalis. Genital area of female without an operculum.

Distribution: The species is only known from the northeastern Pacific Ocean. It appears to be mainly mesopelagic in distribution; results of collections made over a period of three years from the upper 1500 m of water off the central Oregon coast (44° 39' N 125° 15' W) show P. suspiciosum to be most abundant in the depth range of 200-1000 m (Pearcy and Forss, 1966). Specimens in the present study were taken in tows made through the depth ranges of 0-200 m and as deep as 0-3000 m.

Section CARIDEA

Abdomen generally sharply flexed at third abdominal segment. Pleurae of second abdominal segment overlapping those of first and third segments. Third pereopods never chelate. First pleopods of male without petasma. Eggs carried on pleopods by females.

Key to the Families of Caridea

1. Exopods on some or all pereopods; first two pairs of pereopods obviously chelate; second pereopods with an undivided carpus; mandibles imperfectly cleft and with or without a palp 2
- No exopods on any pereopods; first pereopods simple or microscopically chelate; second pereopods with a segmented carpus; mandibles with a three-jointed palp Pandalidae
2. First two pairs of pereopods much longer and stouter than last three pairs Pasiphaeidae
- First two pairs of pereopods shorter than last three pairs Oplophoridae

Family Pasiphaeidae

Rostrum short or represented by a post-frontal gastric spine. First two pairs of pereopods chelate, much longer and stouter than last three pairs, and with carpus undivided. Exopods present on all pereopods, much reduced or absent on second maxillipeds. Terminal joint of second maxilliped attached terminally to preceding

joint. Mandibular palp present or absent mandibles without a molar process.

Key to the Genera of Pasiphaeidae

1. Rostrum in form of a post-frontal spine; no mandibular palp Pasiphaea
- Rostrum a normally directed forward projection arising from frontal margin of carapace; two-jointed palp present in mature forms Parapasiphae

Genus Pasiphaea Savigney, 1816

Rostrum represented by a post-frontal gastric spine. Orbits poorly defined. Fourth pereopods shorter than fifth. Mandible without a palp. Only one species was taken in the study material. The key to species of Pasiphaea includes species not taken during the present study, but known to occur in the study area.

Key to the Species of Pasiphaea

1. Telson distally forked or notched 2
- Telson distally truncate 3
2. Rostrum a sharp-pointed tooth arising from anterior gastric region, falling far short of frontal margin of carapace .. [P. pacifica Rathbun, 1902]
- Rostrum low and elongate in large specimens, extending beyond frontal margin of carapace; in small specimens, rostrum somewhat higher and shorter, reaching to or beyond frontal margin P. tarda

3. Telson terminating in four pairs of spines; rostrum long and slender [P. chacei Yaldwyn, 1962]
- Telson terminating in six pairs of spines and small median unpaired spine; rostrum heavy, triangular in shape
..... [P. magna Faxon, 1893]

Pasiphaea tarda Kröyer

Pasiphaea tarda Kröyer, 1845: 453; Sivertsen and Holthuis, 1957: 23, fig. 17.

Pasiphaea princeps Smith, 1884: 381, pl. 5, fig. 2.

Pasiphaea principalis Sund, 1913: 6, figs. 5-7, 9a-f.

Collection Records: YALOC 66: 849(5); 854(2); 857(1).

Diagnosis: Telson dorsally sulcate, distally forked or notched. Rostrum shape varies with the size of the specimen, in large specimens, the rostrum is low and elongate, extending beyond frontal margin of carapace; in smaller specimens, rostrum is somewhat higher and shorter, reaching to or beyond frontal margin of carapace. Abdominal somites 2-6 dorsally carinate.

Distribution: Pasiphaea tarda has been taken from the northern Atlantic Ocean, where it has been taken as far south as the Bay of Biscay on the European side and to off South Carolina on the North American coast. Rathbun (1904) reported it from Unalaska and off Washington, while Faxon (1895) recorded a specimen from off Ecuador. The species has been reported from depths between 250 and 2400 m (Sivertsen and Holthuis, 1957). Specimens in the present

study were taken in the depth range 0-3000 m. An ovigerous female with a carapace length of 48 mm was taken in a tow through a depth range of 0-2400 m.

Sivertsen and Holthuis (1957) discussed the variation of the rostrum shape with size of the specimens and established the present synonymy of the species.

Genus *Parapasiphae*, Smith, 1884

Rostrum arising from frontal margin. Fourth pereopod shorter than fifth. Mandible with a two-jointed palp in mature forms; Forss (1966) reported that immature forms have no mandibular palp, and that subadult forms have a one-segmented palp.

Key to the Species of *Parapasiphae*

1. Dorsal carina of carapace unarmed, sulcate anteriorly; fingers of second chela not longer than palm..... *P. sulcatifrons*
- Dorsal carina of carapace with one or two spines or sometimes smooth, not sulcate; fingers of second chela distinctly longer than palm *P. cristata*

Parapasiphae sulcatifrons Smith

Parapasiphae sulcatifrons Smith, 1884: 384, pl. 5, fig. 4, pl. 6, figs. 1-7; Pequegnat, 1970: 66.

Collection Records: YALOC 66: 866(1).

Diagnosis: Dorsal carina of carapace unarmed dorsally, but the anterior fourth is broadened and provided with a well-developed groove in adults. Rostrum reaches middle of eyestalk. No spine on anterior edge of lateral portion of carapace. Abdomen with small median spine dorsally at end of fourth somite. Fingers of second chela not longer than palm.

Distribution: Parapasiphae sulcatifrons has been reported in the Atlantic Ocean, from Greenland and Iceland southward to the Gulf of Mexico along the east coast of North America and to off the French Congo and South Africa in the eastern Atlantic. It has also been reported from the southern Indian Ocean. Forss (1966) recorded it for the first time from the Pacific Ocean off Oregon. Butler (1971) recorded a single specimen from off Vancouver Island, British Columbia (51° 26'N 131° 09'W). It has been taken from a depth range of 500-5400 m; Pearcy and Forss (1966) recorded it only from 500-1000 m off Oregon. The specimen in the present study was taken from a depth range of 0-2500 m.

Parapasiphae cristata Smith

Parapasiphae cristata Smith, 1884: 388, pl. 5, fig. 3; Pequegnat, 1970: 65.

Collection Records: SICS-PAC: 613(3).

Diagnosis: Dorsal carina of carapace armed with one or two

teeth above orbit, or if unarmed, not sulcate anteriorly. Rostrum reaches as far as cornea. No spines on anterior edge of lateral portion of carapace. Abdomen with small median spine dorsally at end of fourth somite. Fingers of chela distinctly longer than palm.

Distribution: Parapasiphae cristata has been reported from the North Atlantic, where it has been taken off the east coast of the United States to the Gulf of Mexico and from the Hebrides to the Azores. Forss (1966) recorded it for the first time from the Pacific Ocean off Oregon. Pequegnat (1970) gave a depth range for the species of 1000-2659 m; Percy and Forss (1966) recorded it off Oregon only from 500-1000 m. The three specimens in the present study were taken from an open trawl which sampled the depth range of 0-2450 m.

Family Oplophoridae

Rostrum variable in shape. First two pairs of pereopods chelate, shorter than the last three pairs; carpus of second pereopods undivided. Exopods present on all maxillipeds and pereopods. Terminal joint of second maxilliped attached laterally to the end of the preceding joint. Mandibles imperfectly cleft and with a palp. The family includes seven genera, six of which have been taken previously in the North Pacific; species from five genera were taken in the present study. Meningodora mollis Smith, 1882, a species not

taken in the study, was reported from the northeastern Pacific for the first time by Forss (1966).

Key to the Genera of the Family Oplophoridae (adapted from Holthuis, 1951).

1. Exopods of at least third maxillipeds and first pair of pereopods foliaceous and generally rigid .. Oplophorus
- None of the exopods of pereopods foliaceous or rigid .. 2
2. Last four abdominal somites, at least, dorsally carinate along dorsal midline 3
- Sixth abdominal somites never dorsally carinate 5
3. No straight ridge or carina running entire length of lateral surface of carapace from orbit to hind margin along median lateral line; hind margin of hepatic groove not cut off abruptly by an oblique ridge or carina; incisor process of mandible toothed for its entire length AcanthePHYra
- Carapace with at least one straight carina running entire length of lateral surface of carapace from orbit to hind margin; hind margin of hepatic groove abruptly cut off from branchial region by an oblique carina; anterior half incisor process of mandible unarmed 4
4. A single longitudinal carina on lateral surface of carapace; dorsal margin of carapace not denticulate on posterior three-fourths of its length; abdomen not dorsally carinate on first somite [Meningodora]
- More than one longitudinal carina on lateral surface of carapace; dorsal margin of carapace denticulate for nearly its entire length; abdomen dorsally carinate on all somites Notostomous
5. Eyes very small and poorly pigmented; telson terminating in a truncate, spinose tip, or if not truncate, then not terminating in a sharp-pointed end-piece laterally armed with spines Hymenodora

- Eyes very large and well-pigmented; telson terminating in a sharp-pointed end-piece laterally armed with spines
 Systellaspis

Genus Acanthephyra A. Milne-Edwards, 1881

Carapace without straight carina along lateral surface from orbit to hind margin and without an oblique carina delimiting hind margin of hepatic furrow. Abdomen carinate at least on last four somites. Telson slightly truncate at tip, not ending in a sharply pointed end-piece laterally armed with spines. Exopods of third maxillipeds and pereopods not foliaceous or rigid. Eyes well pigmented even when small. Incisor process of mandible toothed for entire length of its cutting edge.

Four species of Acanthephyra, including one undescribed species, were taken in the samples used in the study. A fifth species, A. microphthalma, has only recently been reported for the first time from the northeastern Pacific (Wasmer, 1972c).

Key to the Species of Acanthephyra

1. Posterior third, at least, of carapace not dorsally carinate 2
- Carapace dorsally carinate throughout its length Acanthephyra n. sp.^{4/}

^{4/} This species will be described separately at a later time.

2. Integument thin and membranous; rostrum short, reaching only to end of eyes; 3rd-5th abdominal somites serrated in dorsal midline A. prionota
- Integument hard and firm; rostrum reaching beyond eyes; 3rd-5th abdominal somites not serrated in dorsal midline 3
3. Eyes minute, very much narrower than eyestalks
..... [A. microphalma Smith, 1885]
- Eyes normal, slightly broader than eyestalks 4
4. Rostrum triangular, shorter than carapace .A. curtirostris
- Rostrum long and slender A. quadrispinosa

Acantheephyra curtirostris Wood-Mason

Acantheephyra curtirostris Wood-Mason, 1891: 195; Chace, 1940: 143, fig. 21; Figueira, 1957: 28.

Collection Records: SICS-PAC: 607(1); 608(4); 611(7);

612(2); 613(4).

YALOC 66: 866(2).

Diagnosis: Integument firm. Rostrum triangular, dorsally toothed, with one ventral tooth. Carapace not carinate in posterior third. Branchiostegal spine supported by a carina extending to posterior part of branchial region. All but first abdominal somite dorsally carinate; median posterior spine on third, fourth, fifth and sixth somites. Telson dorsally sulcate proximally, armed with 6-15 dorsolateral spines.

Distribution: This species ranges from the eastern Atlantic

off the east coast of Africa through the Indian Ocean, Indo-Pacific, and Pacific from the Philippines, Japan and Hawaii to off the west coast of the American Continent (Vancouver Island, British Columbia to Panama and Peru). It seems to be more rare in the Atlantic where it has been taken off the west coast of Africa and Madeira, and from off the Bahamas and Cuba. It has been taken from nets fishing as deep as 2000 m in the eastern Atlantic (Crosnier and Forest, 1968); Percy and Forss (1966) reported it only from 200-1000 m off Oregon. The specimens in the present study were taken from tows made in the upper 280 m and from 0-2500 m.

Acanthephyra quadrispinosa Kemp

Acanthephyra batei Stebbing, 1905: 107, pl. 24.

Acanthephyra purpurea Stebbing, 1910: 395 (in part).

Acanthephyra quadrispinosa Kemp, 1939: 576; Barnard, 1950: 668, fig. 124, g.

Collection Records: JRM-22: 25(1).

HMS-30: 23(11); 30(13); 51(5);

65(1); 72(2); 75(1).

SICS-PAC: 607(3); 609(3); 611(2);

612(2); 613(1).

YALOC 66: 826(1); 831(3); 834(3);

835(5).

Trans-PAC: 14(2); 16(2); 24(1); 25(4).

Diagnosis: Integument firm. Rostrum long and slender, armed with dorsal and ventral teeth. Carapace not dorsally carinate posteriorly. Branchiostegal spine strong, flared outwards, supported by a short carina. Posterior tooth on 3rd-6th abdominal somites; tooth on 4th somite a little smaller than that on 5th. Telson with four pairs of dorsolateral spines.

Distribution: Kemp (1939) considered the range of A. quadrispinosa to be the South Atlantic from 32°S to 40°S, the Indo-Pacific from the East African coast to 163°W, and from 25°N to 42°S. Aizawa (1969) reported the species from off Central Japan. Butler (1971) recorded a single specimen from off Vancouver Island, British Columbia (50°56.4'N 130°12.2'W). Aizawa (1969) concluded that the species migrates vertically, with a daytime distribution between 400-1000 m and a nighttime distribution between 200-400 m. The specimens in the present study were taken in tows made in the upper 320 m and in one deeper tow (0-2400 m).

Acanthephyra prionota Foxton

Acanthephyra prionota Foxton, 1971: 35, figs. 1, 2A-2H.

Collection Records: SICS-PAC: 610(2).

Diagnosis: Integument membranous. Rostrum short, forming the termination of a convex dorsal crest which occupies the

anterior third of carapace; crest armed with five or six procumbent teeth. Carapace carinate for three-quarters or less of its length. No branchiostegal carina. Last five abdominal somites dorsally carinate; each of last four with dorsal tooth, that on the third somite large, reaching to middle of fourth somite. Dorsal serrations present on dorsal carina of 3rd-5th abdominal somites. Telson dorsally sulcate proximally, armed with four pairs of dorsolateral spines on distal half.

Acanthephyra prionota is the smallest known species of Acanthephyra; the carapace length of the type, an adult, is only 7.1 mm.

Distribution: Acanthephyra prionota was described in MS by Dr. Kemp sometime prior to 20 March 1941 on the basis of five specimens taken off the east coast of Africa to the north of the Mozambique Channel and from comparable latitudes in the Central Atlantic; Kemp's description was never published (Foxton, 1971). Foxton recorded additional specimens from recent cruises as far north in the Atlantic as the Cape Verde Islands and also from the central Indian Ocean. It has also been taken in collections made in the Eastern and Central Pacific by others (Foxton, 1971) who had recognized it as belonging to a new species. The specimens from this study were recognized as representing a new species in 1967 by Dr. Carl Forss and the author.

Foxton (1971) recorded the species only from depths below 700 m both by day and by night. The specimens in the present study were taken in a trawl which sampled the depth range 0-2450 m.

Acanthephyra new species

Collection Records: YALOC 66: 849(1); 866(4).

Diagnosis: Integument pliable. Rostrum triangular, with 6-7 dorsal teeth and one ventral tooth. Carapace carinate throughout its length. Last four abdominal somites carinate and dorsally spined. Telson dorsally sulcate, armed with 3-4 pairs of lateral spines in its distal half.

Distribution: Specimens of this new species of Acanthephyra have been taken south of the Alaskan Peninsula and in the north-eastern Pacific off the central Oregon coast. The species has been taken in trawls which sampled the depth range 0-2500 m.

Genus Notostomous A. Milne-Edwards, 1881

Lateral surface of carapace with more than one straight carina from orbit to posterior margin of carapace, and with an oblique carina delimiting hind margin of hepatic furrow. Dorsal carina of carapace denticulated throughout its length. All abdominal somites dorsally carinate. Telson apically truncate. Eyes well pigmented.

Incisor process of mandible toothed for only half length of its cutting edge.

Key to the Species of *Notostomous*

1. Gastro-orbital carina continuous with lower lateral rostral carina *N. perlatus*
- Gastro-orbital carina not continuous with lower lateral rostral carina *N. japonicus*

Notostomous japonicus Bate

Notostomous japonicus Bate, 1888: 830, pl. 135, fig. 1; Stevens and Chace, 1965: 277, fig. 2-4.

Collection Records: HMS-30: 88(3)

YALOC 66: 857(5).

Trans-PAC: 2(1); 6(4).

Diagnosis: Dorsal margin of carapace not strongly arched. Posterior half of lateral surface of carapace with four longitudinal carinae. Upper lateral rostral carina present. Gastro-orbital carina not continuous with lower lateral rostral carina. Short carina directed obliquely upward and backward from middle of gastro-orbital carina.

A female specimen from YALOC 66 Station 857 with a carapace length of 37 mm was ovigerous; this is the first record of the species which gives a clear indication of the size at which the species

becomes mature. The male holotype is the only specimen of N. japonicus on record which is larger (c. l. = 42 mm) than this ovigerous female. The eggs measure 1.3 mm in largest diameter, and are eyed.

Distribution: Notostomous japonicus was described from a single specimen trawled by the "Challenger" south of Honshu Island, Japan, from a depth of 1034 m. Stevens and Chace (1965) recorded the species from 180 to 850 miles off the west coast of North America, between the latitudes of the southern end of Queen Charlotte Island, British Columbia, and Cape Blanco, Oregon, in mid-water depths of 225-400 m. Collection of the specimens during the Hugh M. Smith Cruise 30 and the Canadian trans-Pacific cruise now make it possible to extend the range of the species into the North Central Pacific in the region south of the Alaskan Peninsula. Pearcy and Forss (1966) recorded the species only from a depth range of 200-1000 m off the central Oregon coast. Specimens in the present material were generally taken in tows made in the upper 320 m; the ovigerous female was taken in a trawl towed through a depth range of 0-3000 m.

Notostomous perlatus Bate

Notostomous perlatus Bate, 1888: 831, pl. 134, fig. 2; Kemp, 1913: 66, pl. 7, fig. 10; Chace, 1940: 170, fig. 42.

Collection Records: YALOC 66: 823(1).

Diagnosis: Integument soft. Carapace greatly inflated, dorsal margin minutely dentate for its entire length. Four lateral carinae on posterior half of carapace. No upper lateral rostral carina at base of rostrum. Gastro-orbital carina continuous with lower lateral rostral carina. Abdomen carinate on every somite and with a posterior tooth on third, fourth, fifth somites.

Distribution: The single small specimen (c. l = 7 mm) taken in the study material has been tentatively assigned to this species. Although it is in a somewhat mutilated condition due to the fragile nature of its integument, it does appear to agree with the diagnostic characters given by Chace (1940) for the species and with the published figures of the species. The specimen was taken in a trawl towed through a depth range of 0-2700 m.

All the recorded specimens of N. perlatus (except for three) have been taken within ten degrees of the equator off the coast of Brazil, off the west and east coasts of Africa, in the Indian Ocean and south of the Philippines. Chace (1940) recorded a small specimen taken south of Bermuda and mentioned the presence of two specimens in the U. S. National Museum which were taken in the Gulf of Mexico; these three records are the only known specimens outside the apparent equatorial distribution of the species.

If the present specimen is N. perlatus, then it becomes

possible to extend the known range of the species to 23°N in the North Central Pacific.

Genus *Hymenodora* G. O. Sars, 1877

Carapace without a straight carina along lateral surface from orbit to hind margin, and without an oblique carina delimiting the hind margin of the hepatic furrow. Abdominal somites not dorsally carinate. Telson apically truncate or ending in an elongate, rounded end-piece laterally armed with spines. Endopod of first maxilliped composed of only two segments. The two inner distal lobes of second maxilliped broad and not projecting beyond the basal lobe. Eyes small, feebly pigmented. Incisor process of mandible toothed for entire length of its cutting edge.

Four species of *Hymenodora* have been described. Three of the species are present in the materials taken in this study; the fourth species, *Hymenodora acanthitelsonis* Wasmer, 1972a, has only recently been described and is known only from waters off the coast of Oregon.

Key to the Species of *Hymenodora*

1. Telson distally truncate 2
- Telson terminates in an elongate, rounded end-piece laterally armed with spines [*H. acanthitelsonis* Wasmer, 1972a]

2. Rostrum short, reaching to tips of eyes 3
- Rostrum long, extending beyond eyes H. frontalis
3. Podobranch present on second maxilliped , H. gracilis
- No podobranch present on second maxilliped
 H. glacialis

Hymenodora frontalis Rathbun

Hymenodora frontalis Rathbun, 1902: 904, 1904: 28, fig. 8.

Collection Records: SICS-PAC: 610(5); 611(9); 612(1);
 613(42).

YALOC 66: 840(39); 849(194);
 854(62); 857(113); 866(188).

Trans-PAC: 1(1); 4(2); 26(1); 28(1);
 32(2).

Diagnosis: Integument rugose, thin, but not membranous.

Rostrum longer than eyes, reaching distal segment of antennular peduncle. Telson distally truncate, armed with three to six small dorsolateral spines and two pairs of terminal spines, the outer pair longer than the inner.

Distribution: Rathbun (1902; 1904) reported the species from the Bering Sea to off Monterey Bay, California, and from Kamchatka in the western Pacific. Aizawa (1969), who reported the species from depths of 500 m to 1300 m, concluded that the species does not

migrate vertically. Pearcy and Forss (1966) reported the species mainly from depths of 200-1000 m off the central Oregon coast. Specimens in the present study were taken in tows made in the depth range of 0-220 m, as well as in deeper tows (0-3000 m).

Hymenodora glacialis (Buchholz)

Pasiphae glacialis Buchholz, 1874: 279, pl. 1, fig. 2.

Hymenodora glacialis Smith, 1885: 501; 1886: 678, pl. 15, fig. 3, 10; Sivertsen and Holthuis, 1956: 15, fig. 11.

Collection Records: SICS-PAC: 610(9).

YALOC 66: 840(24); 849(74); 854(18);
857(37); 866(15).

Diagnosis: Integument soft and membranous. Rostrum not extending beyond eyes, convex on lower margin, with up to four spines on dorsal surface. Groove passing upward and backward from middle of hepatic groove connected to supra-branchial groove by one whose convex portion is directed anteriorly. Second maxilliped with an epipod, but no podobranch. Telson truncate, armed with five pairs of dorsolateral spines and three pairs of terminal spines.

Distribution: This species appears to be nearly restricted to arctic and temperate waters (Sivertsen and Holthuis, 1956). It has, however, been reported from the Gulf of Panama. Chace (1940)

did not report the species off Bermuda, but it was taken from off the Bahamas, nearly ten degrees further south (Chace, 1947).

There are many records of this species in the literature, but since H. glacialis and H. gracilis have been considered to be synonyms in the past (Sivertsen and Holthuis, 1956), many of the references to this species can not be trusted.

The species has been found in depths to 3900 m (Sivertsen and Holthuis, 1956). Forss (1966) reported the species from off Oregon in depths to 1000 m. Specimens of the species in this study were taken from tows made to depths as deep as 3000 m.

Hymenodora gracilis Smith

Hymenodora gracilis Smith, 1886: 681, pl. 12, fig. 6; Sivertsen and Holthuis, 1956: 16, figs. 11, 13.

Collection Records: SICS-PAC: 610(1); 611(9); 612(1).

YALOC 66: 844(14); 854(7); 857(36).

Diagnosis: Integument thin. Rostrum not extending beyond eyes, armed with up to four spines on dorsal surface. A groove passes upward and backward from middle of hepatic groove, but none converging toward the first from suprabranchial groove. Second maxilliped has an epipod and a podobranch. Telson truncate, armed with four pairs of dorsolateral spines and two pairs of terminal spines.

Distribution: This species has been reported in all oceans (Sivertsen and Holthuis, 1956; Pearcy and Forss, 1966). It has been taken from depths of 500 to 5300 m. Pearcy and Forss (1966) reported it mainly from 200-1000 m. Specimens of the species in the present study were taken in tows made in the depth range 0-200 m as well as in tows made to as deep as 3000 m.

Genus *Systellaspis* Bate, 1888

Carapace without a straight carina along lateral surface from orbit to hind margin and without an oblique carina delimiting the hind margin of the hepatic furrow. Sixth abdominal somite not dorsally carinate. Telson not truncate at tip, ending in a sharply pointed end-piece laterally armed with spines. Eyes well pigmented, usually large. Incisor process of mandible toothed for entire length of its cutting edge. Luminous organs present in some species.

Five species of *Systellaspis* are known, two of which were present in the material in this study. A third species, *S. cristata* (Faxon) has recently been reported from the northeastern Pacific (Wasmer, 1972c).

Key to the Species of *Systellaspis*

1. Abdomen not dorsally carinate on any somite; rostrum about one-third as long as carapace *S. braueri*

- Abdomen carinate on third and fourth somites; rostrum more than half as long as carapace 2
- 2. Hind margins of fourth and fifth abdominal somites crenate on either side of the median spine S. debilis
- Hind margins of fourth and fifth abdominal somites not crenate on either side of the median spine
[S. cristata (Faxon), 1893]

Systellaspis braueri (Balss)

? Systellaspis echinurus Coutière, 1911: 158.

Acanthephyra braueri Balss, 1914: 594.

Systellaspis braueri, Chace, 1940: 180, fig. 50.

Collection Records: SICS-PAC: 610(1); 611(2) 613(4).

YALOC 66: 840(1); 849(1); 854(1);

857(1); 866(4).

Diagnosis: Rostrum triangular, less than half as long as carapace. No dorsal carina on any abdominal somite. A deep notch in lower posterior of fifth abdominal pleuron. Telson armed laterally with about thirty spines, one pair of which is large and distally placed; telson terminates in a sharp end-piece.

Distribution: Systellaspis braueri has been reported from the Bay of Biscay, the Gulf of Guinea, the Bay of Bengal, the Azores, off Bermuda, off Newfoundland, and off the west coast of North America. Sivertsen and Holthuis (1956) reported that the species has been taken from depths between 1300 and 4000 meters. Percy

and Forss (1966) reported it mainly from depths of 200-1000 m off the Oregon coast. Specimens of the species in the present study were taken in tows made as shallow as 0-220 m as well as in deeper tows (0-3000 m).

Systellaspis debilis (A. Milne-Edwards)

Acanthephyra debilis A. Milne-Edwards, 1881; 13.

Systellaspis debilis, Chace, 1940: 181; fig. 51; Figueira, 1957: 31, fig. 2

Collection Records: HMS-30: 3(2); 9(1); 15(1).

YALOC 66: 823(4).

Diagnosis: Rostrum slender, usually longer than carapace.

Abdomen dorsally carinate on most of third and posterior portion of fourth somites; hind margins of fourth and fifth somites denticulate on either side of median spine. A notch in lower posterior of fifth abdominal somite. Telson with three to five pairs of dorsal spines, apically with five pairs, the first pair much stouter than the others; telson terminates in a sharp end-piece. Photophores present on carapace, abdomen, eye-stalks, and bases of appendages (Dennell, 1955, q.v. for other references).

Distribution: Systellaspis debilis is most abundant in the North Atlantic, but it has also been recorded from the eastern South Atlantic, the Indian Ocean, the Malay Archipelago and the Hawaiian

Islands. Foxton (1971a) reported that the species migrates vertically, with a daytime range between 650 and 850 m; the night migration involves the whole population and results in its concentration at about 150 m. Specimens taken in the present study were taken in the upper 250 m, in a depth range of 500-1000 m, and in a tow made in a depth range of 0-2700 m.

Genus *Oplophorus* A. Milne-Edwards, 1837

Carapace without a straight carina along lateral surface from orbit to hind margin and without an oblique carina delimiting hind margin of hepatic furrow. Abdomen armed with long spines on either the second, third and fourth or the third, fourth and fifth somites. Telson terminating in a sharp point which may or may not be armed with lateral spines. Exopods of third maxillipeds and pereopods foliaceous and often rigid. Eyes large and well pigmented. Outer margin of antennal scale usually armed with series of spines. Incisor process of mandible toothed for entire length of its cutting edge. Luminous organs may or may not be present.

Five species of *Oplophorus* are known; two of these were taken in the present study.

Key to the Species of *Oplophorus*

1. Abdomen armed with long spines on second, third and fourth somites *O. spinicauda*

- Abdomen armed with long spines on third, fourth and fifth somites O. spinosus

Oplophorus spinicauda A. Milne-Edwards

Oplophorus spinicauda A. Milne-Edwards, 1883; Chace, 1940: 184, fig. 54.

Oplophorus foliaceus Rathbun, 1906: 922, pl. 20, fig. 8.

Collection Records: HMS-27: 23-2(3); 71(1)

HMS-30: 9(2).

YALOC 66: 820(2); 823(2); 824(3).

Diagnosis: Second, third and fourth abdominal somites terminating in a long spine. No spine at posterolateral angle of carapace. Outer margin of antennal scale spinose. Exopods of all pereopods foliaceous, but not rigid. Telson terminating in end-piece armed with lateral spines. Photophores present on eye-stalk, appendages, and uropods (see Chace, 1940, p. 186).

Distribution: Oplophorus spinicauda has been recorded from off the coast of British Honduras, the West Indies, Bermuda, off the east coast of Florida and off the coast of Morocco in the Atlantic. It has also been taken in the Indian Ocean and in the Philippine region, and from south of the Hawaiian Islands. Chace (1940) recorded the species from depths ranging from 549 to 1464 m. The specimens of the species from the present study were taken in tows made in depths ranging from 100 to 2700 m.

Oplophorus spinosus (Brulle)

Palaemon spinosus Brullé, 1839: 18, fig. on p. 3.

Hoplophorus grimaldii Coutière, 1905a: 1114; 1905b: 1, fig. 1.

Oplophorus spinosus, Holthuis, 1949: 229; Sivertsen and Holthuis, 1956: 19, fig. 15, pl. 3, figs. 1-2; Figueira, 1957: 36.

Collection Records: JRM-22: 2(1); 6(1); 8(1); 10(2);
12(12); 25(2); 27(8).
HMS-27: 25-1(1); 28-1(7); 35(1);
40(1); 62(2).
HMS-30: 3(1); 6(2); 12(6); 15(5);
18(2); 23(4); 27(10); 51(13); 54(1); 57(1); 60(3); 65(1); 67(5); 69(6);
72(1); 75(3); 101(4); 107(3); 113(1).
SICS-PAC: 606(1); 607(2); 609(2);
610(3); 613(1).
YALOC 66: 820(1); 824(1); 826(1);
830(2); 831(2); 832(1); 833(6); 834(1).
Trans-PAC: 16(2).

Diagnosis: Third, fourth and fifth abdominal somites terminating in a long spine. Usually no spine at posterolateral angle of carapace. Antennal scale with distinct barb on inner margin near tip; outer margin of scale spinose. Exopods of all pereopods foliaceous and more or less rigid. Telson terminating in a long

spine, but not in an end-piece armed with lateral spines. Photophores present on appendages, side of carapace and on uropods (see Chace, 1940, pp. 187-188; Yaldwyn, 1963).

Distribution: The species is known from the North Atlantic (off the east coast of the U.S.A., near Bermuda, the Bahamas, west of Madeira, off the Canary Islands), from north of Tristan da Cunha in the South Atlantic, from the eastern Indian Ocean, and from south of Japan and near Easter Island in the Pacific. It has been found in depths between 0-1800 m (Sivertsen and Holthuis, 1956). The present specimens extend the geographical range eastward in the North Pacific.

Foxton (1970a) recorded the species from depth ranges between 100 and 500 m, and concluded that the species does not migrate vertically. The species was taken in the present study from tows made in depth ranges between 95 and 2400 m.

Family Pandalidae

Rostrum usually long, laterally compressed and dentate. Mandible bifid, with three-jointed palp. Chelae of first pair of pereopods microscopically small or absent; chelae of second pair of pereopods small and slender. Carpus of second pereopods subdivided into two or more joints. No exopod on any of the pereopods.

Only one genus of Pandalidae was taken in the materials used

in this study. A key to the genera of the Pandalidae can be found in Holthuis (1955).

Genus *Parapandalus* Borradaile, 1899

No lateral longitudinal carinae on carapace. Rostrum immovable and armed dorsally with fixed spines and sometimes with movable spines as well. Eyes wider than eye-stalks. Third maxillipeds with an exopod. No epipods on any of the pereopods. Carpus of second maxillipeds composed of more than three segments.

Only one species, *Parapandalus richardi* (Coutière) was taken.

Parapandalus richardi (Coutière)

Pandalus (*Stylopandalus*) *Richardi* Coutière, 1905a: 18, fig. 6; 1905b: 1115.

Plesionika nana Murray and Hjort, 1912: 585, 668.

Parapandalus zurstrasseni Balss, 1914: 597; 1925: 281, pl. 27.

? *Pandalus* (*Plesionika*) *gracilis* Borradaile, 1915: 208; 1917: 398, pl. 58, fig. 1.

Parapandalus richardi, De Man, 1920: 140 (in key).

Parapandalus zur strasseni, De Man, 1920: 139, 141, pl. 12, figs. 32-32d.

Parapandalus richardi, Pequegnat, 1970: 86.

Collection Records: HMS-30; 12(1); 15(3); 18(1); 60(3); 63(1); 65(1); 113(1),

SICS-PAC: 610(1).

YALOC 66: 830(9); 831(1).

Other Material Examined:

Parapandalus zurstrasseni Balss, 1914: 1 syntype obtained from the Zoological Museum, Berlin, East Germany.

Parapandalus zurstrasseni Balss: 7 specimens discussed by De Man (1920), from the Siboga Expedition; obtained from Zoological Museum, Amsterdam.

Parapandalus zurstrasseni Balss: 4 specimens from the Snellius Expedition (1929-1930), identified by Dr. Holthuis; obtained from Rijksmuseum van Natuurlijke Historie, Leiden.

Parapandalus richardi (Coutière): 1 specimen from "Ombango" Cruise 13, identified by Crosnier and Forest (1967); obtained from Museum National D'Histoire Naturelle, Paris.

Diagnosis: Rostrum about three times as long as carapace, armed on dorsal surface with more or less widely spaced teeth along the entire length, including two larger teeth above the eye; ventral surface armed with more regularly spaced teeth. A slender, movable middorsal spine on posterior margin of third abdominal somite. Sixth abdominal somite at least three times as long as high and about two and two-thirds times as long as fifth somite.

Remarks: The specimen recorded from the SICS-PAC Cruise was identified (Wasmer, 1967) as Parapandalus richardi (Coutière), as were the specimens taken during the YALOC 66 Cruise. The specimens from the HMS-30 Cruise had been identified, apparently by Isaac Ikehara and Allen Shimomura (of the POFI lab), as

Parapandalus zurstrasseni Balss. Since all these latter specimens agreed with the specimens previously identified as P. richardi, they were considered by the author to be the latter species.

The distributional records for P. richardi revealed that the species had not previously been recorded from the Pacific Ocean; the only species of Parapandalus from the Indo-Pacific which closely resembled P. richardi was P. zurstrasseni Balss, 1914. The resemblance of the two species was noted by Chace (1940, p. 194), who mentioned that P. zurstrasseni apparently lacks the slender spine on the third abdominal somite, and also noted that this spine is often broken off in specimens of P. richardi.

In view of the apparent close resemblance of the two species, and of the fact that the figure of P. zurstrasseni in Balss (1925, pl. 27) seemed to indicate the presence of a slender spine on the third abdominal somite (even though Balss did not mention it in his description), it was decided that specimens of both species should be examined to see if, in fact, the two were identical.

In the course of obtaining the specimens of the two species listed on p. 71, I was informed by Dr. J. Forest (letter of 20 September, 1971) that he and Dr. Crosnier had concluded that Parapandalus zurstrasseni Balss was synonymous with P. richardi (Coutière) and that they had a paper in press in which the synonymy is established. Examination of the specimens obtained on loan

substantiated this conclusion.

All the specimens obtained on loan, including the syntype of P. zurstrasseni, have the slender movable spine (or an indication of it having been present, but broken off) on the third abdominal somite. The tip of the telson of the syntype of P. zurstrasseni is like that of the type of P. richardi as shown in figure 6 of Coutière (1905a) rather than as shown in figure 59 of Balss (1925). The only apparent differences between the specimens were in the spacing of the proximal teeth on the dorsal surface of the rostrum, but Crosnier and Forest state that "L'écartement des quatre où cinq premières petites dents peut varier assez considérablement suivant les spécimen." (in press, quoted from letter of 20 September, 1971).

It is very probable that Pandalus (Plesionika) gracilis Borradaile, 1915, is in reality Parapandalus richardi. The type of Pandalus (Plesionika) gracilis is on deposit in the University Museum of Zoology, Cambridge; I was unable to obtain the type on loan because it is a unique specimen and somewhat damaged. However, Dr. C. B. Goodhart of Cambridge informed me (letter of 21 October, 1971) that Dr. Holthuis had re-examined the specimen in 1956 and that at that time he regarded it as identical with Parapandalus zurstrasseni Balss.

Distribution: Parapandalus richardi has been taken from the western Atlantic east of Newfoundland, near Bermuda, throughout

the Gulf of Mexico; eastern Atlantic near the Azores, west of Gibraltar, west of Madeira, near the Canary Islands, Gulf of Guinea, throughout the Mediterranean, Adriatic and Red Sea; in the Central Atlantic between the Azores and Bermuda (Pequegnat, 1970). It has also been recorded from the Indo-Pacific region (as P. zurstrasseni and Pandalus (Plesionika) gracilis). The present records of the species from the North Central Pacific represent a significant extension of the range of the species northward and eastward in the Pacific.

The species is known from depths between 12.5 and 1800 m (Sivertsen and Holthuis, 1956). Foxton (1970a) concluded that the species migrates vertically, with a possible daytime population maximum at 650 m and a nighttime maximum at 150 m. All the specimens of the species from the present study were taken in tows made in the upper 250 m.

Summary of Quantitative Results

Forty-one species of pelagic shrimps representing thirteen genera and five families were identified in this study. The species taken, arranged according to the number of specimens of each collected, are listed in Appendix A.

Twenty-five species of Penaeidea and sixteen of Caridea were present. The Sergestidae were the most numerous, both in number

of species (16) and in number of specimens taken (7017); the Oplophoridae were next in abundance with 11 species and 1111 specimens. Sergestes (Sergestes) similis, Hymenodora frontalis, and H. glacialis together contributed over 90% of the total catch, with Sergestes (Sergestes) similis by far the most numerous. Thirty-five species each made up less than 1% of the total.

The 16 species marked with an asterisk (*) in Appendix A were recorded from the Pacific for the first time, or have had their Pacific ranges extended into the study area further as a result of this work. These species are indicative of the fact that the pelagic fauna (at least the shrimps) of this region is much less known compared with that in the Atlantic and Indian Oceans. The Challenger expedition was the only great exploratory cruise into the North Pacific during that period when faunal collections were being made by England, Monaco, France and Norway.

ZOOGEOGRAPHY AND SPECIATION

The following discussion of the zoogeography and speciation of pelagic shrimps in the North Pacific Ocean stresses the importance and influence of the water masses as defined physico-chemically and biologically. A zoogeographical study of this sort should investigate the importance of isolation within and adaptations to subtly different environments. However, since deep-sea shrimps are not easy to use in experimental research, the reasons for their distributions can be suggested only through a descriptive approach which attempts to show correlation between their distributions and environmental features. Although such correlations do not prove causal relationships, it is possible to hypothesize likely relationships between the distribution of particular species and similarly distributed environmental features when such correlations are found (Ebeling, 1962).

Characteristics and Formation of Water Masses

Water masses can be identified on the basis of their temperature-salinity characteristics (Sverdrup et al, 1942). An area is called a water mass because within its boundaries there exists a certain consistency of the temperature-salinity relationships. Below 100-200 meters, plots of temperature versus salinity (T-S curves) constructed from hydrographic data taken from a particular

water mass fall within certain limits; these limits define the water mass envelope, which has a characteristic shape and is used to identify the water mass.

A water mass is formed at the sea surface, where it acquires its particular temperature-salinity relationship through heating, cooling, evaporation and precipitation. As these changes take place at the sea surface, the water sinks and spreads in a manner which depends on its density in relation to the surrounding waters. Each parcel of water with the same temperature and salinity throughout is a water type. As each water type moves away from its point of formation, it becomes mixed with other waters. As stated above, the large bodies of water thus formed are called "water masses" and are characterized by similar temperature-salinity curves.

Oceanic currents also play an important part in bringing about the unique temperature characteristics of the water masses. For example, Bierl (1959) pointed out that the large current gyres in the Subarctic and Central Water Masses in the North Pacific function to maintain the small range of the temperature and salinity values characteristic of these waters.

Thus, the physico-chemical features of each water mass depends mainly upon the latitude of the region, the degree of isolation, and the types of currents (Sverdrup et al, 1942). As was stated in the introduction, the biological characteristics of each water mass

depend ultimately on its physico-chemical features.

Current Systems and Water Masses of the North Pacific

The currents and water masses of the North Pacific were defined by Sverdrup et al. (1942). They defined the Subarctic Pacific Water Mass, the Eastern and Western North Pacific Central Water Mass, and the Pacific Equatorial Water Mass on the basis of temperature-salinity relations below the surface layer.

The major current systems of the North Pacific Ocean are shown by Figure 4. Figure 5 shows the horizontal extent of the water masses in the area of this study. Figure 6 is a temperature-salinity diagram showing the water mass envelopes used to characterize and identify the water masses in the study area.

The Subarctic Boundary near 40°N separates the Subarctic Water of low temperature and salinity to the north from the North Pacific Central Water of higher temperature and salinity to the south. This boundary is generally identified by a nearly vertical isohaline of 34.0‰ which extends from the surface to a depth of 200 to 400 m (Dodimead, Favorite and Hirano, 1963).

North of the boundary in the Subarctic Region, the salinity is lowest at the surface and increases with depth. South of the boundary, in the Subtropic Region, the salinity is highest at the surface and decreases to a distinct minimum below 500 m, but the water column is stable due to the temperature structure (Dodimead, et al., (1963).

Favorite and Hanavan (1963) defined two fronts in the North

Pacific: a temperature front associated with an almost vertical isotherm of 4°C , and a salinity front associated with the isohaline of $34^{\circ}/_{\text{‰}}$. They considered the area to the north of the temperature front to be the Subarctic Region, the area between the two fronts to be the Transition Region, and the area to the south of the salinity front to be the Subtropic Region. Subarctic water are characterized by a temperature minimum and Subtropic waters by a salinity minimum at middle depths. Transition waters do not have a temperature or salinity minimum. The two fronts coincide and form a sharp boundary in the Western Pacific, but in the Central Pacific they are about 300 miles apart.

The surface circulation in the extreme Western Pacific consists of the warm saline Kuroshio Current which flows northward along the Japanese Islands with the main flow turning eastward at about 36°N . This water continues eastward as the North Pacific Current to about 150°W where it moves southward. Part of the Kuroshio continues northeast to the vicinity of 40°N where it meets the cold, less saline Oyashio Current which moves southward along the eastern side of the Kurile and northern Japanese Islands. Extensive horizontal and vertical mixing occurs where these two currents meet. These mixed waters move eastward as the "West Wind Drift" with a slight northern component carrying it to about 45°N in the vicinity of 180°E . From there it continues eastward to approximately 300 miles from the Washington-Oregon coasts. Here the current divides, a part turns south to form the California current, and a small part

intrudes into the area off the coast of Vancouver Island and then flows southward along the coast; the remainder flows north into the Gulf of Alaska. The part of the Oyashio Current that does not actively mix with the Kuroshio moves northeastward to within 60 miles of the Aleutian Islands in the vicinity of 180°E . Most of this water moves east as the Subarctic Current. It eventually flows into the Gulf of Alaska and around the Alaskan gyre, making its return in the strongly westward flowing Alaskan stream to the south of the Aleutian Islands. The remainder of the water forms the Western Subarctic Gyre centered at about 50°N , 165°E . The water at the edge of the gyre mixes with the water of the Alaskan Stream, moves westward to the end of the Aleutian Islands, where a portion enters the Bering Sea. Although some of this water flows northward to the Arctic Ocean through the Bering Strait, most of it forms a cyclonic circulation which flows southward along the Siberian coast. One part of this southward flow becomes the East Kamchatka Current and the other is absorbed into the cyclonic gyre in the central Bering Sea (Dodimead et al., 1963).

The Transition Region off the coast of California lies in the California Current where Subarctic, Central, and Equatorial waters converge. The California Current Extension, in conjunction with the west-flowing North Equatorial Current, serves to return the flow of water to the Western Pacific, completing the large central gyre in

the Subtropic Region.

Because of extensive vertical mixing, the Subarctic Waters are rich with nutrients transported up from the deeper layers. This results in high production and a large food supply for these waters, especially near the Aleutian Islands (Fleming, 1955).

The properties of the North Pacific Central Water Mass differ sharply from those of the Subarctic Water. Because it has been warmed for considerable time in the large central gyres, this water mass has a stable thermocline and a deep mixed layer, which is relatively warm and saline. Since there is very little mixing through the thermocline, the nutrients in the surface layer are virtually exhausted and the productivity is low.

A limited amount of mixed water is formed at the convergence of the Kuroshio and Oyashio currents off Kamchatka and the Kurile Islands (Reid, 1965). This water sinks to form a relatively shallow layer of Intermediate Water. This water mass flows southward and eastward at a depth of about 500 m below the Central Water and the Kuroshio and is recognized by a distinct core of water with a salinity minimum. It serves to distribute nutrients produced in high latitudes to intermediate depths below the Central Water Mass (Ebeling, 1962).

Vertical sections of temperature, salinity, and dissolved oxygen along a north-south track at 158° W illustrate the structure of

the water masses in the North Pacific (Figures 7, 8, 9). These vertical sections were made using data from one of the cruises which supplied shrimp for this study, the Hugh M. Smith Cruise 30, and are reproduced in the NorPac Atlas (NorPac Committee, 1960a). The salinity structure shows a distinct vertical isohaline of 34.0‰ extending from the surface to a depth of about 200 m between stations 96 and 97 (about 40°N); this represents the Subarctic Boundary. The upper 500 meters of the subarctic region to the north are distinguished by low values for temperature and salinity and by high concentrations of oxygen related to the increased productivity of the region. The northern edge of the Transition Region, that area between Central waters to the south and Subarctic waters to the north (Favorite and Hanavan, 1963) is indicated by the almost vertical 4°C isotherm at 200 m between stations 86 and 87. The salinity minimum, $<34\text{‰}$, extends southward from the boundary at depths of 500 to 700 m below the Central Water; this core of water represents the Intermediate Water.

The North Pacific Central Water to the south of the boundary differs markedly from water to the north. The water mass here is warmer - up to 10°C at 400 m, and more saline, with surface values reaching above 35‰ . Oxygen values do not show the higher near-surface values characteristic of the zone of higher production to the north.

These vertical sections of temperature, salinity, and dissolved oxygen at 158°W are in general agreement with the vertical sections shown by Park (1967) for that portion of the YALOC-66 cruise of R/V Yaquina which crossed the subarctic boundary near 170°W, except that the Subarctic boundary was crossed at 42°N rather than at 40°N as in the Hugh M. Smith Cruise 30.

Temperature and salinity sections along the inbound track (the more eastwardly track of the two tracks on Figure 1) of the SICS-PAC cruise of the R/V Yaquina (Figures 10 and 11) show that this cruise crossed three adjacent oceanic regions (Coleman, n.d.). Stations 616 and 615 were in water which was largely Subarctic in nature, characterized by the presence of a well defined halocline at depths of 75 to 175 m and by the absence of a thermocline. Water temperatures in this region ranged from 7.88° to 10.62°C at the surface and from 6.64° to 7.64°C at 200 m. Salinities ranged from 31.92 to 32.61‰ at the surface and from 33.87 to 34.00‰ at 200 m. Stations 614 to 611 were in waters transitional between the Subarctic Water to the northeast and Eastern North Pacific Central Water to the southwest. These waters were characterized by the gradual erosion of the halocline and the formation of a distinct thermocline. Temperatures at the surface ranged from 10.62° to 16.00°C and from 7.64° to 10.62°C at 200 m. Salinities ranged from 32.75 to 33.75‰ at the surface and from 33.75 to 34.00‰ at 200 m.

Station 610 was in the Eastern North Pacific Central water mass, characterized by relatively high surface salinities which ranged from 33.75 to 34.60‰ at the surface and from 34.00 to 34.24‰ at 200 m. A distinct salinity minimum was present at a depth of about 500 m at the extreme southwest end of the cruise tract. Temperatures in this region were high, ranging from 16.00° to 17.50°C at the surface and from 10.62° to 11.91°C at 200 m.

Distribution of Shrimps Relative to North Pacific Water Masses

In order to locate species of pelagic shrimps in temperature-salinity defined water masses, captures of each species were not only plotted on distribution maps, but the T-S curves associated with the capture stations were superimposed on water mass envelopes. Only the positive stations were plotted on surface distribution maps which also indicated the horizontal extents of the various water masses in the study area in the North Pacific Ocean. T-S curves for each capture station were constructed from hydrographic data taken concurrently at each station. The family of T-S curves representing all the capture stations were plotted on Temperature-Salinity capture diagrams on which the North Pacific water mass envelopes were also indicated.

No attempt was made to plot the part of the T-S curve

representing only the portion of a water column occupied by a species. Since most captures were made with open nets which either sampled only the upper limits of an extensive vertical range or sampled so thick a layer that the depth of capture cannot be determined, the water-mass habitat was identified by plotting the full T-S curve. In some cases, when the family of T-S capture curves fell in a rather narrow range of temperature and salinity values, or when curves from a number of capture stations were to be plotted, capture envelopes were constructed instead of plots of each individual curve because the curves tended to merge anyway. In this method of establishing distributions relative to water masses, when the curves for a certain species fall mostly within a single water mass envelope, the indications are that that species lives only in the water mass in the North Pacific defined by this envelope.

Bieri's (1959) investigation of chaetognath distributions in the North and South Pacific and the similiar study on euphausiids by Brinton (1957) indicate the great variety of distributional patterns shown by such groups when studied over such immense areas. In the light of these studies, no attempt was made to predict distributions of species of shrimps in the Pacific outside of the region investigated even though many of the species occur elsewhere.

Hydrographic data used in constructing T-S curves were taken from the following sources for each cruise:

Hugh M. Smith 27 - Scripps Institution of Oceanography,
1962.

Hugh M. Smith 30 - NorPac Committee, 1960b.

SICS-PAC - Wyatt et al., 1967.

YALOC 66 - Barstow et al., 1968.

Transpac - F.R. B. C., MS. 1970.

The forty-one species of shrimp discussed in this work can be divided into four groups based on their zoogeographical distributions in relation to the water masses of the North Pacific Ocean. These four groups are: Subarctic-Transitional, Transitional, Central-Transitional, and Central.

Subarctic-Transitional Species: Twelve species were included in this group. All have ranges which include all or part of the Subarctic Water, but which also extend into Transitional waters, so that it is probable that the southern boundary of this latter region is the southern limit of their distribution. The species included in this group are Bentheogennema borealis, Bentheogennema n. sp., Sergestes similis, S. (Sergia) japonicus, Petalidium suspiriosum, Pasiphaea tarda, Notostomous japonicus, Hymenodora frontalis, H. glacialis, H. gracilis, and Systellaspis braueri.

Sergestes (Sergestes) similis is the one species most representative of this group of species. It occurs throughout the northern North Pacific from Suruga Bay, Japan, to the coast of Oregon and

California as far south as the Gulf of California. The surface distribution map and temperature-salinity capture diagram (Figures 12, 13) for the species indicates clearly its association with Subarctic and Transitional waters. It is apparently the only oceanic sergestid found north of the Subarctic boundary in the mid-Pacific, but the records of Sergestes japonicus and S. tenuiremis from above 50°N to the east of 140°W indicate that at least two other sergestid species extend into this region in the northeastern Pacific.

Milne (1968) reported that Sergestes similis has also been taken in the South Pacific off Chile (Cecchini, 1928) and in the Benguela Current in the southeastern Atlantic (Illig, 1927). These records are apparently of Sergestes arcticus Hansen, a species found in the North Atlantic and circumpolarly in the southern hemisphere, as Yaldwyn (1957) includes these records in his discussion of the distribution of this species. Thus Sergestes similis is a species which is apparently endemic to the Subarctic and Transitional waters of the northern North Pacific. Many other species of fish and invertebrates have ranges which include only Subarctic and Transitional waters in the North Pacific Ocean (Bieri, 1959; Brinton, 1962; Ebeling, 1962; McGowan, 1960).

Bentheogennema borealis ranges broadly throughout the Subarctic and Transitional waters of the North Pacific from Japan to Southern California, although it was not taken west of 175°E in the

present study (Figures 14, 15). Its presence at SICS-PAC Station 610 was somewhat surprising and elicits some comment.

The temperature-salinity diagram for Station 610 indicates that the water here was essentially Western North Pacific Central in character. (The Eastern and Western North Pacific Central water masses were distinguished by Sverdrup et al., (1942), but are not now generally believed to distinct gyres.) It will be noted that not only were shrimps with Subarctic-Transitional distributions taken at this station, but Central-Transitional and Central species were also taken here. There must have been a broad overlap of conditions at this station to account for the presence of species having such different zoogeographical ranges. This is also a good indication that distributions of oceanic shrimps are probably not controlled solely by temperature-salinity characteristics of the waters in which they are found. A possible explanation of the occurrence of species having such diverse distributional features at this one station is that the station was sampled with a 10-foot trawl towed through a depth range of 0-2450 m, so that it more effectively sampled the shrimp actually occurring in the water column. Station 609 of the same cruise, also from Central waters, was sampled only to a depth of 250 m with a 6-foot trawl, and while it included Central-Transitional and Central species, it lacked species characteristic of Subarctic-Transitional waters.

The distributional maps and temperature-salinity capture diagrams of Hymenodora frontalis (Figures 16, 17), H. glacialis (Figures 18, 19), H. gracilis (Figures 20, 21), Systellaspis braueri (Figures 22, 23), and to some extent Acantheephyra n. sp. (Figures 24, 25) present essentially the same picture, that is, that these species occur in Subarctic-Transitional waters in the North Pacific Ocean. The records of Hymenodora glacialis from the Gulf of Panama (Faxon, 1895) brings to mind the somewhat similar distribution of the planktonic worm Poecobius meseres, reported by McGowan (1960) generally from Subarctic and mixed Transitional waters in the North Pacific, but with some records from near the equator between the Galapagos Islands and 6°S in the terminal part of the Peru current. It was hypothesized that the tropical records were sterile expatriates from the Subarctic and Transitional waters to the north, and that their occurrence near the equator implied a relationship between Intermediate Water in the eastern tropics and Subarctic Water.

Bentheogennema n. sp. (Figures 26, 27) and Petalidium suspiriosum (Figures 28, 29) have much the same distributional maps and temperature-salinity capture diagrams. While both of them inhabit Subarctic-Transitional Waters, they are not found as extensively throughout the Subarctic region as are the preceding species of this group. They are, in fact, only known from waters to the east of 140°W which have a more transitional character.

Sergestes (Sergia) japonicus was taken at only one station, Station 857 of YALOC-66 (Figure 30). The temperature-salinity capture diagram for this species shows the presence of considerable Subarctic Water, with the intrusion of Intermediate Water at mid-depths (Figure 31). The recent record for the species from 44° 46.3'N 131°25.6'W indicates that the species occurs also in waters more typically transitional, so it has been included in this group of species rather than in a strictly Subarctic group as the single T-S curve would seem to indicate. Sergestes (Sergia) japonicus thus becomes the second sergestid species to be recorded from north-eastern Pacific in Subarctic-Transitional waters. Only Sergestes similis had previously been reported from this area.

Pasiphaea tarda was recorded from three stations above 50°N (Figure 32). The temperature-salinity capture diagram (Figure 33) indicates the subarctic nature of the water at these stations. The species has previously been reported from off the coast of Washington (Rathbun, 1904), so it has been included in those species found in both Subarctic and Transitional waters. The record of the species from off Ecuador (Faxon, 1895) indicates that the species has a much broader Pacific range than indicated here.

Notostomous japonicus was taken at only four stations (Figure 34) whose waters show some Subarctic features, but approaching Transitional waters at mid-depths (Figure 35). The other records

for the species (Stevens and Chace, 1965; Forss, 1966) indicate that it occurs in Transitional waters off the coasts of Oregon and Washington.

Transitional species: Three species are included in this group. They are Parapasiphae cristata, P. sulcatifrons, and AcanthePHYRA curtirostris. Parapasiphae cristata (Figures 36, 37) and P. sulcatifrons (Figures 38, 39) were only taken at one station each in the Northeastern Pacific in waters clearly of a Transitional character. The previous Pacific records for both species are only from waters of this region, and presumably all under more or less the same transitional influences.

AcanthePHYRA curtirostris was only taken from stations in the northeastern Pacific which were under strong influence of Transitional waters (Figures 40, 41), and on the basis of this study one would have to conclude that it belongs to the Transition group of species. However, the species has a much broader distribution in the Pacific, from Japan, the Philippines, Hawaii, and from Washington to Panama and Peru. It is possible that its absence from collections made in the vicinity of Hawaii was the result of its not being caught, rather than its not being there. Further studies of this type are needed before its complete distribution in the Pacific can be known.

Other species of fish and invertebrates are known only from Transitional waters in the North Pacific. The chaetognath Sagitta

scrippsae, the euphausiids Nematoscelis difficilis and Thysanoessa gregaria, and the melamphid Melamphaes parvus are examples of species limited to the Transitional Water of the North Pacific (Alvarino, 1962; Brinton, 1962; Ebeling, 1962).

As pointed out by Brinton (1962), the plankton species of central waters can be grouped according to the extent to which their ranges conform to the Central Water as distinguished by its characteristic envelope of T-S curves. The last two groups of species described in this study both include central species, but the first includes those whose ranges extend into Transitional Waters around the margin of the Central water mass, while the last group includes species whose ranges tend to conform to the warm, barren mid-parts of the North Pacific Central water masses.

Central-Transitional Species: Nine species are included in this group. They are Gennadas incertus, G. parvus, G. propinquus, G. tinayrei, Sergestes armatus, S. sargassi, S. prehensilis, S. tenuiremis, AcanthePHYra quadrispinosa, and Oplophorus spinosus.

Oplophorus spinosus is typical of the species of this group. The distributional map and temperature-salinity capture diagram (Figures 42, 43) clearly indicate that while the species inhabits Central waters, its range extends out into the Transitional waters at the margins of its range.

The distributional maps and temperature-salinity capture

diagrams for Gennadas propinquus (Figures 44, 45), Gennadas tinayrei (Figures 46, 47), Sergestes armatus (Figures 48, 49), and Acanthephyra quadrispinosa (Figures 50, 51) are all quite similar, and show that these species also inhabit Central waters, but extend into Transitional waters at the margins of their ranges. The temperature-salinity capture diagrams differ slightly from that of Oplophorus spinosus in that those for the former species indicate that perhaps these species do not extend quite as far into Transitional waters as does O. spinosus.

Sergestes sargassi was recorded from seven stations (Figure 52) six of which were decidedly in Central waters (Figure 53). The seventh station, SICS-PAC 608 was weakly Transitional in its features, and so this species has been included in this group.

Gennadas incertus was recorded from sixteen stations in this study (Figure 54). The temperature-salinity capture diagram (Figure 55) would seem to indicate that this species belongs in the next group to be discussed, the Central species. However, when other records for the species from off the coasts of Oregon (Pearcy and Forss, 1966) are considered, it is seen that the species clearly belongs to the Central-Transitional group.

Gennadas parvus was taken at only three stations, all above 40°N in the western half of the Pacific (Figure 56). The temperature-salinity capture diagram (Figure 57) is not very complete, but does

seem to indicate that the species is found in Central-Transitional waters, and it has been placed here accordingly.

Sergestes (Sergia) tenuiremis was recorded from only two stations in this study (Figure 58), but the temperature-salinity capture diagram (Figure 59) indicates the Central-Transitional nature of the water in which it was found. Sergestes tenuiremis is the third sergestid to be reported from the northeastern Pacific in an area from which only S. similis had previously been reported. It has been recorded from Hawaii (Rathbun, 1906) and its absence in the present collection from the area must be due to its not being caught.

Sergestes consobrinus was only taken at two stations (Figure 60) in the present study. Both stations were in North Pacific Central waters, (Figure 61), and on the basis of these two records the species would appear to belong to the next group, the Central species. However, that this is clearly not the case is evident when the records for the species cited by Milne (1968) are considered. She records it from off the coast of California south of $41^{\circ}10'N$, about 385 miles west of Cape Mendocino, to $32^{\circ}06'N$ $128^{\circ}51'W$, west of the California-Mexico border, in waters which could be considered to be Transitional in nature (Aron, 1962). Therefore, S. consobrinus is considered here to be a Central-Transitional species.

Sergestes (Sergia) prehensilis (Figure 62) was taken at only Station TP-16-10 of the Canadian Trans-Pacific cruise.

Unfortunately, there was no temperature-salinity data for this station, so it is impossible to say anything definite concerning the nature of water in which it was taken. The species is only known from this region off Japan, this being the third record for the species. For sake of convenience, it has arbitrarily been included in this group because Oplophorus spinosus, Acanthephyra quadrispinosa, Gennadas incertus, and Gennadas propinquus, all species with Central-Transitional distributions, were also taken at this station. This decision could, of course, be in error, and the species be Subarctic-Transitional, because Sergestes similis (a Subarctic-Transitional species) was also taken at this station. Further records for the species are needed before its distribution will be known with some surety.

Examples of what are here called Central-Transitional species from other groups of organisms include the euphausiid Euphausia mutica, the arrow worm Sagitta pseudoserratodentata, and the foraminiferan Globotalia truncatulinoides. Although each of these are found towards the central parts of the Central water masses, their ranges extend out toward the margins of the Central waters into transitional areas where the central environment impinges on the waters of Subarctic region eastern boundary currents, and the Equatorial water mass where the waters are more fertile (Johnson and Brinton, 1963).

Central Species: Sixteen species are included in this group.

The distributional maps and temperature-salinity capture diagrams of all sixteen clearly indicate that these species have ranges which conform to the more barren mid-parts of the North Pacific Central water masses. The species included in this group are Gennadas bourvieri (Figures 63, 64), G. capensis (Figures 65, 66), Funchalia taaningi (Figures 67, 68), Sergestes atlanticus (Figures 69, 70), S. orientalis (Figures 71, 72), S. pectinatus (Figures 73, 74), S. vigilax (Figures 75, 76), Sergestes (Sergia) bigemmus (Figures 77, 78), S. (Sergia) gardineri (Figures 79, 80), S. (Sergia) scintillans (Figures 81, 82), S. (Sergia) talismani (Figures 83, 84), Acanthephyra prionota (Figures 85, 86), Notostomus perlatus (Figures 87, 88), Systellaspis debilis (Figures 89, 90), Oplophorus spinicauda (Figures 91, 92), and Parapandalus richardi (Figures 93, 94).

The euphausiids Nematoscelis atlanticus, Euphausia brevis and E. hemigibba are examples of other organisms which inhabit the warm, barren mid-parts of the North Pacific Central water masses (Brinton, 1962).

It should be remembered that the four distributional patterns of shrimp discussed here apply only to the North Pacific Ocean exclusive of the Equatorial water mass. While some of the species almost certainly have distributional patterns showing differing

amounts of antitropicality in waters of the Southern Hemisphere, the complex distributions shown for chaetognaths (Bieri, 1959) and euphausiids (Brinton, 1962) when the entire Pacific is considered is cause for caution towards making predictions of distribution of shrimp outside the region investigated.

Environmental Isolating and Integrating Factors

The preceeding discussion of the distributions of oceanic shrimp in the North Pacific Ocean has revealed that most of the species do not follow the boundaries of the physico-chemically defined water masses, but tend to either overlap boundaries or to localize within one water mass in the case of many of the Central species. It can be concluded therefore, that there is only a tendency for species to associate with physico-chemically defined water masses and that the species are most likely not limited solely by temperature and salinity.

Physico-chemical factors such as currents, oxygen and nutrient content of the water, and biological factors such as productivity and food supply have been suggested as factors which may function directly or indirectly to establish faunal boundaries within or between water masses (Ebeling, 1962).

Temperature by itself is probably not a factor functioning to limit the horizontal distributions of oceanic shrimps. Many of the

mesopelagic species carry out extensive diurnal migrations that carry them through greater temperature differences than they would encounter at depth outside of their horizontal range. In addition, their horizontal distributions may range across areas delineated by different isotherms, or may not completely fill one such area. This is not to say that temperature does not have a great importance to the ecology of open ocean organisms. Bruun (1957) stressed its importance in vertical zonation. Certain physiological functions carried out at depths may also have limiting temperatures. Salinity is probably of less importance than temperature in limiting distributions since it varies only slightly from water mass to water mass (Ebeling, 1962). It may function to limit breeding areas of species which shed their buoyant eggs into the water column. Even slight changes in salinity might influence the depth at which the eggs are carried by the water and directly affect the survival and development of eggs and larvae.

Current gyres in the North Pacific Ocean most likely serve to integrate and concentrate pelagic shrimps. The gyres help form and maintain unique regimes of physico-chemical and biological properties which then can support their included faunas. Ebeling (1962) cited the isolation of the melamphid Melamphaes pumilus which occurs entirely within the western gyre of the North Atlantic as a probable example of this type of isolation. The large central

gyres in the North Central Pacific may function to concentrate and isolate certain of the species of shrimp in the more barren mid-parts of the Central water mass.

Convergences and divergences of currents, and other mixing processes in waters at boundaries between water masses, by altering nutrient content, temperature, and concentrations of chemicals, may support certain populations of shrimp. The several examples of species of shrimp limited to Transitional waters may be examples of this. Similiar explanations have been given for Sagitta minima and Melamphaes parvus, two other organisms inhabiting mixed regions between water masses (Bieri, 1959; Ebeling, 1962).

Ebeling (1962) indicated that it is improbable that dissolved oxygen concentration is often a critical factor limiting the distribution of bathypelagic organisms. He based this on the fact that large concentrations of fishes and invertebrates live within oxygen-minimum layers in the eastern tropical Pacific off Central America where the oxygen concentrations measure less than 0.1 ml/l at depths between 100 and 500 meters.

Biological factors such as the rate of organic production, food supply, and the availability of certain dissolved metabolites have been shown to influence the distributions of bathypelagic fishes and invertebrates (Ebeling, 1962; Roper, 1969).

Primary production of phytoplankton and the resulting food

supply in general are greatest in those areas where the euphotic zone is replenished with dissolved nutrients that have accumulated below the depth where photosynthesis just balances respiration, the compensation depth. This replenishment of nutrients is greatest in regions of intense upwelling and vertical mixing and in areas close to runoff from land. Areas of upwelling occur along eastern boundaries of the oceans and in divergences of oceanic water masses. Because of this, boreal and eastern equatorial waters, with their shallow and unstable thermoclines which permit vertical replenishment of nutrients, are areas of high productivity. The central water masses are relatively sterile because of their deep, stable thermoclines which prevent vertical mixing.

The zoogeographical importance of increased primary production in a given water mass is the support of a fauna which is distinct from the faunas of less productive adjacent areas (Ebeling, 1962). The productive areas may support higher densities of larger species. Ebeling found that the four dwarf species of Melamphaes usually inhabited central waters of low food supply while most of the larger species were found in more productive waters. It is of interest to note that the smallest species of Sergestes from this study, S. pectinatus, was generally taken in Central water.

The annual productivity of the mid-Subarctic Pacific Region in 1966-68 ranged between 80 and 100 g C/m² (Larrance, 1971), while

in oceanic waters off Washington and Oregon it was estimated to be 125 g C/m^2 (Anderson, in press, cited in Larrance, 1971). Productivity in the Central North Pacific is in the vicinity of 50 g C/m^2 / year or less. Thus one would expect these two areas and the zone of transition between to support distinct faunas.

The distribution of oceanic shrimps in the area investigated in this study fulfill the above expectation and are in general agreement with other studies of this sort done with other groups of organisms (Bieri, 1959; Brinton, 1962; Ebeling, 1962, and others). Ebeling (1962) concluded that the ranges of species of Melamphaes generally follow the water masses, but where they depart, they usually follow contours of productivity. Roper (1969) in his investigation of the zoogeography of the bathypelagic squid Bathyteuthis, concluded that while its distribution was governed in part by physico-chemical characteristics, the primary limiting factor was high primary productivity.

Thus, we find that in the North Pacific Ocean, four groups of oceanic shrimps can be distinguished: a Subarctic-Transitional group inhabiting waters having a fairly high level of primary productivity, a Transitional group inhabiting mixed waters between the Subarctic and Central water masses, a Central-Transitional group with species occurring in the relatively unproductive Central waters but whose ranges

extend into the somewhat richer Transitional waters at the margins of their ranges, and a Central group found only in the more barren mid-parts of the Central waters.

Speciation and Water Mass Boundaries

Ebeling (1962) considered that the speciation of melamphids and other bathypelagic fishes relative to water masses could best be considered in three stages: (1) initial period of dispersal, perhaps vertically as well as horizontally, (2) a gradual cessation of gene flow between contiguous populations, and finally, (3) reinforcement of the initial isolation by competition between these populations.

Because of the uncertain influences of water mass boundaries as absolute barriers which function to isolate populations between water masses (Van der Spoel, 1971, discussed factors and problems involved in speciation in the open ocean), only the three north-south continental land masses which divide the Atlantic, Pacific, and Indian Ocean can be considered as absolute barriers between low latitude pelagic organisms. A broad tropical or subtropical belt separating a range into an antitropical pattern of distribution can also establish absolute isolation of northern and southern populations. Brinton (1962) used the paired roles of continental and tropical barriers to consider the speciation of euphausiid species. In doing this, isotherms that agree with the limits of recent distributions

were used to extrapolate the limits of the hypothetical distributions which may have existed during past epoch under warmer and cooler ocean conditions.

David in discussing speciation in Chaetognatha, stated:

If isolation is necessary, and some formed barrier is the 'cause' of isolation, then barriers exist in the ocean. Evolution is a continuous process, taking place all the time, and one may therefore suppose that by studying the factors controlling the present day distribution of animals one could discover the barriers which are now operating in the formation of new species . . . yet in the ocean one tends to think that if the controlling factors of distribution were known one would know also how species were formed, this may be so, but it is not necessarily so (David, 1963, p. 130).

He then gave five possible mechanisms responsible for distribution patterns using the barrier concept; these mechanisms then were used to explain speciation in the chaetognaths. Van der Spoel (1971) was of the opinion that none of the five mechanisms mentioned by David (1963) are effective as barriers in speciation, although they may determine the present distribution of species.

The finding of geographical races or subspecies in pelagic species suggests that morphological differentiation may arise in segments of a series of communicating regions. For example, Brinton (1962) discussed several Pacific variants of the euphausiid Stylocheiron affine which he considered as forming a Rassenkreis along the anticyclonic circulation of the tropical and subtropical North Pacific. McGowan (1963) discussed the geographical variation of

Limacina helicina in the Subarctic water, Gulf of Alaska, and California current. Little is known of the possible effectiveness of oceanographic barriers in isolating such populations from one another. Environmental gradients exert continuing but variable pressure on the adaptive capacity of all planktonic populations. Therefore, the populations are constantly subject to both physiological and genetic adaptations, but the implications of these to speciation are clear only when gene pools that are not in communication with each other have been established (Johnson and Brinton, 1963).

It appears that the present study, which is limited to shrimp of the North Pacific, does not provide data on which one can form conclusions regarding factors which may function to isolate gene pools.

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APPENDICES

APPENDIX A

Species of oceanic shrimp taken, arranged according to number of each collected. Asterisk(*) indicates a first Pacific record for the species, or a range extension for the species.

<u>Species</u>	<u>Number Taken</u>
<u>Sergestes (Sergestes) similis</u>	6770
<u>Hymenodora frontalis</u>	590
<u>Hymenodora glacialis</u>	177
<u>Oplophorus spinosis</u> *	134
<u>Petalidium suspiriosum</u>	101
<u>Bentheogennema borialis</u>	94
<u>Acanthephyra quadrispinosa</u>	71
<u>Hymenodora gracilis</u>	68
<u>Bentheogennema n. sp.</u>	65
<u>Gennadas propinquus</u>	59
<u>Gennadas tinayrei</u> *	59
<u>Gennadas incertus</u>	48
<u>Sergestes (Sergestes) armatus</u> *	29
<u>Sergestes (Sergia) scintillans</u> *	25
<u>Parapandalus richardi</u> *	22
<u>Acanthephyra curtirostris</u>	20

<u>Species</u>	<u>Number Taken</u>
<u>Sergestes (Sergestes) pectinatus</u> *	17
<u>Systellaspis braueri</u>	15
<u>Oplophorus spinicauda</u>	13
<u>Funchalia taaningi</u> *	12
<u>Sergestes (Sergestes) sargassi</u> *	12
<u>Notostomous japonicus</u>	12
<u>Sergestes (Sergia) talismani</u> *	11
<u>Systellaspis debilis</u>	8
<u>Pasiphaea tarda</u>	8
<u>Sergestes (Sergestes) vigilax</u> *	7
<u>Sergestes (Sergestes) consobrinus</u>	7
<u>Sergestes (Sergia) prehensilis</u>	7
<u>Sergestes (Sergia) gardineri</u> *	5
<u>Gennadas bouvieri</u>	4
<u>Gennadas parvus</u>	4
<u>Sergestes (Sergestes) atlanticus</u>	4
<u>Sergestes (Sergia) tenuiremis</u>	4
<u>Sergestes (Sergia) bigemmeus</u> *	3
<u>Sergestes (Sergia) japonicus</u> *	3
<u>Parapasiphaea cristata</u>	3
<u>Sergestes (Sergestes) orientalis</u> *	2

<u>Species</u>	<u>Number Taken</u>
<u>Acanthephyra prionota</u>	2
<u>Gennadas capensis</u> *	1
<u>Parapasiphaea sulcatifrons</u>	1
<u>Notostomous perlatus</u> *	1

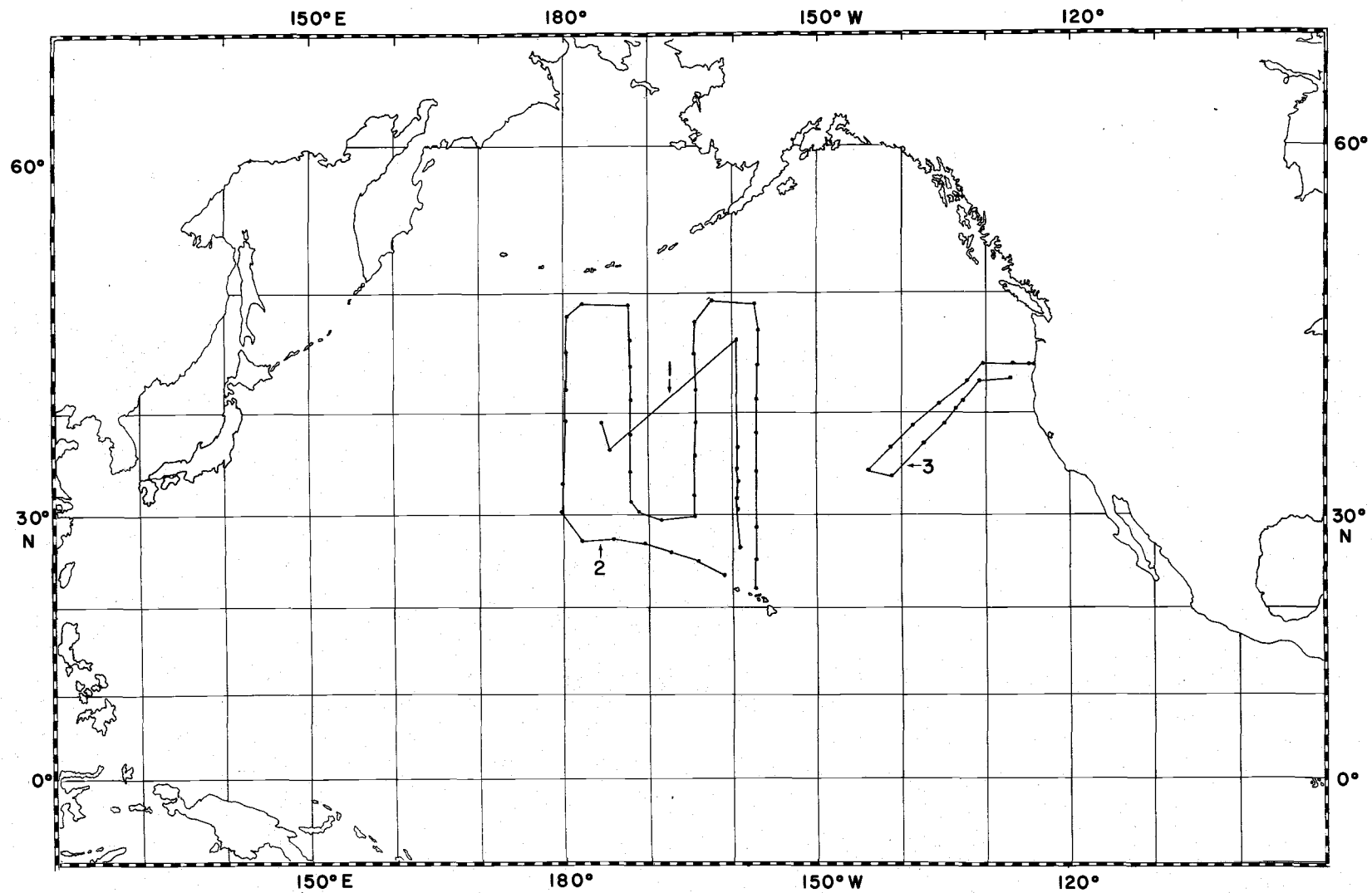


Figure 1. Study area and cruise tracks, showing midwater trawl stations from which shrimp samples were taken. (1) John R. Manning 22, (2) Hugh M. Smith (30), (3) SICS-PAC.

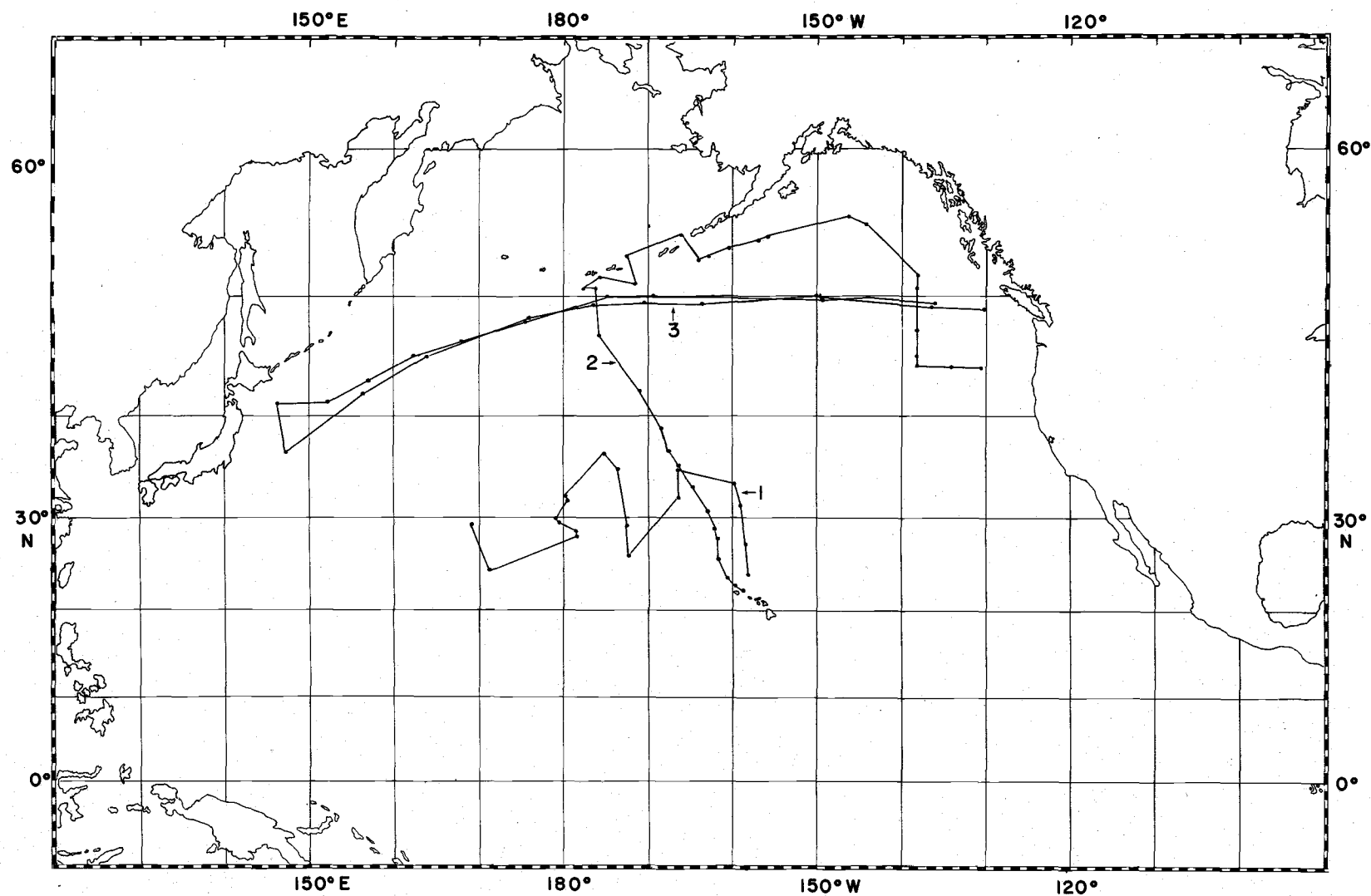
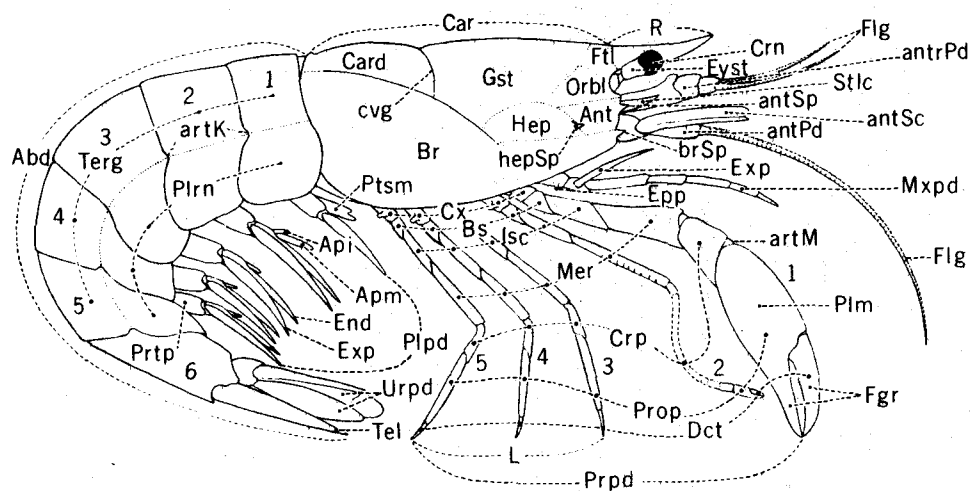


Figure 2. Study area and cruise tracks, showing midwater trawl stations from which shrimp samples were taken. (1) Hugh M. Smith 27, (2) YALOC 66, (3) Canadian trans-Pacific.



Abd = abdomen
 Ant = antennal region
 antPd = antennal peduncle
 antrPd = antennular peduncle
 antSc = antennal scale
 antSp = antennal spine
 Api = appendix interna
 Apm = appendix masculina
 artK = articular knob
 artM = articular membrane
 Br = branchial region
 brSp = branchiostegal spine
 Bs = basis
 Car = carapace
 Card = cardiac region
 Crn = cornea

Crp = carpus
 cvg = cervical groove
 Cx = coxa
 Dct = dactyl
 End = endopod
 Epp = epipod
 Exp = exopod
 Eyst = eyestalk
 Fgr = finger
 Flg = flagellum
 Ftl = frontal region
 Gst = gastric region
 Hep = hepatic region
 hepSp = hepatic spine
 Isc = ischium
 L = walking leg

Mer = merus
 Mxp = third maxilliped
 Orbl = orbital region
 Plm = palm
 Plpd = pleopod
 Plrn = pleuron
 Prop = propodus
 Prpd = pereopod
 Prtp = protopodite
 Ptsm = petasma
 R = rostrum
 Stlc = stylocerite
 Tel = telson
 Terg = tergum
 Urpd = uropod

Figure 3. Diagrammatic shrimp in lateral view showing terms used in keys and descriptions. (After Chace and Hobbs, 1969).

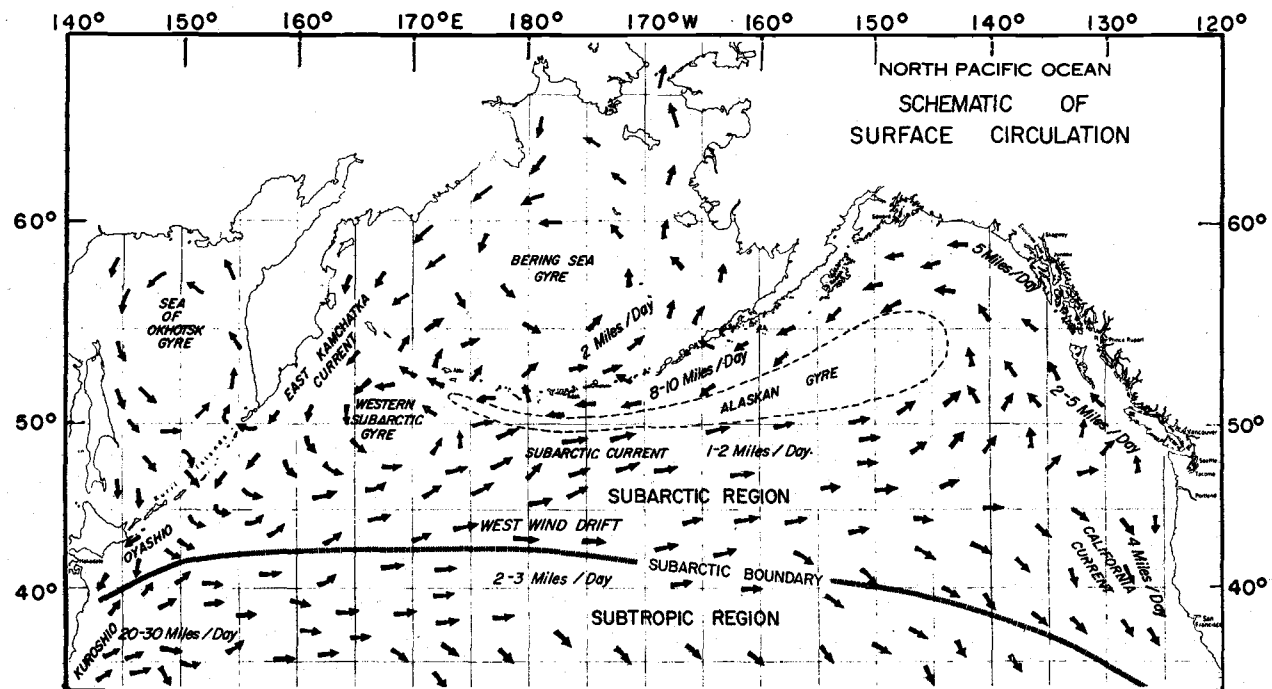


Figure 4. Schematic diagram of surface circulation in the North Pacific Ocean. (After Shepard, Hartt and Yonemori, 1968).

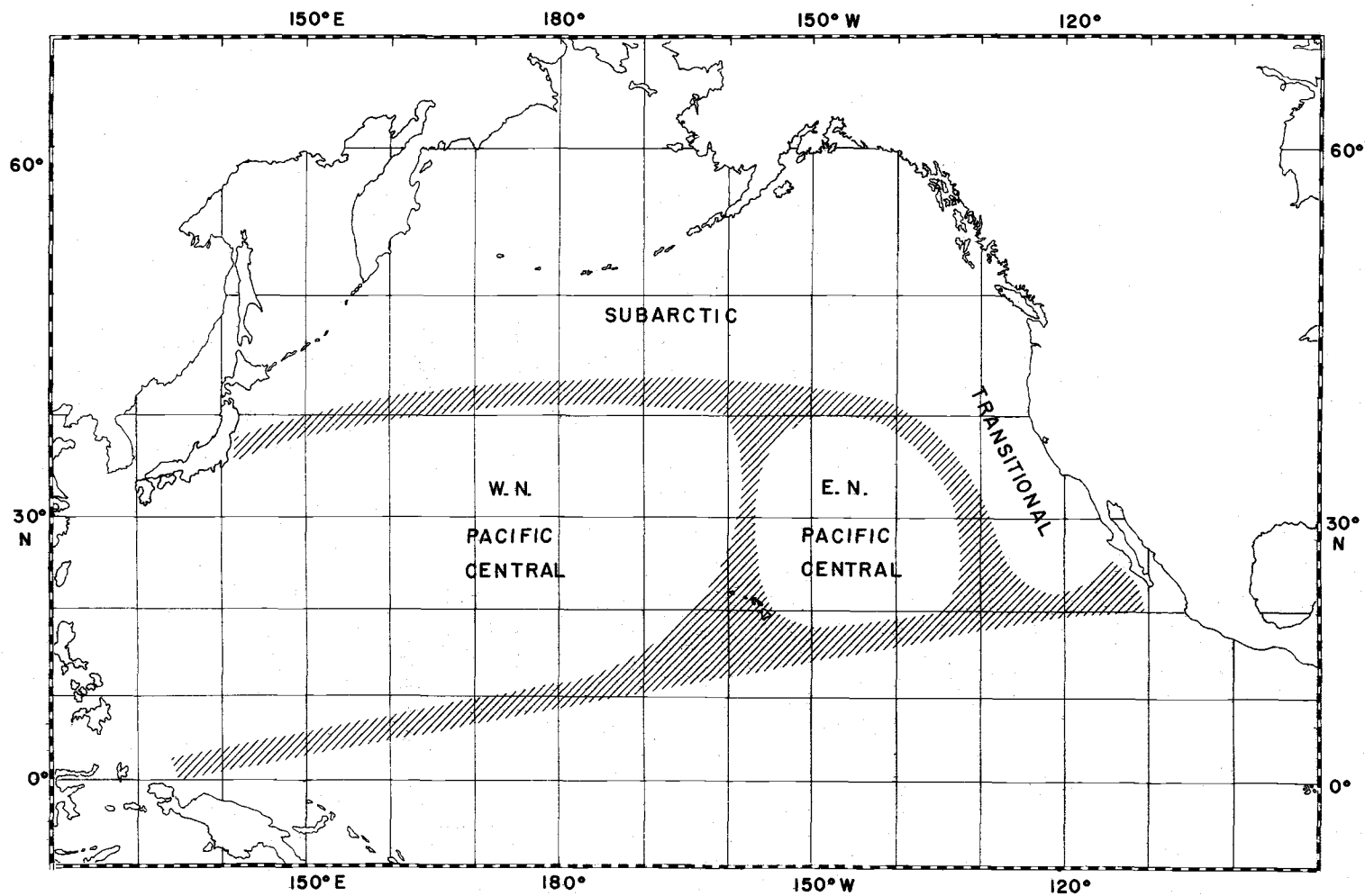


Figure 5. Major water masses of the North Pacific Ocean. Hatched bands delimit the water masses. (After Sverdrup *et al.*, 1942).

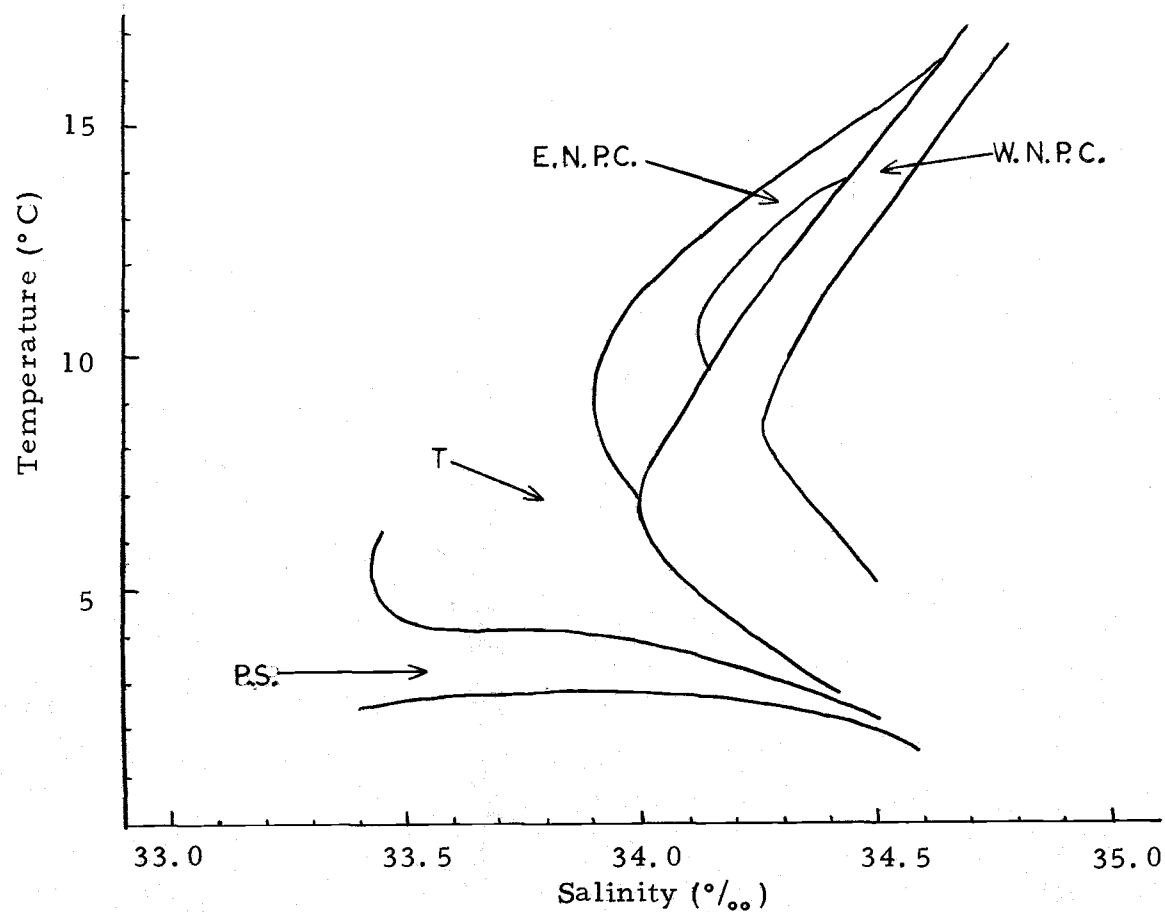


Figure 6. Temperature-salinity diagram showing water mass envelopes for water masses in the study area of the North Pacific Ocean: P. S. = Pacific Subarctic water mass; E. N. P. C. = Eastern North Pacific Central water mass; W. N. P. C. = Western North Pacific Central water mass; T = Transitional waters.

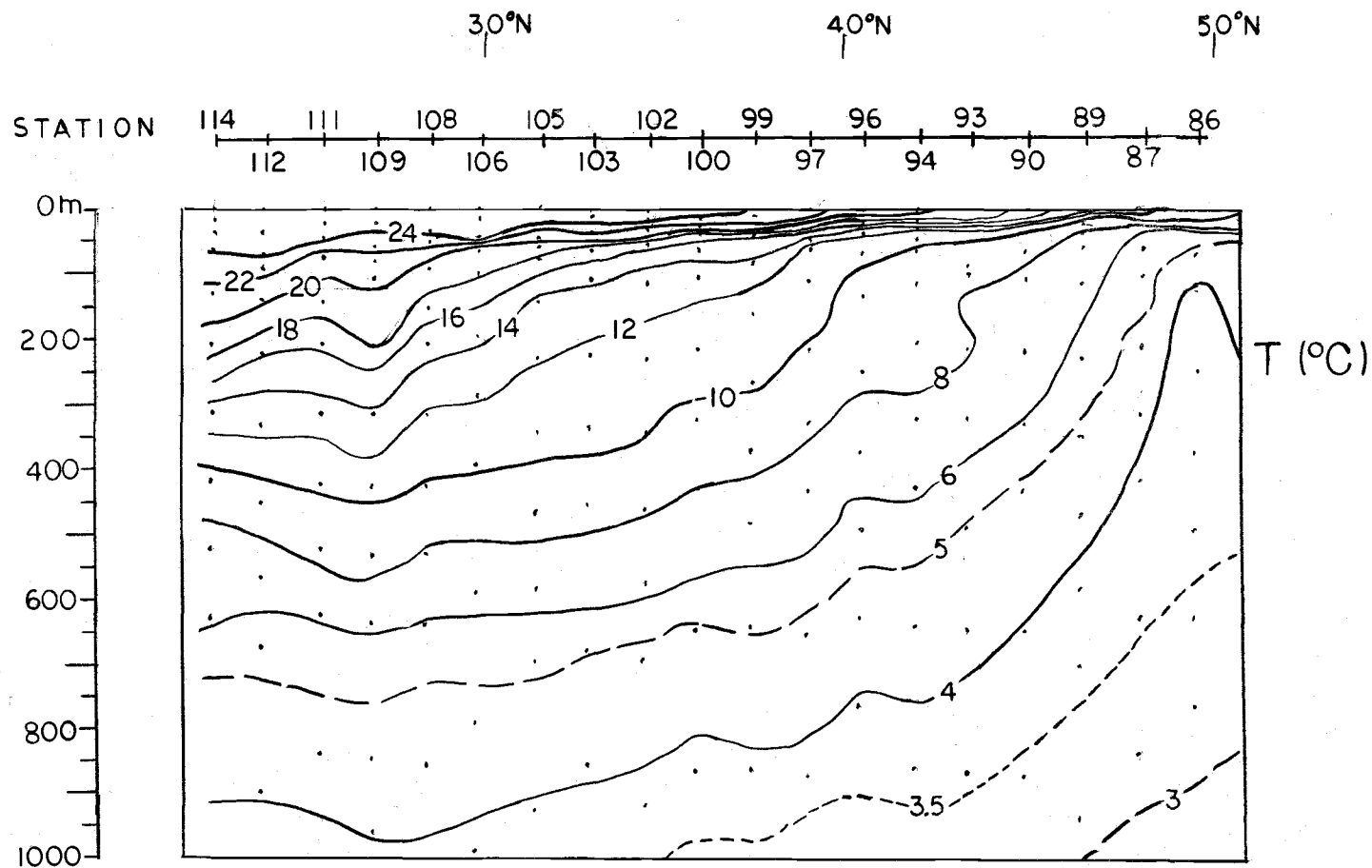


Figure 7. Temperature profile along a north-south track of Hugh M. Smith Cruise at 158°W, from 48°04'N (Station 86) to 22°30'N (Station 114).

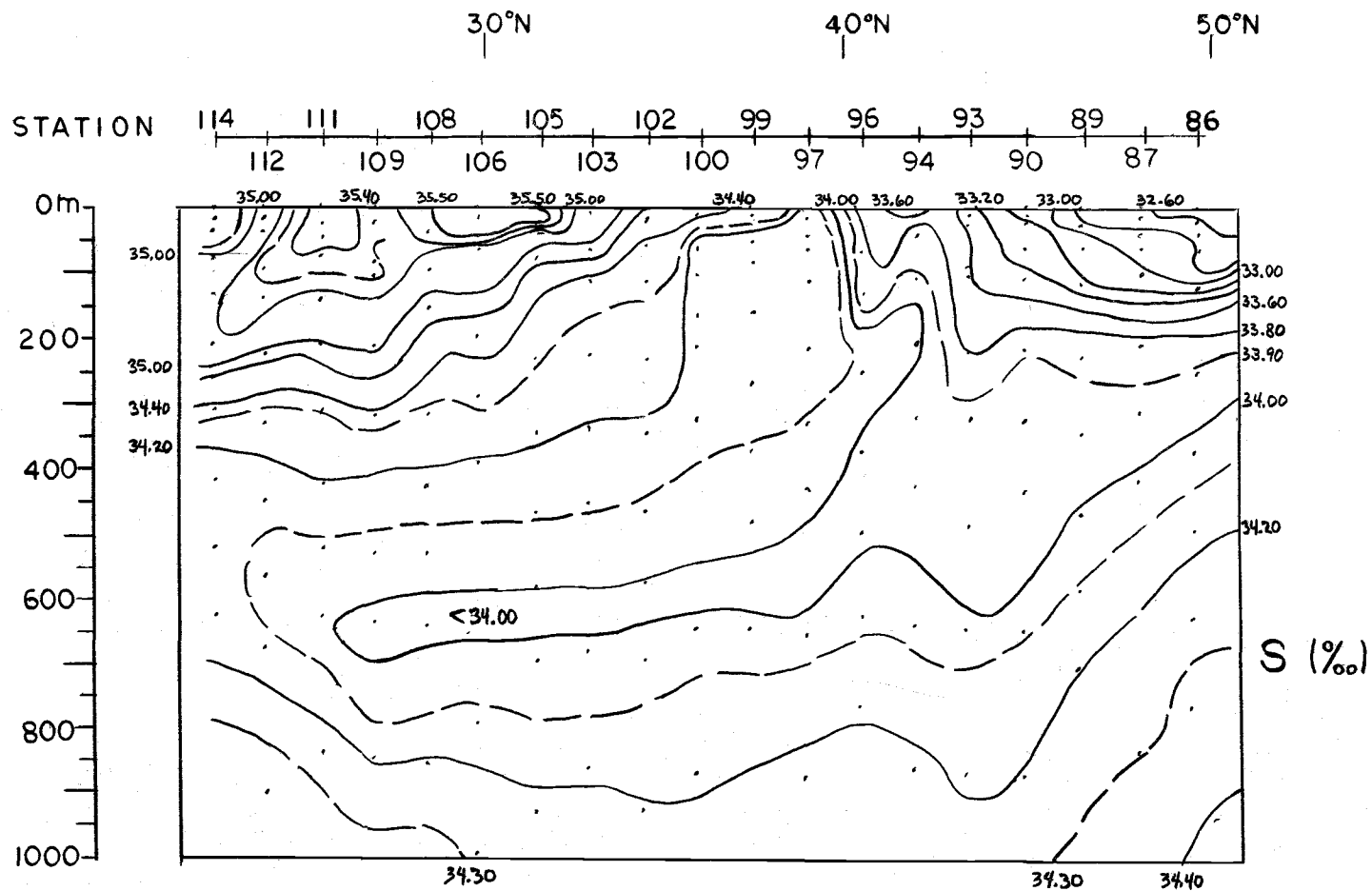


Figure 8. Salinity profile along a north-south track of Hugh M. Smith Cruise 30 at 158°W, from 48°04'N (Station 86) to 22°30'N (Station 114).

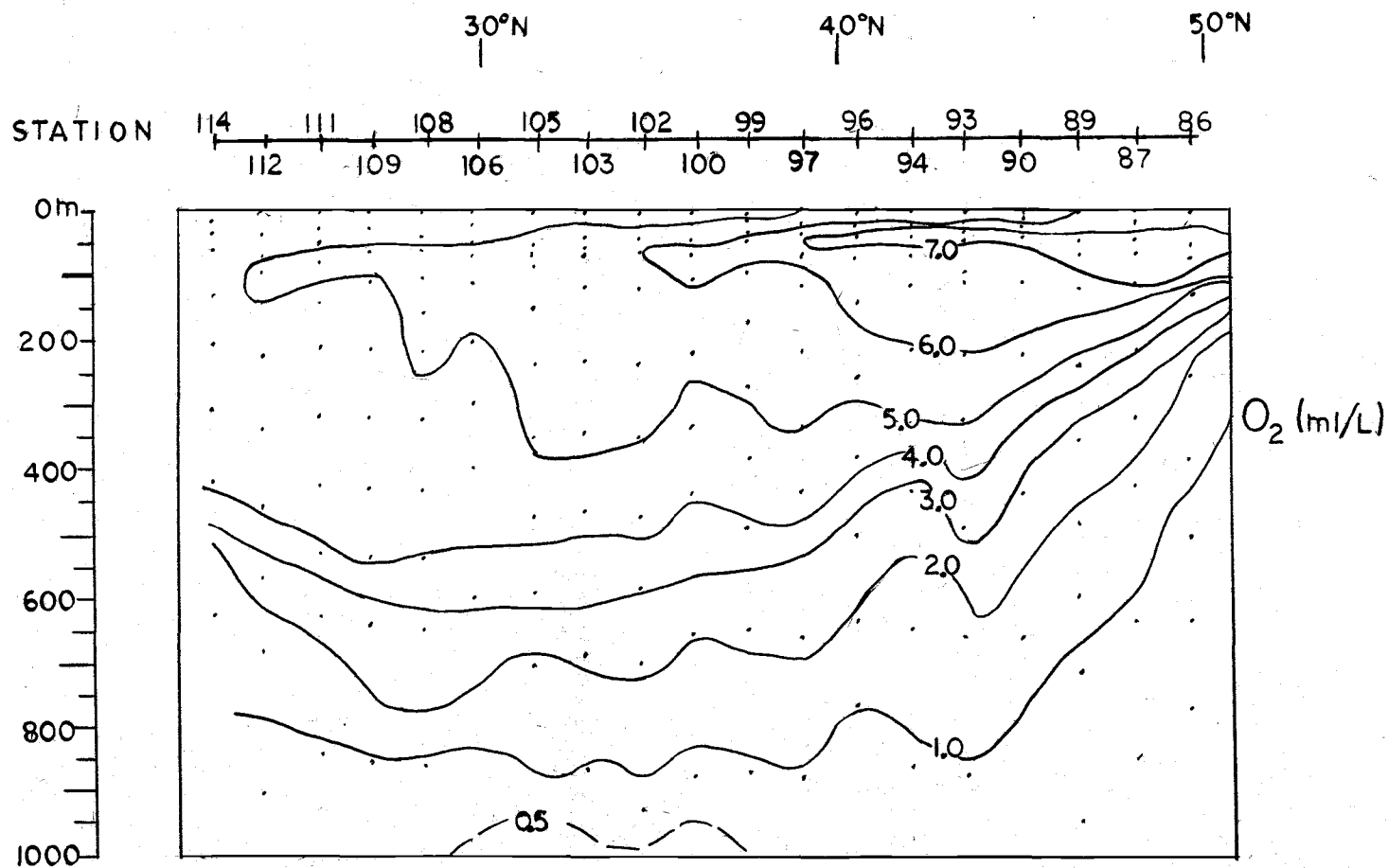


Figure 9. Oxygen profile along a north-south track of Hugh M. Smith Cruise 30 at 158°W, from 48°04'N (Station 86) to 22°30'N (Station 114).

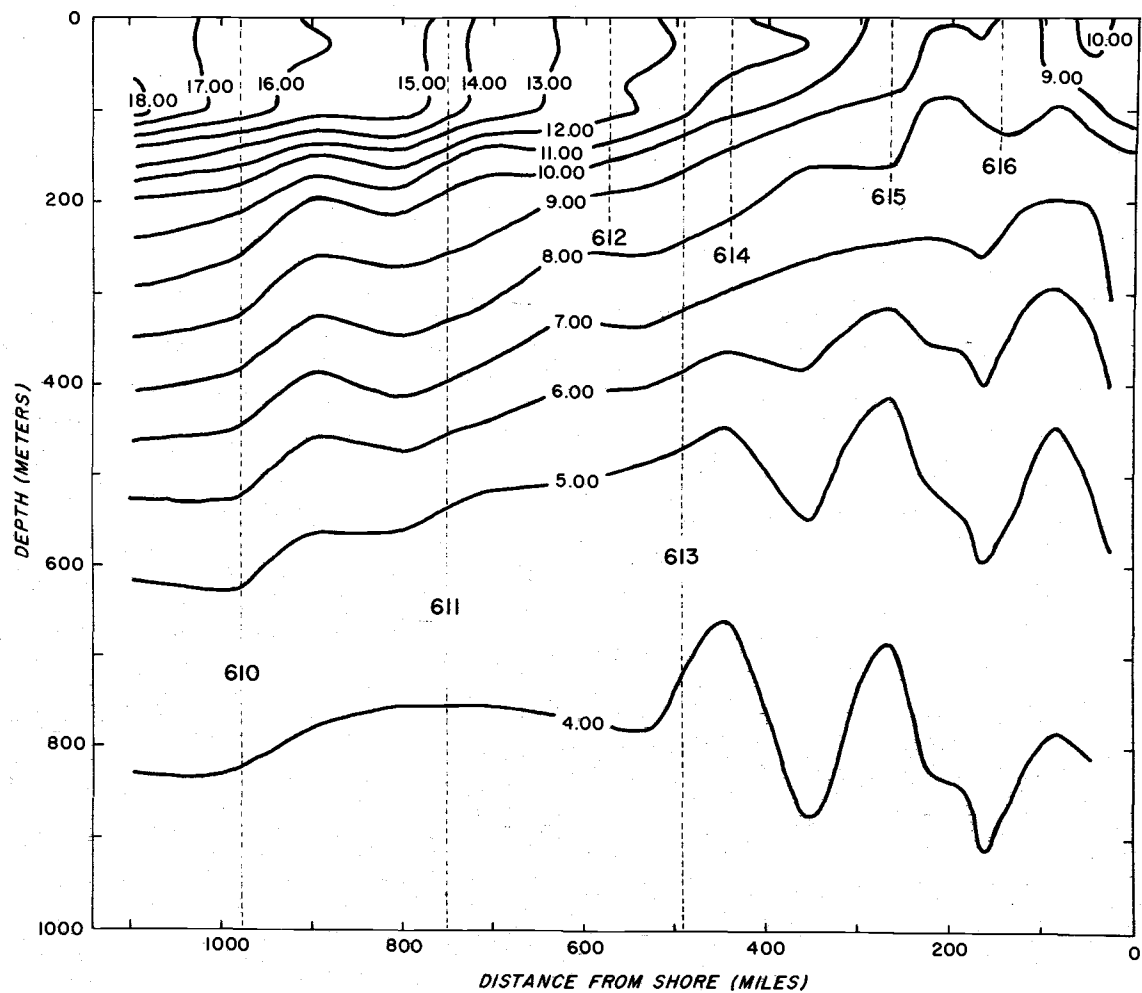


Figure 10. Temperature profile along the inbound track of the SICS-PAC cruise of the R/V Yaquina, from 34°31.8'N (Station 610) to 43°20.6'N (Station 616). Vertical dash lines indicate midwater trawl stations.

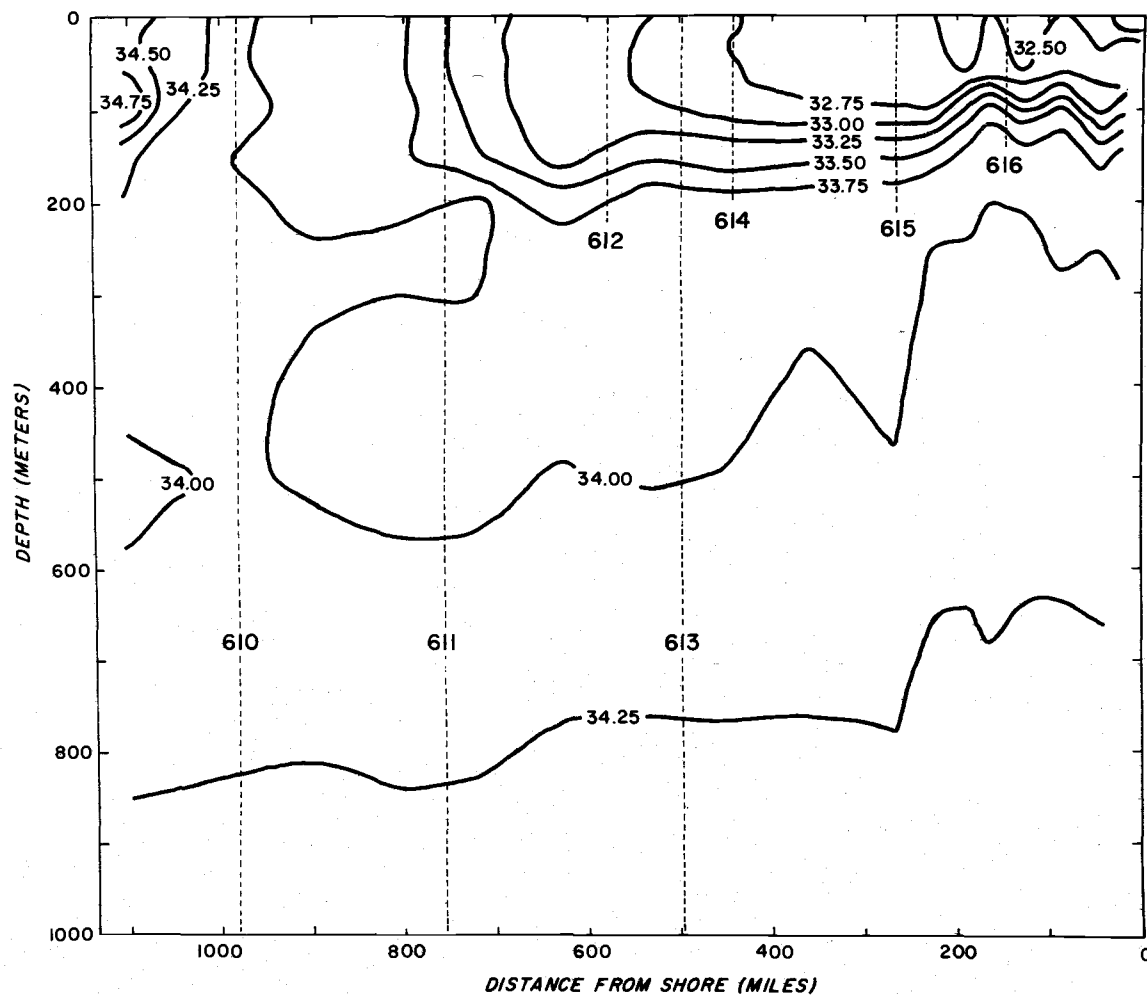


Figure 11. Salinity profile along the inbound track of the SICS-PAC cruise of the R/V Yaquina, from 34° 31.8'N (Station 610) to 43° 20.6'N (Station 616). Vertical dash lines indicate midwater trawl stations.

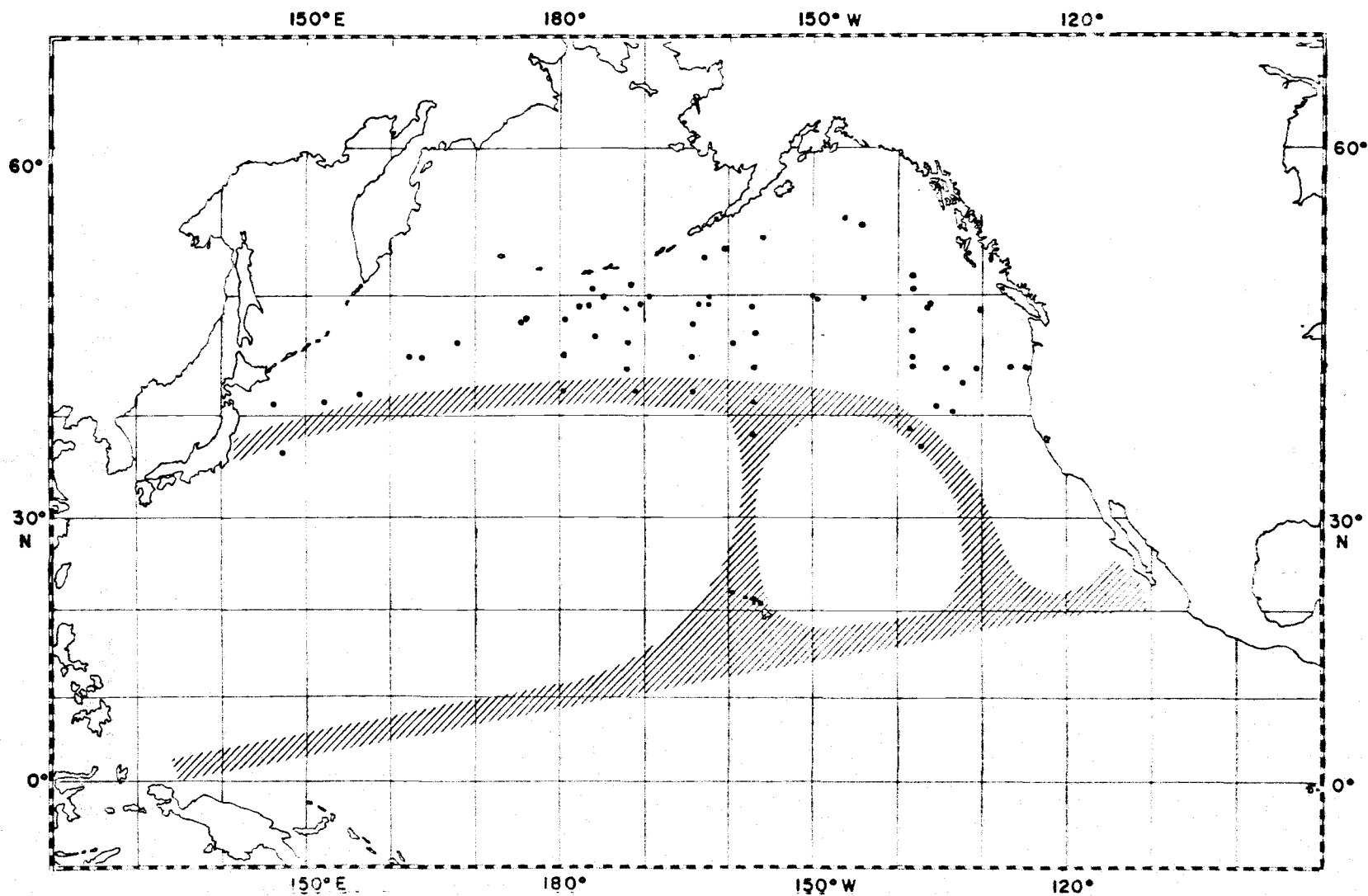


Figure 12. Distribution of *Sergestes similis* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

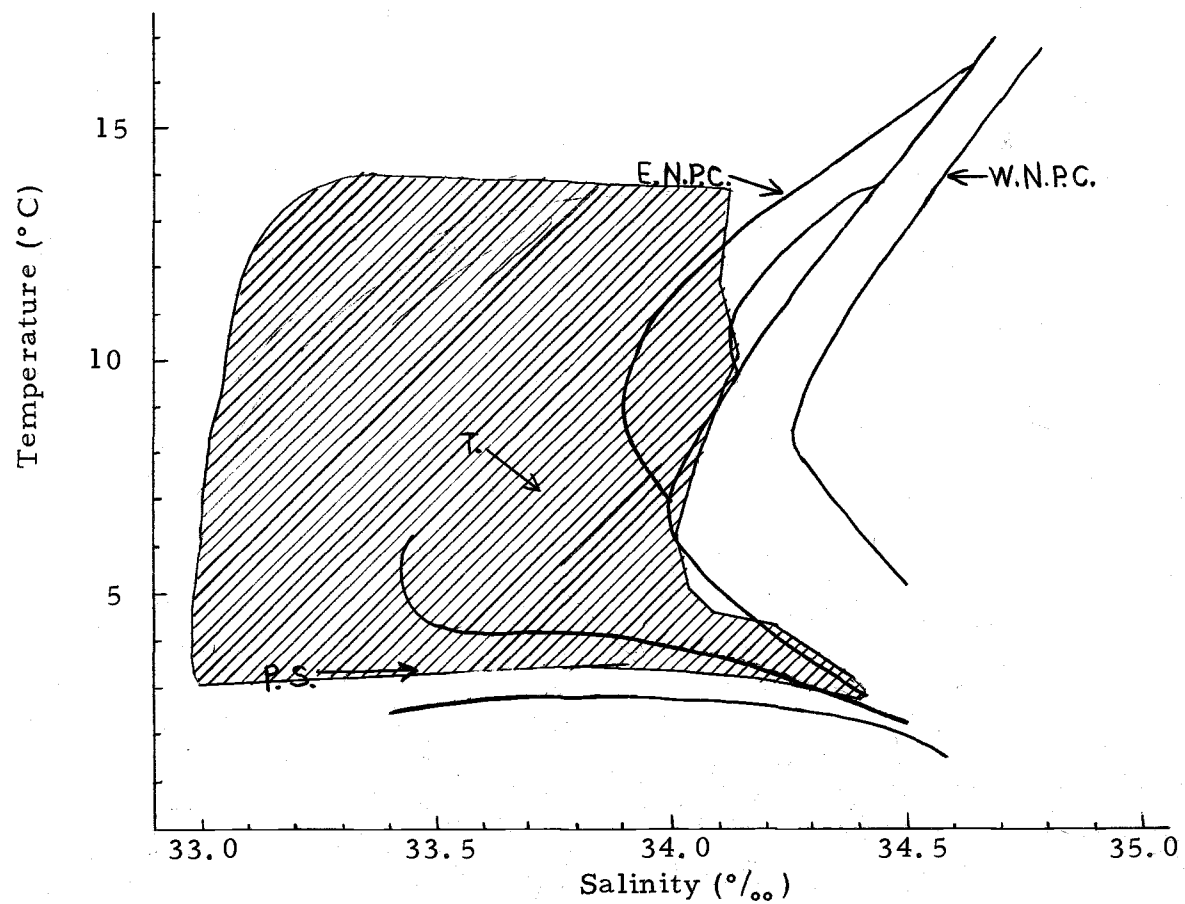


Figure 13. Temperature-salinity capture diagram for *Sergestes similis*. Water masses as in Figure 6.

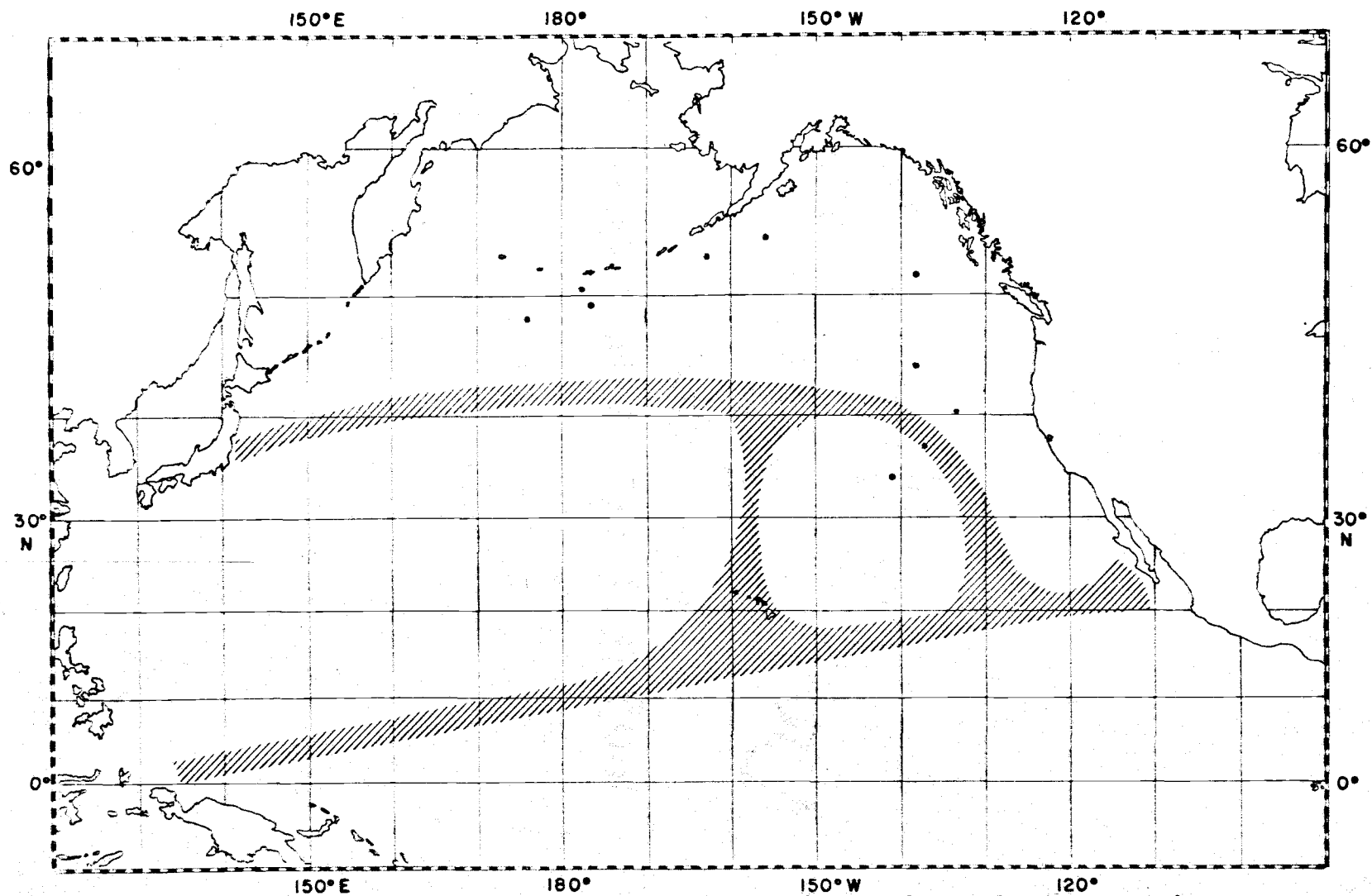


Figure 14. Distribution of Bentheogennema borealis in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

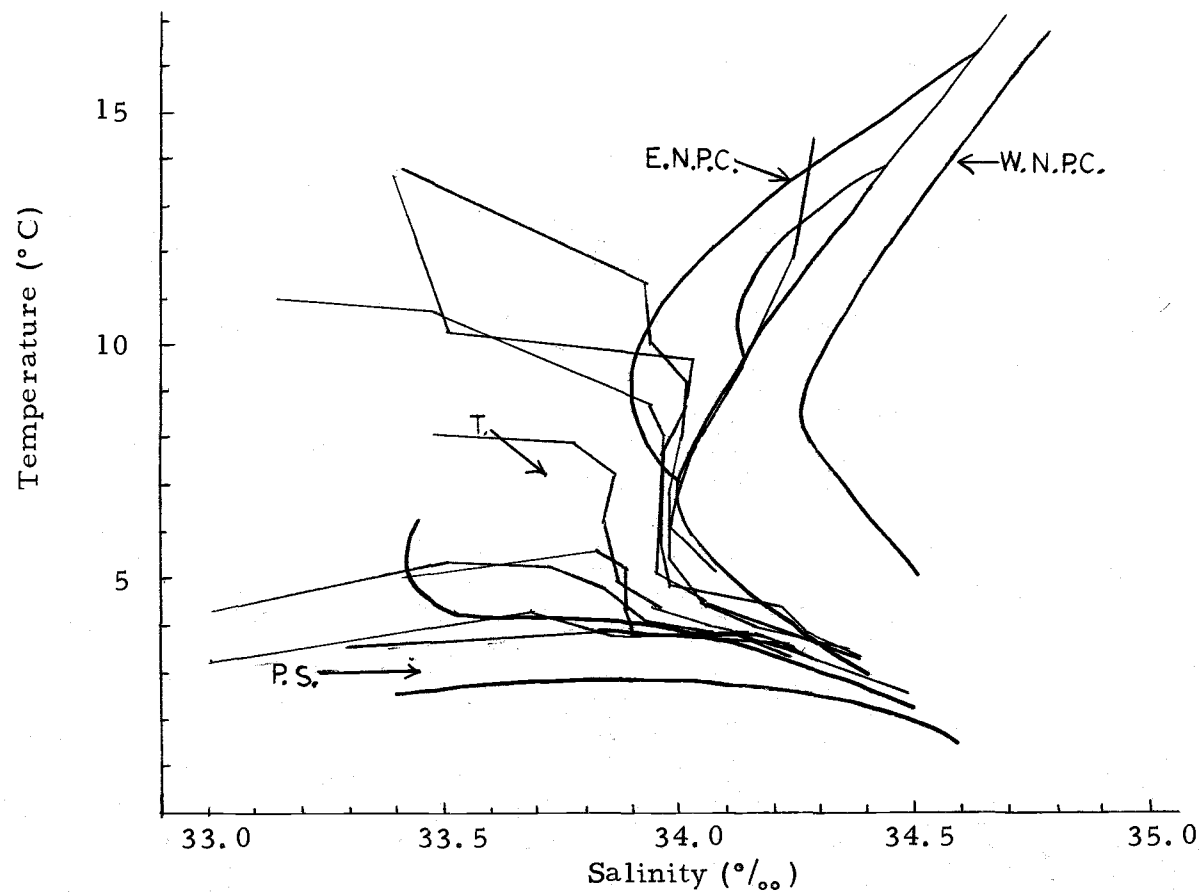


Figure 15. Temperature-salinity capture diagram for Bentheogennema borealis. Water masses as in Figure 6.

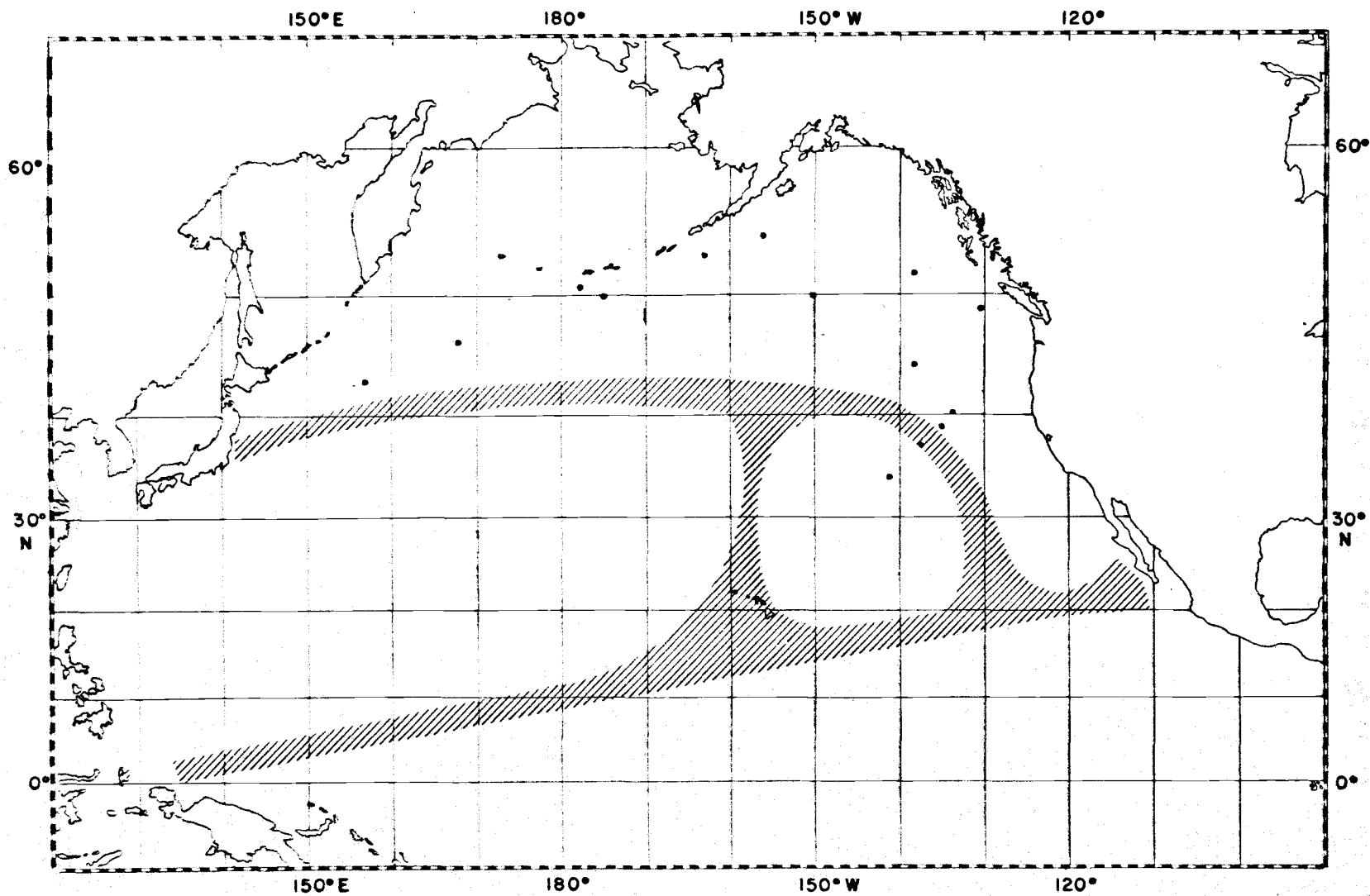


Figure 16. Distribution of *Hymenodora frontalis* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

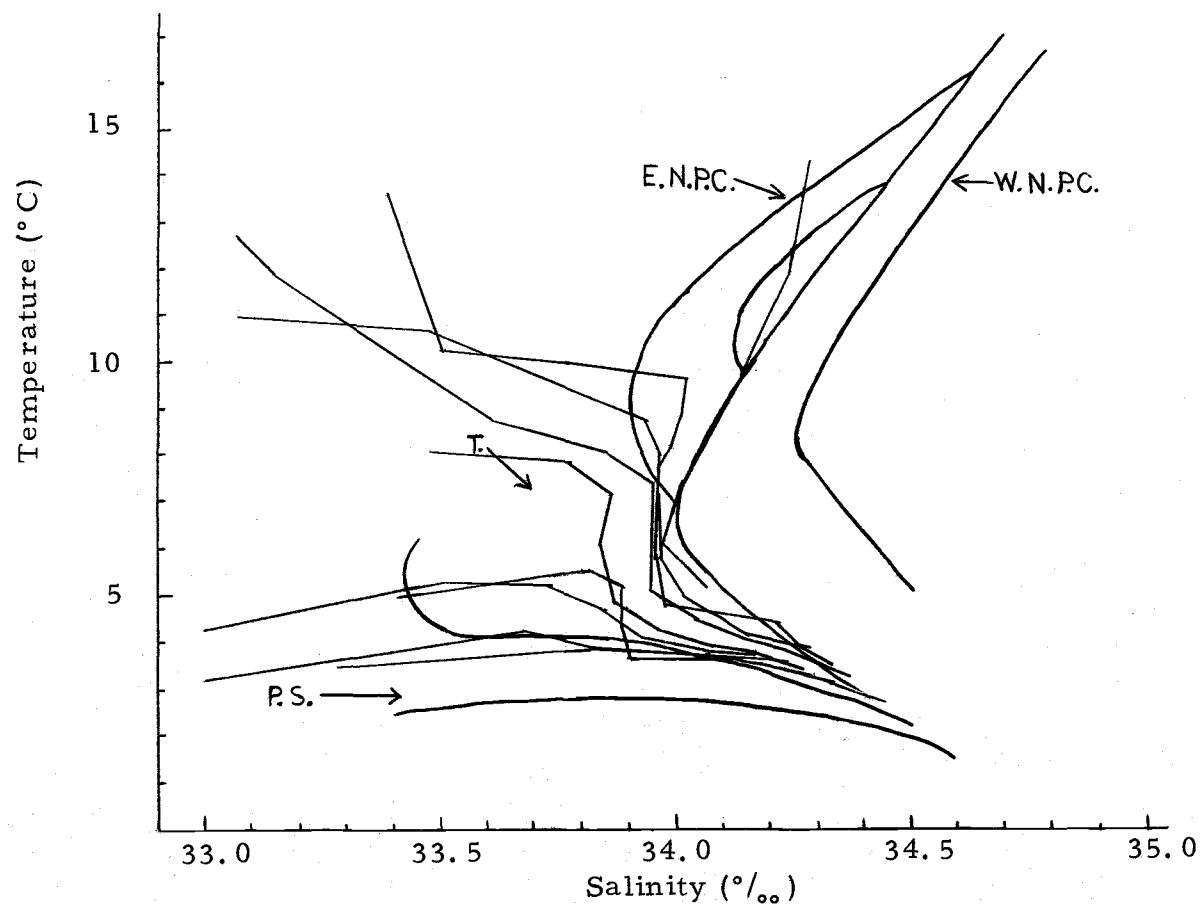


Figure 17. Temperature-salinity capture diagram for Hymenodora frontalis. Water masses as in Figure 6.

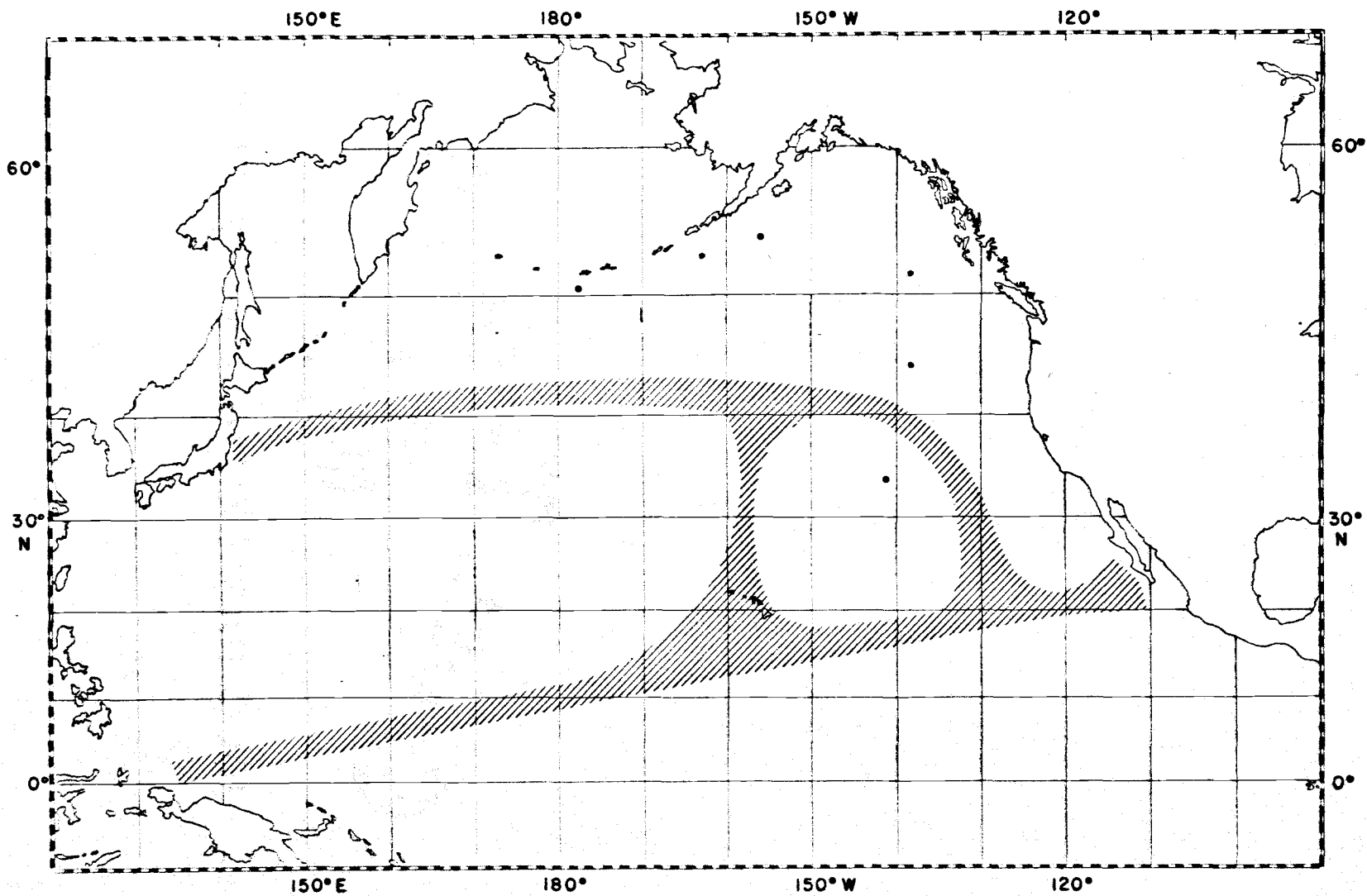


Figure 18. Distribution of *Hymenodora glacialis* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

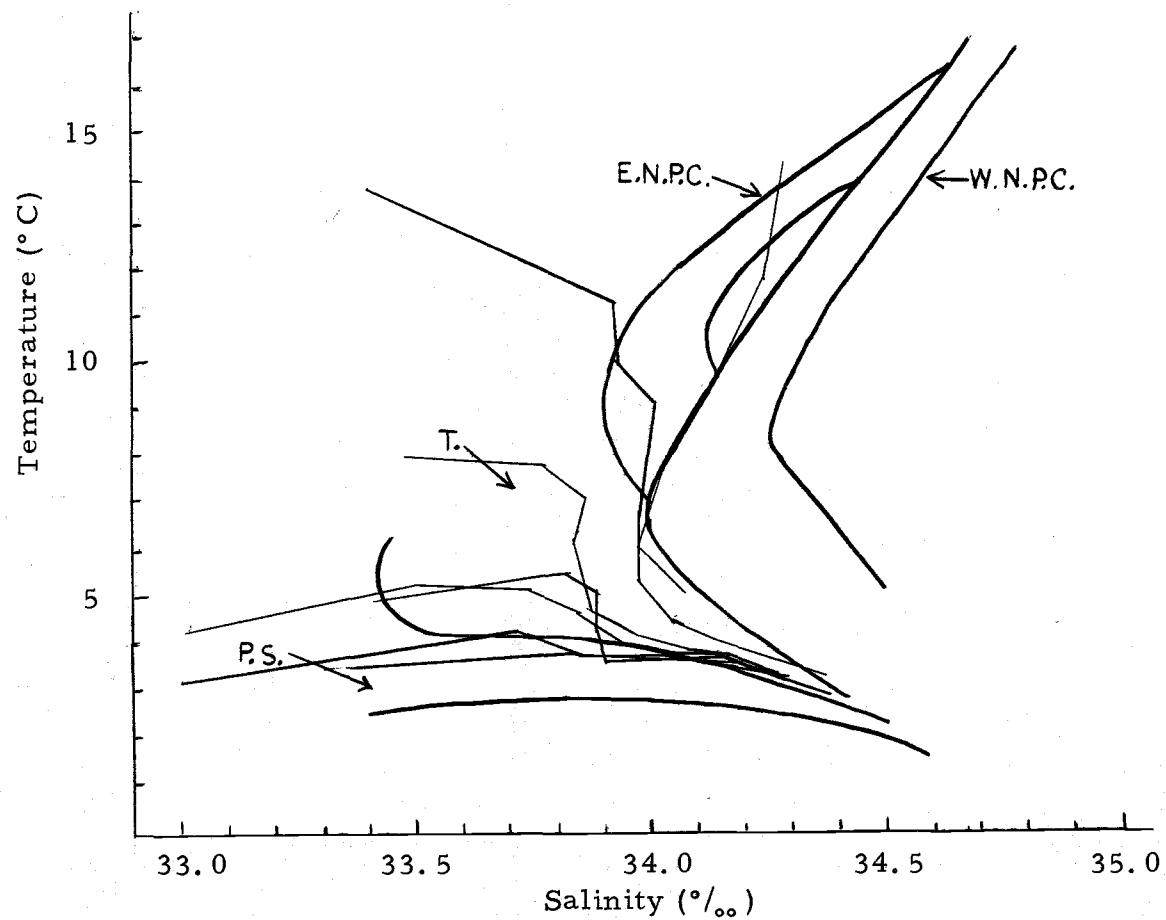


Figure 19. Temperature-salinity capture diagram for Hymenodora glacialis. Water masses as in Figure 6.

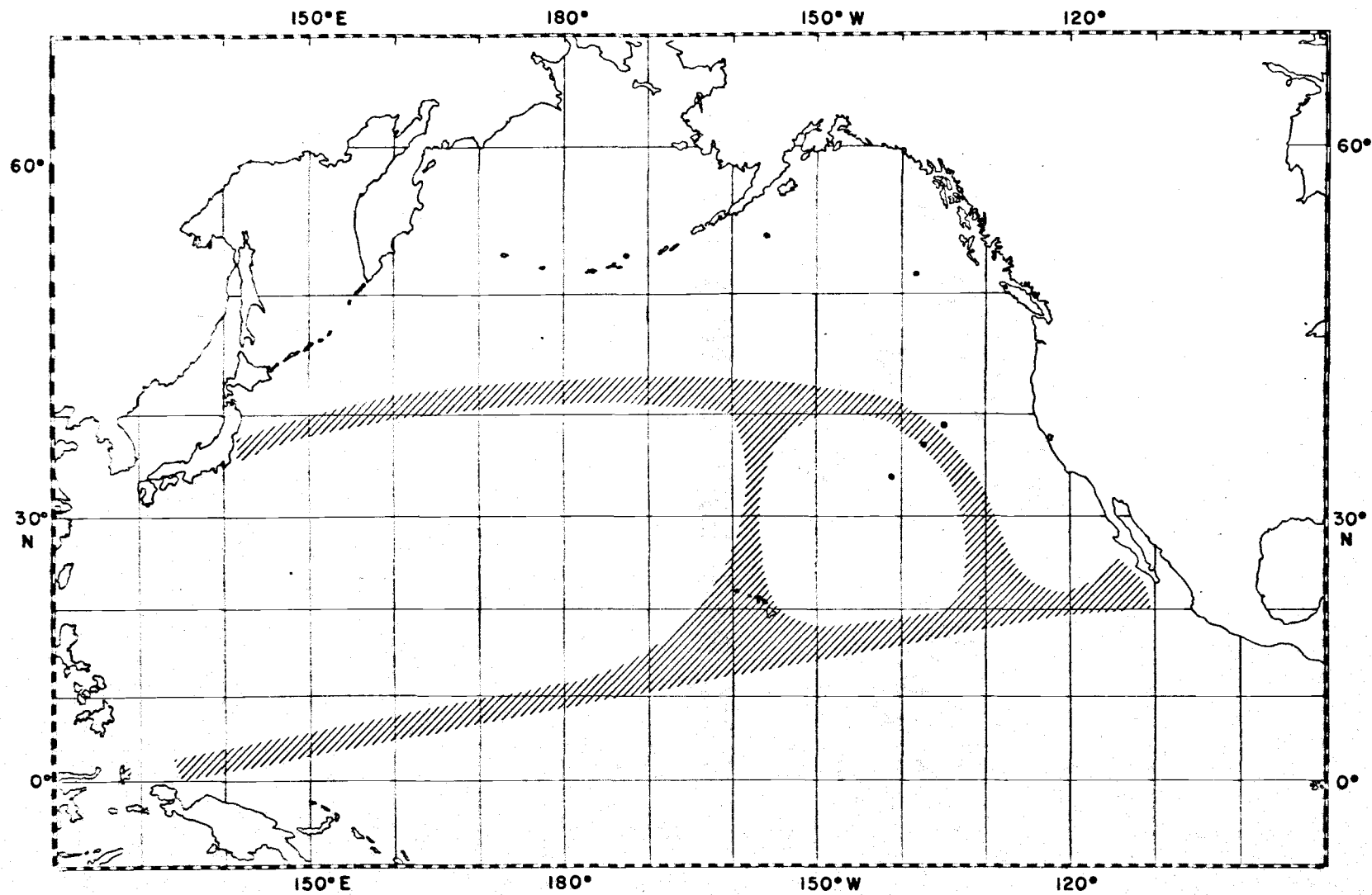


Figure 20. Distribution of *Hymenodora gracilis* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

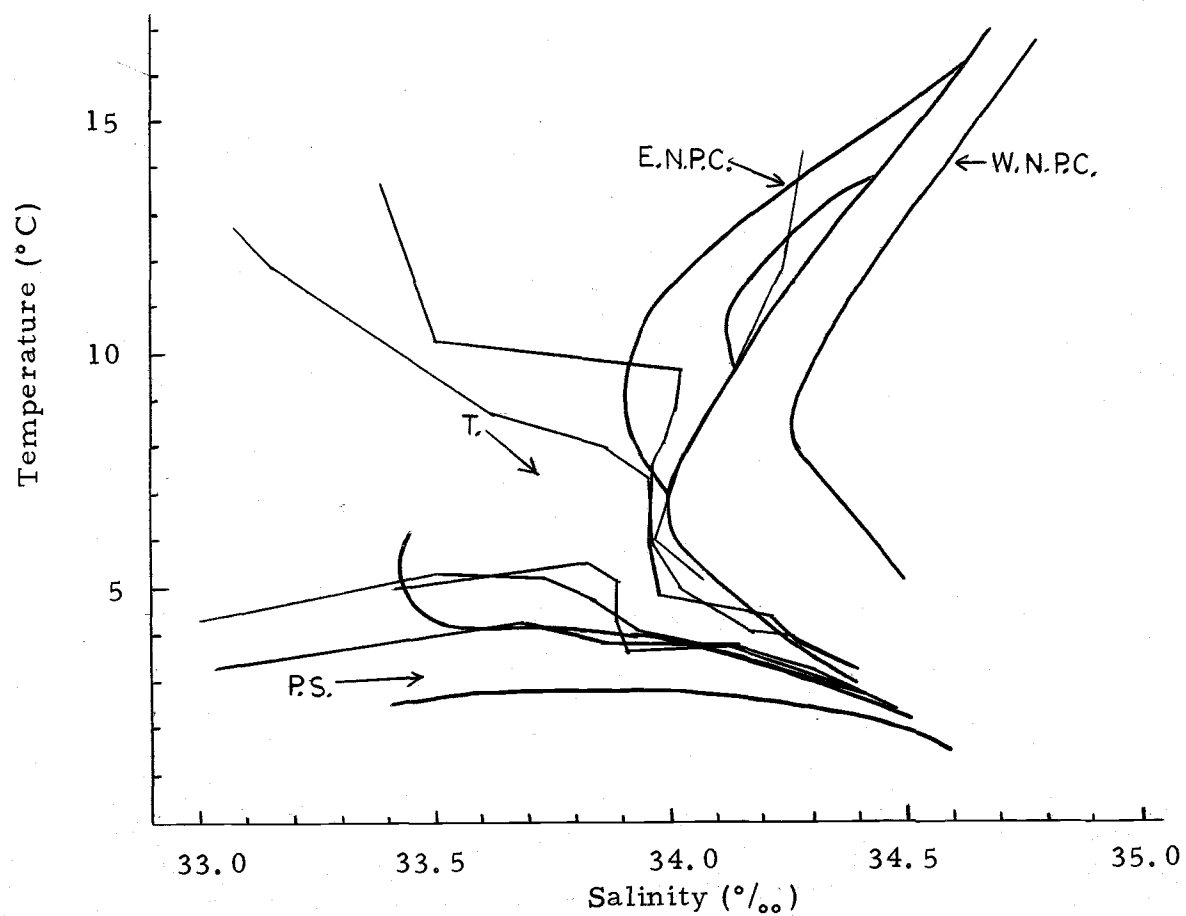


Figure 21. Temperature-salinity capture diagram for Hymenodora gracilis. Water masses as in Figure 6.

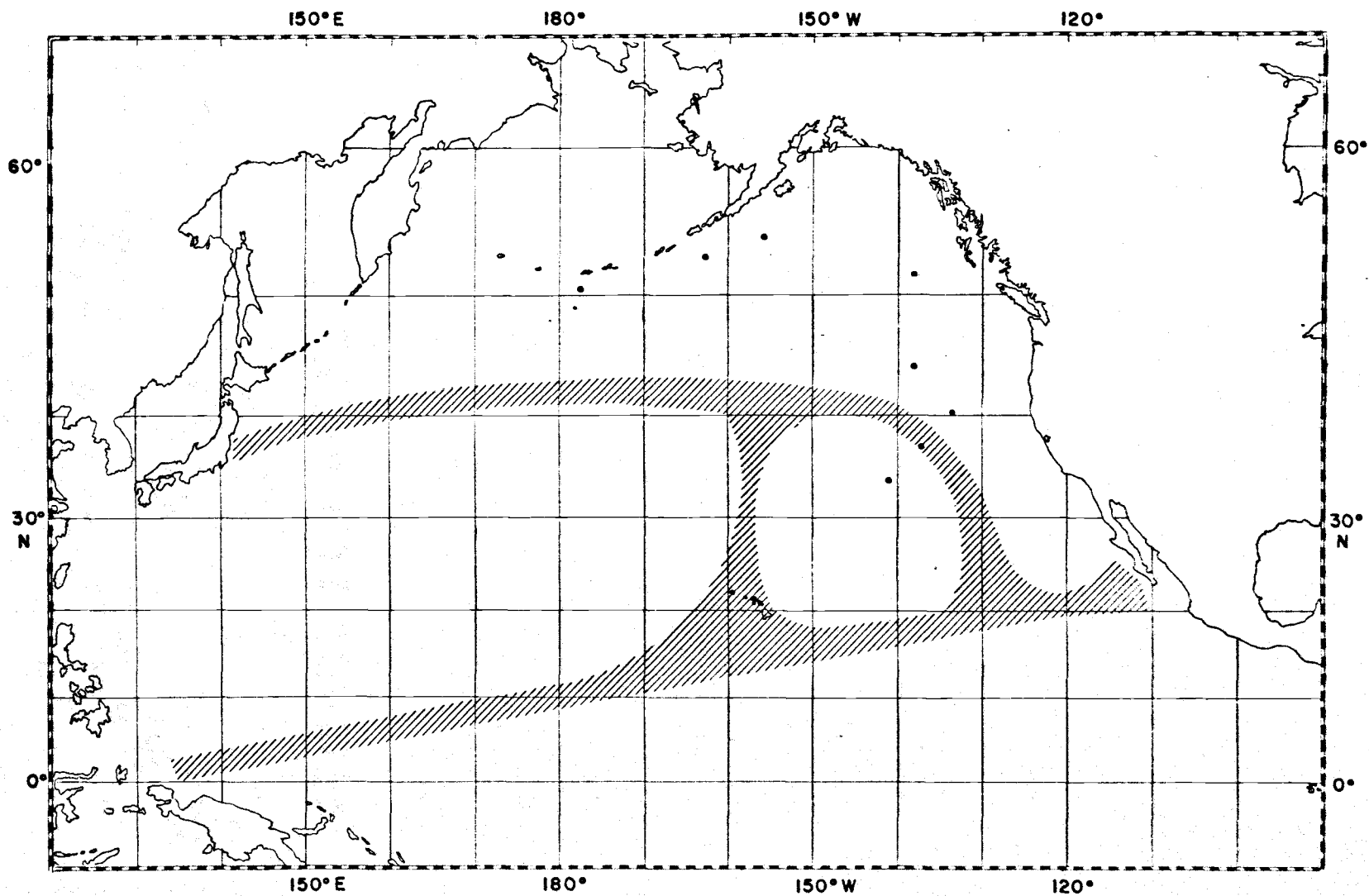


Figure 22. Distribution of *Systellaspis braueri* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

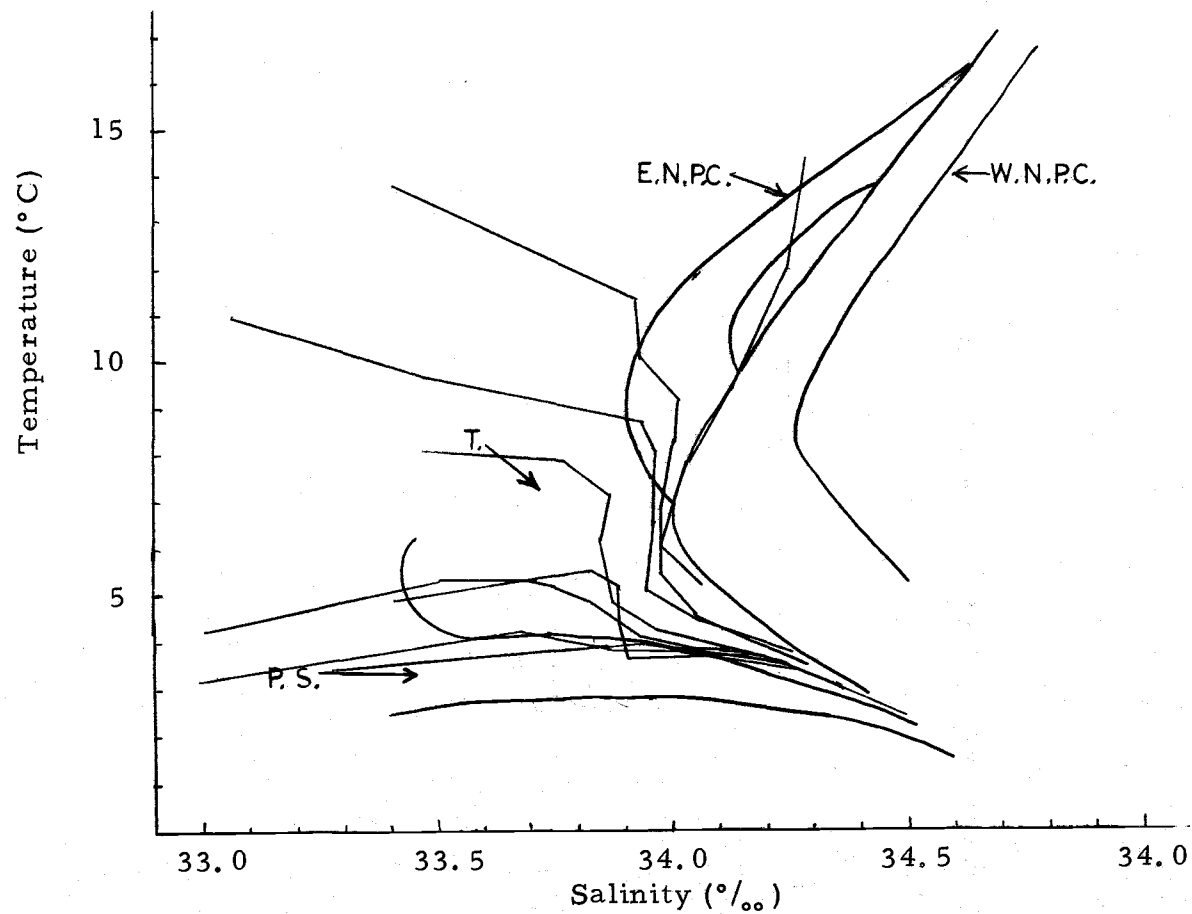


Figure 23. Temperature-salinity capture diagram for Systellaspis braueri. Water masses as in Figure 6.

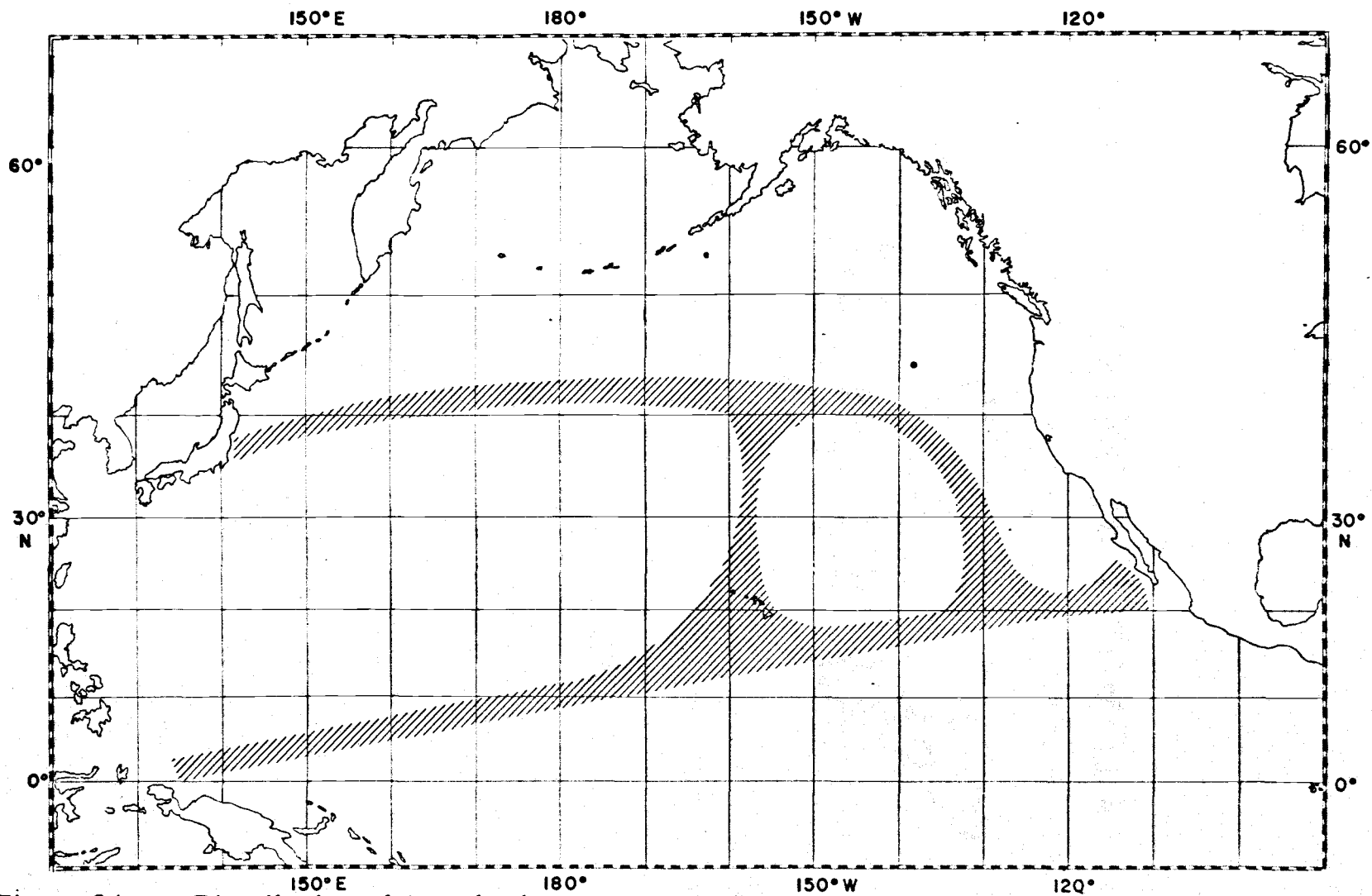


Figure 24. Distribution of *Acantheephyra n. sp.* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

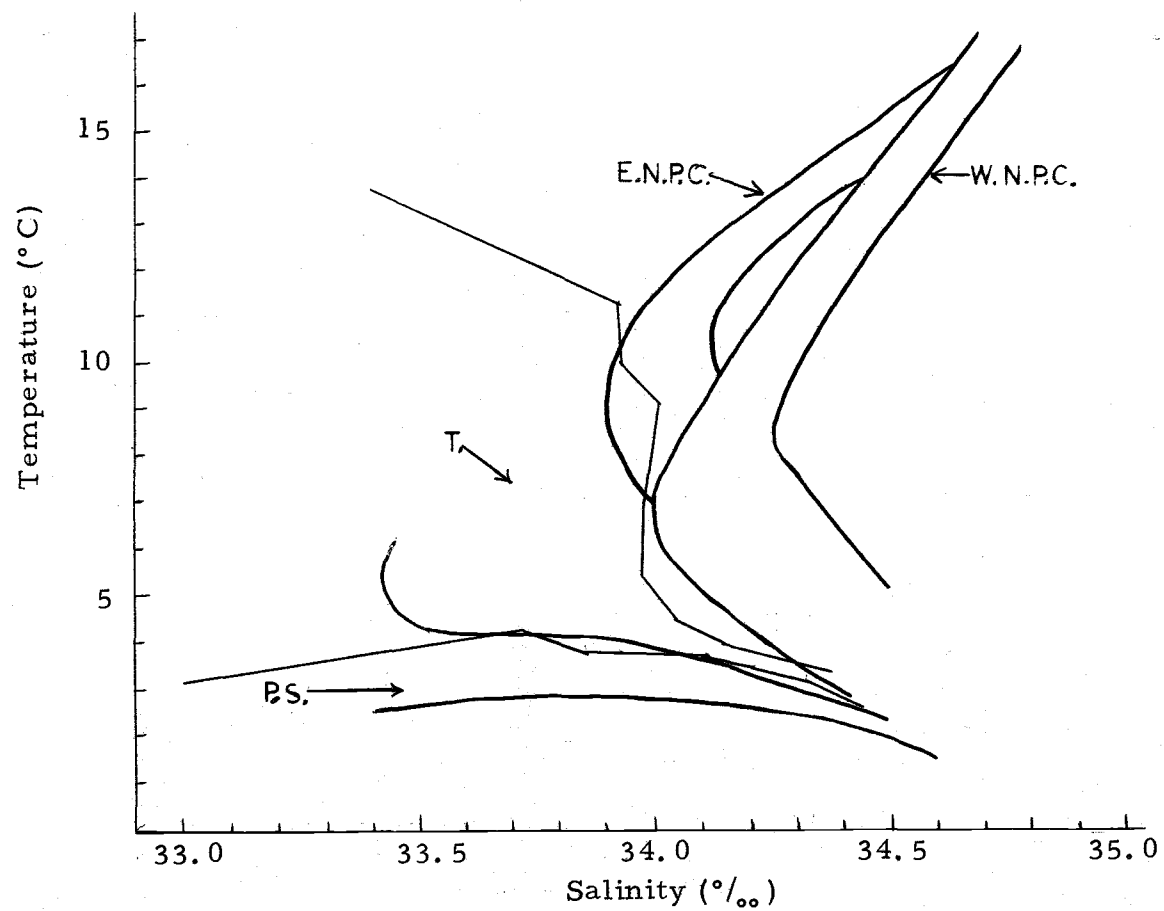


Figure 25. Temperature-salinity capture diagram for *Acanthephyra n. sp.* Water masses as in Figure 6.

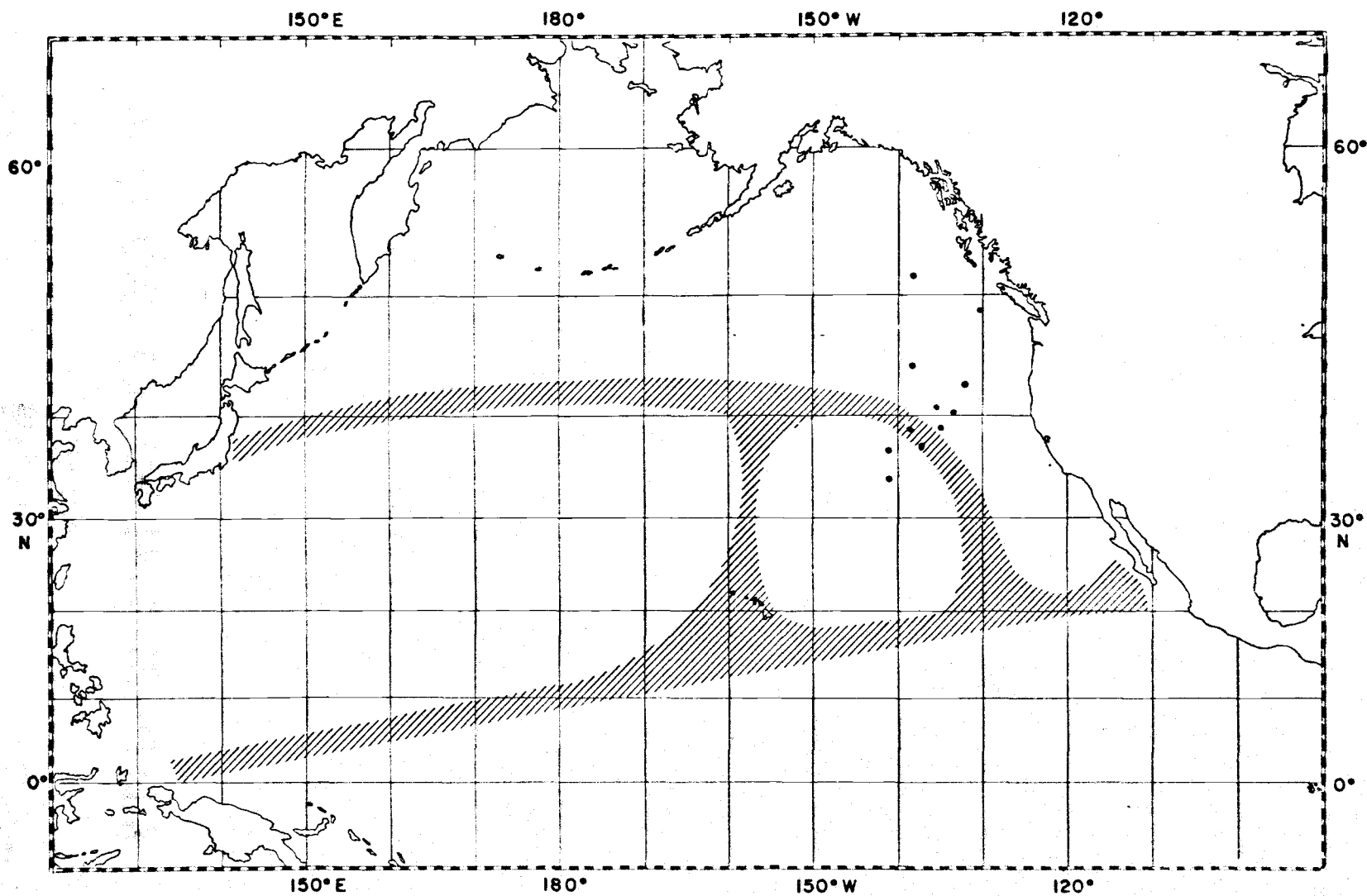


Figure 26. Distribution of *Bentheogennema* n. sp. in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

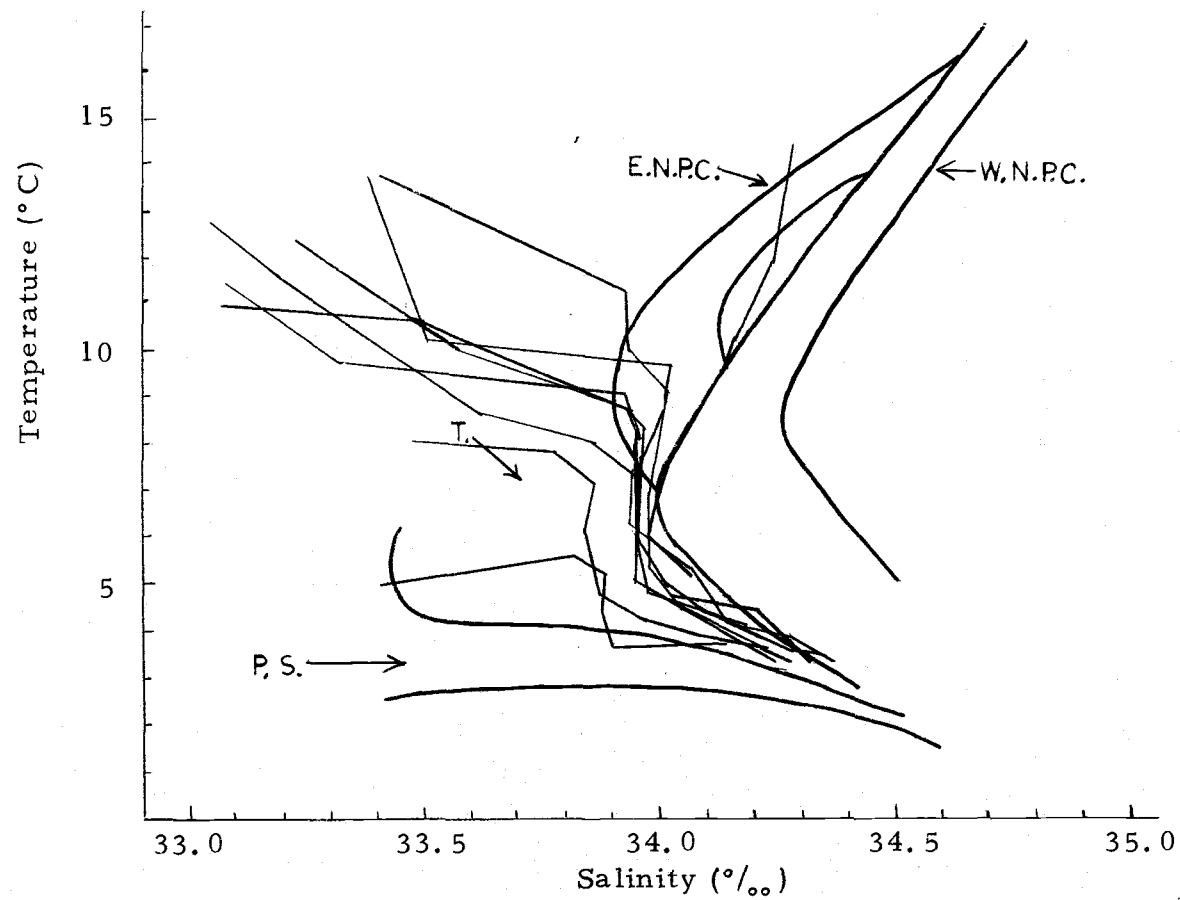


Figure 27. Temperature-salinity capture diagram for *Bentheogennema n. sp.* Water masses as in Figure 6.

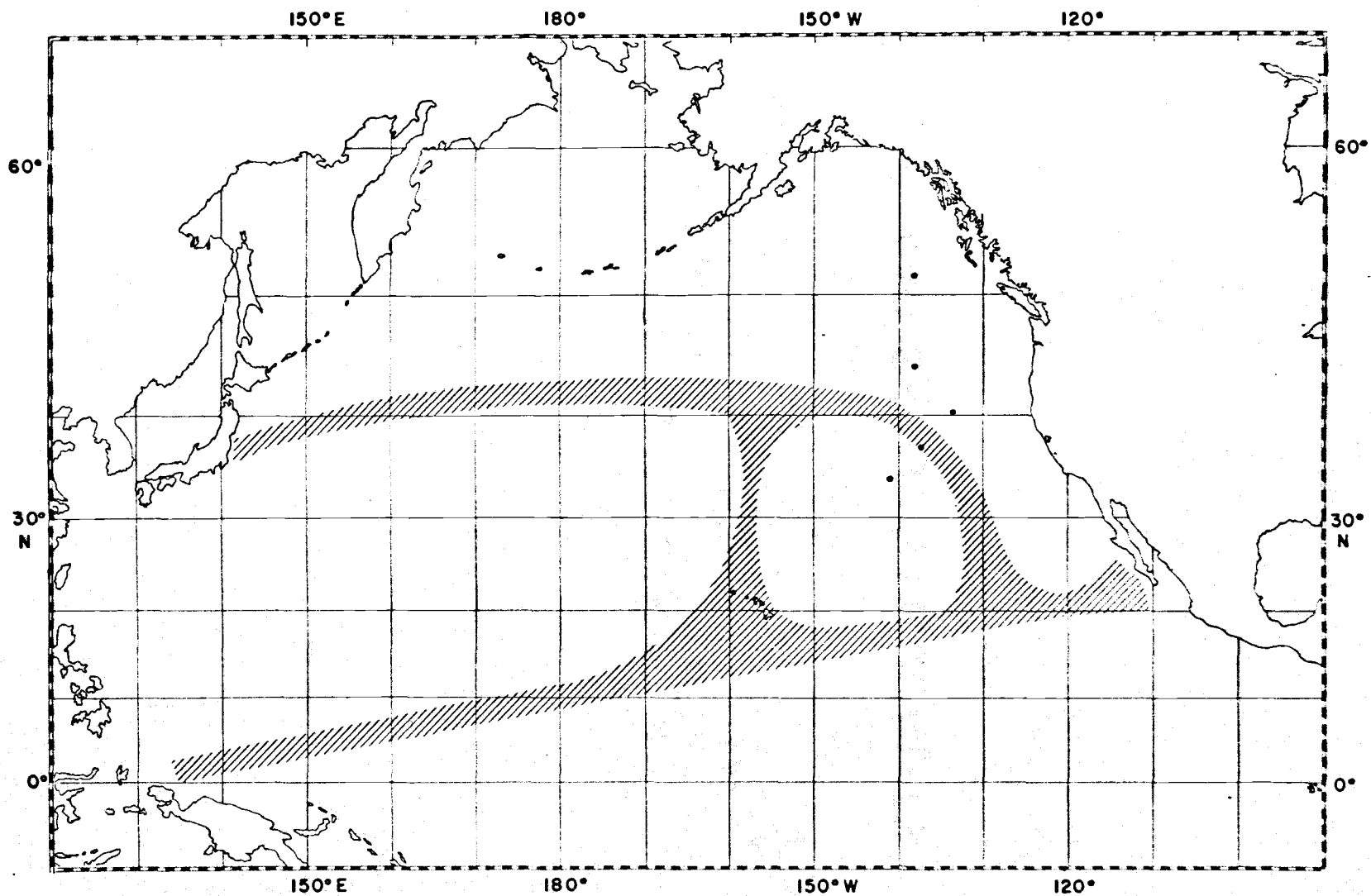


Figure 28. Distribution of *Petalidium suspensum* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

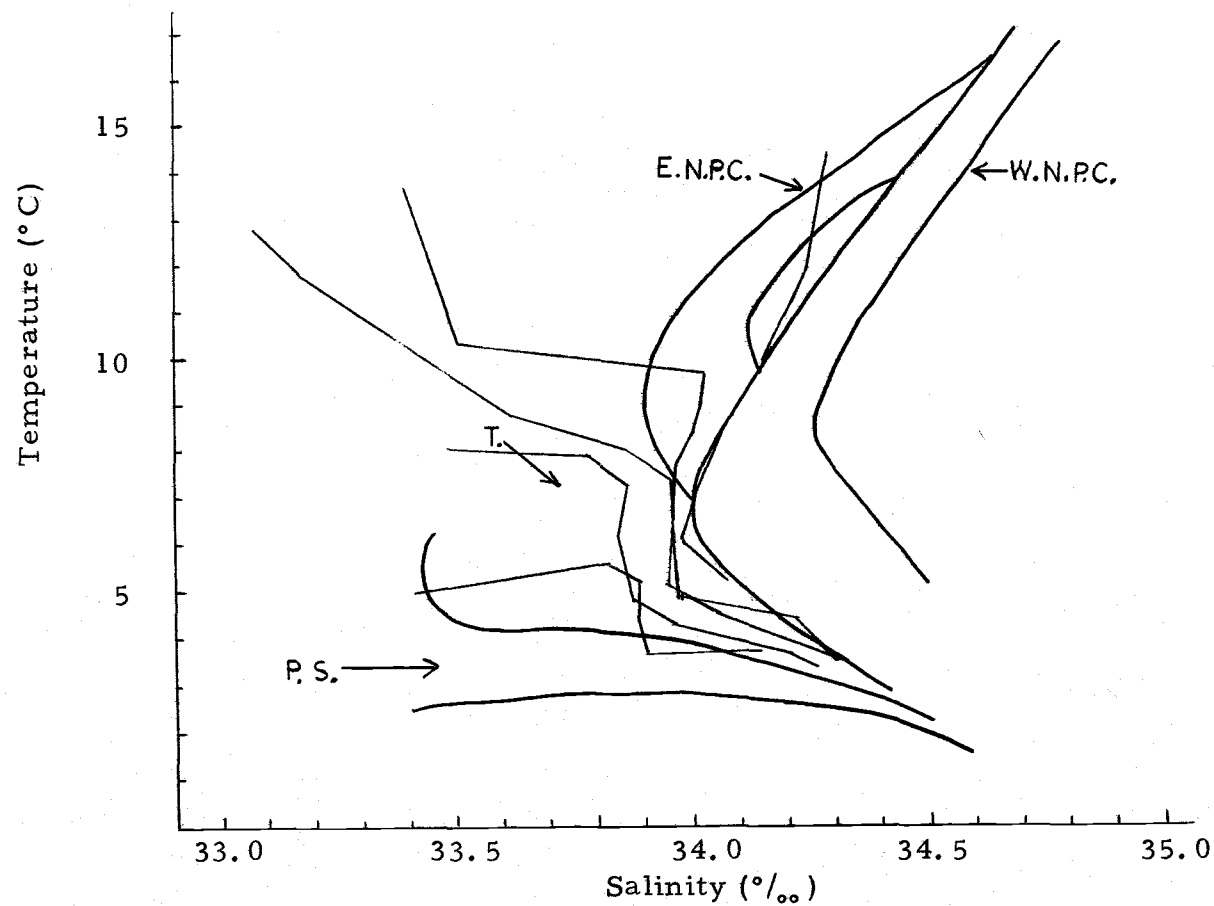


Figure 29. Temperature-salinity capture diagram for Petalidium suspensum. Water masses as in Figure 6.

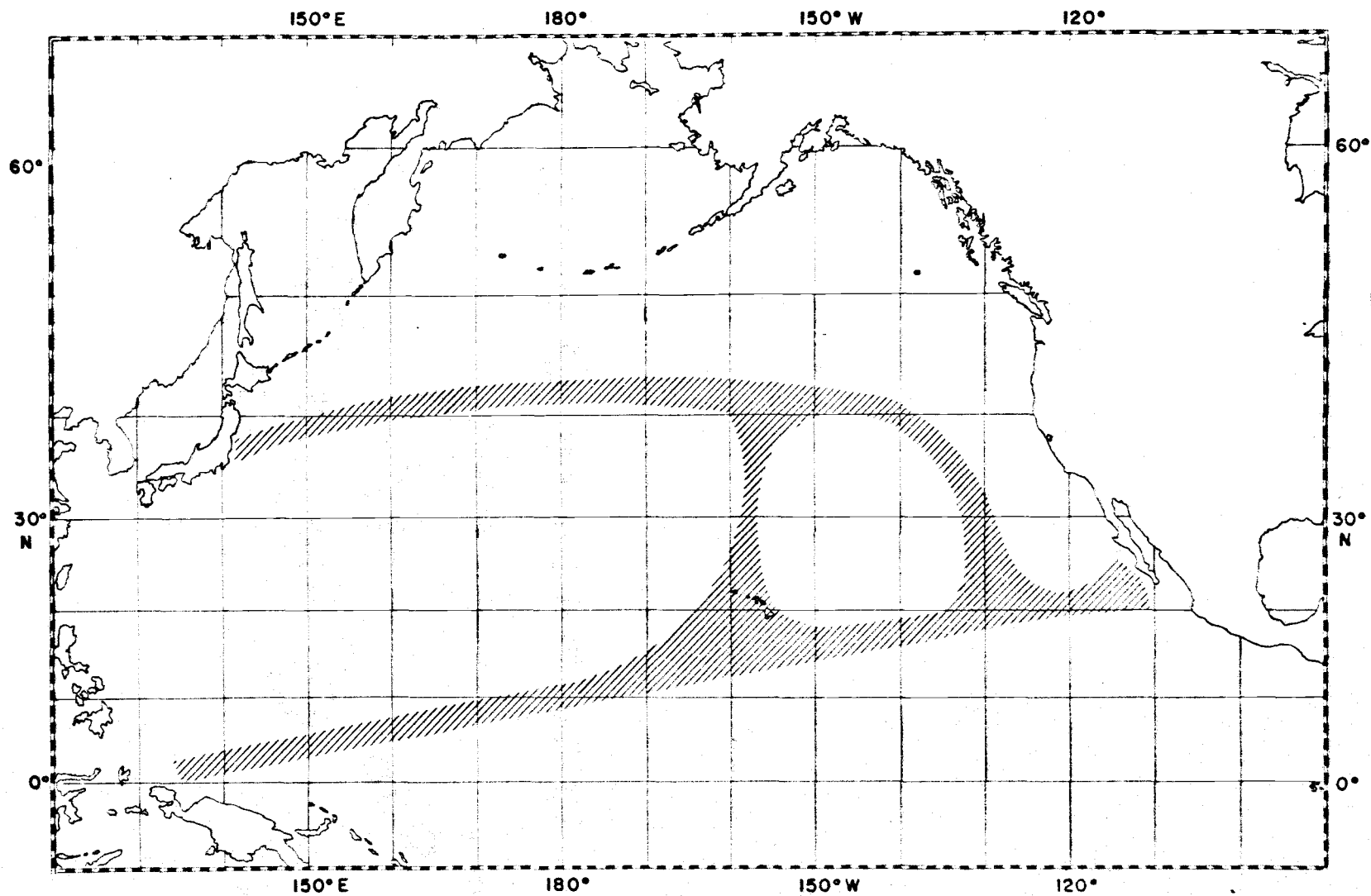


Figure 30. Distribution of *Sergestes japonicus* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

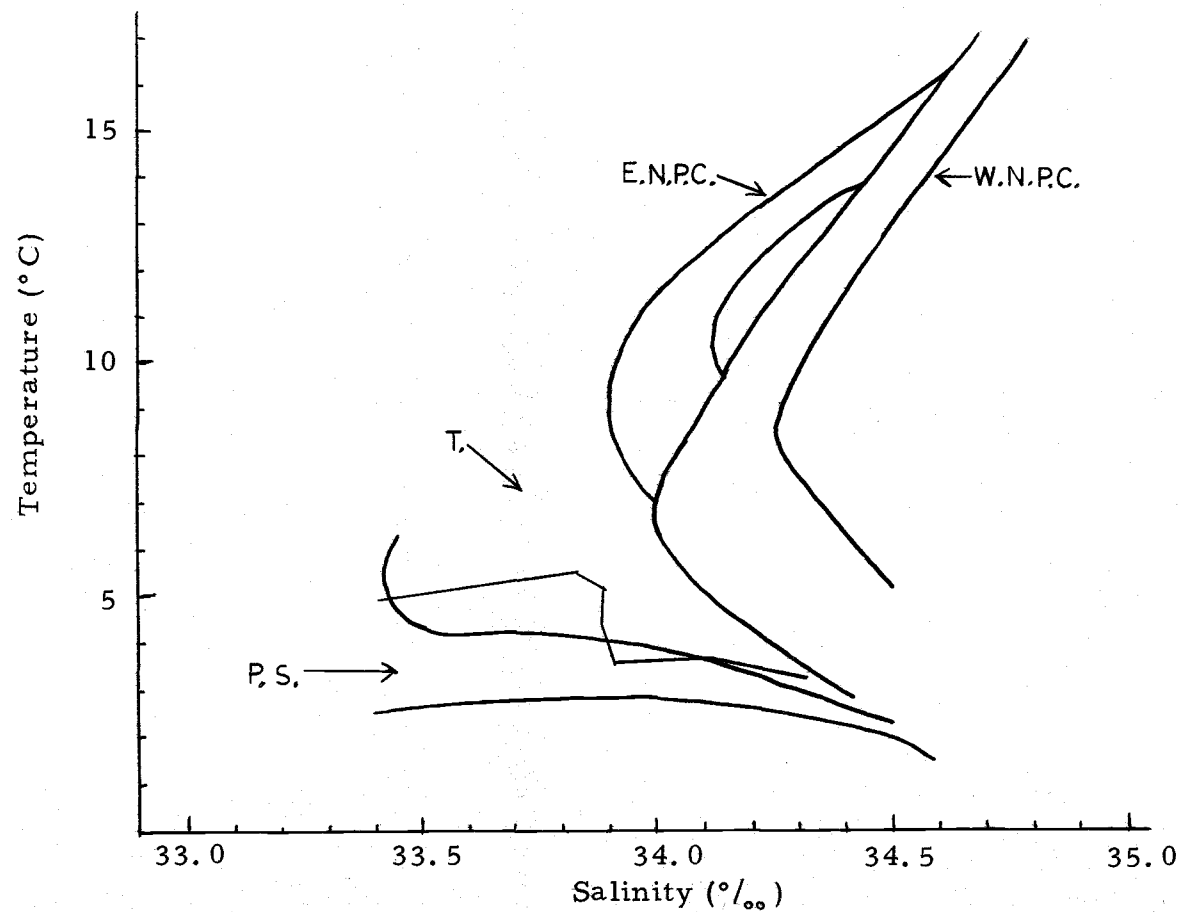


Figure 31. Temperature-salinity capture diagram for Sergestes japonicus. Water masses as in Figure 6.

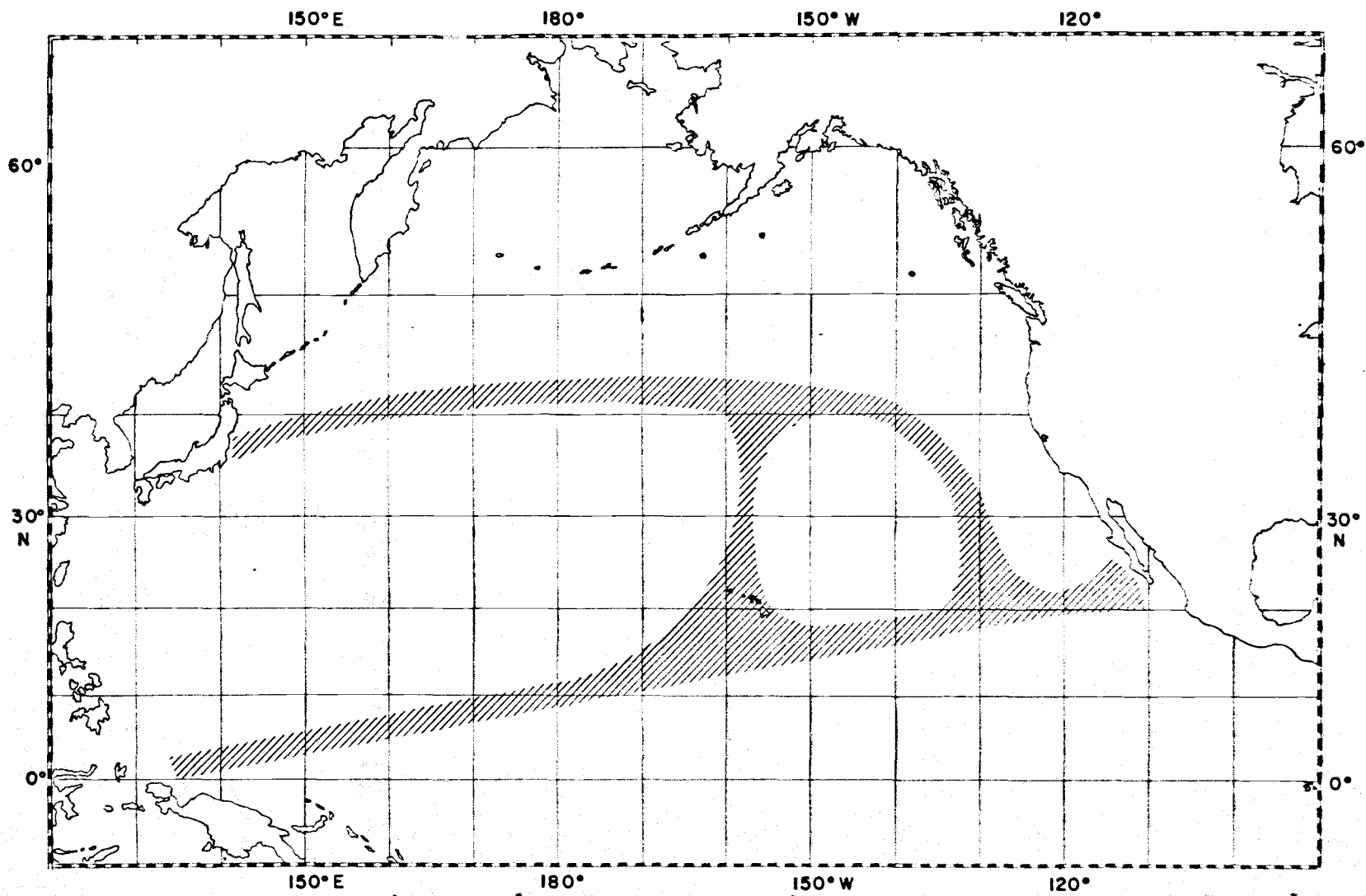


Figure 32. Distribution of *Pasiphaea tarda* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

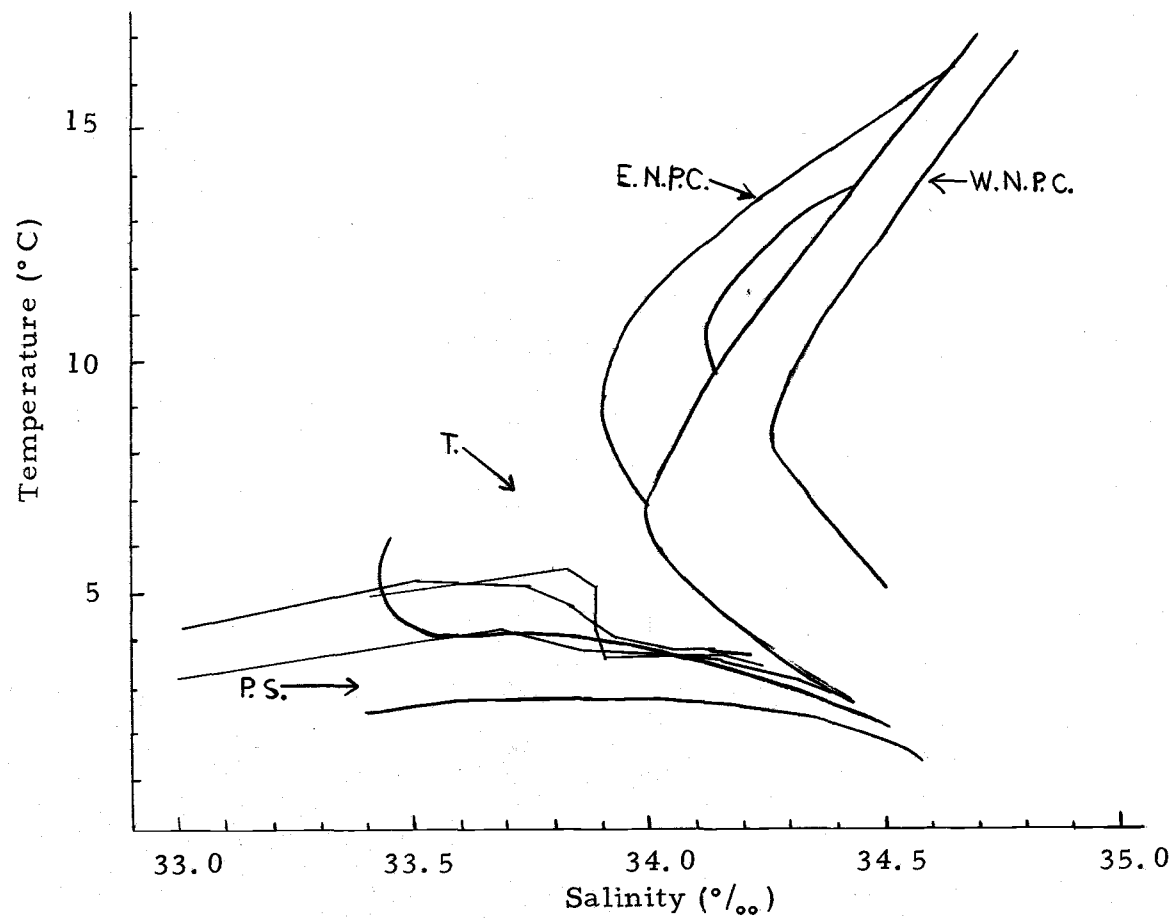


Figure 33. Temperature-salinity capture diagram for *Pasiphaea tarda*. Water masses as in Figure 6.

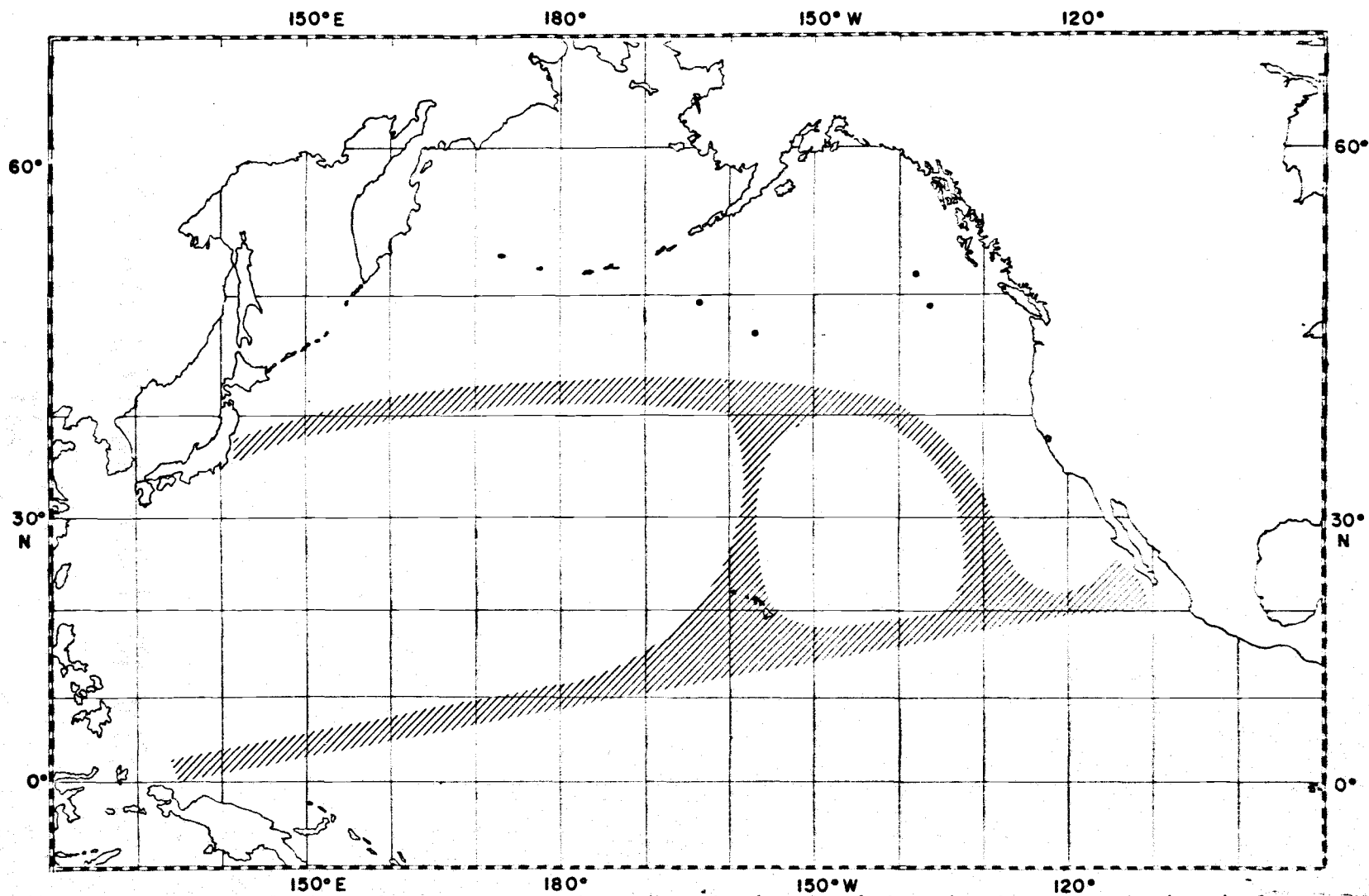


Figure 34. Distribution of *Notostomous japonicus* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

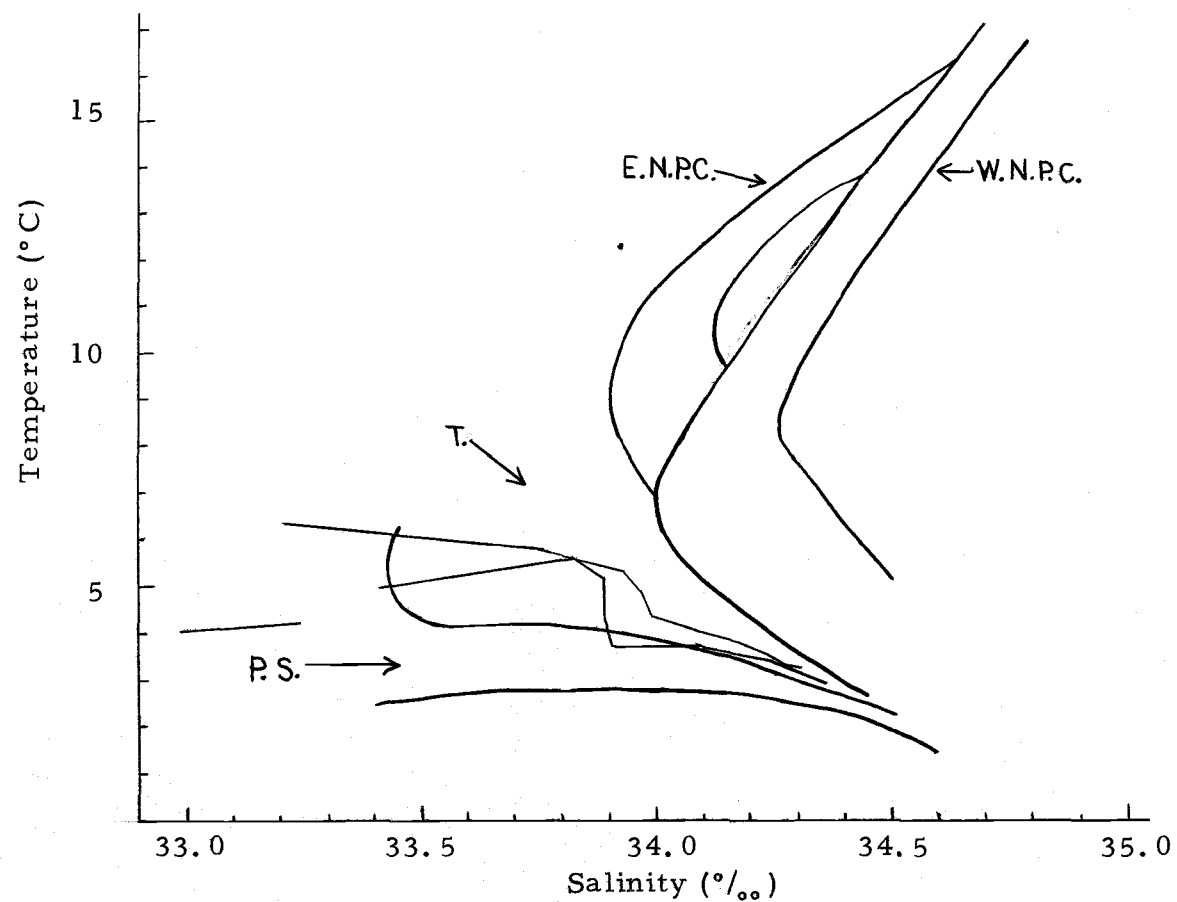


Figure 35. Temperature-salinity capture diagram for Notostomous japonicus. Water masses as in Figure 6.

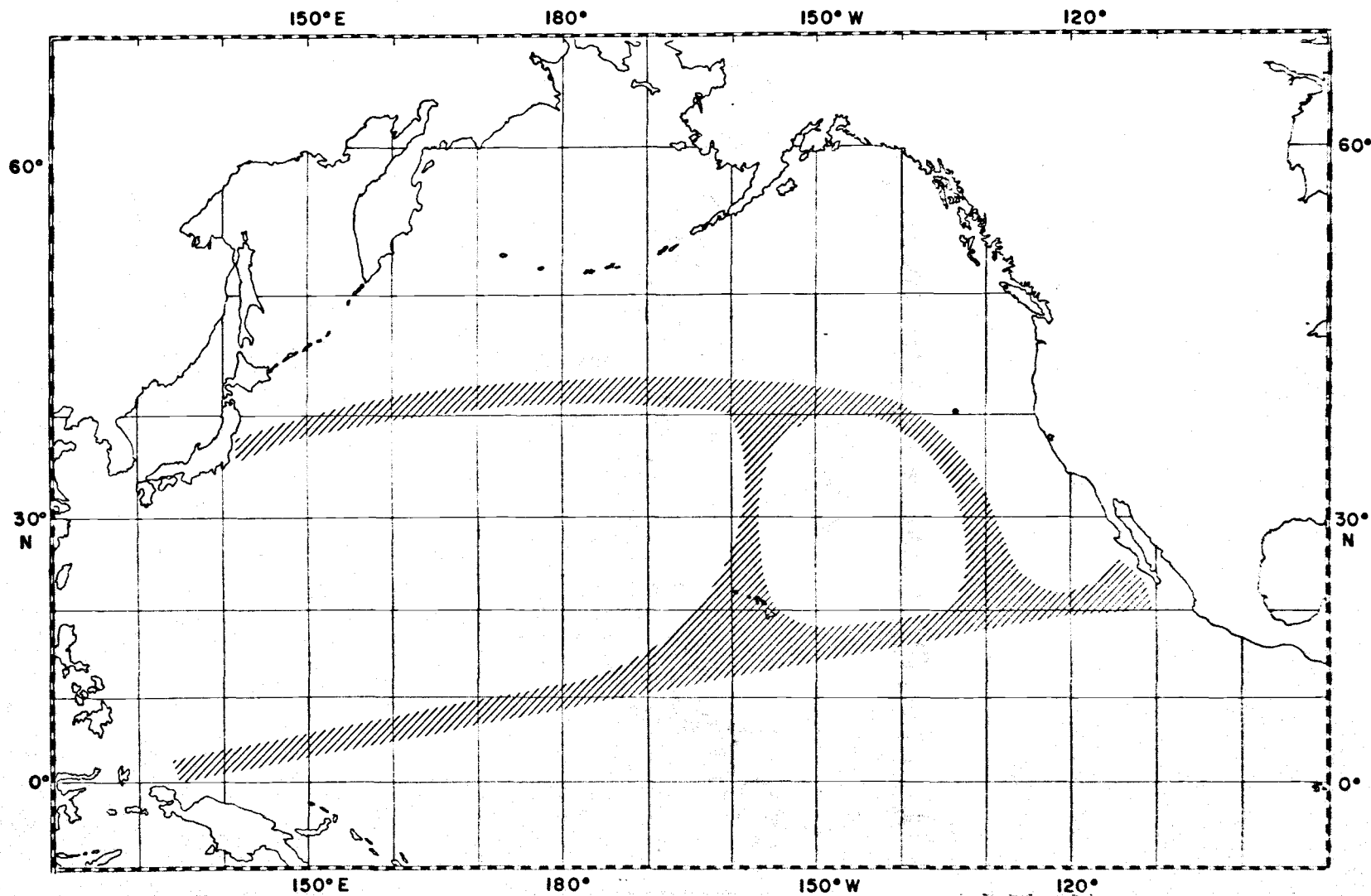


Figure 36. Distribution of *Parapasiphae cristata* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

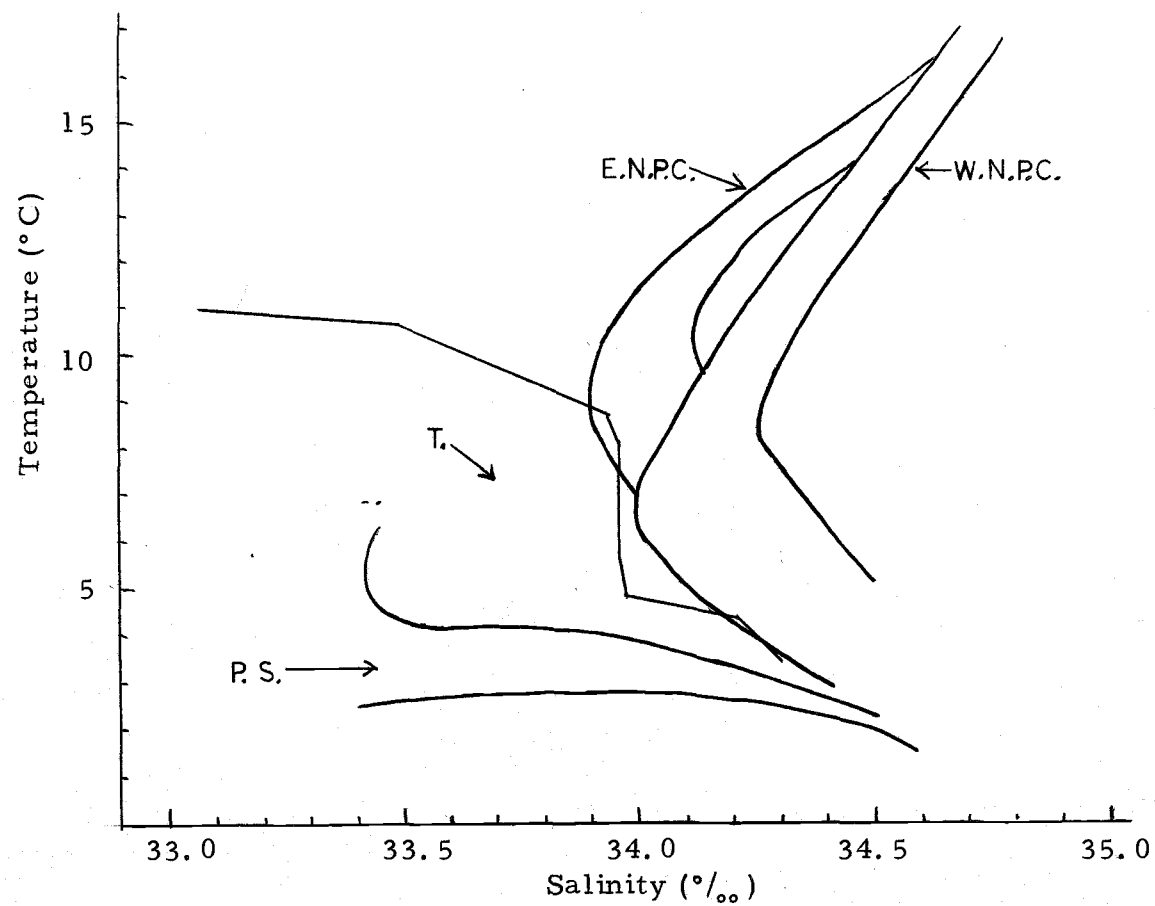


Figure 37. Temperature-salinity capture diagram for Parapasiphae cristata. Water masses as in Figure 6.

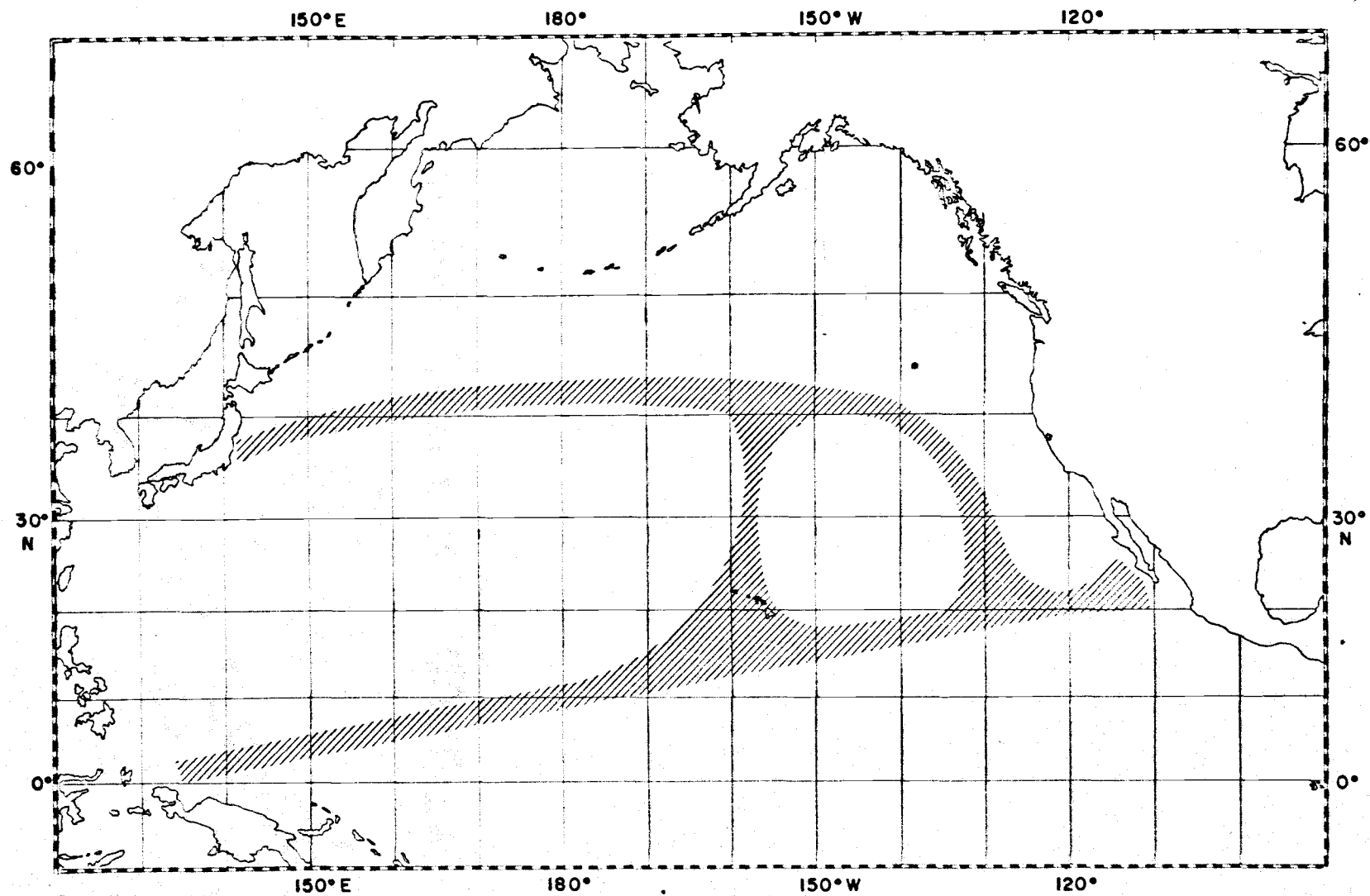


Figure 38. Distribution of Parapasiphae sulcatifrons in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

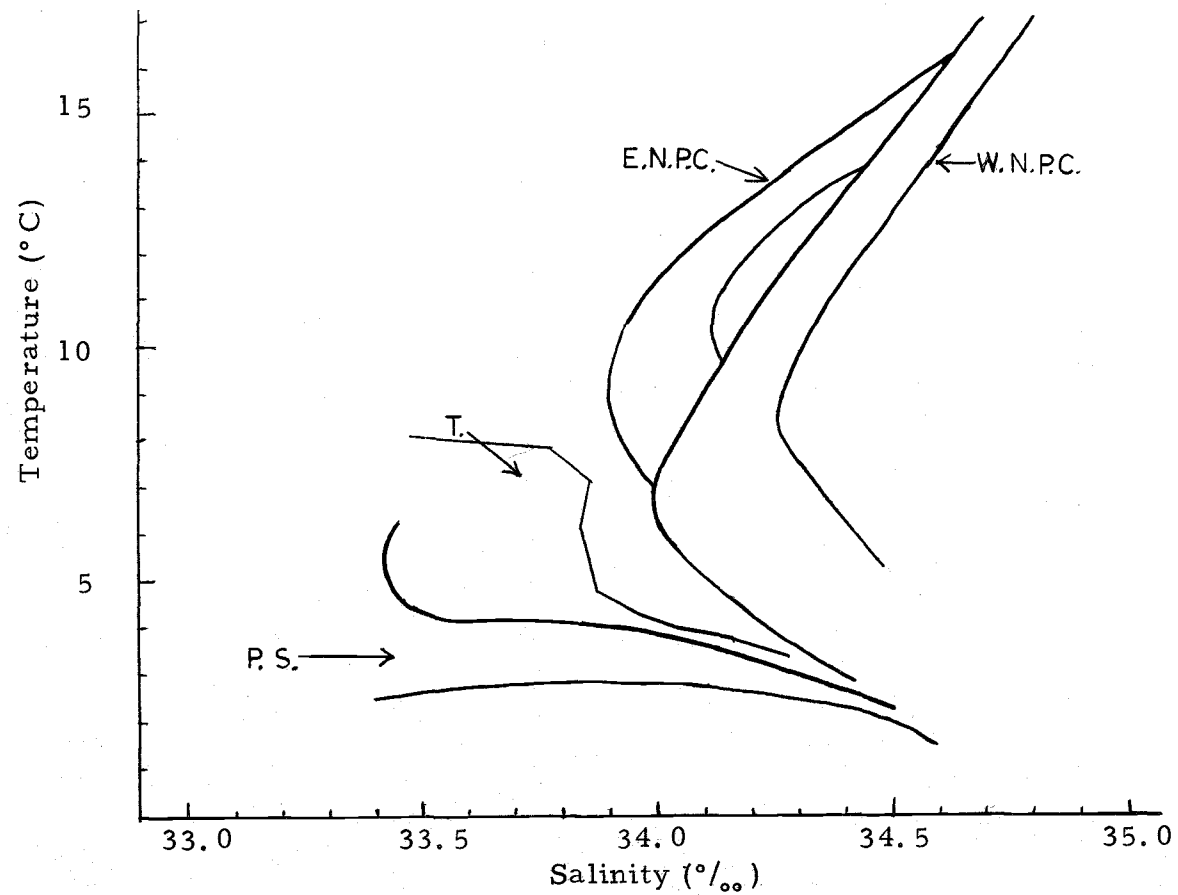


Figure 39. Temperature-salinity capture diagram for Parapasiphae sulcatifrons. Water masses as in Figure 6.

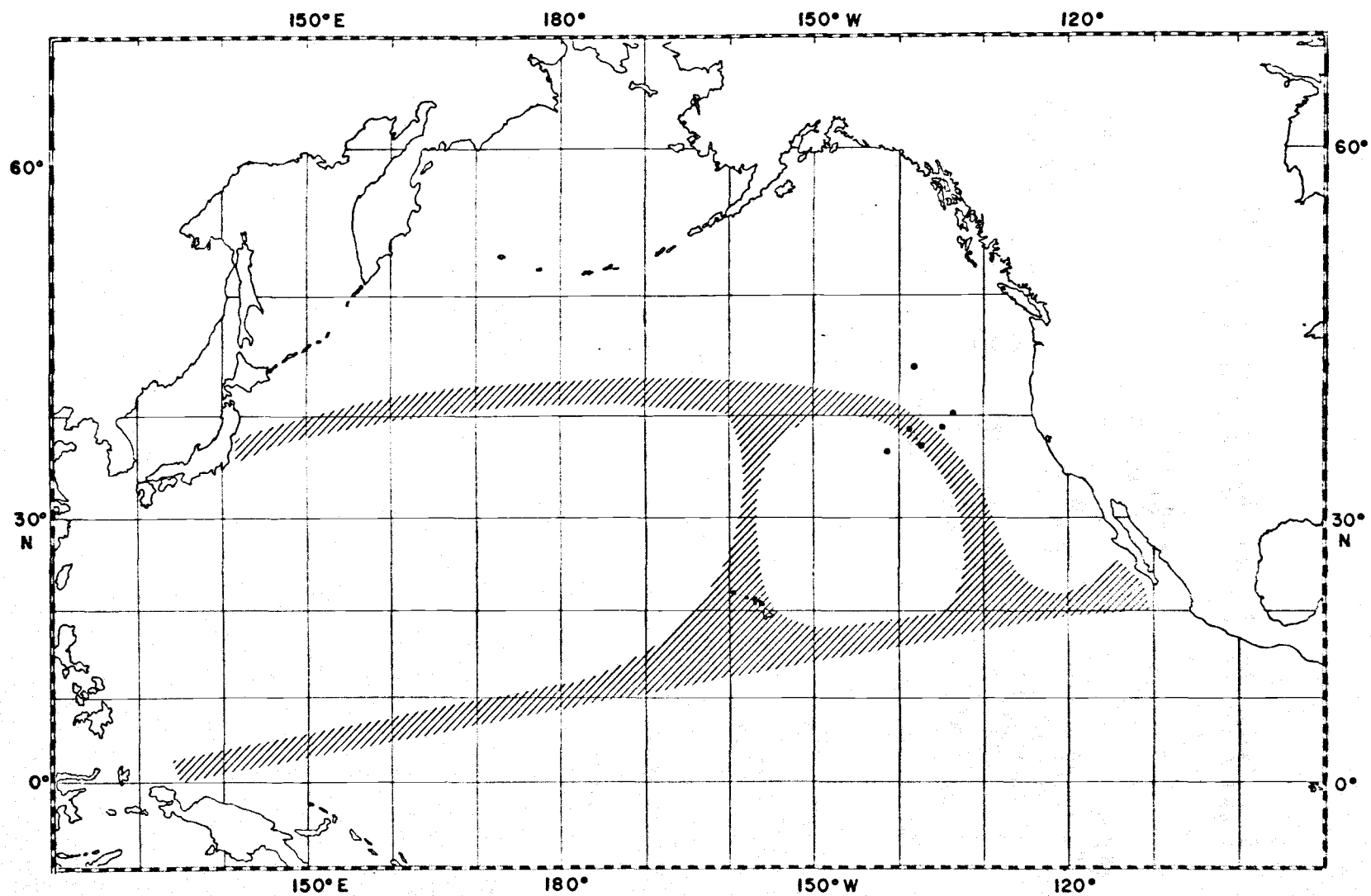


Figure 40. Distribution of *Acantheephyra curtirostris* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

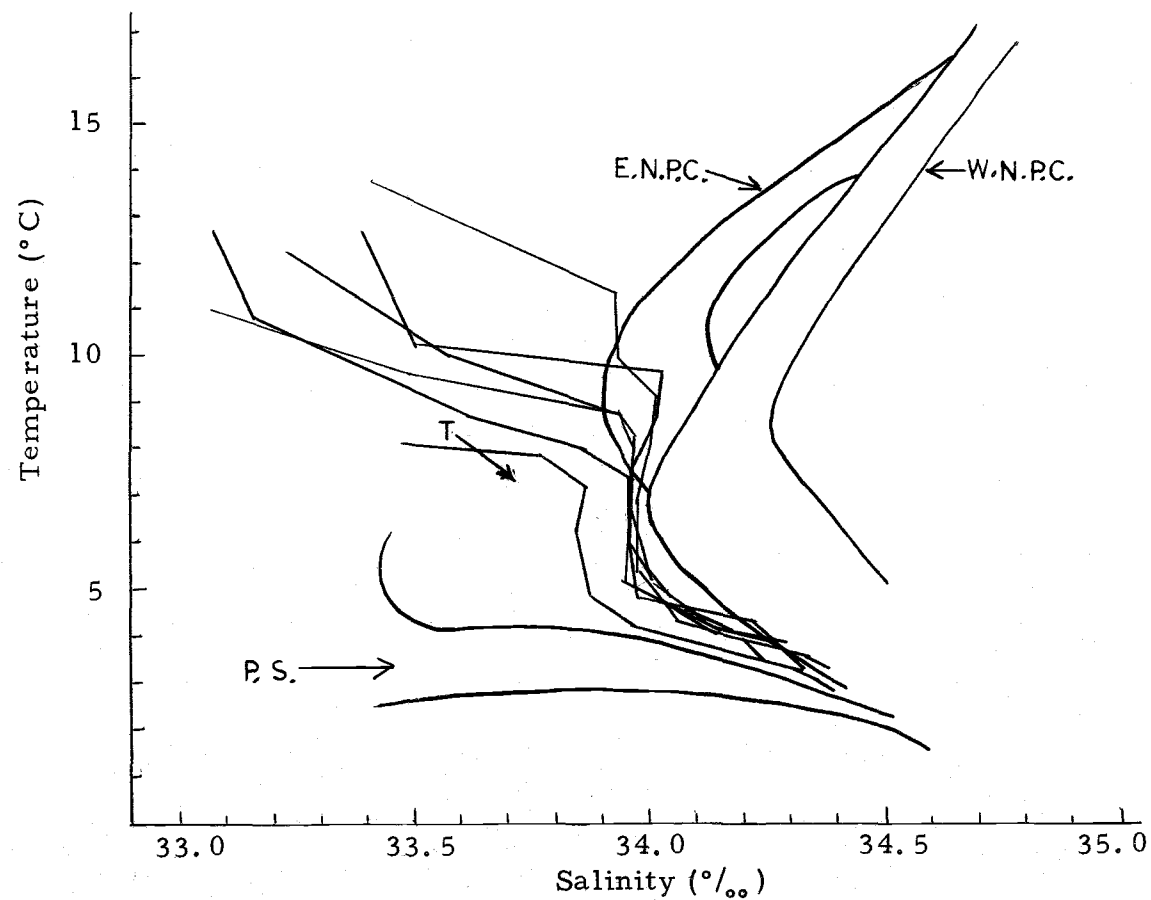


Figure 41. Temperature-salinity capture diagram for Acanthephyra curtirostris. Water masses as in Figure 6.

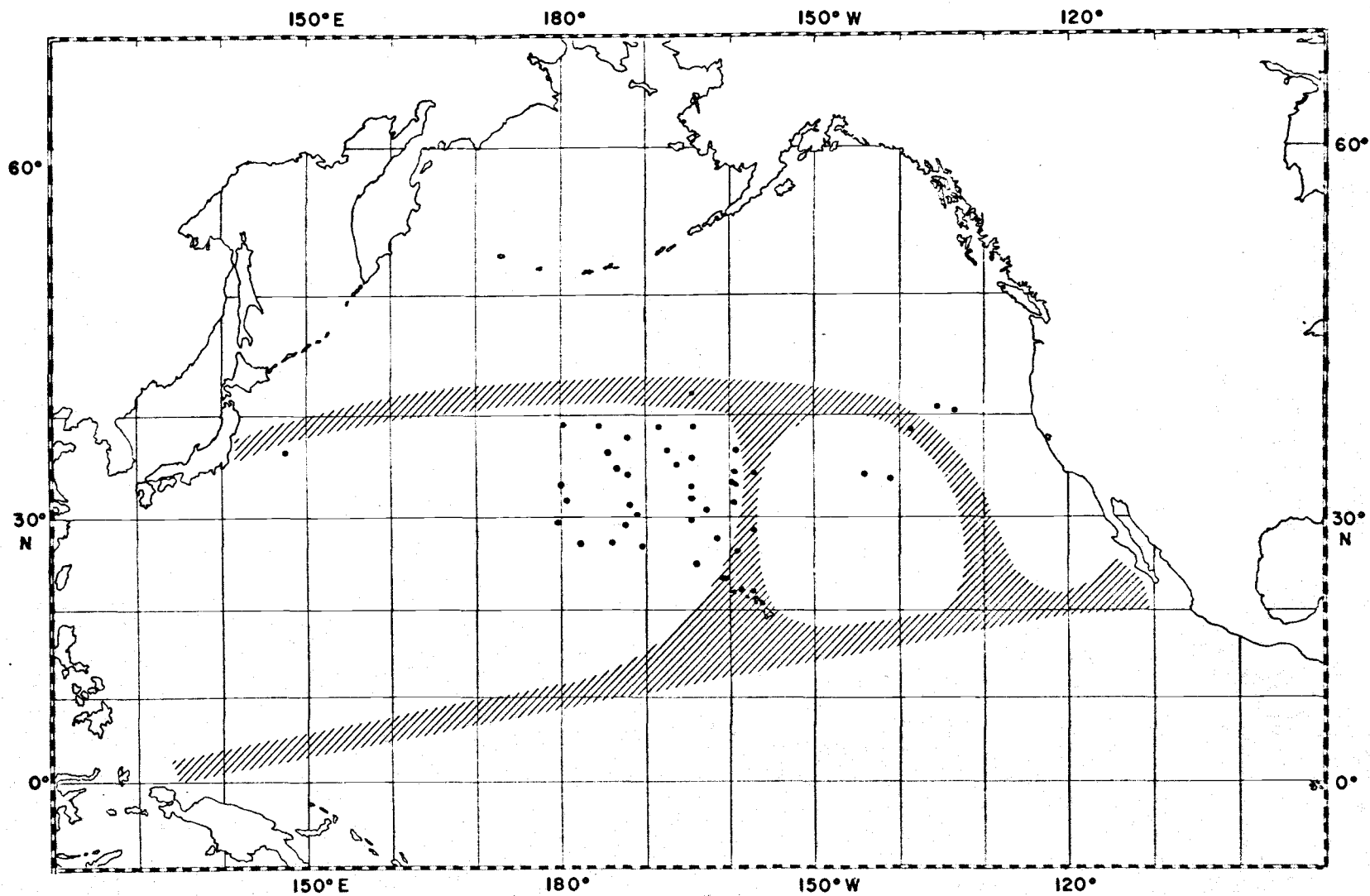


Figure 42. Distribution of Oplophorus spinosus in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

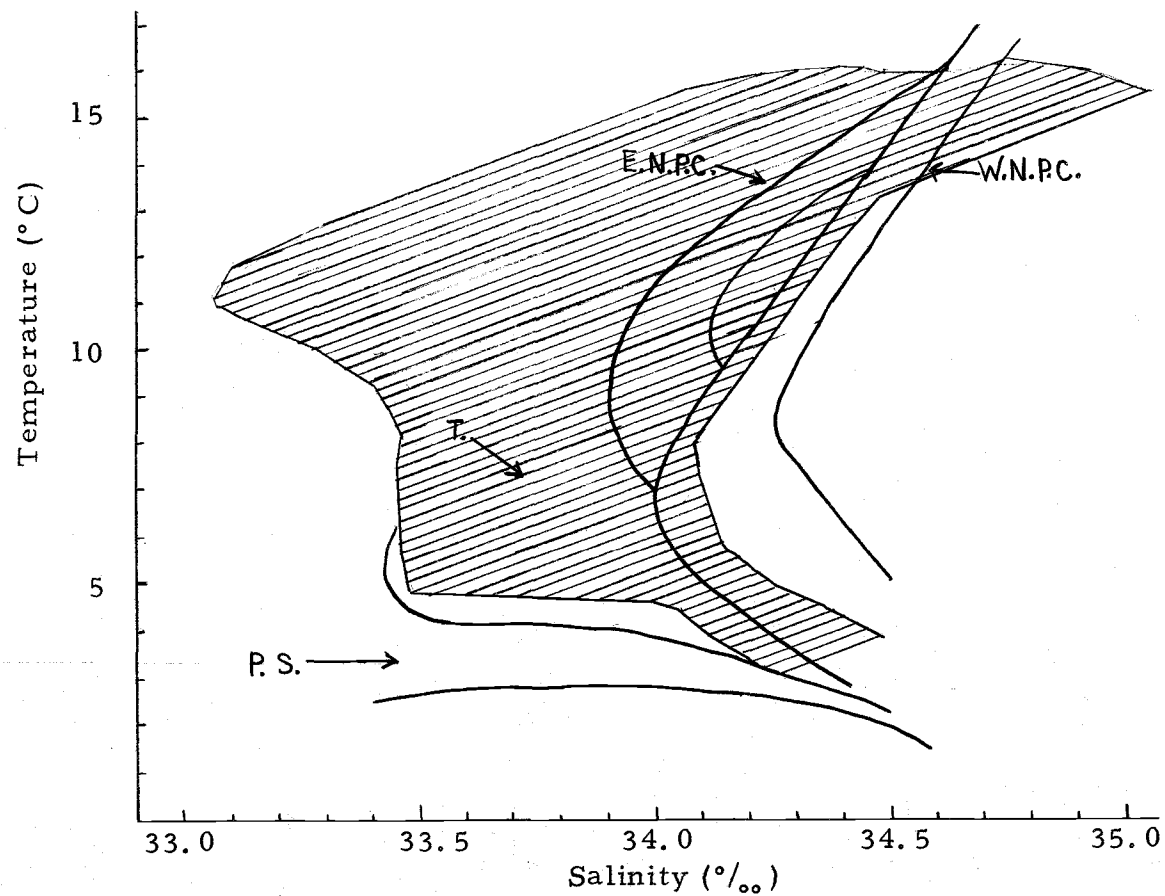


Figure 43. Temperature-salinity capture diagram for Oplophorus spinosus. Water masses as in Figure 6.

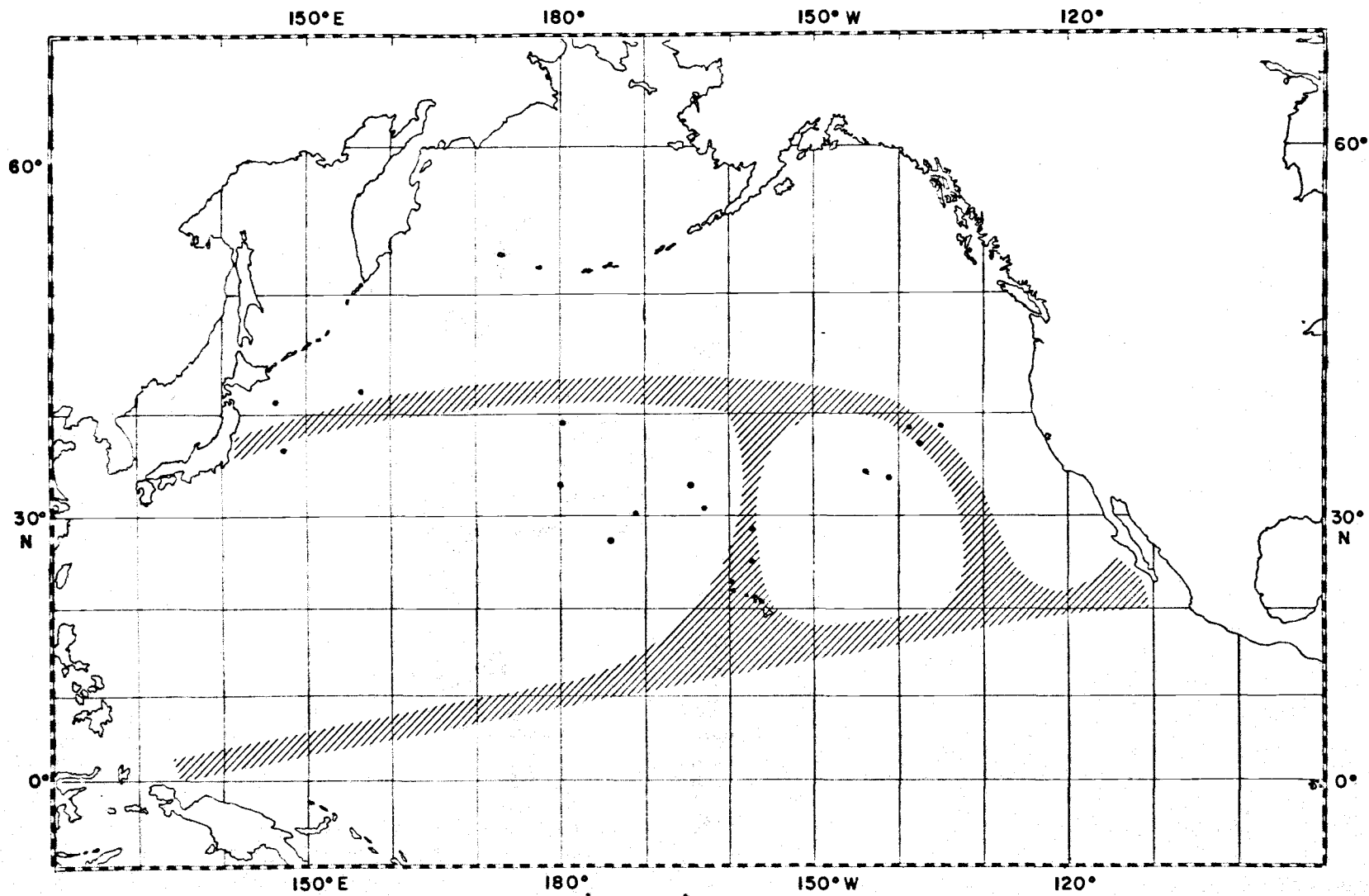


Figure 44. Distribution of Gennadas propinquus in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

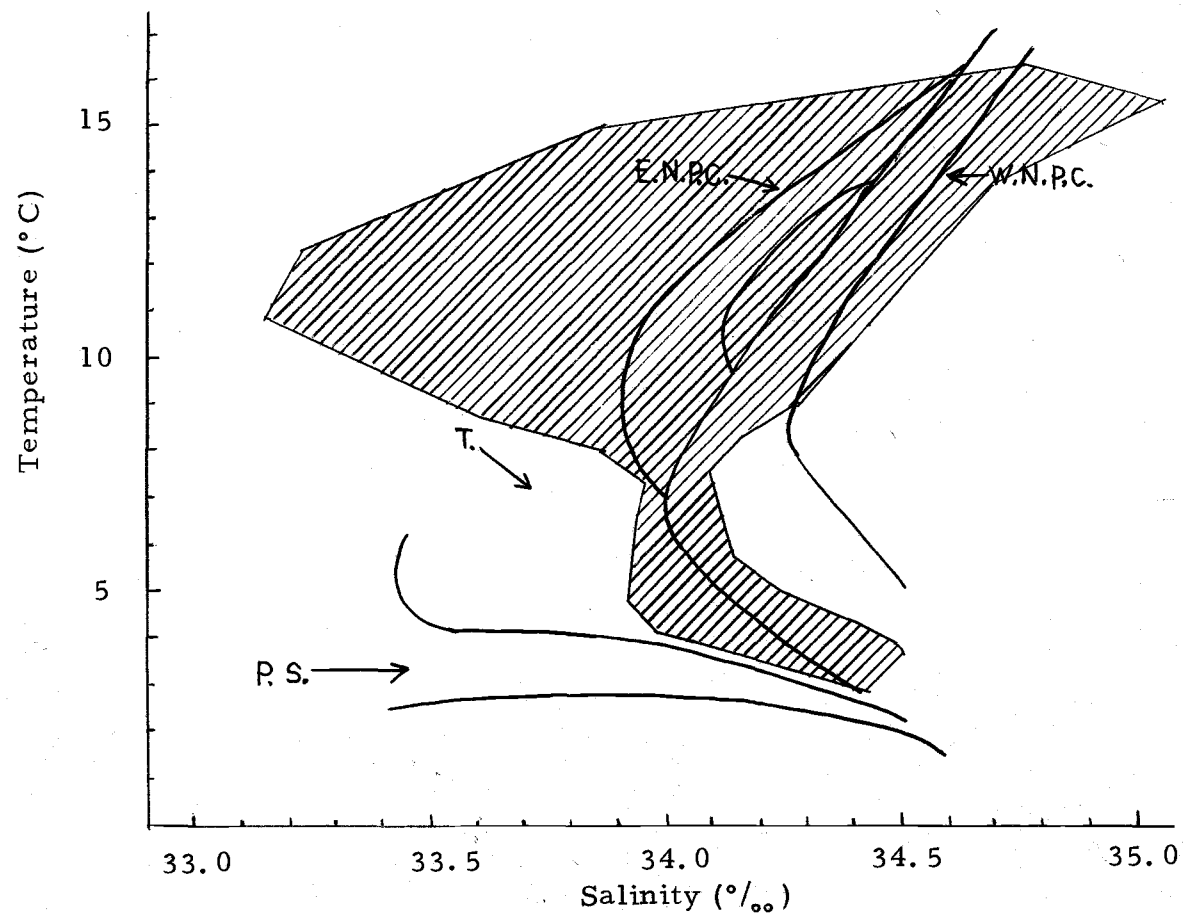


Figure 45. Temperature-salinity capture diagram for Gennadas propinquus. Water as in Figure 6.

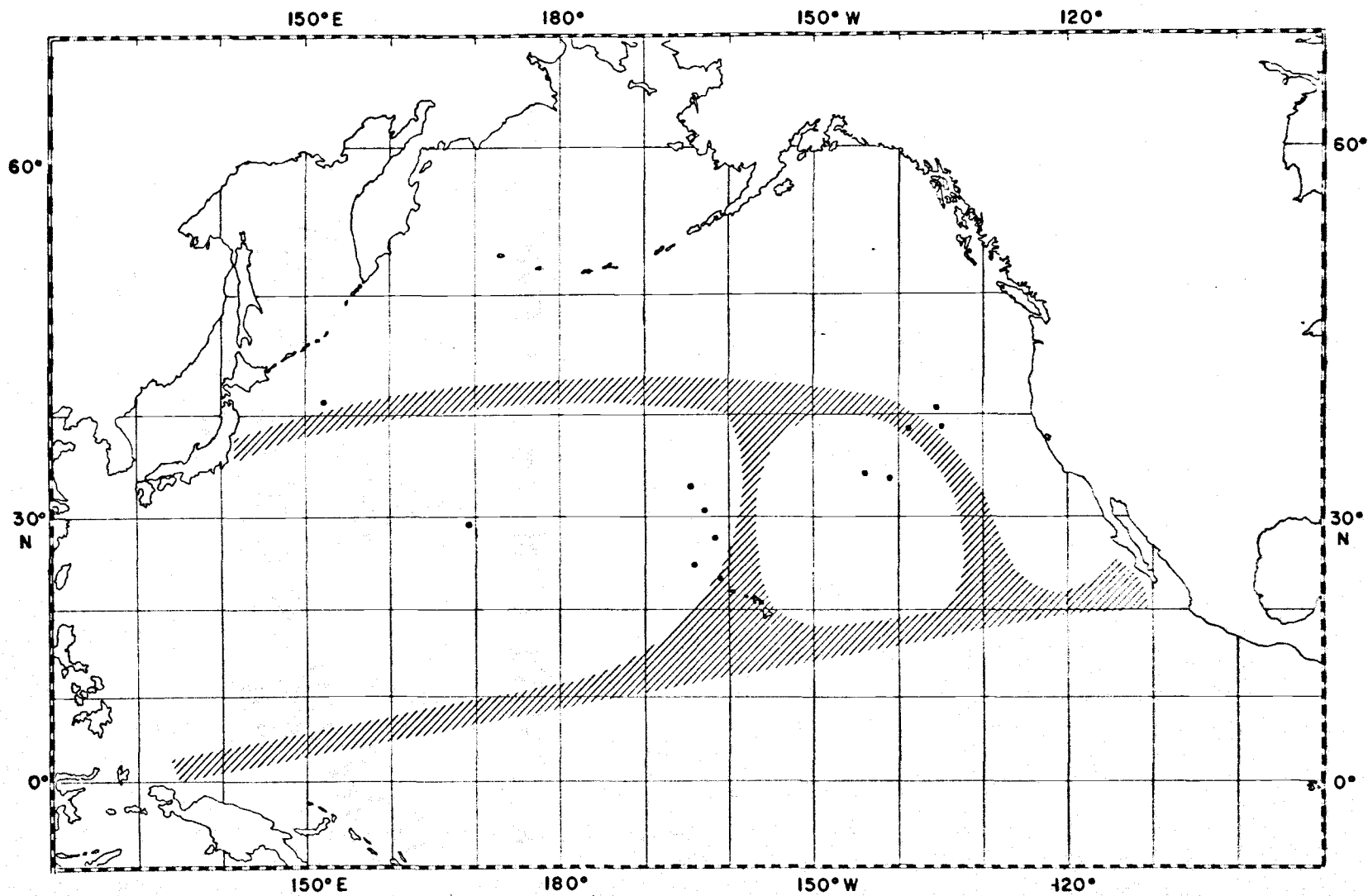


Figure 46. Distribution of Gennadas tinayrei in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

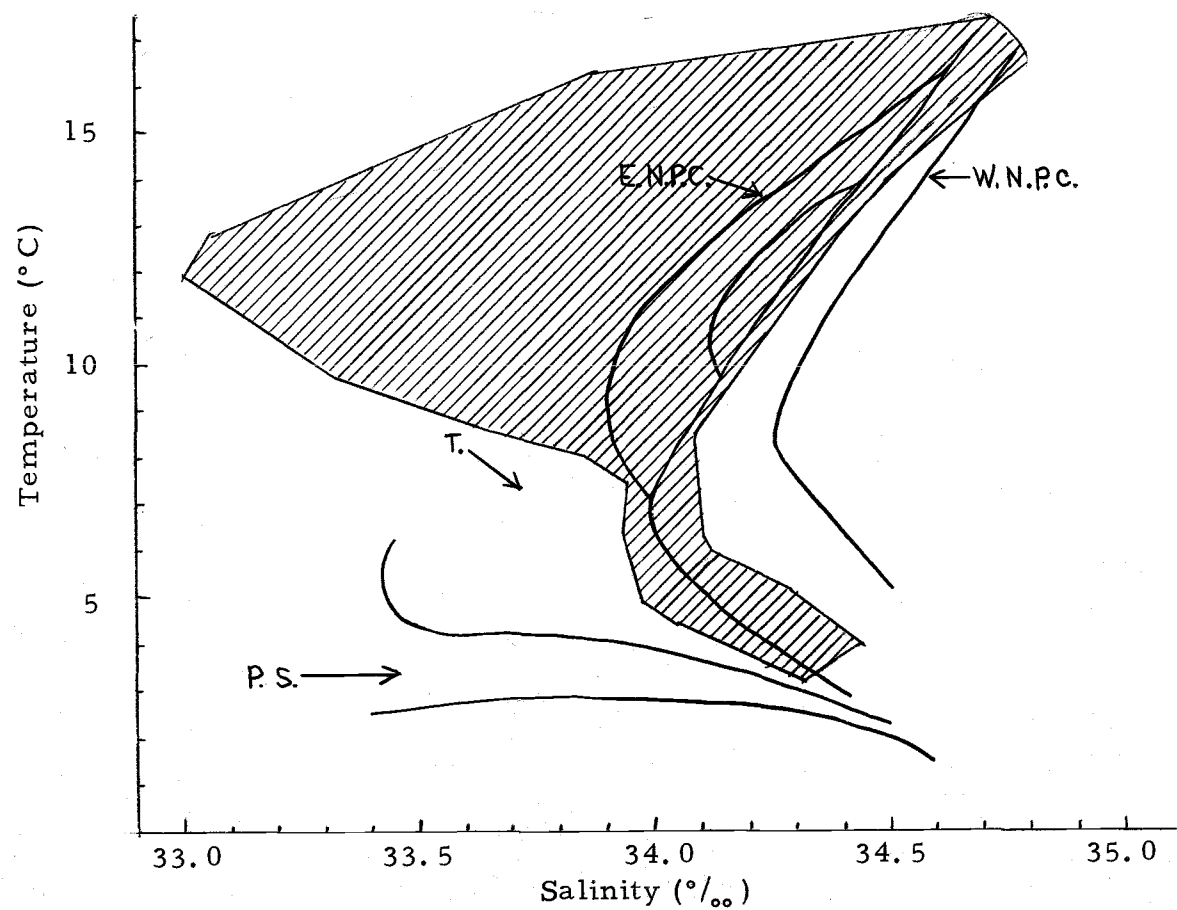


Figure 47. Temperature-salinity capture diagram for Gennadas tinayrei. Water masses as in Figure 6.

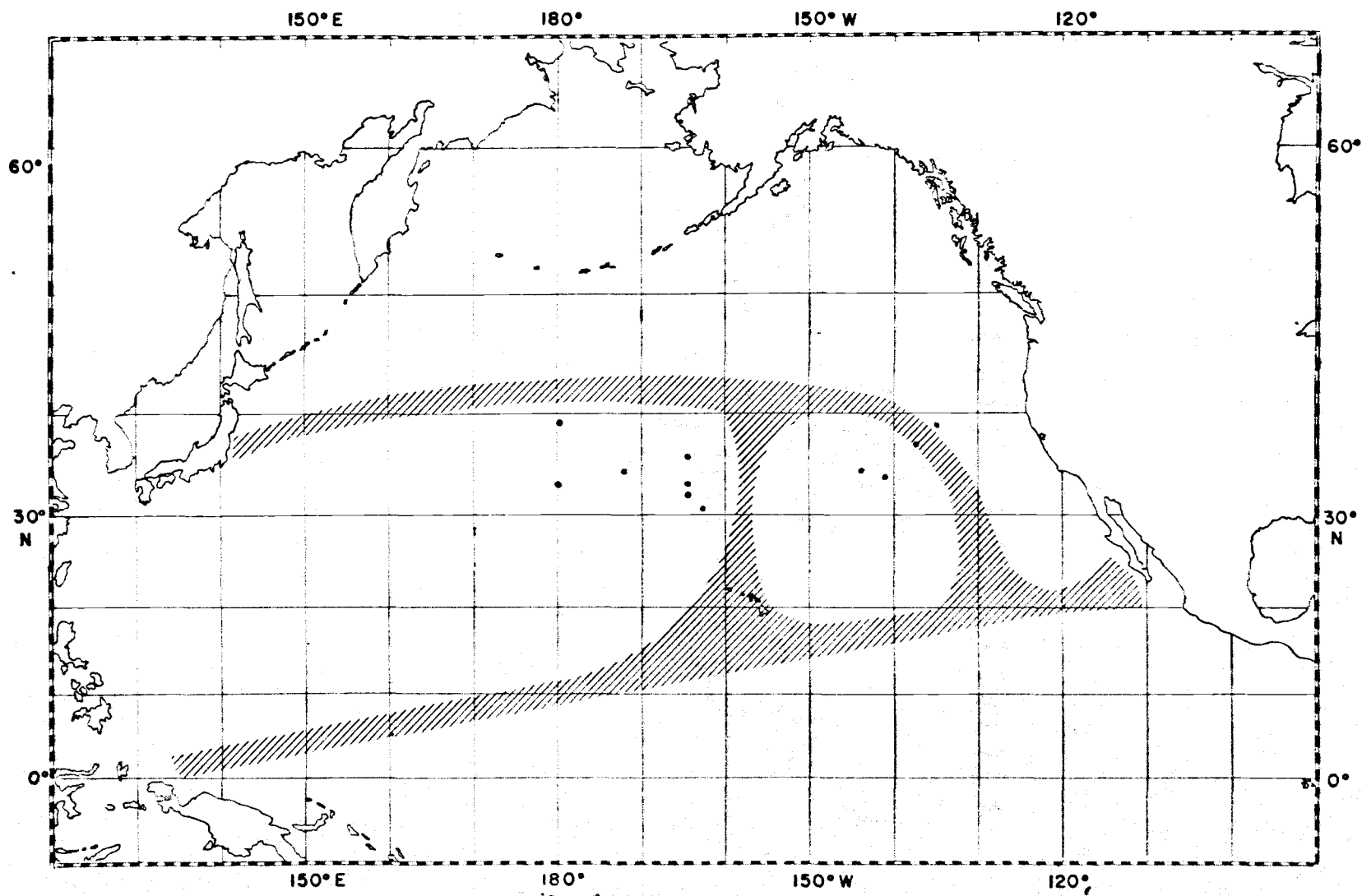


Figure 48. Distribution of *Sergestes armatus* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

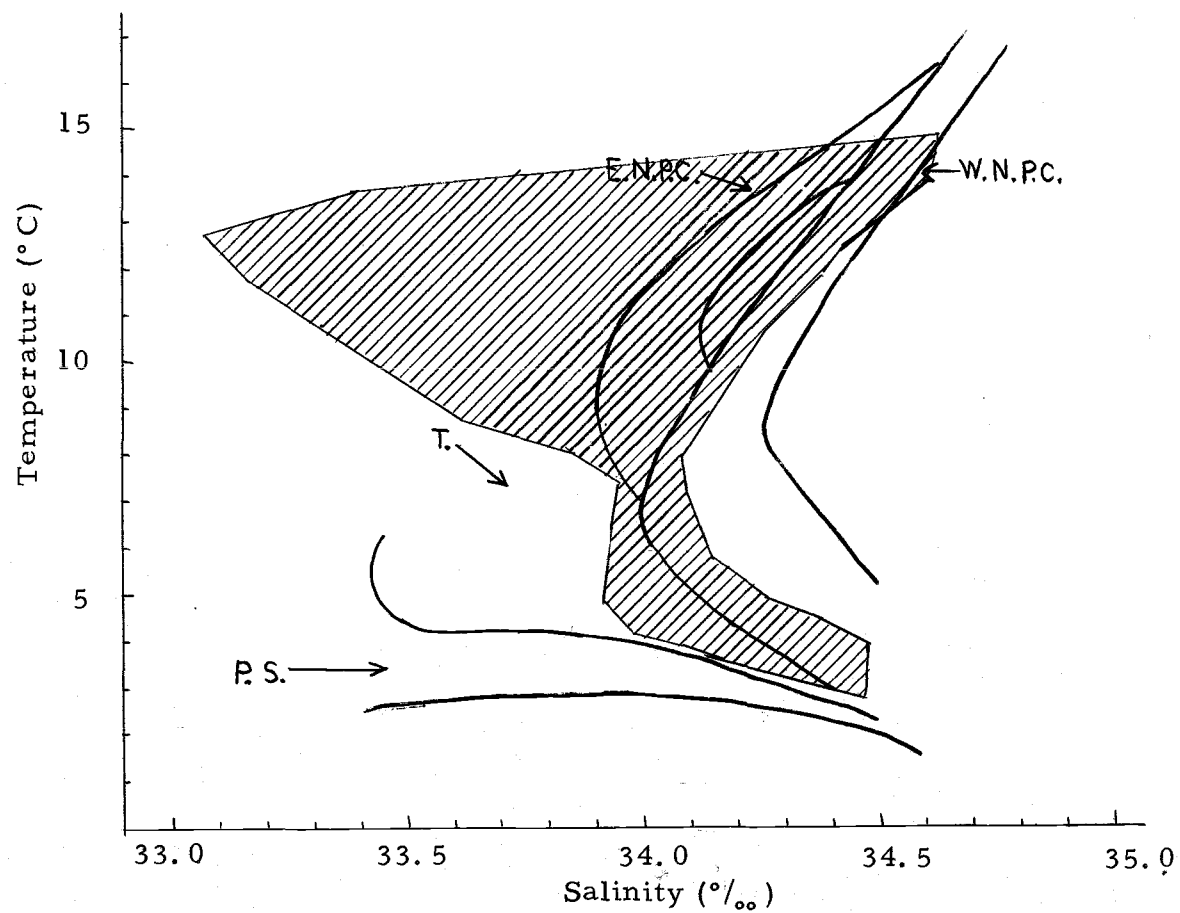


Figure 49. Temperature-salinity capture diagram for *Sergestes armatus*. Water masses as in Figure 6.

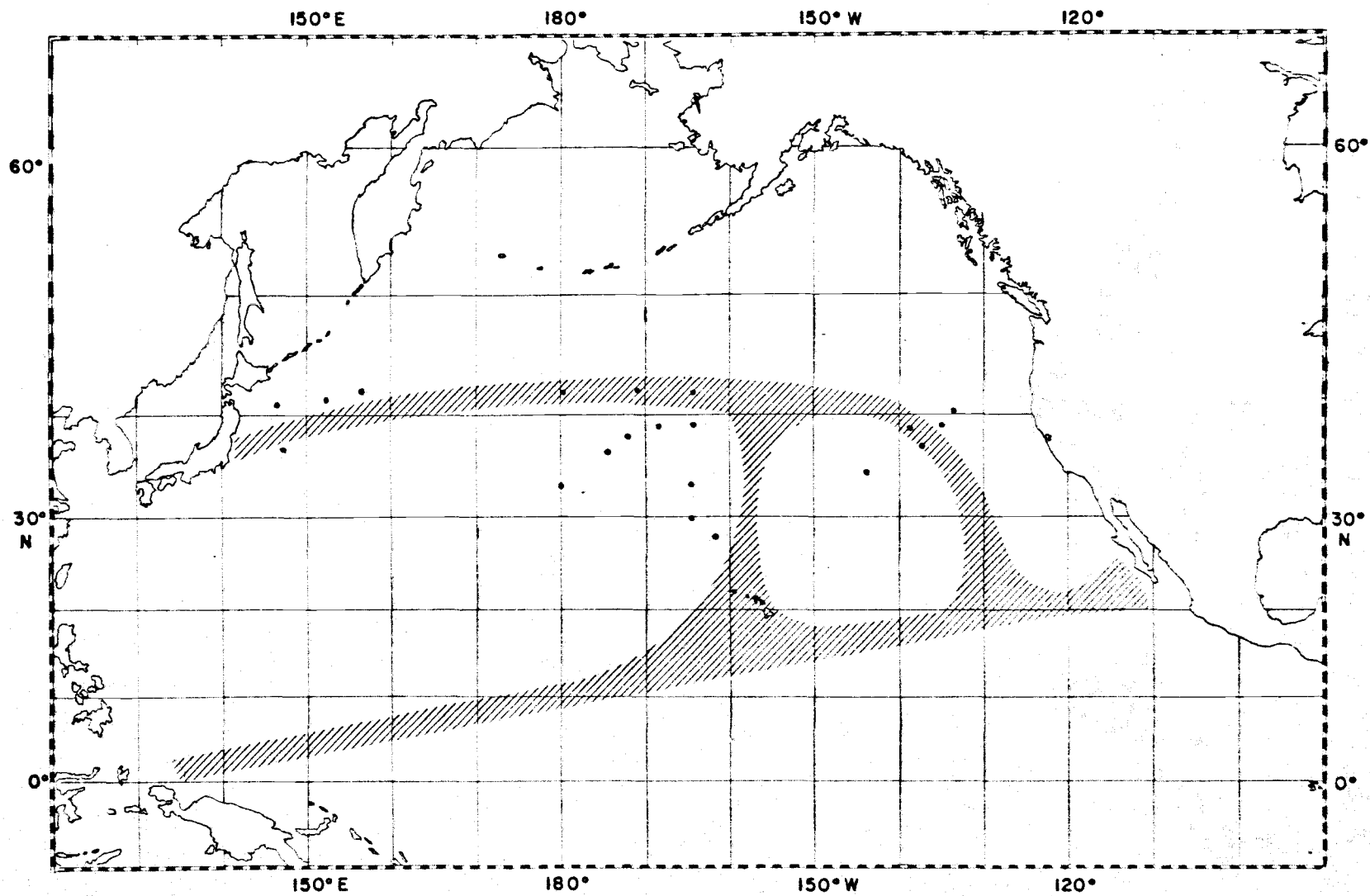


Figure 50. Distribution of *Acantheephyra quadrispinosa* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

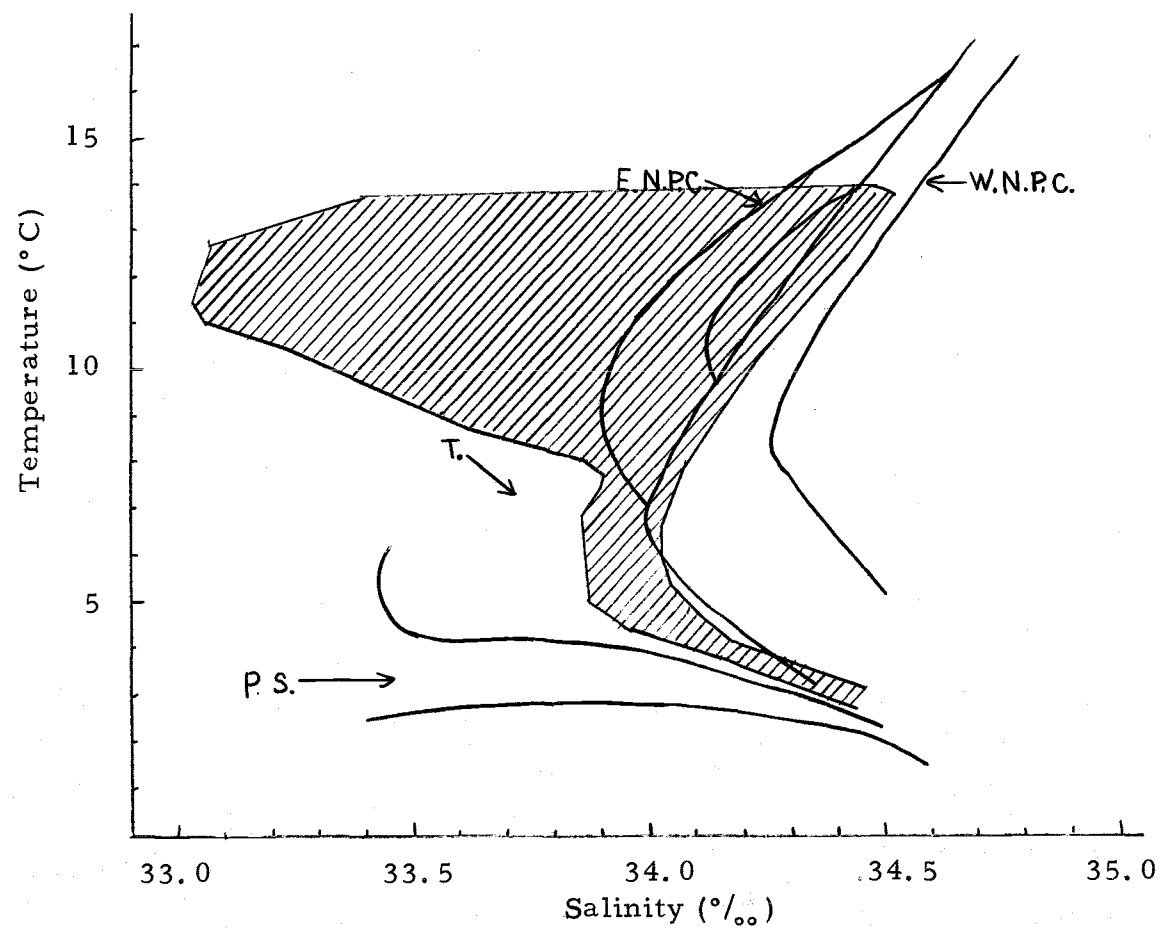


Figure 51. Temperature-salinity capture diagram for *Acantheephyra quadrispinosa*. Water masses as in Figure 6.

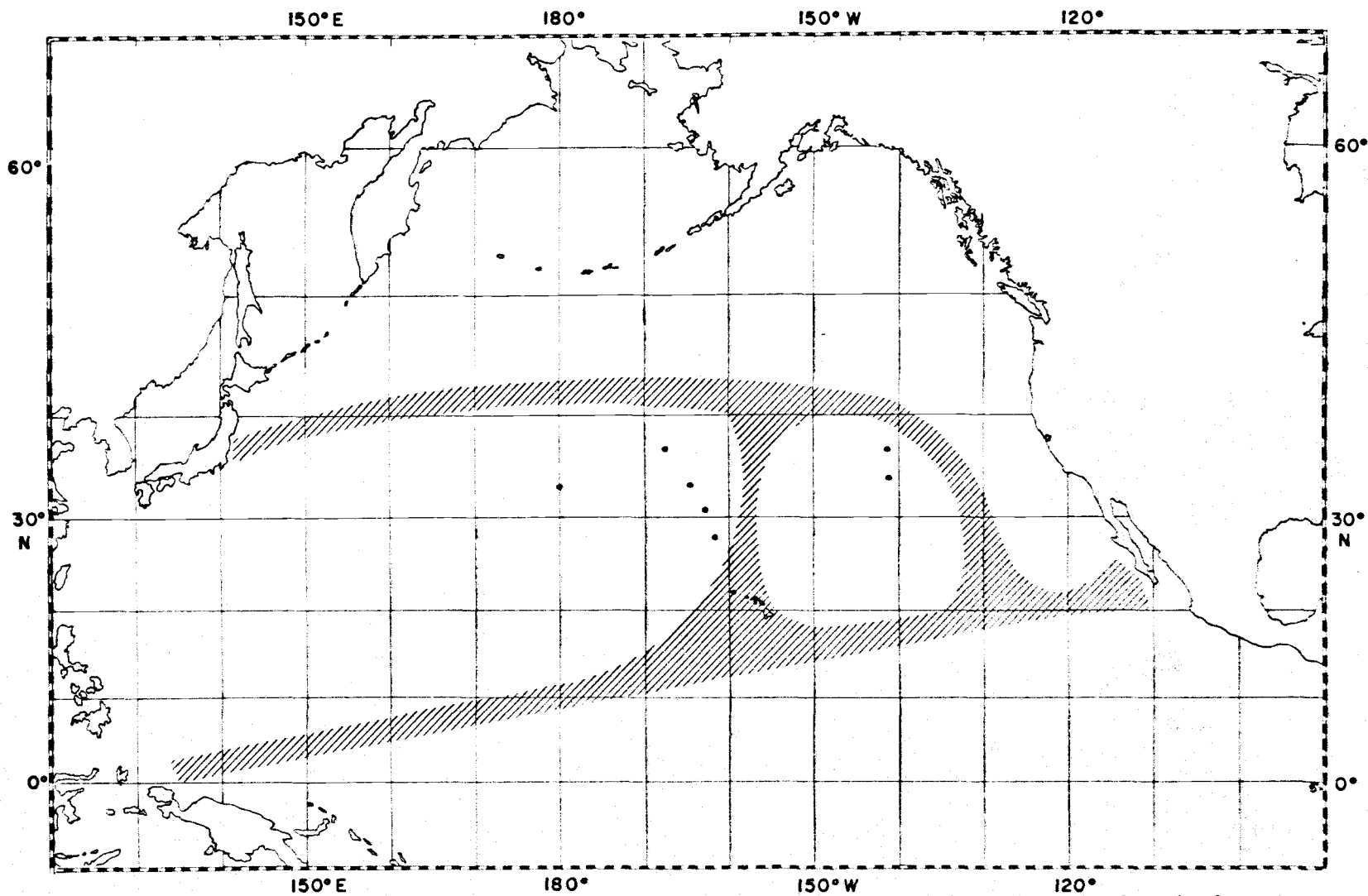


Figure 52. Distribution of *Sergestes sargassi* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

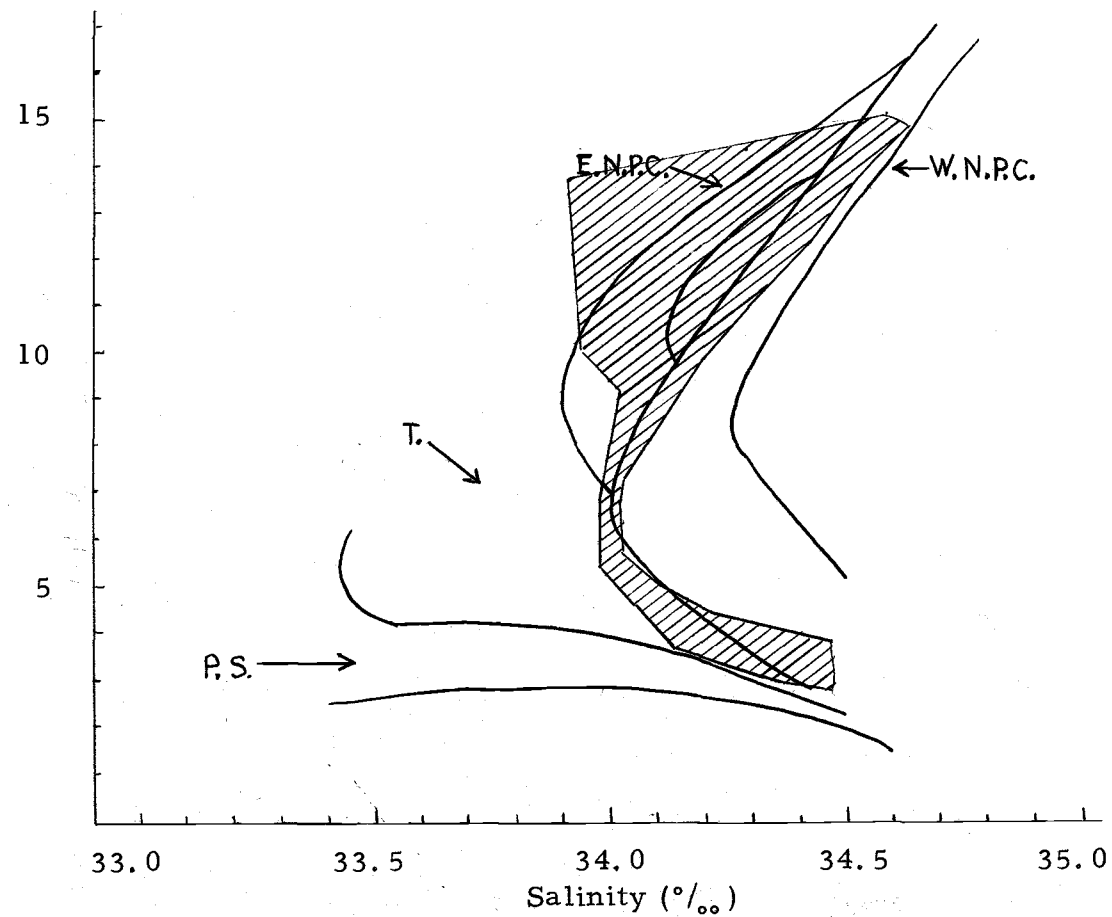


Figure 53. Temperature-salinity capture diagram for *Sergestes sargassi*. Water masses as in Figure 6.

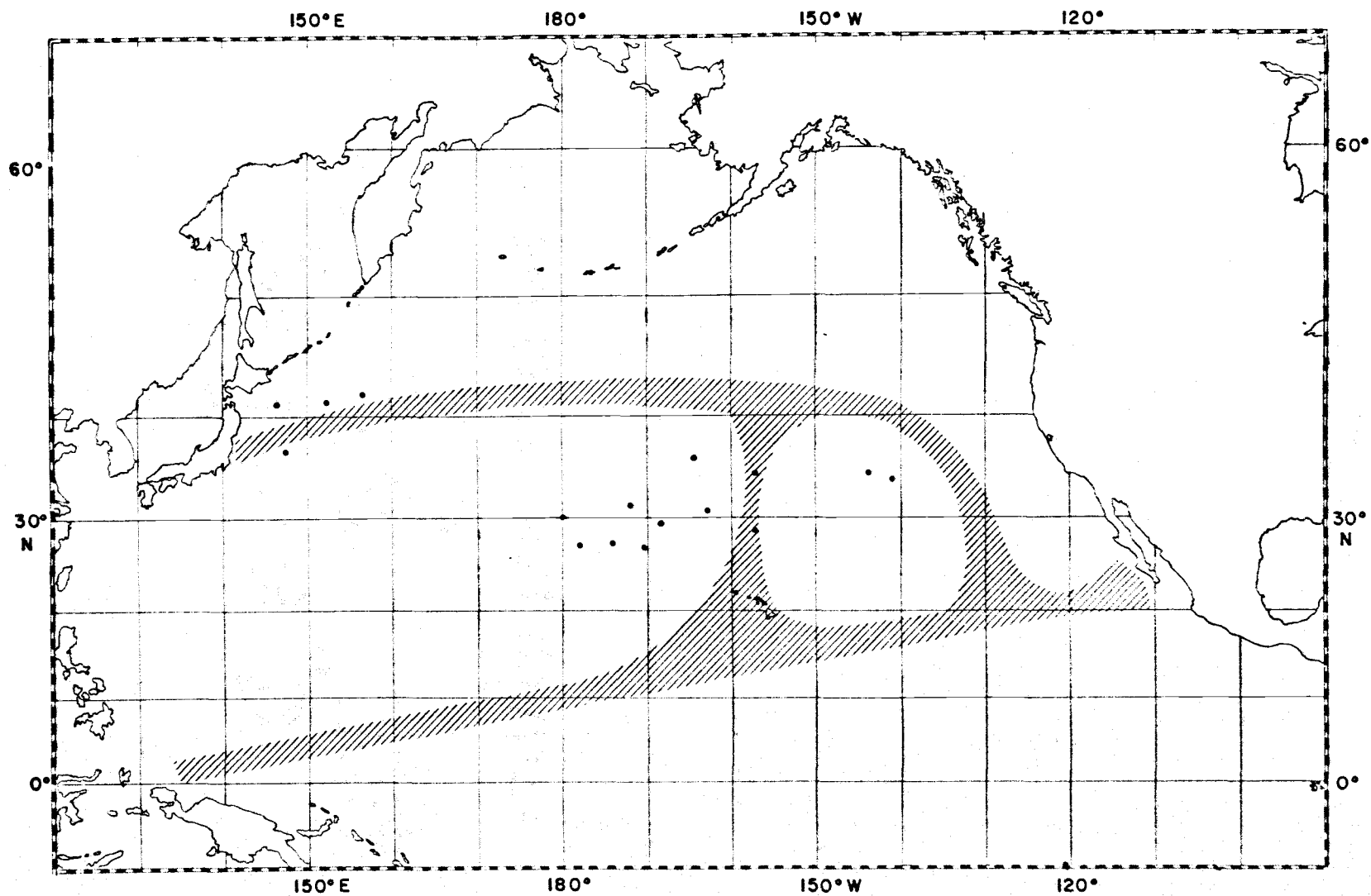


Figure 54. Distribution of *Gennadas incertus* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

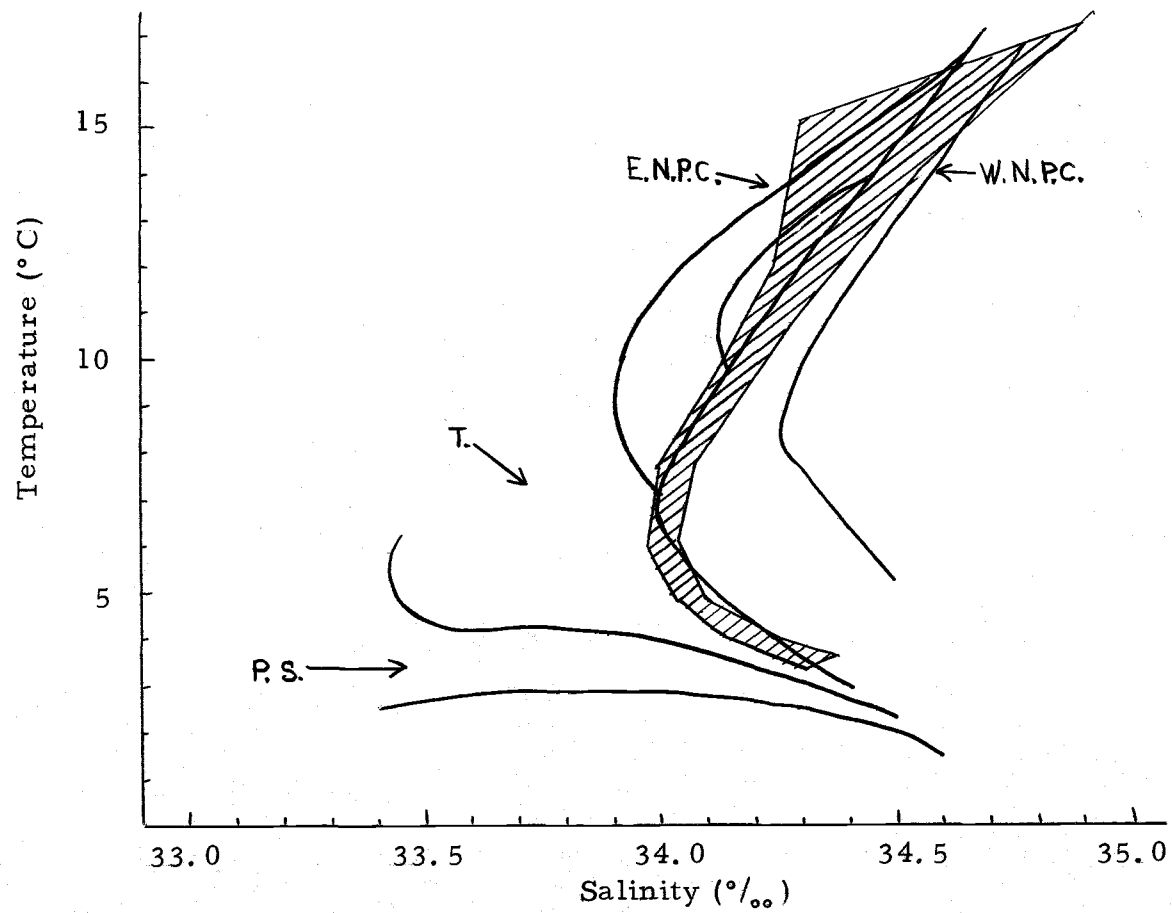


Figure 55. Temperature-salinity capture diagram for Gennadas incertus. Water masses as in Figure 6.

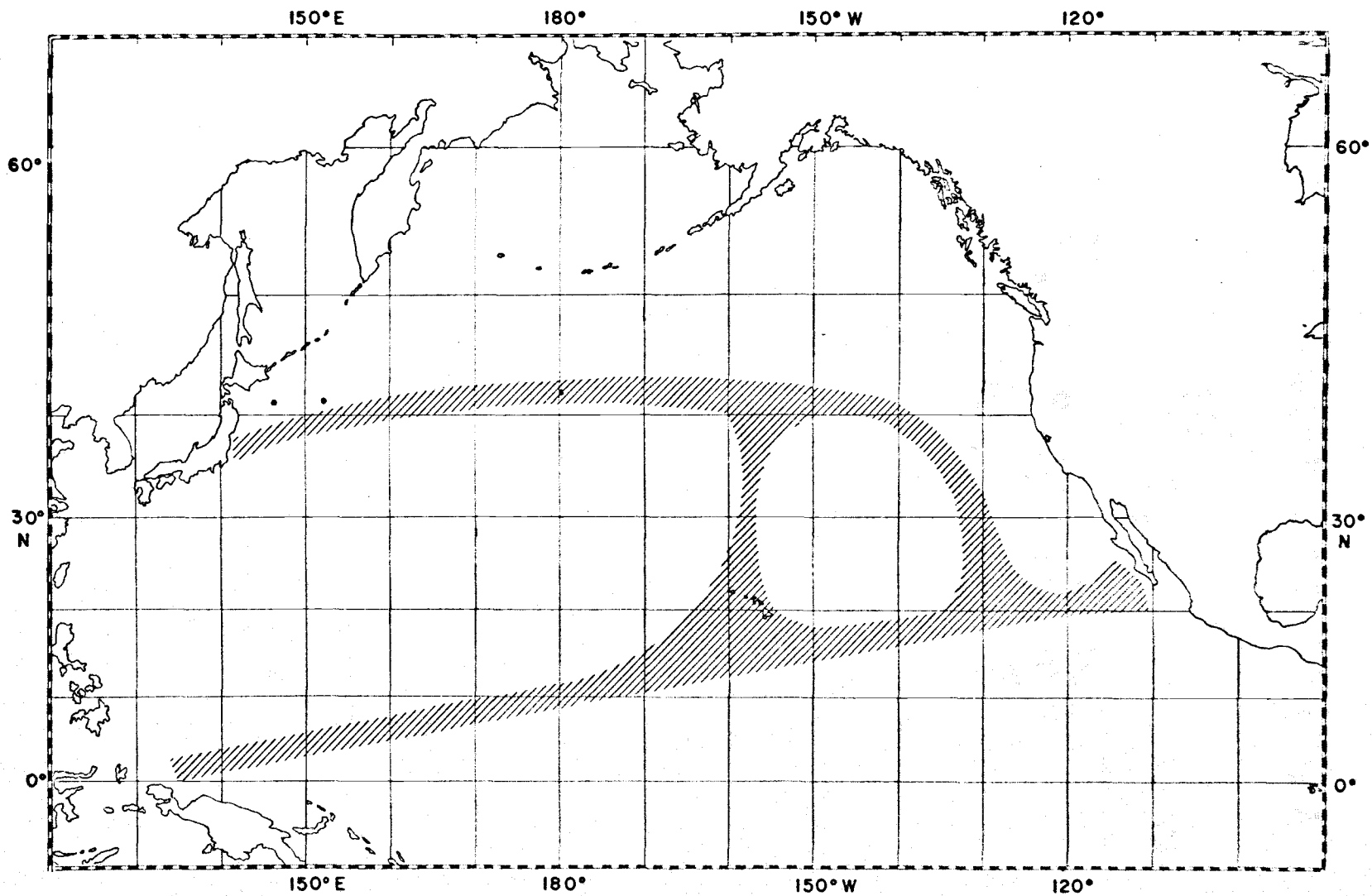


Figure 56. Distribution of *Gennadas parvus* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

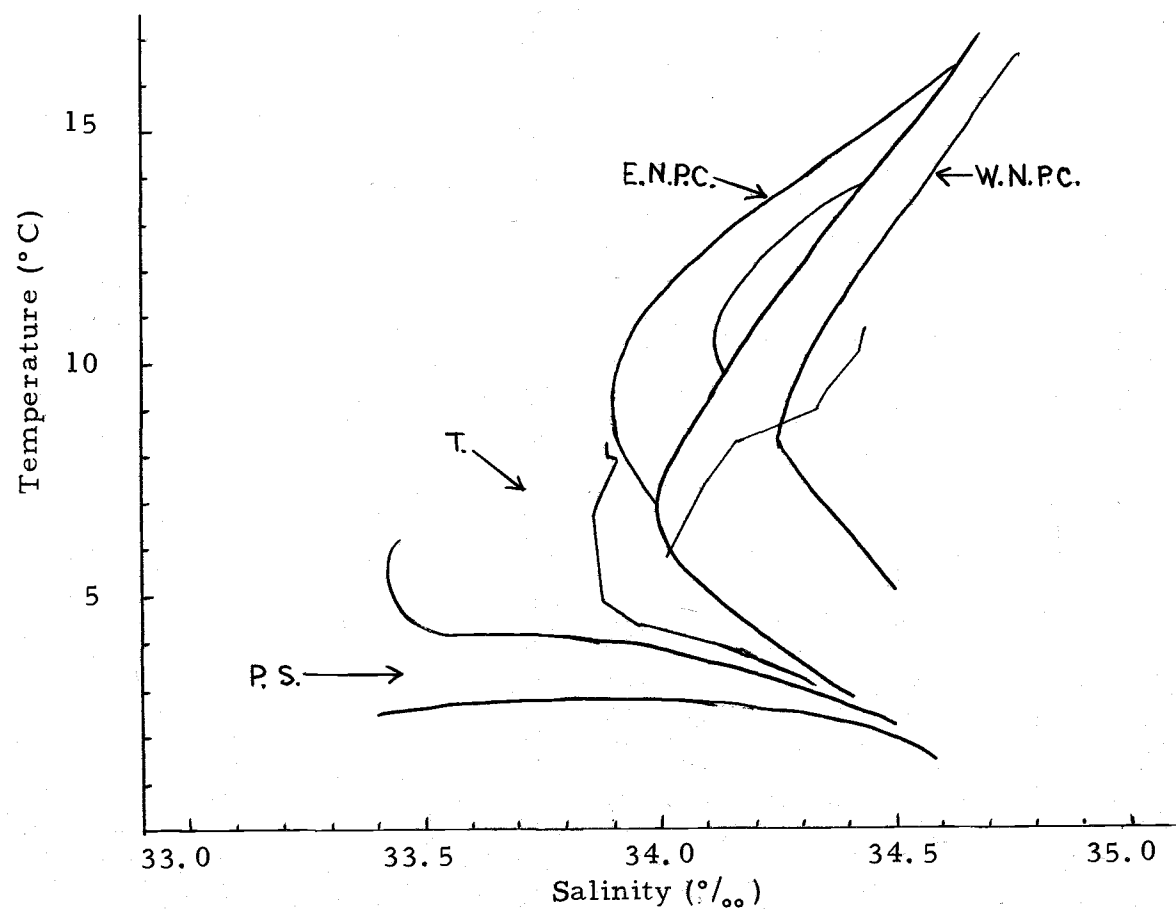


Figure 57. Temperature-salinity capture diagram for Gennadas parvus. Water masses as in Figure 6.

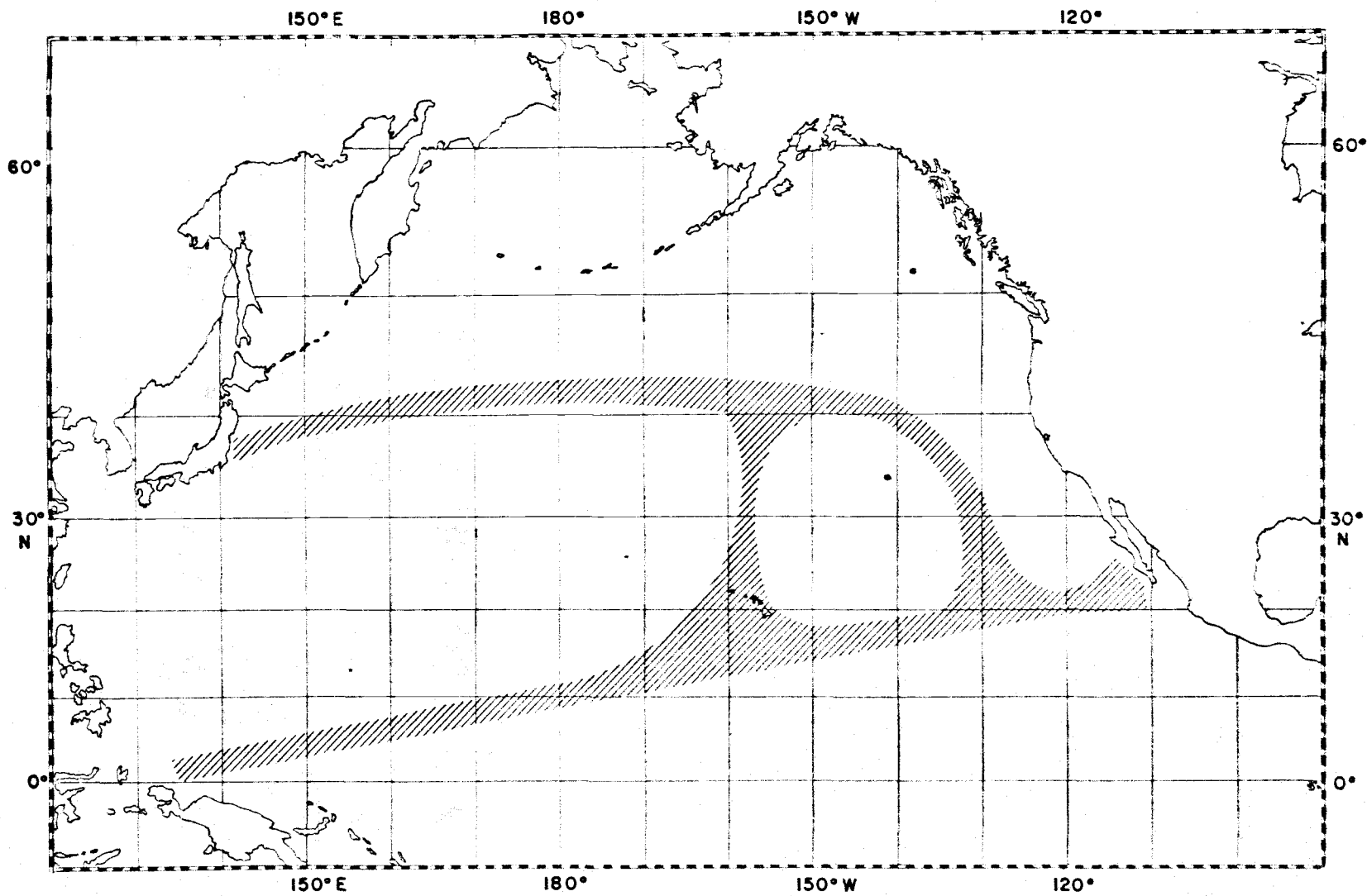


Figure 58. Distribution of *Sergestes tenuiremis* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

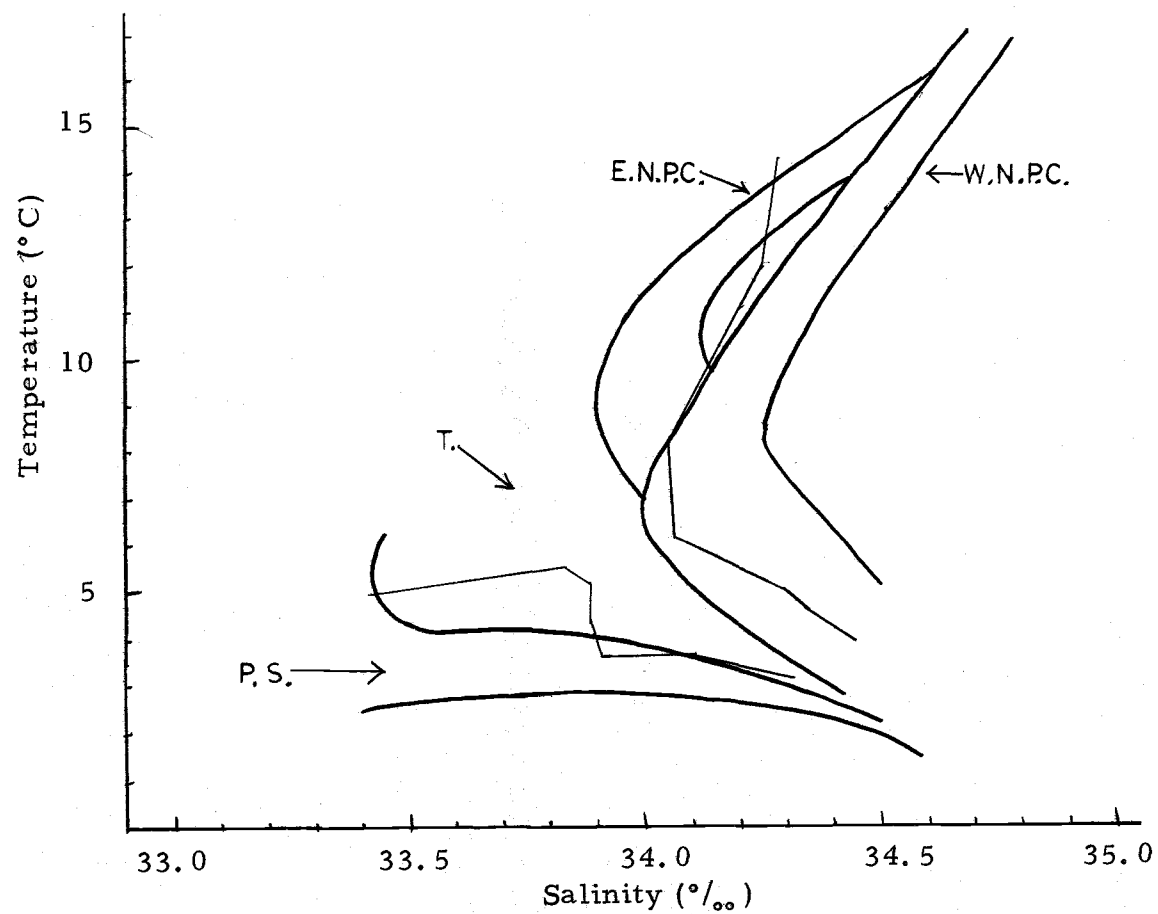


Figure 59. Temperature-salinity capture diagram for *Sergestes tenuiremis*. Water masses as in Figure 6.

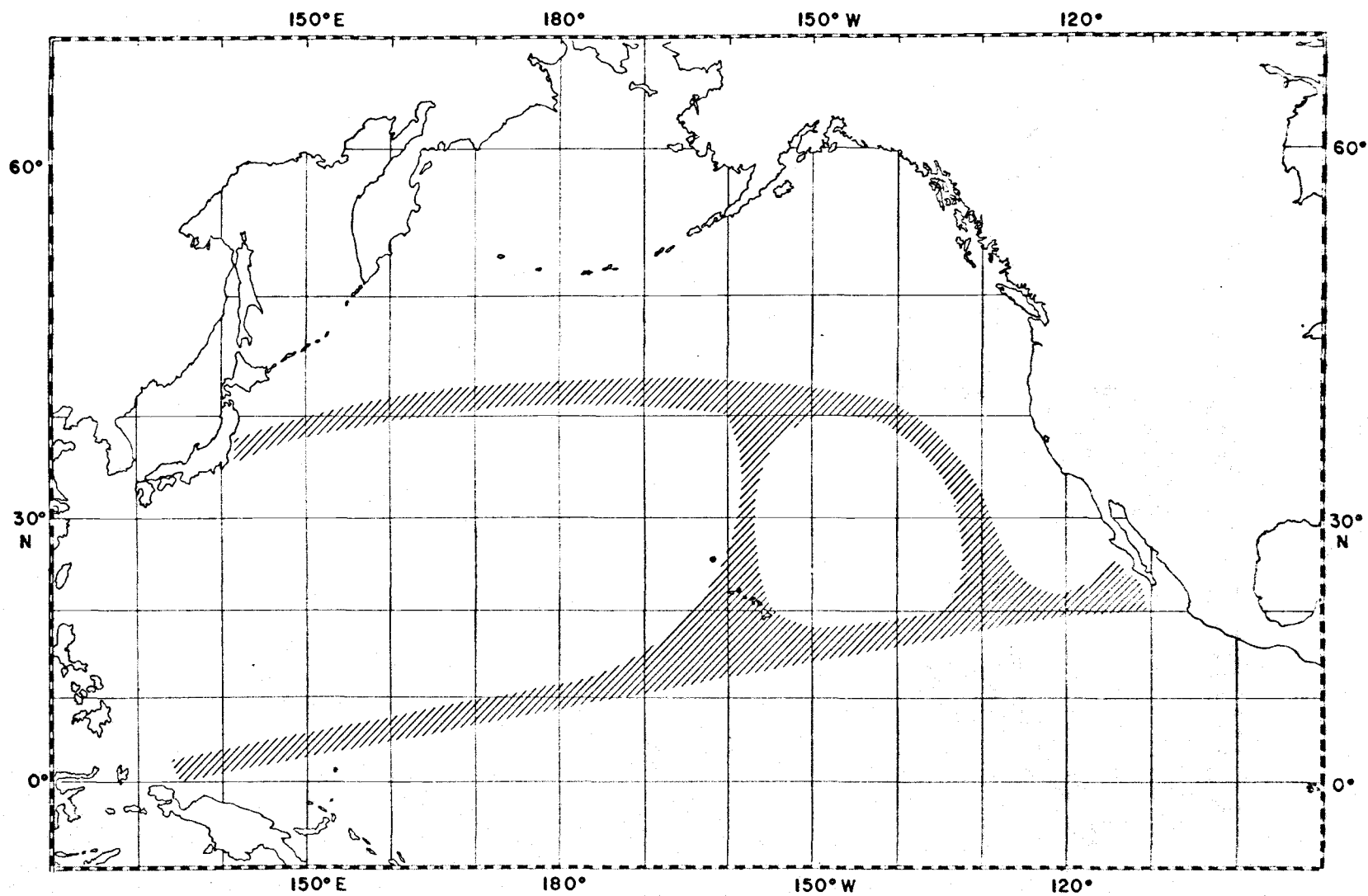


Figure 60. Distribution of Sergestes consobrinus in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

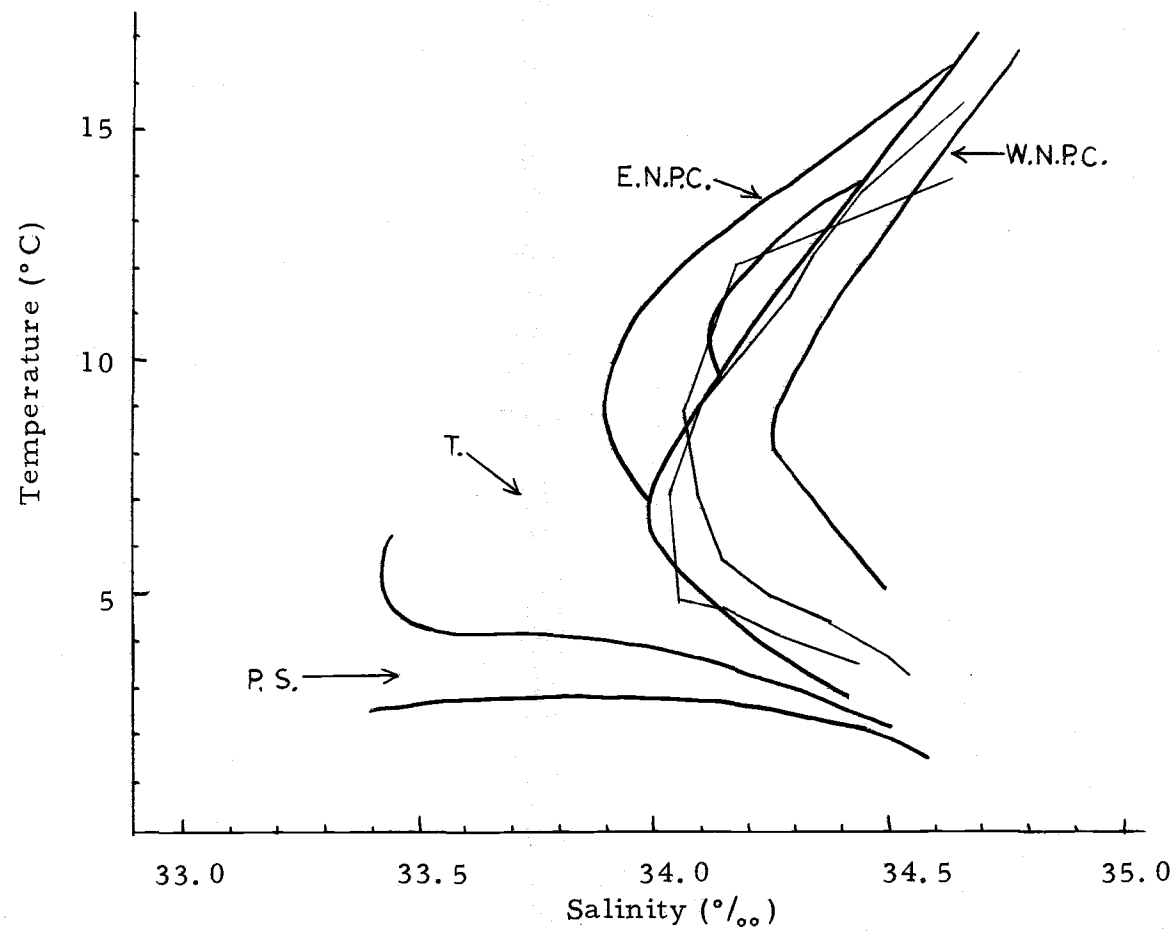


Figure 61. Temperature-salinity capture diagram for Sergestes consobrinus. Water masses as in Figure 6.

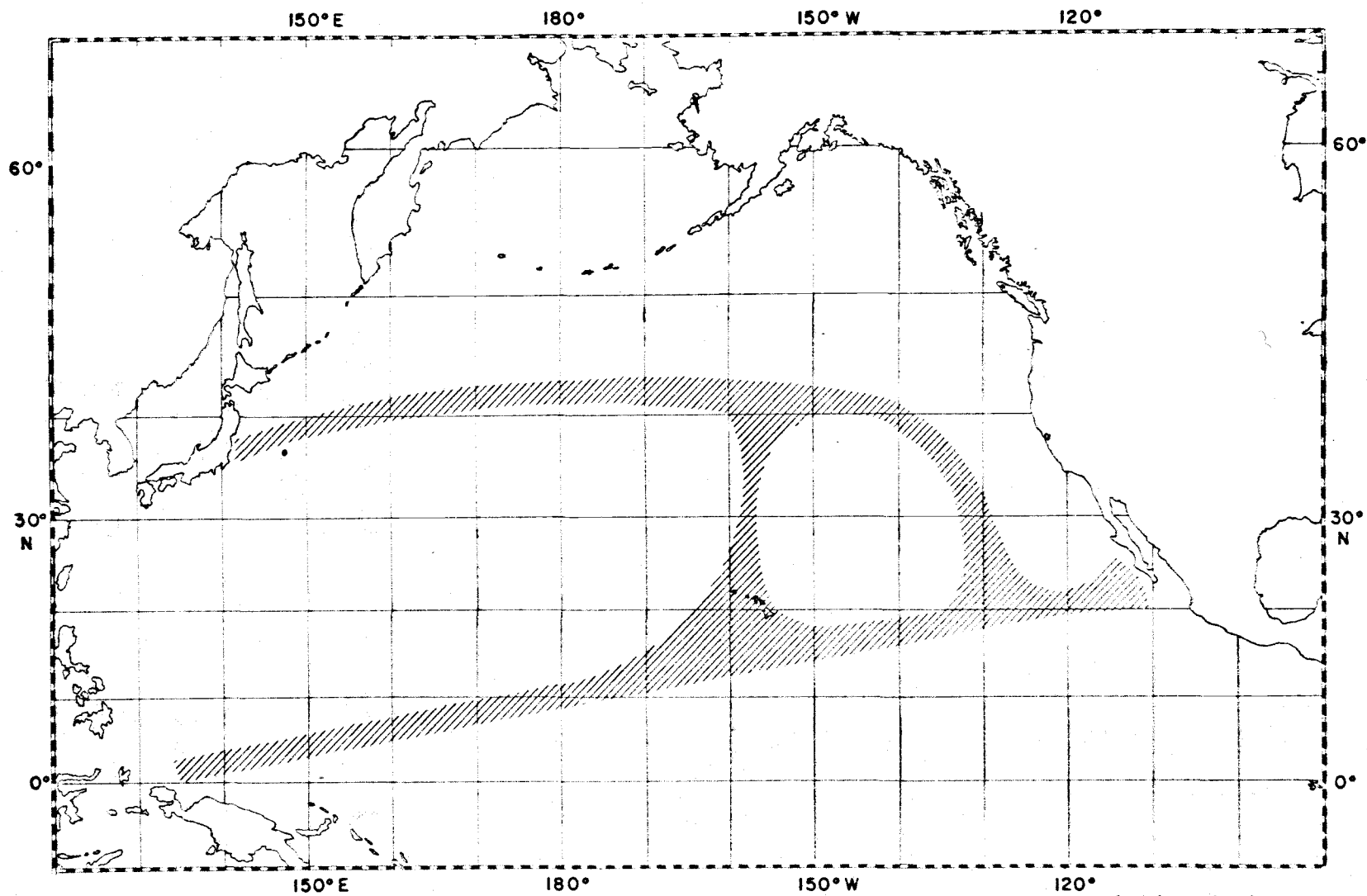


Figure 62. Distribution of *Sergestes prehensilis* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

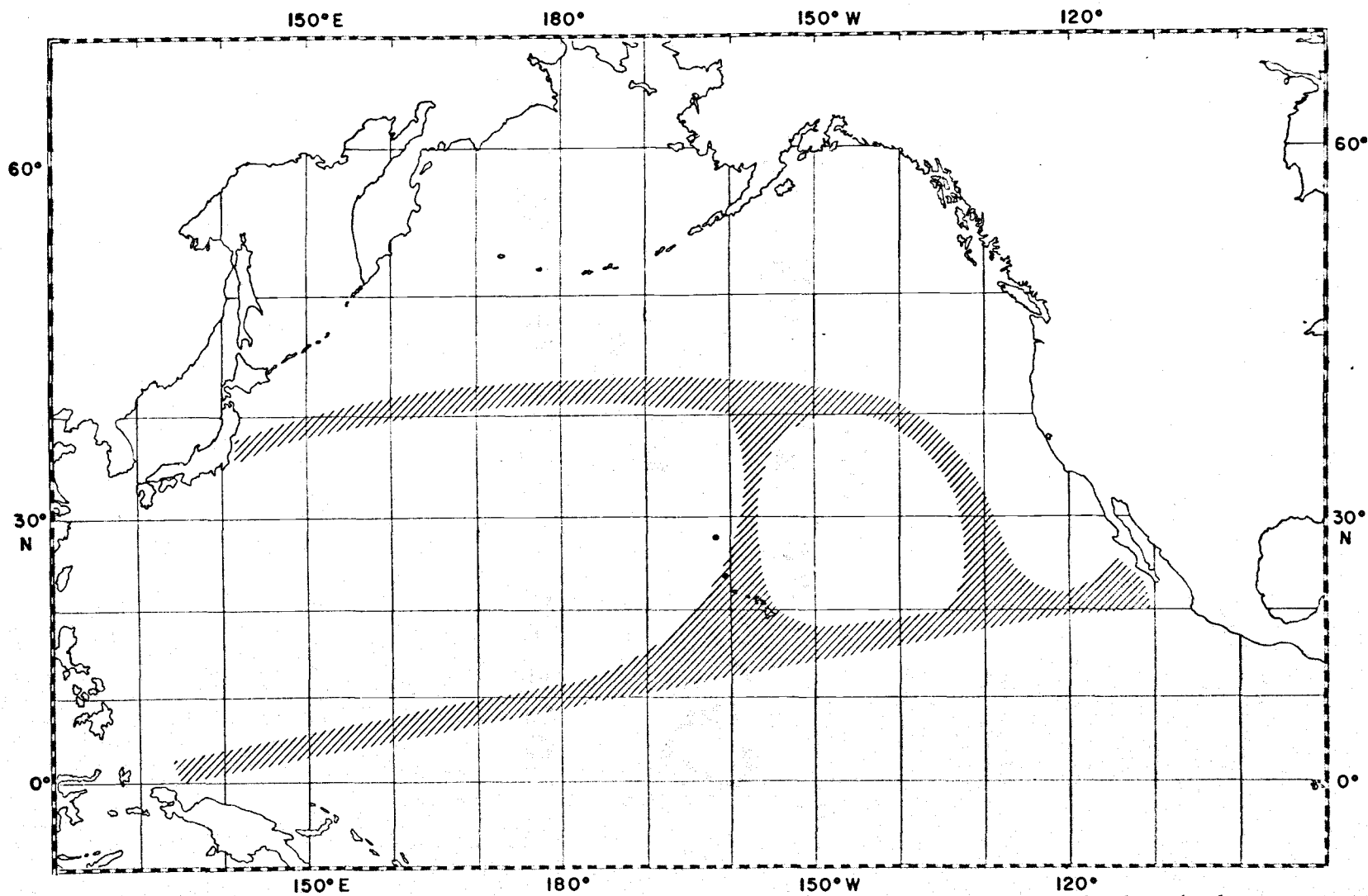


Figure 63. Distribution of *Grennadas bouvieri* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

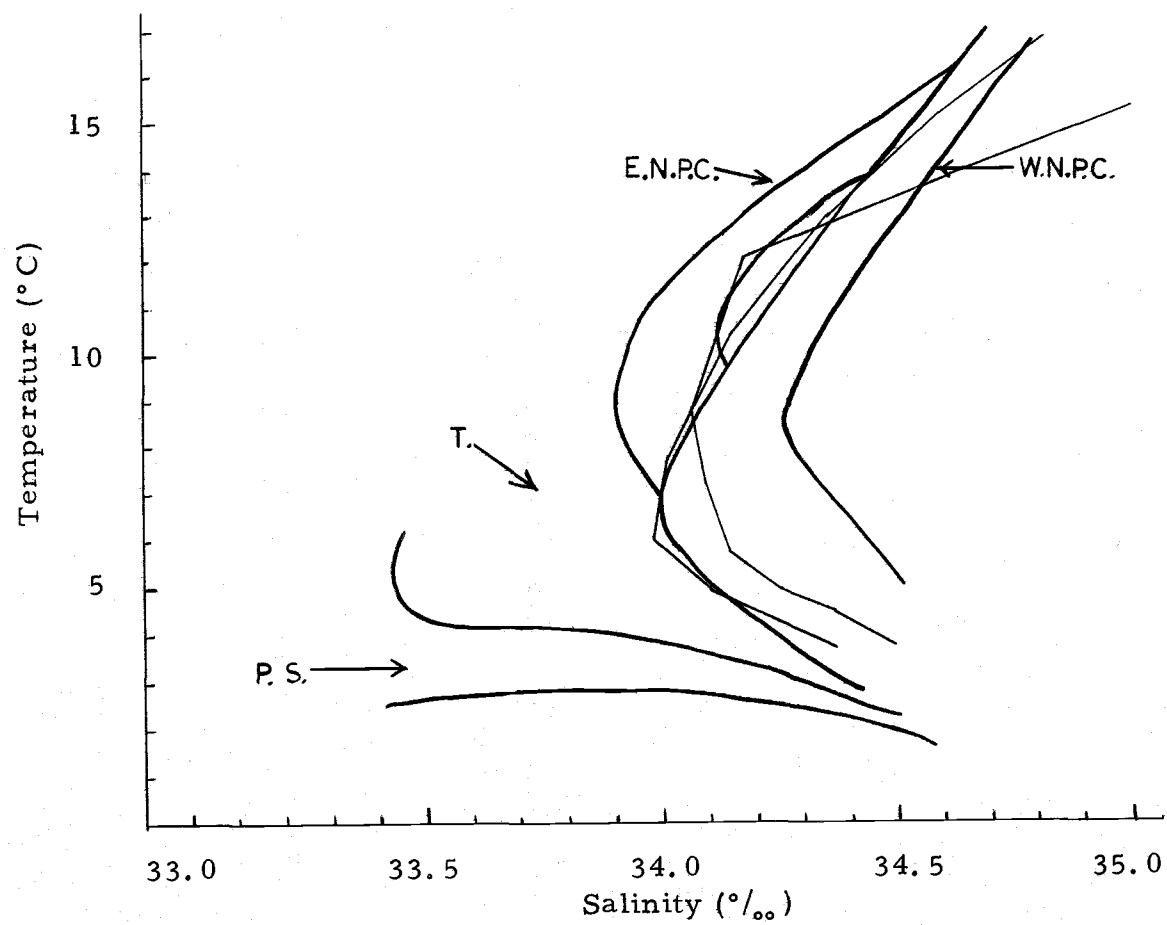


Figure 64. Temperature-salinity capture diagram for Grennadas bouvieri. Water masses as in Figure 6.

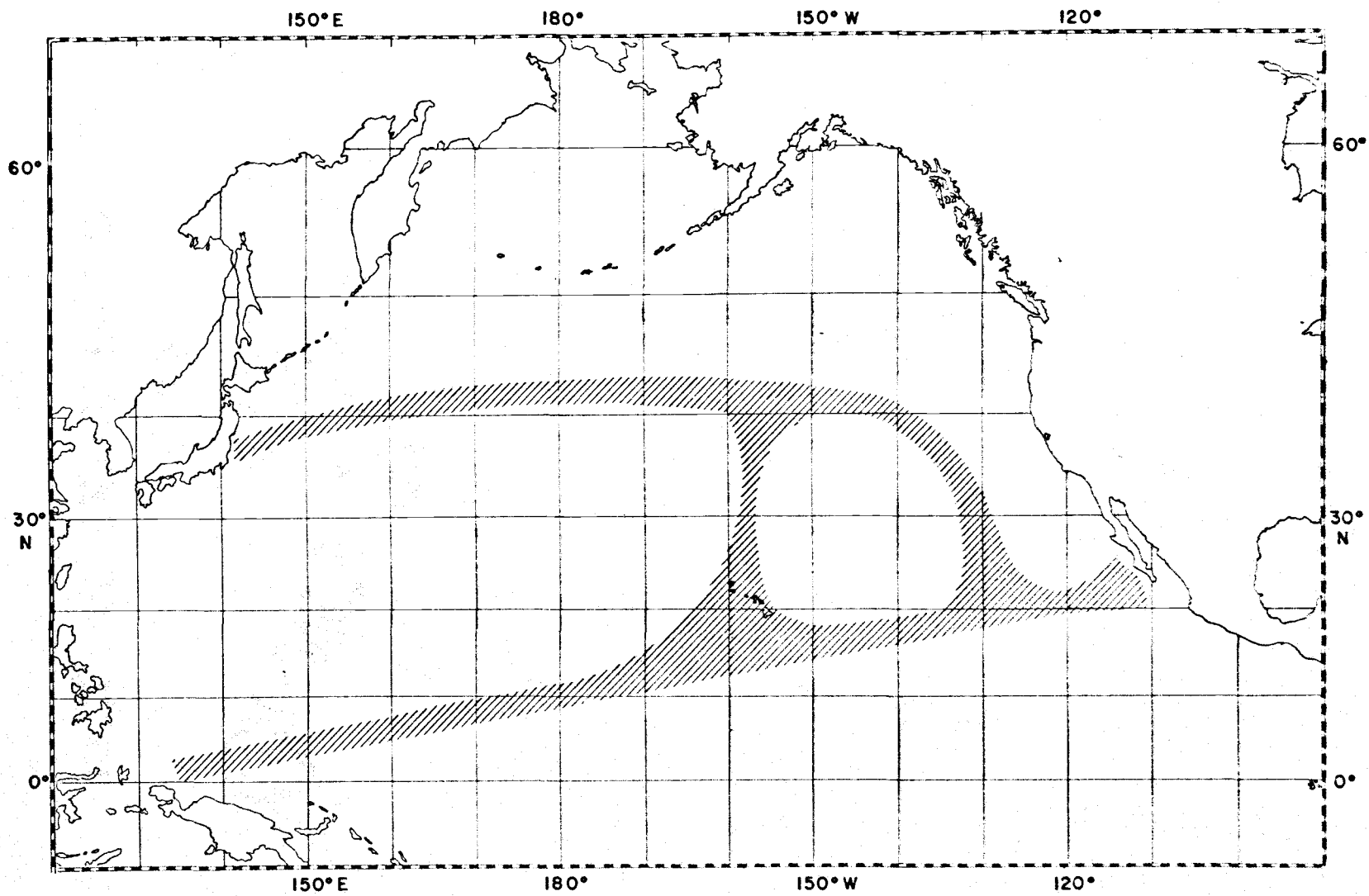


Figure 65. Distribution of *Gennades capensis* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

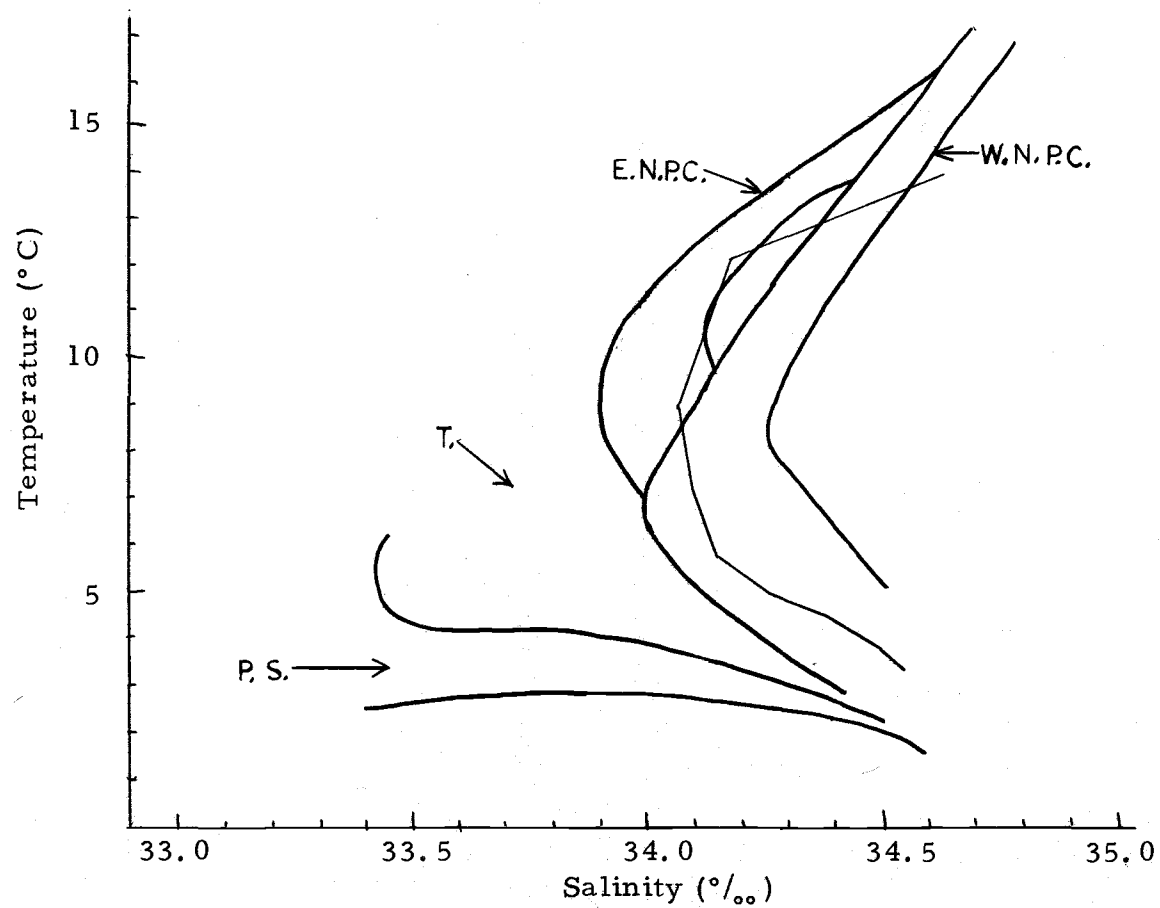


Figure 66. Temperature-salinity capture diagram for Gennadas capensis. Water masses as in Figure 6.

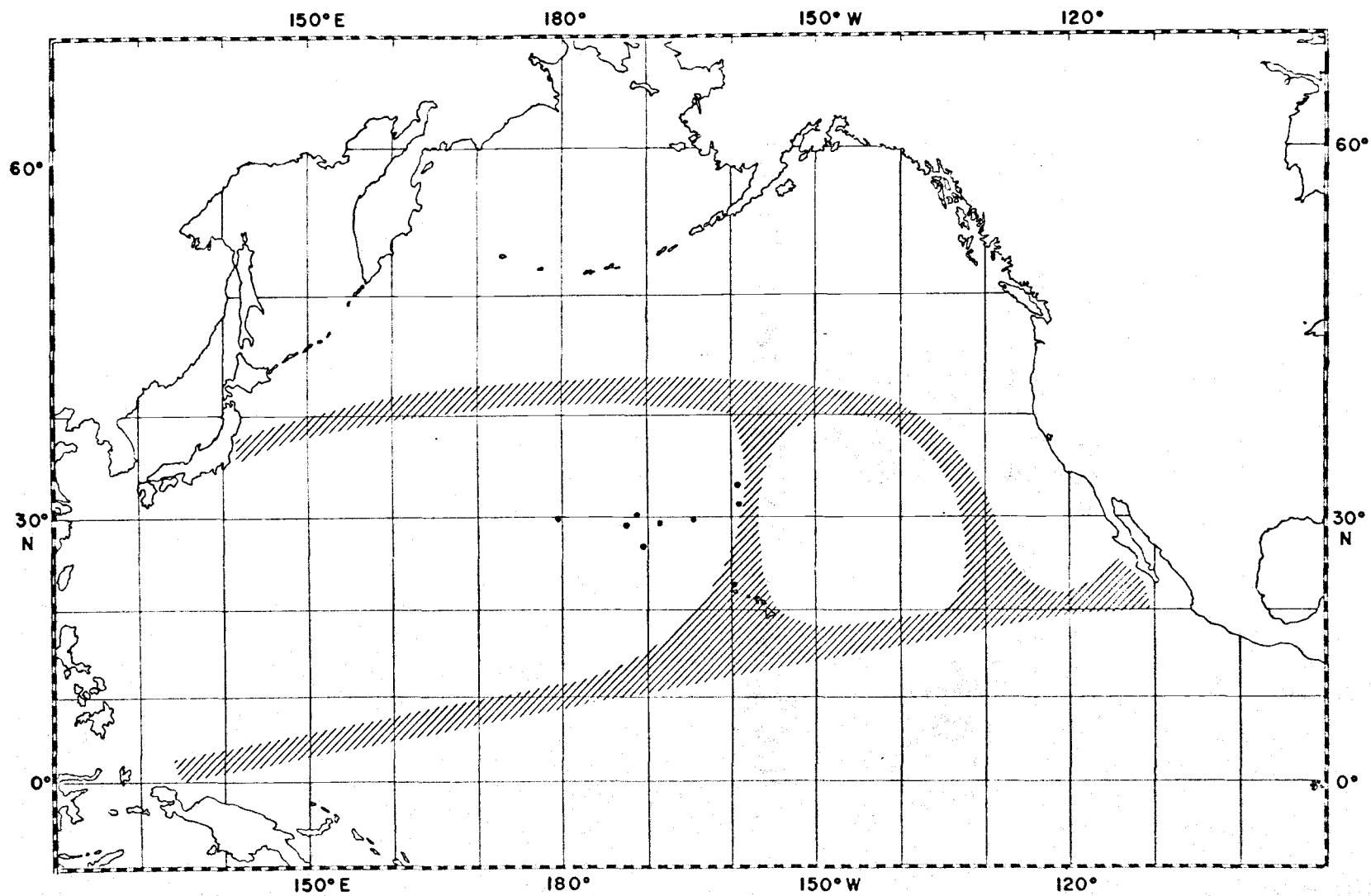


Figure 67. Distribution of *Funchalia taaningi* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

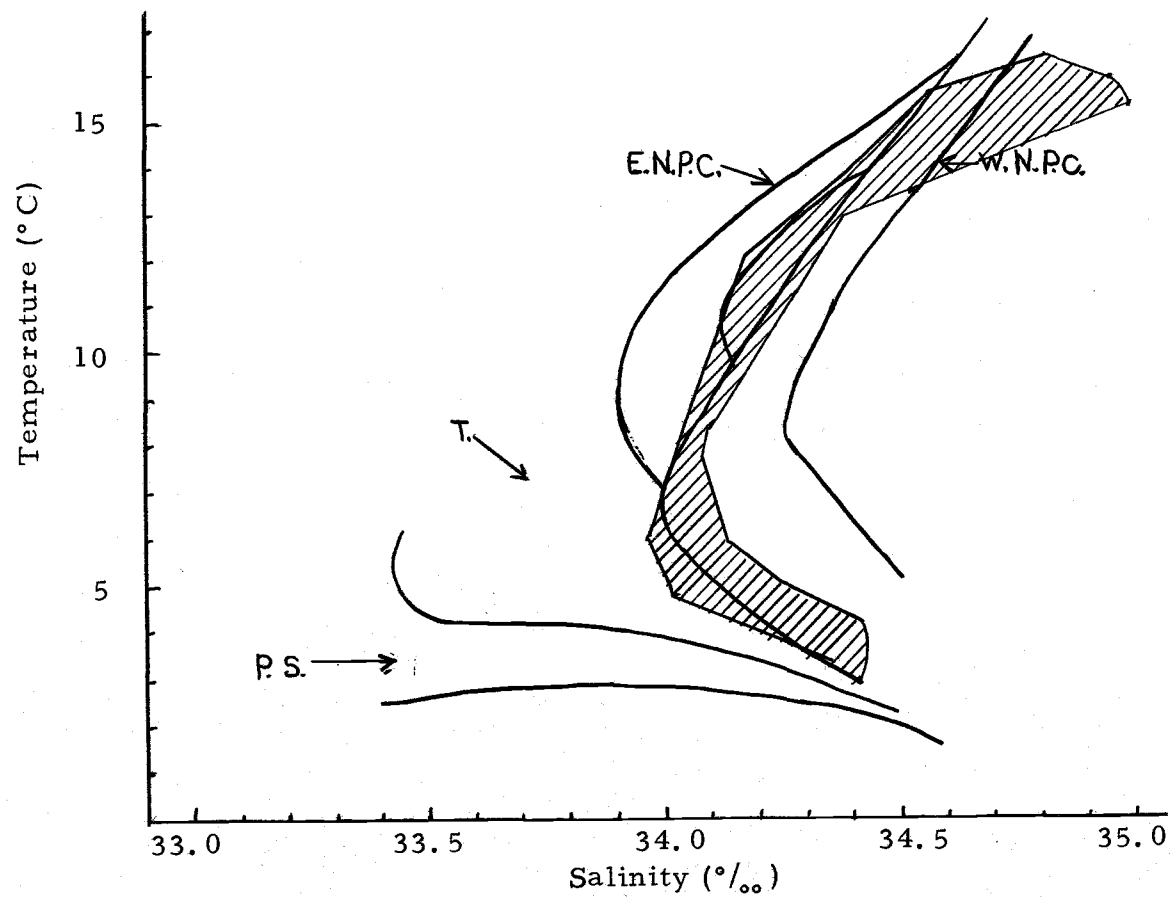


Figure 68. Temperature-salinity capture diagram for Funchalia taaningi. Water masses as in Figure 6.

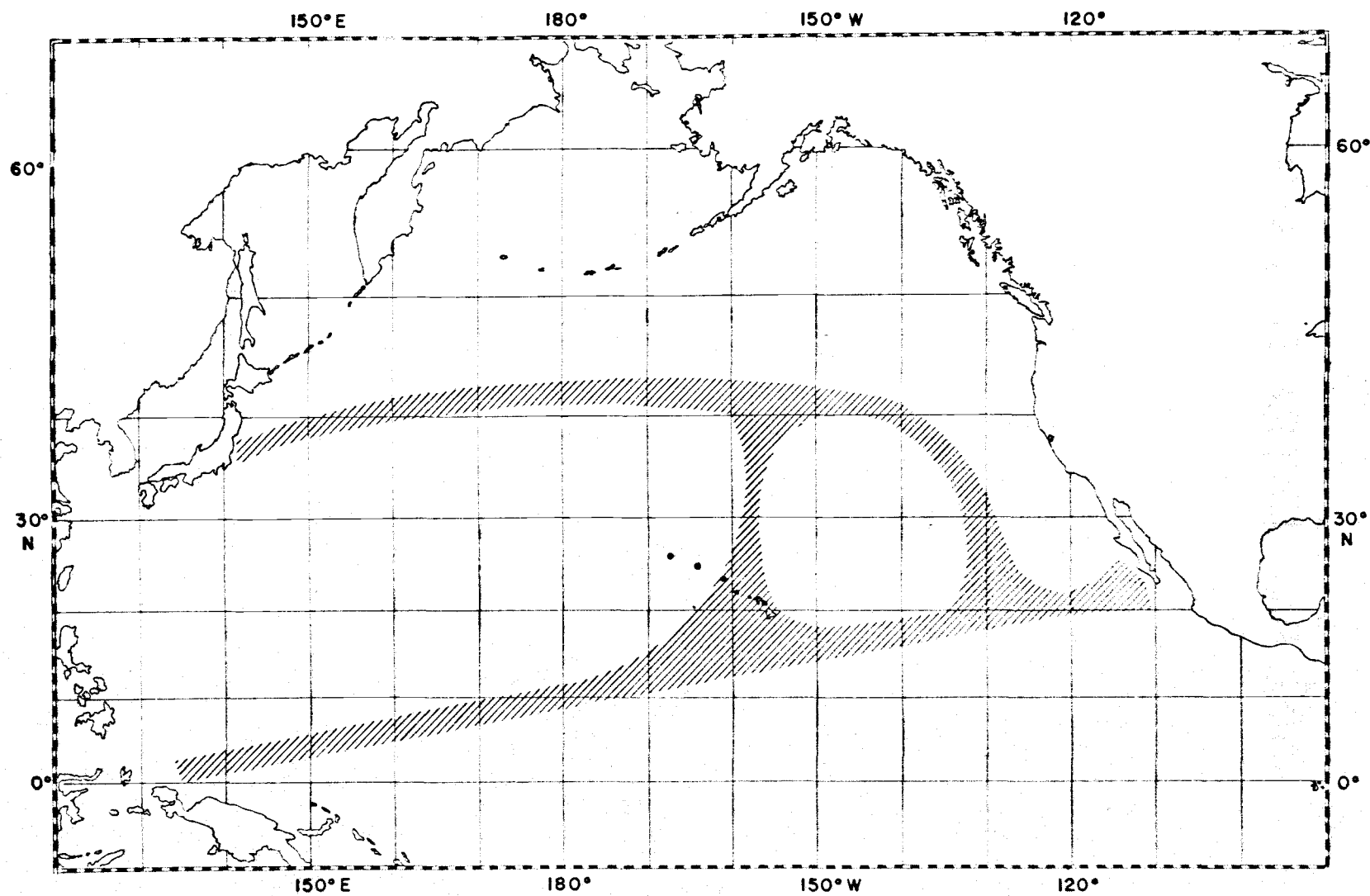


Figure 69. Distribution of Sergestes atlanticus in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

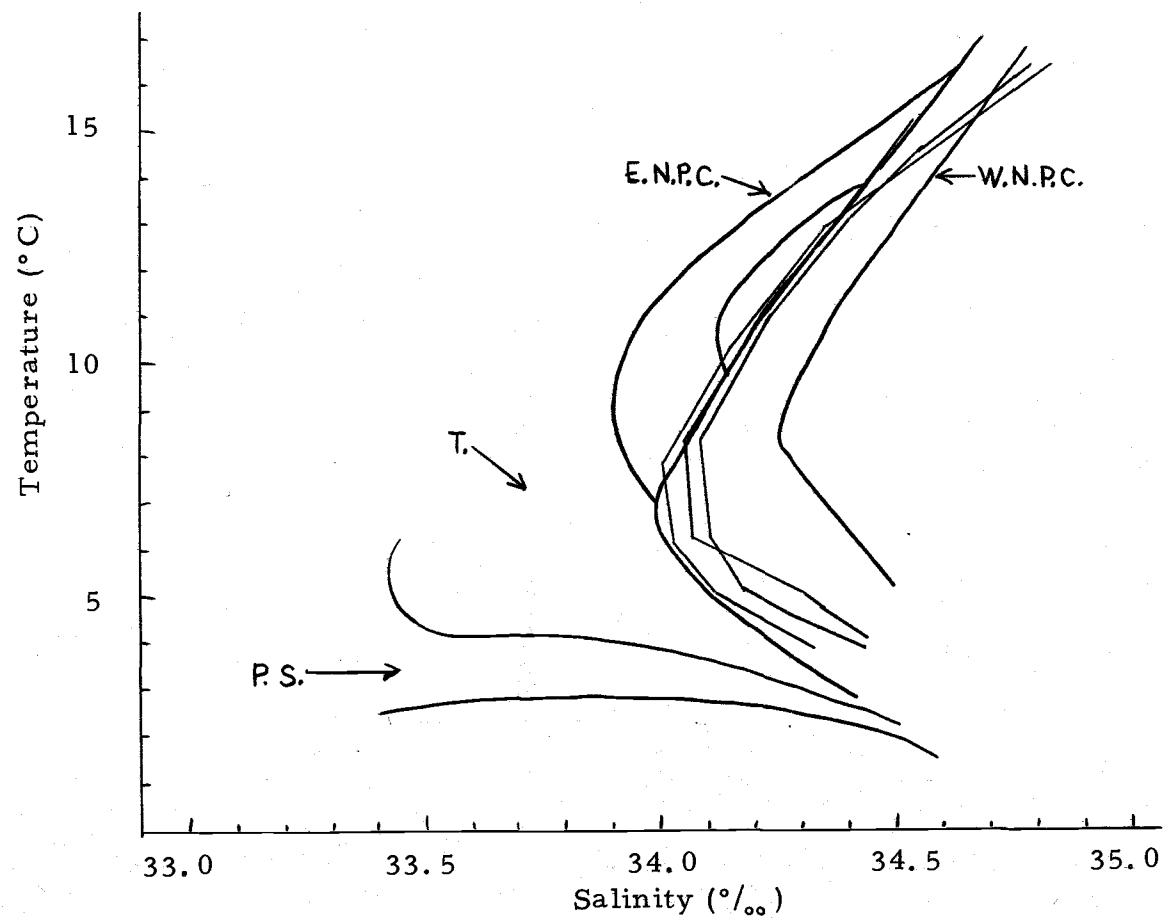


Figure 70. Temperature-salinity diagram for Sergestes atlanticus. Water masses as in Figure 6.

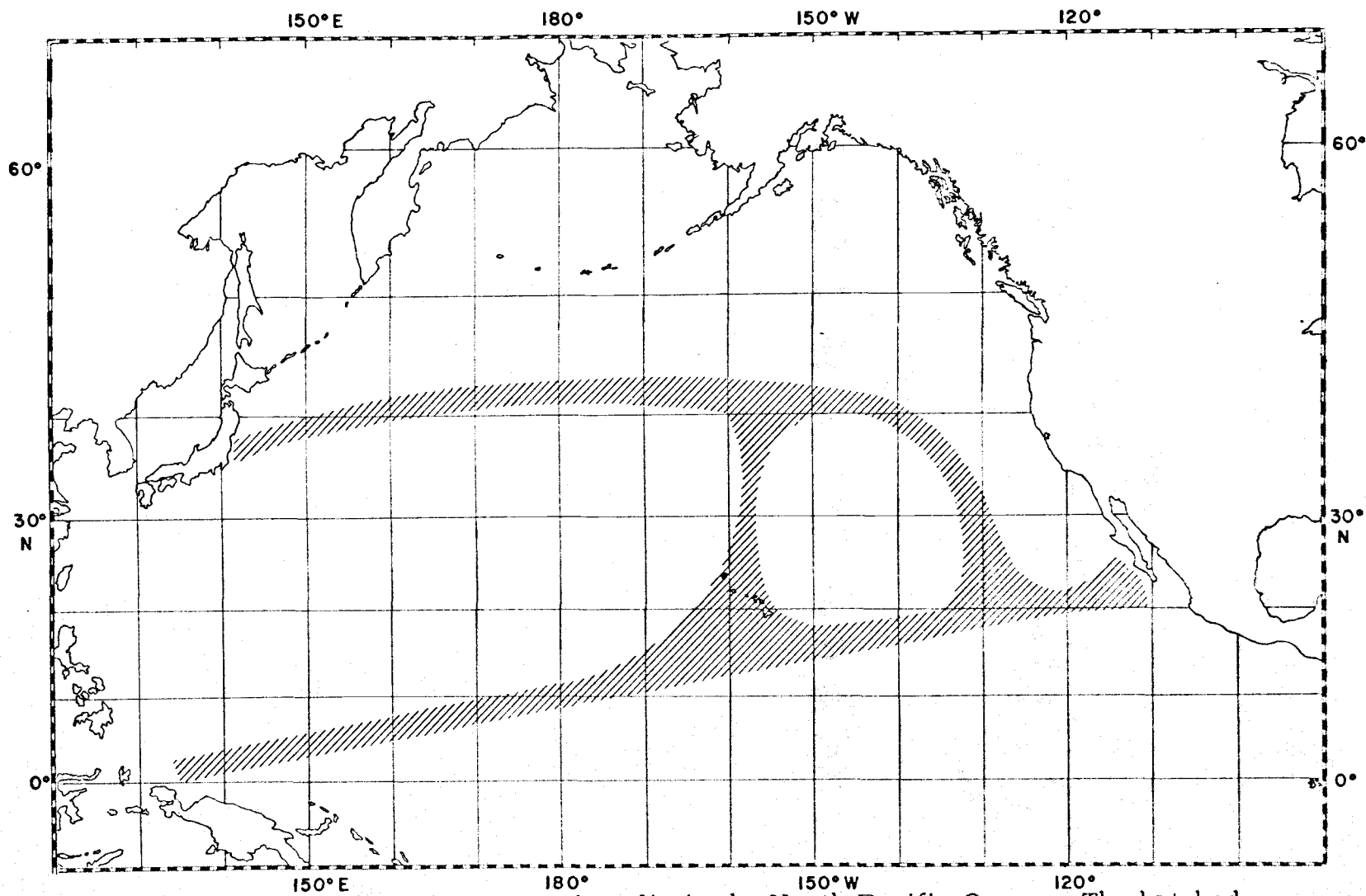


Figure 71. Distribution of *Sergestes orientalis* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

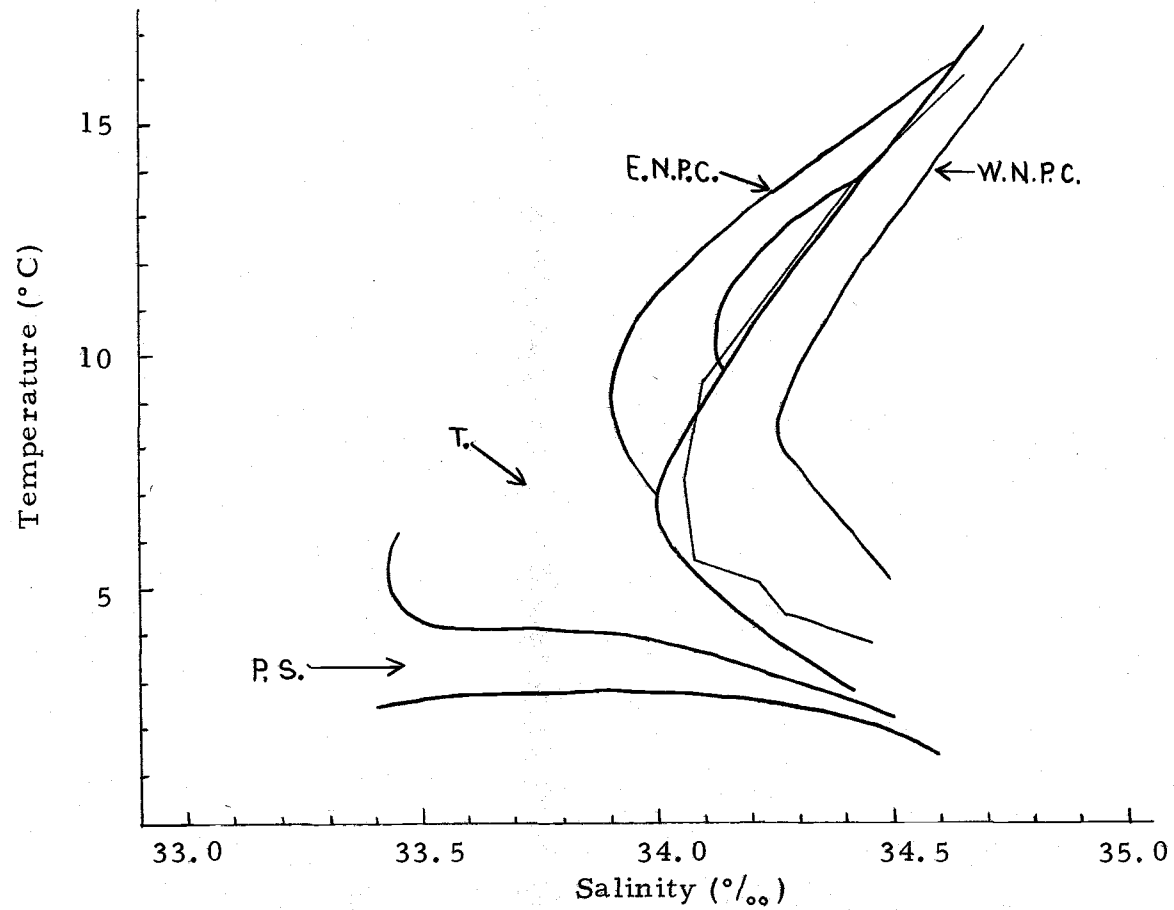


Figure 72. Temperature-salinity capture diagram for *Sergestes orientalis*. Water masses as in Figure 6.

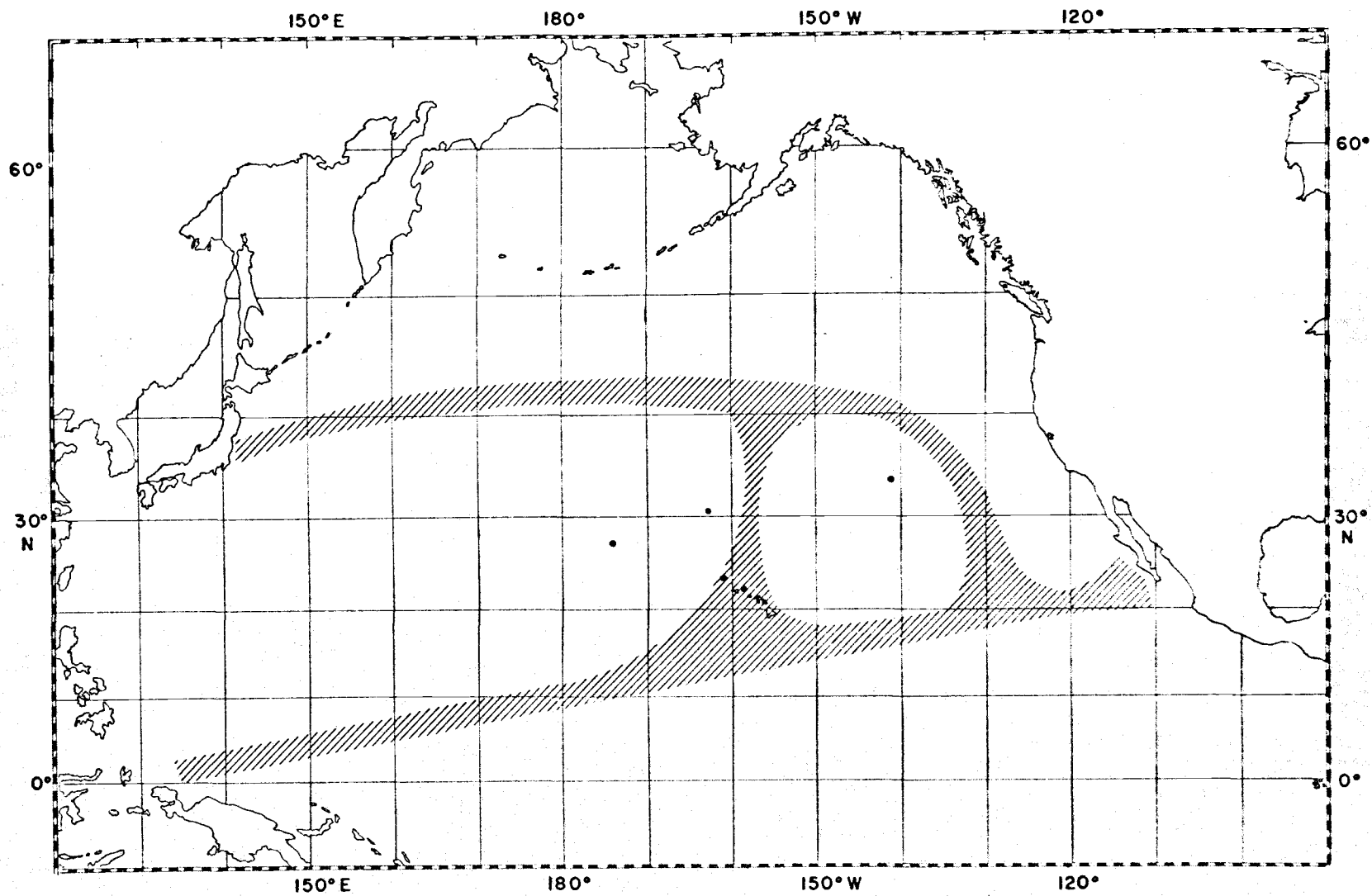


Figure 73. Distribution of *Sergestes pectinatus* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

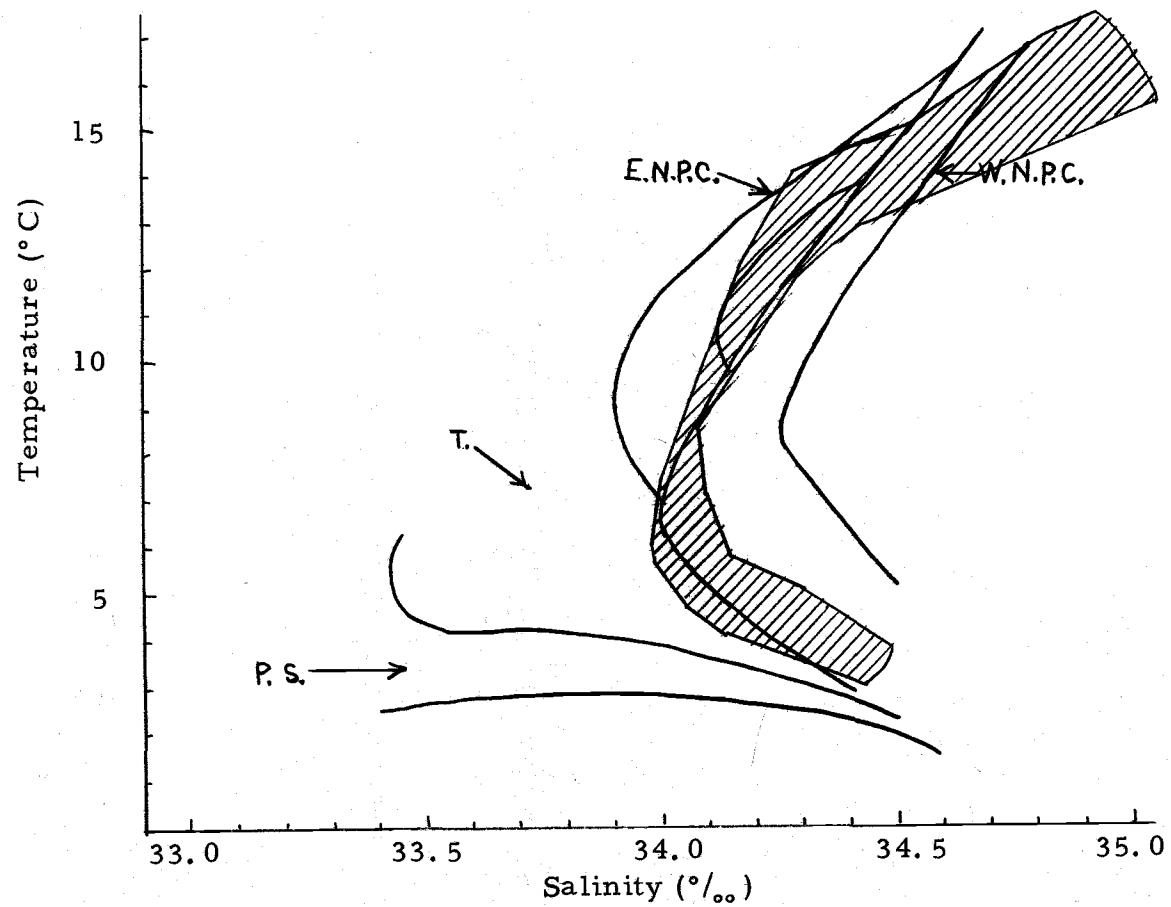


Figure 74. Temperature-salinity capture diagram for Sergestes pectinatus. Water masses as in Figure 6.

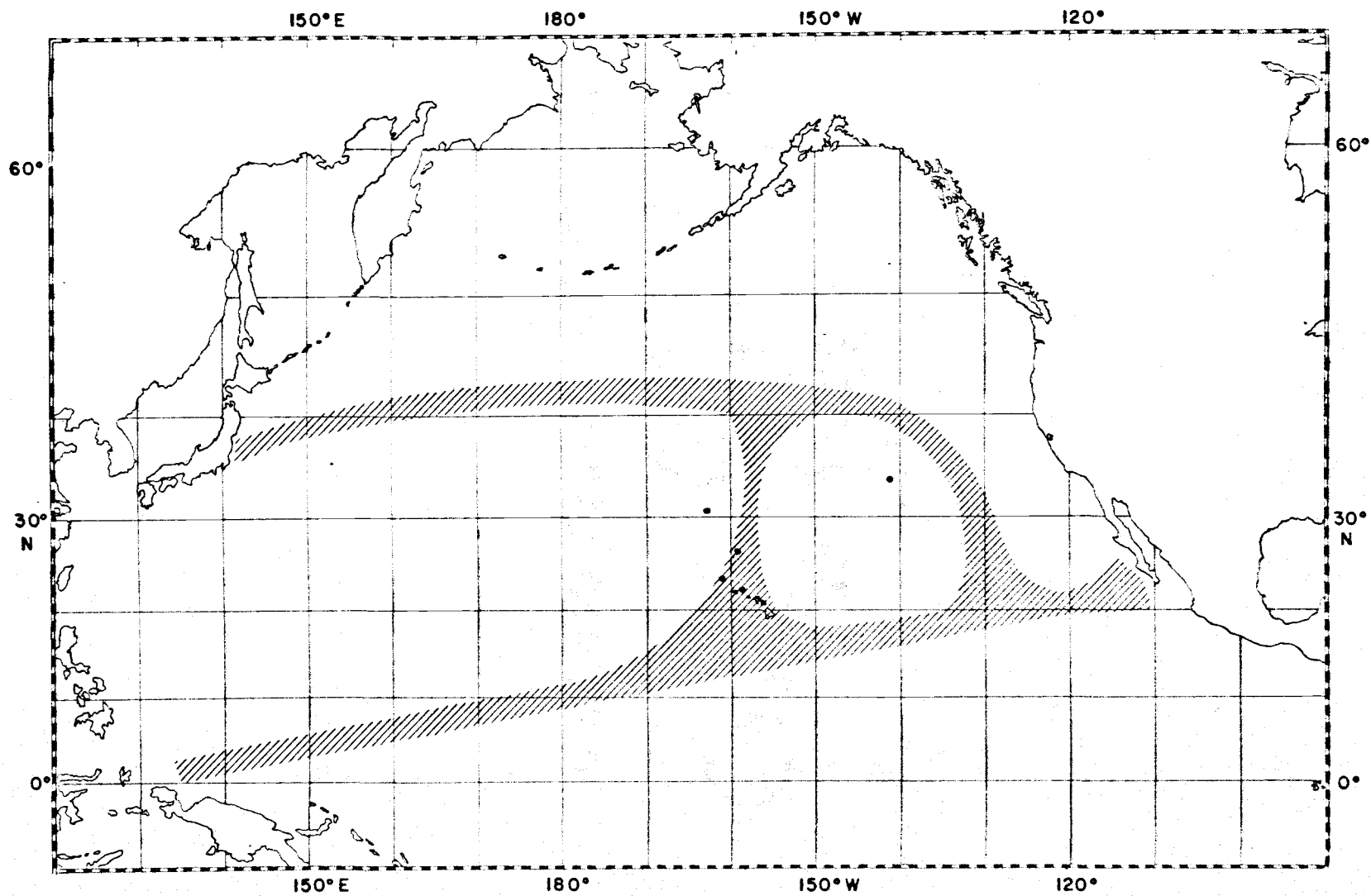


Figure 75. Distribution of *Sergestes vigilax* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

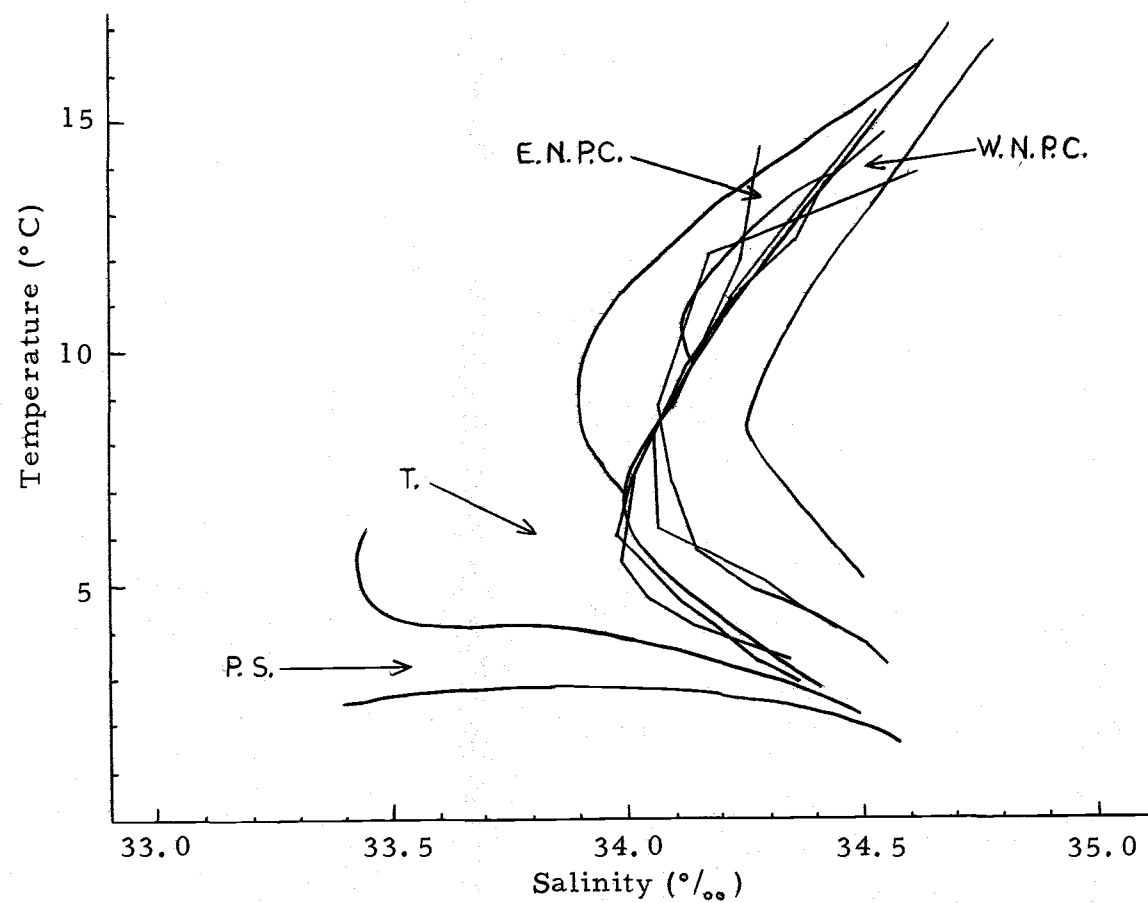


Figure 76. Temperature-salinity capture diagram for *Sergestes vigilax*. Water masses as in Figure 6.

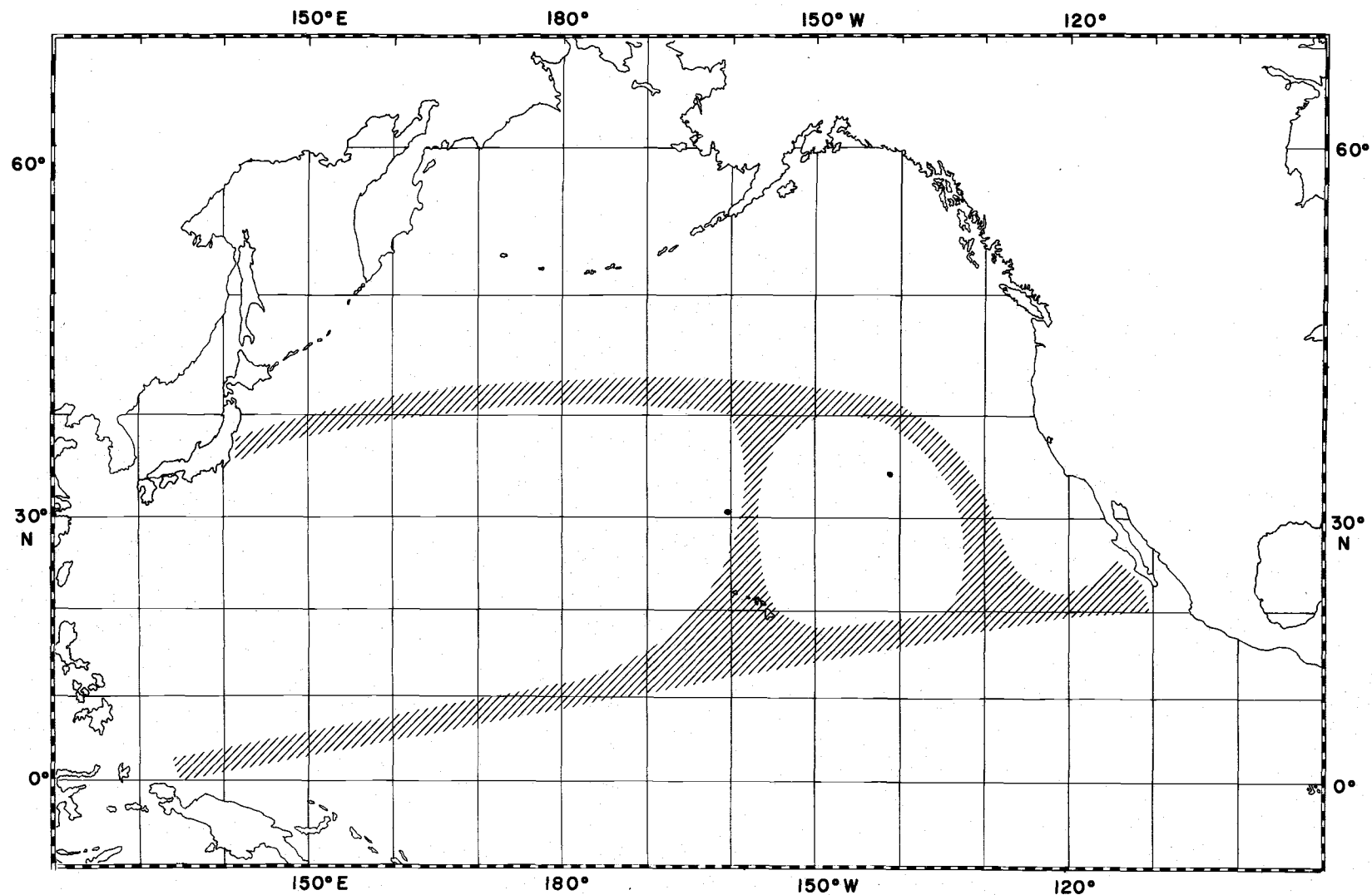


Figure 77. Distribution of *Sergestes bigemmus* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

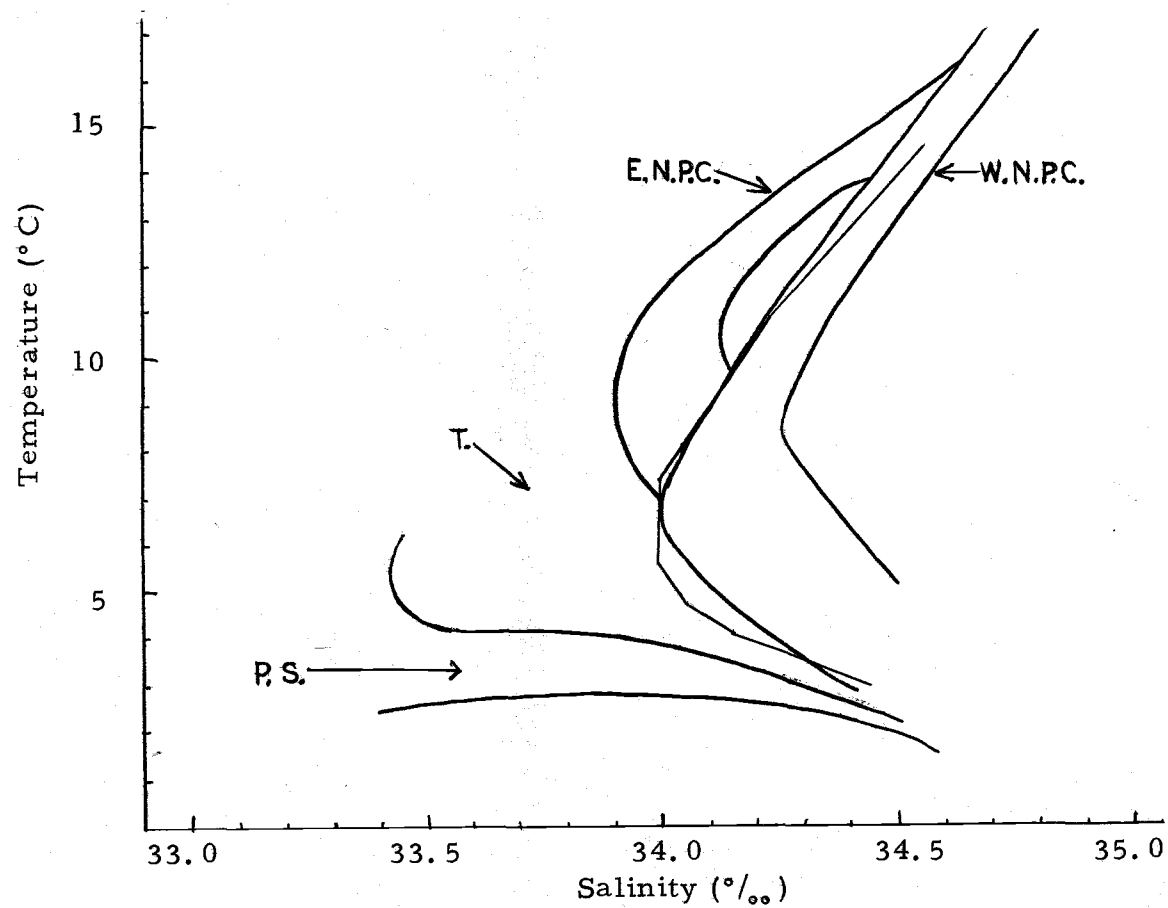


Figure 78. Temperature-salinity capture diagram for Sergestes bigemmus. Water masses as in Figure 6.

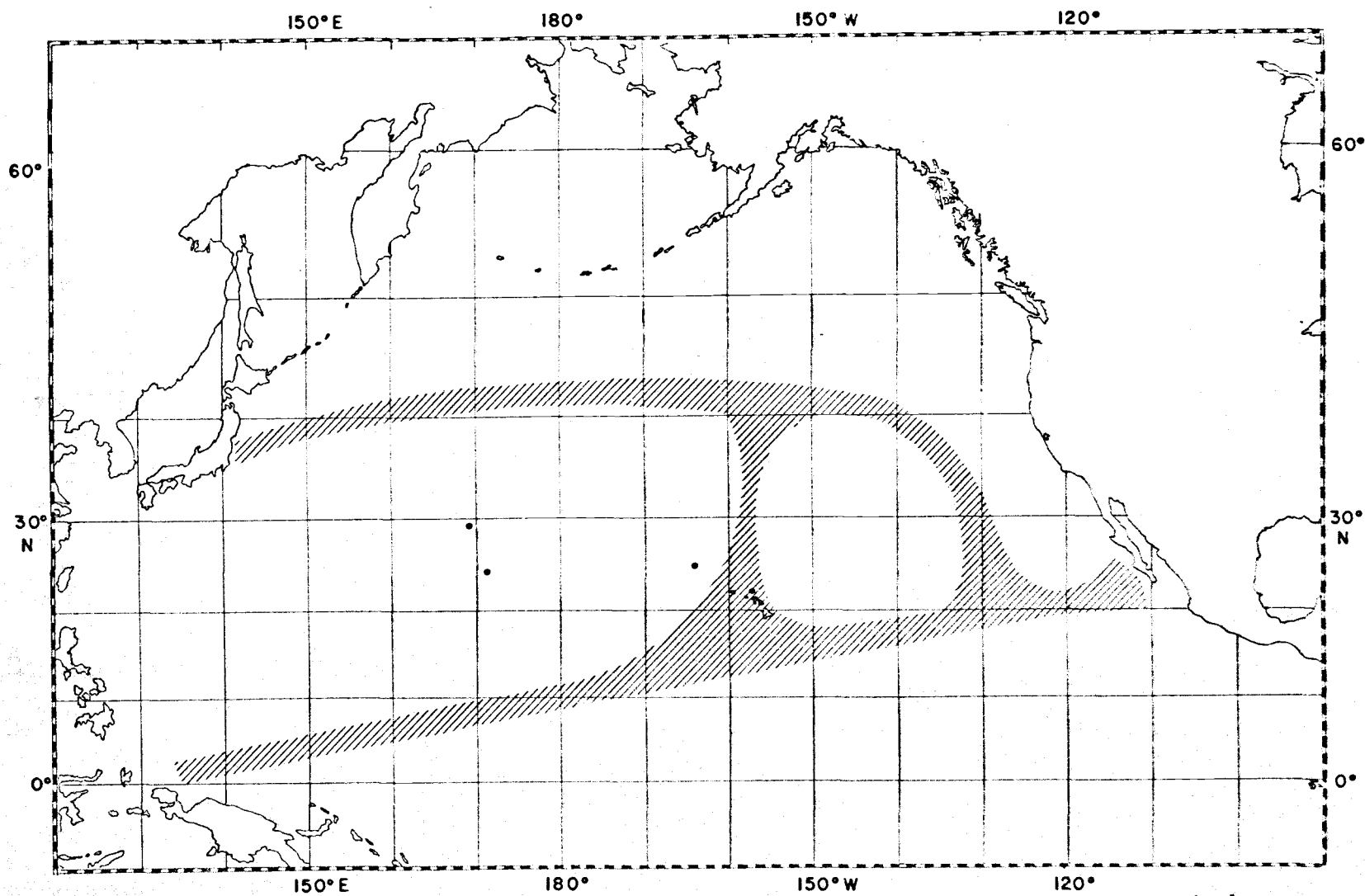


Figure 79. Distribution of *Sergestes gardineri* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

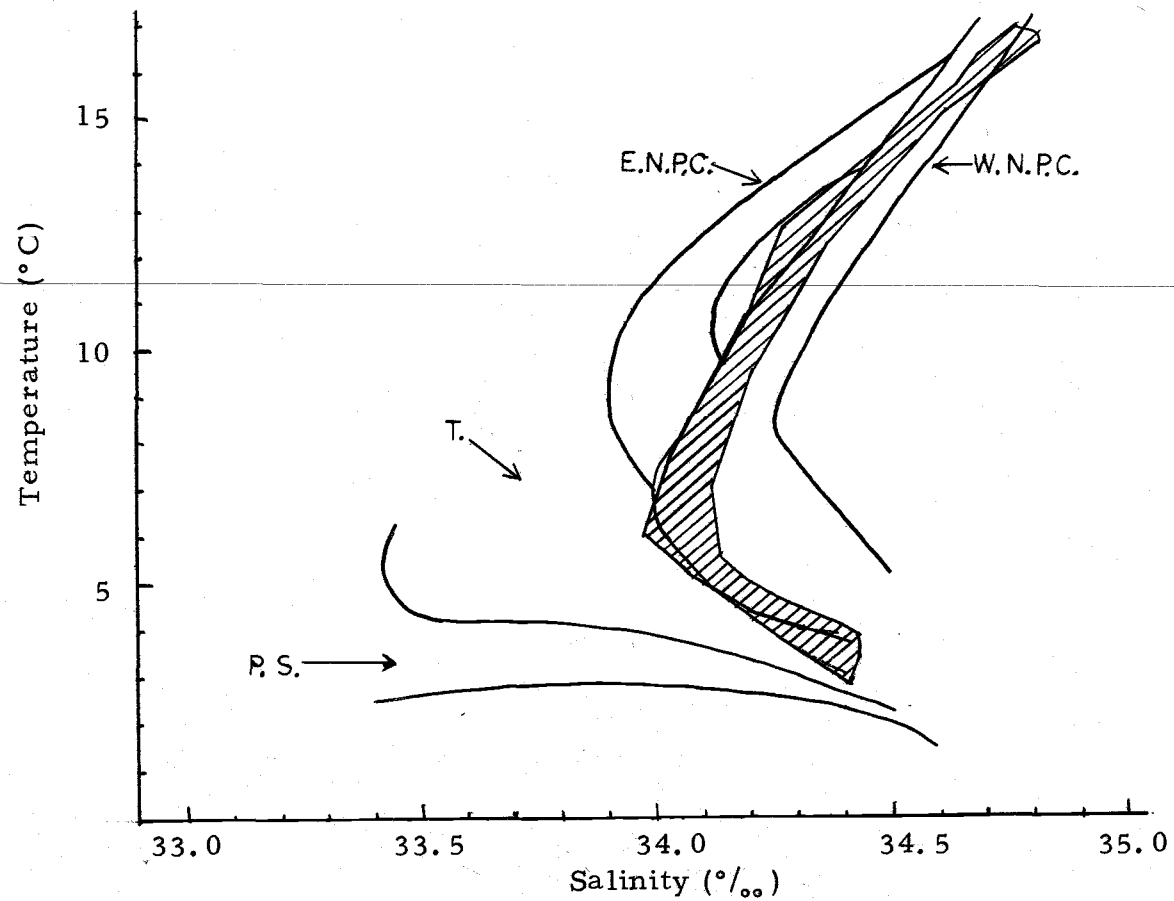


Figure 80. Temperature-salinity capture diagram for *Sergestes gardineri*. Water masses as in Figure 6.

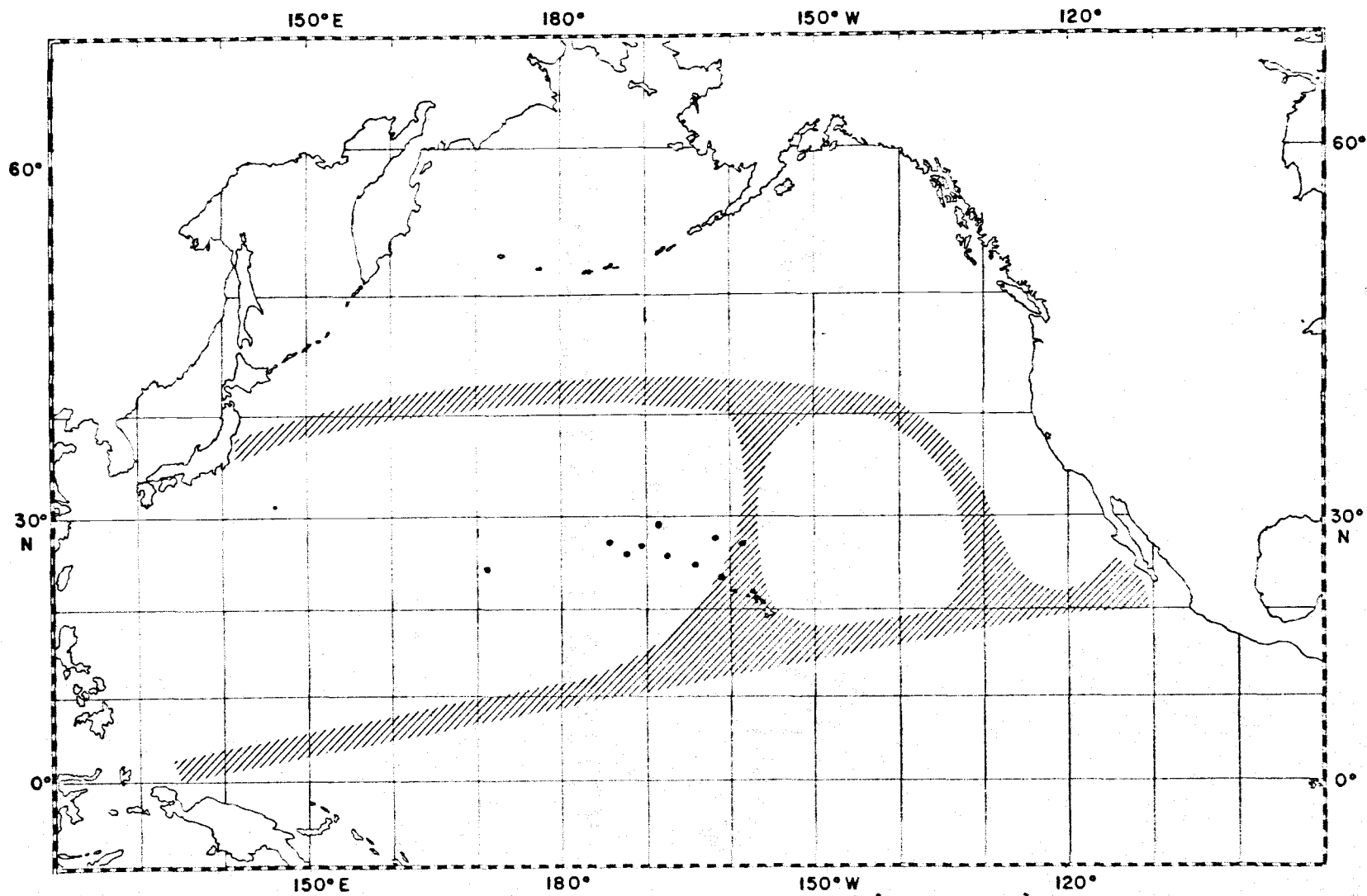


Figure 31. Distribution of *Sergestes scintillans* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

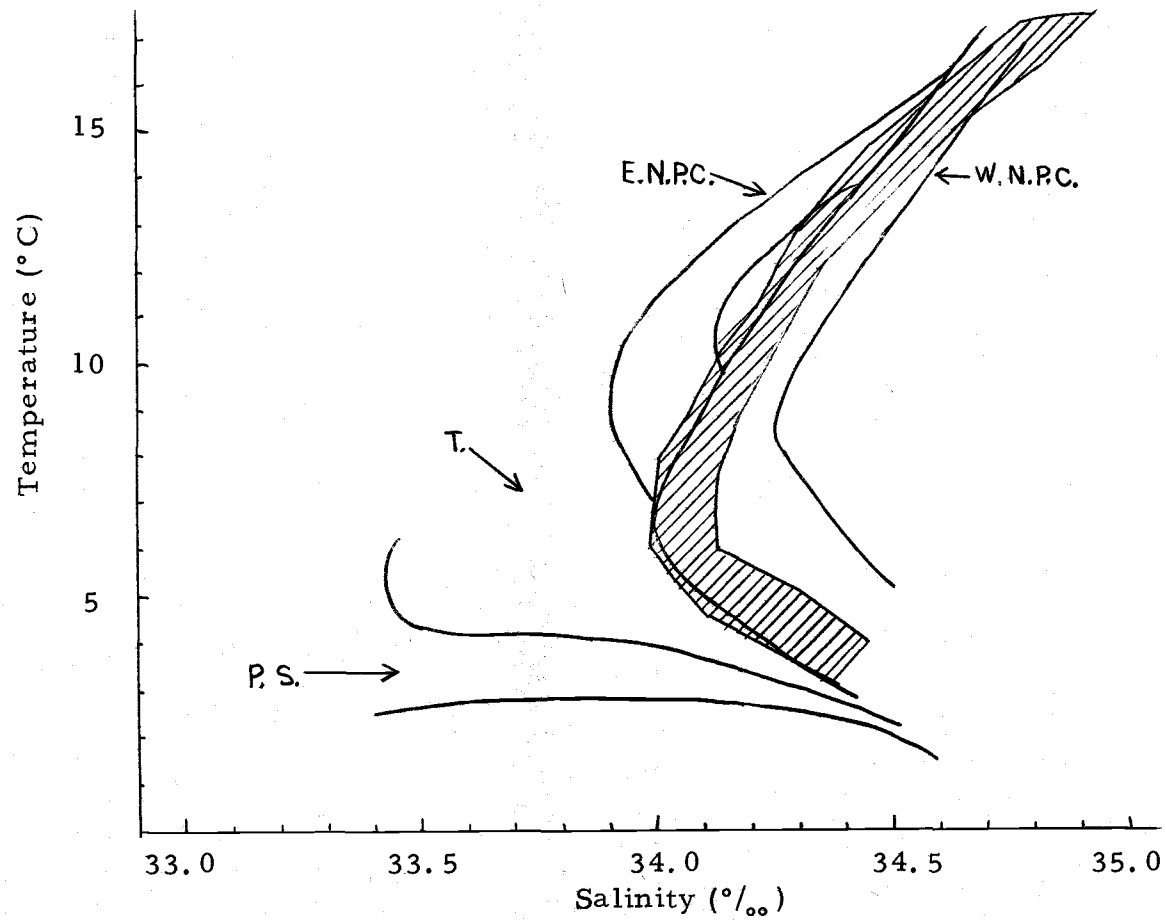


Figure 82. Temperature-salinity capture diagram for Sergestes scintillans. Water masses as in Figure 6.

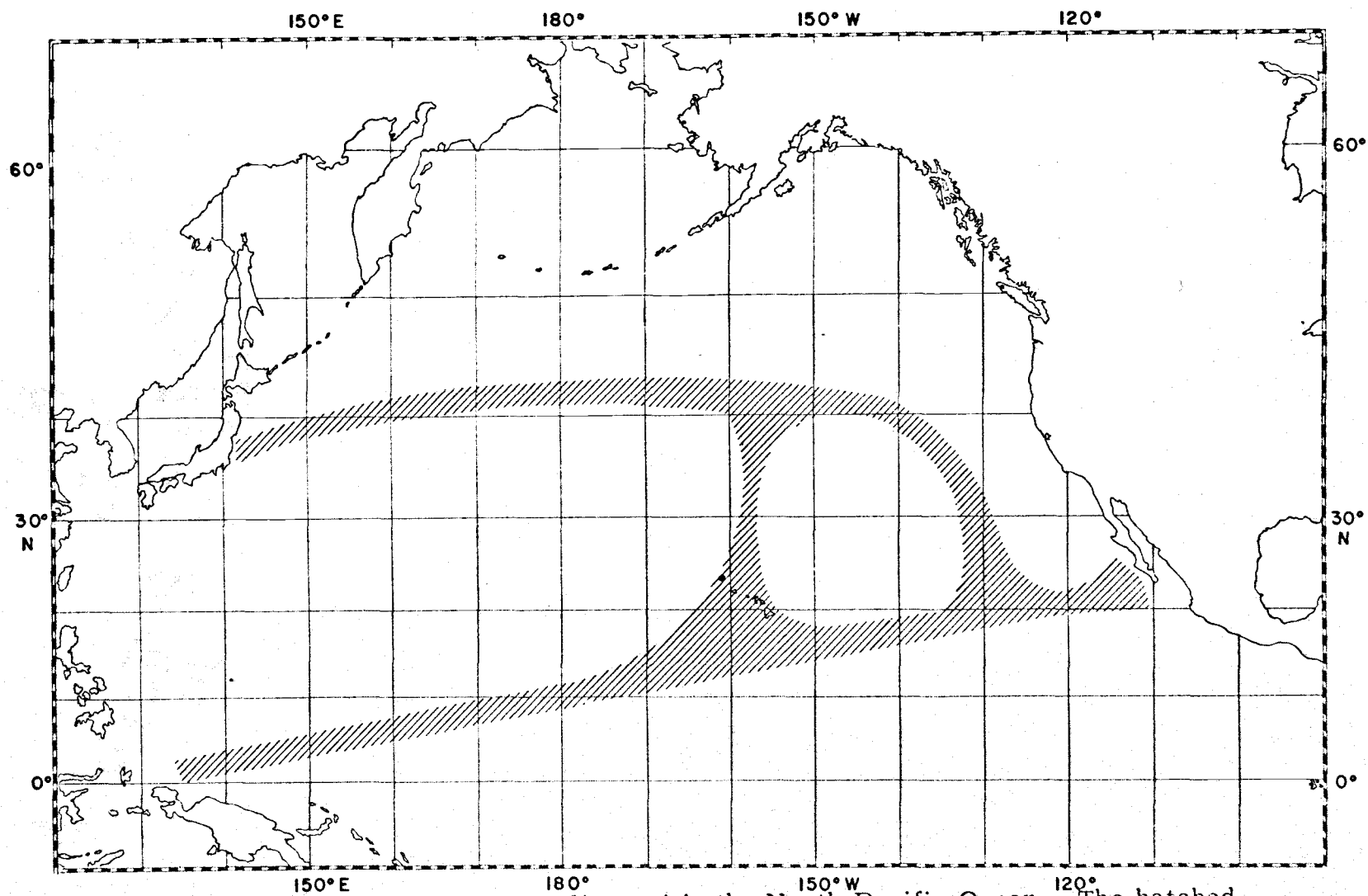


Figure 83. Distribution of *Sergestes talismani* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

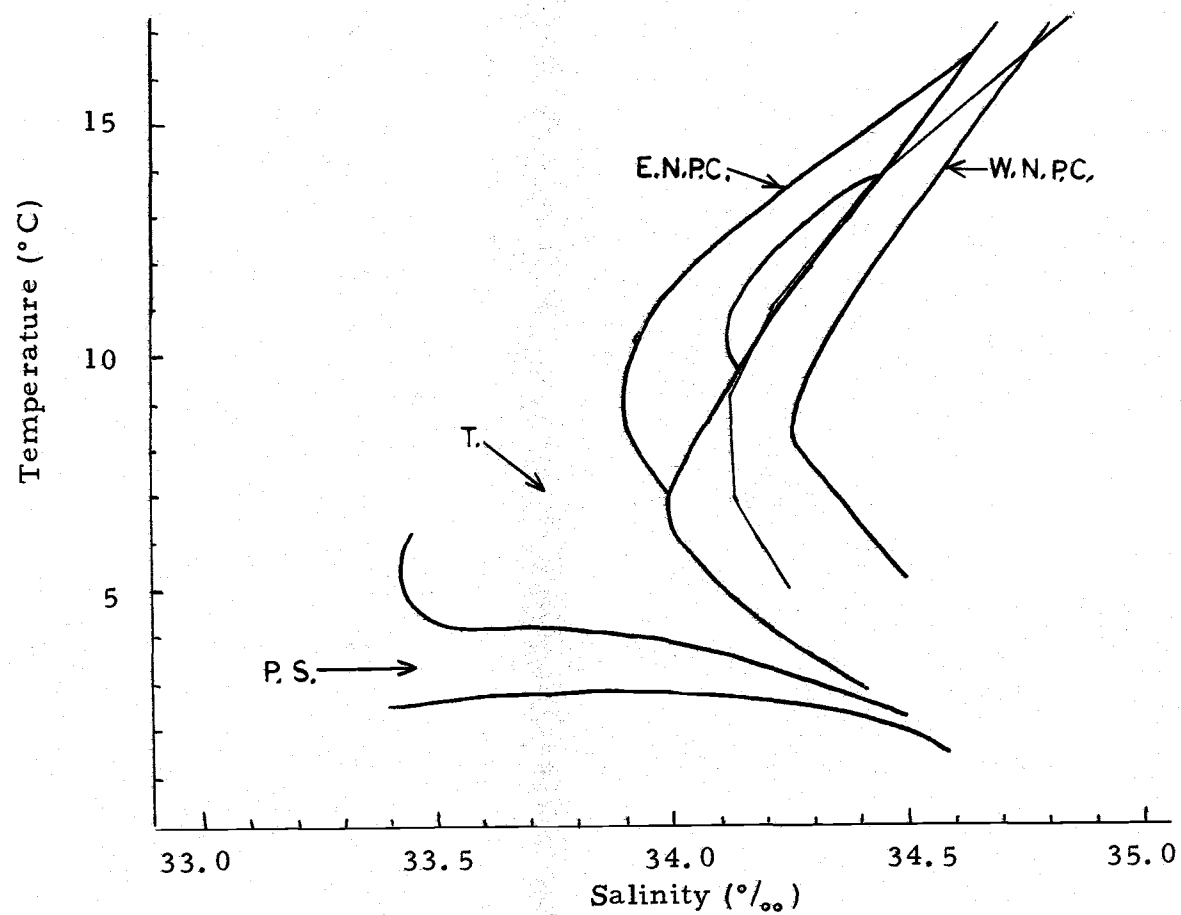


Figure 84. Temperature-salinity capture diagram for Sergestes talismani. Water masses as in Figure 6.

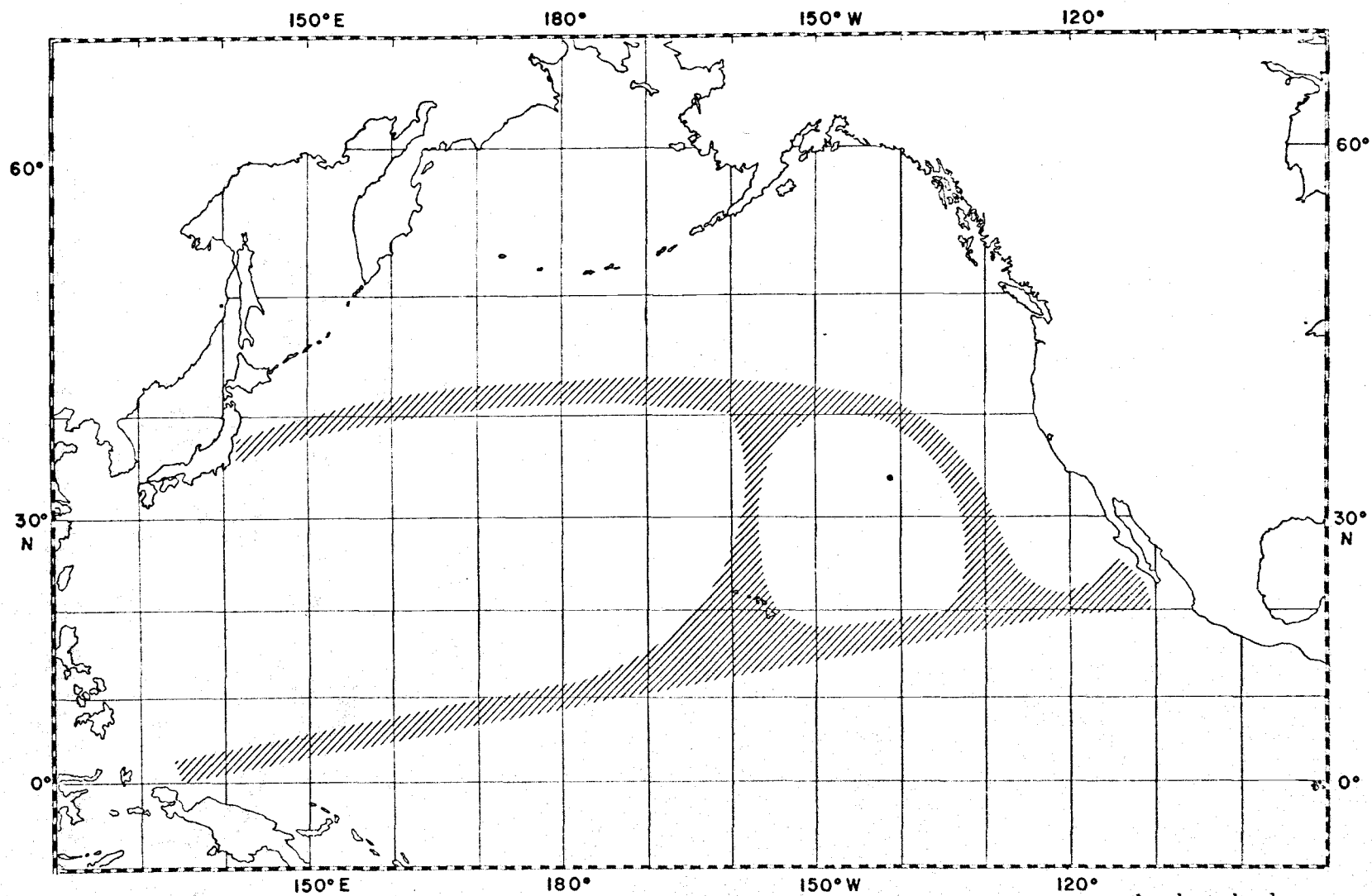


Figure 35. Distribution of Acantheephyra prionota in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

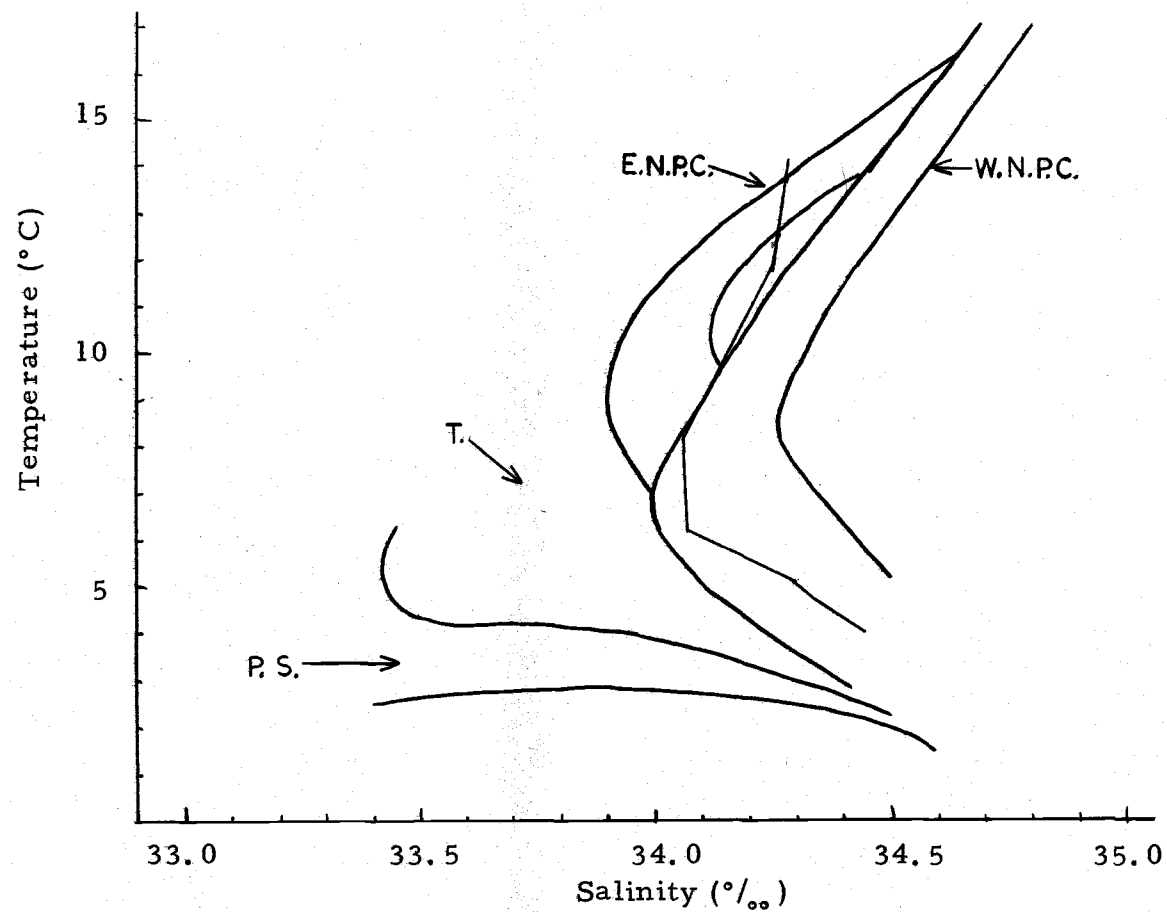


Figure 86. Temperature-salinity capture diagram for Acantheephyra prionota. Water masses as in Figure 6.

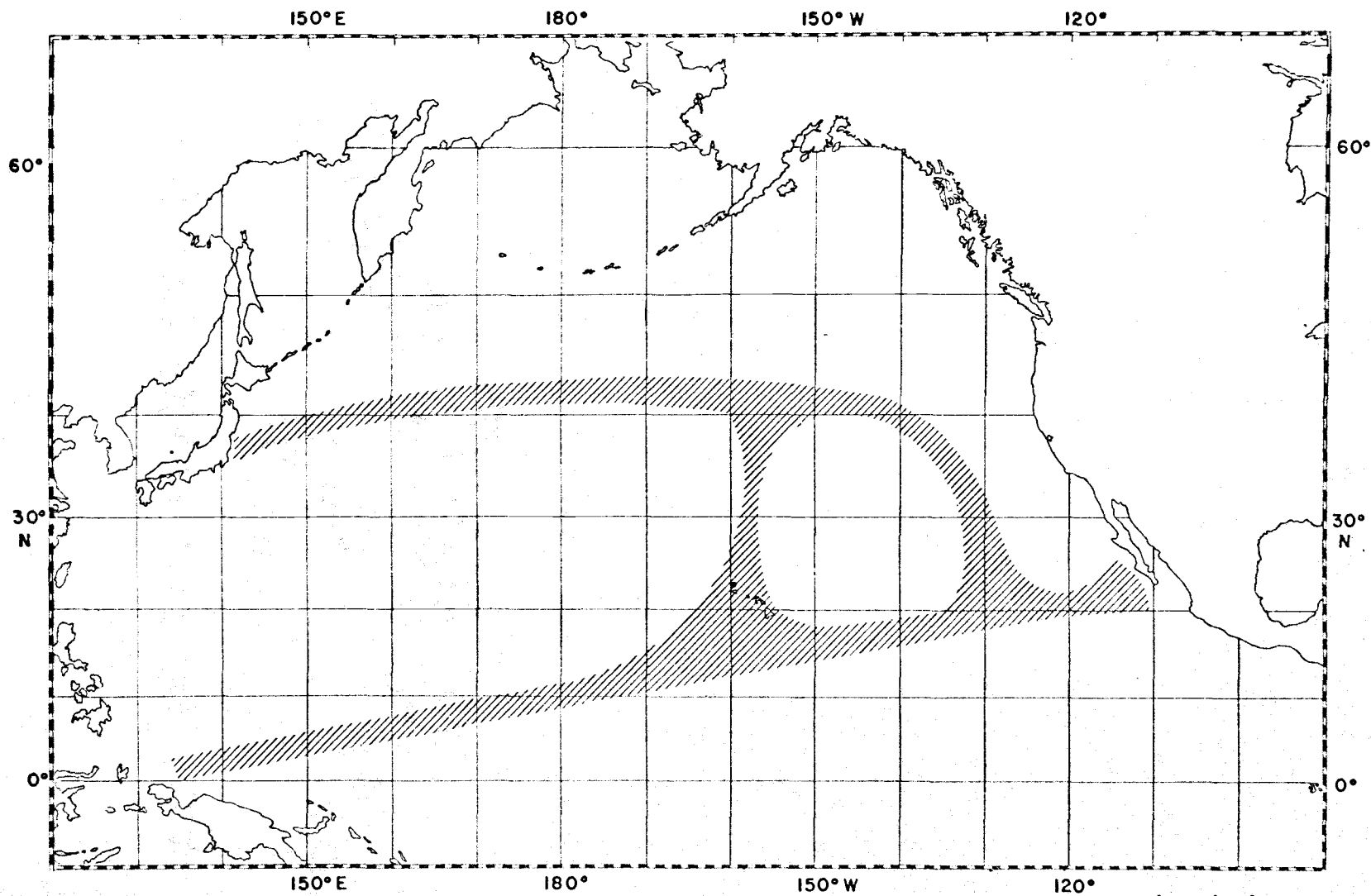


Figure 87. Distribution of *Notostomous perlatus* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

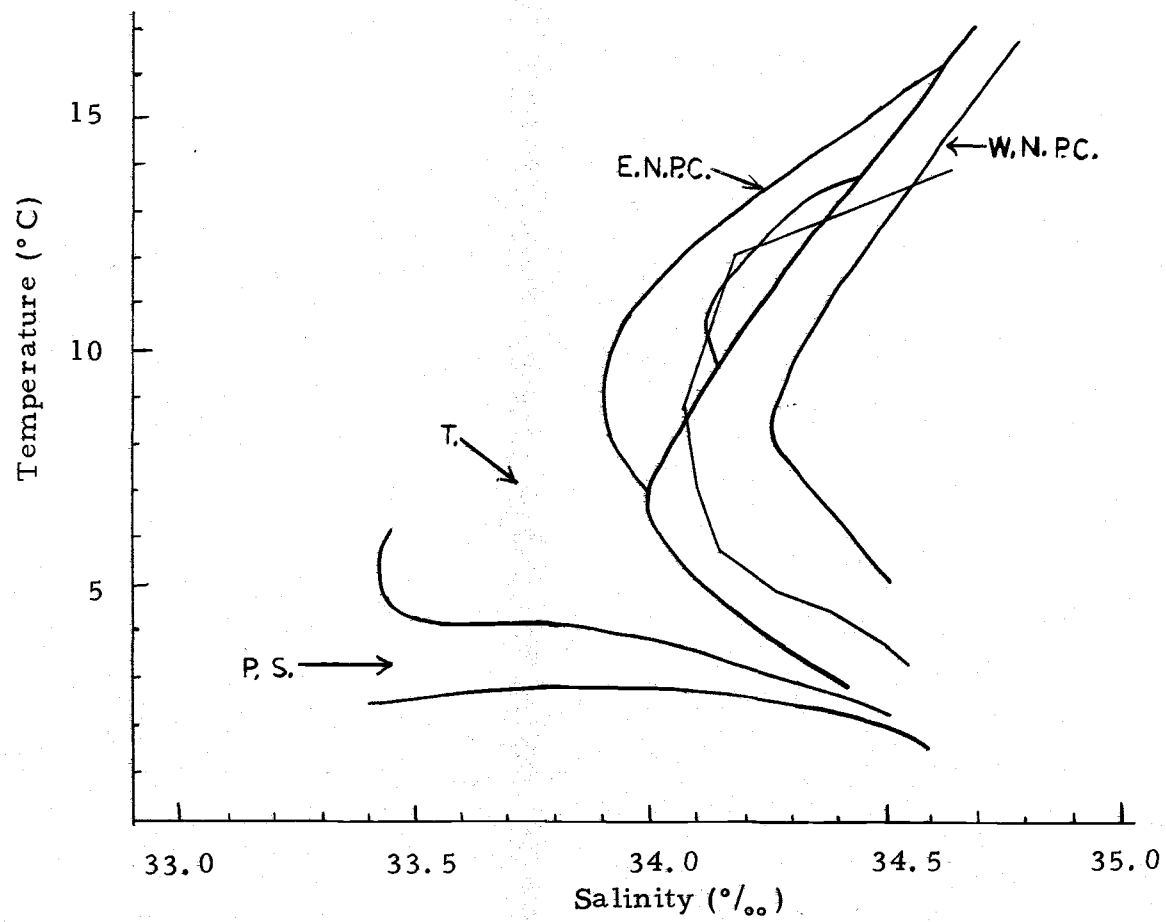


Figure 88. Temperature-salinity capture diagram for Notostomous perlatus. Water masses as in Figure 6.

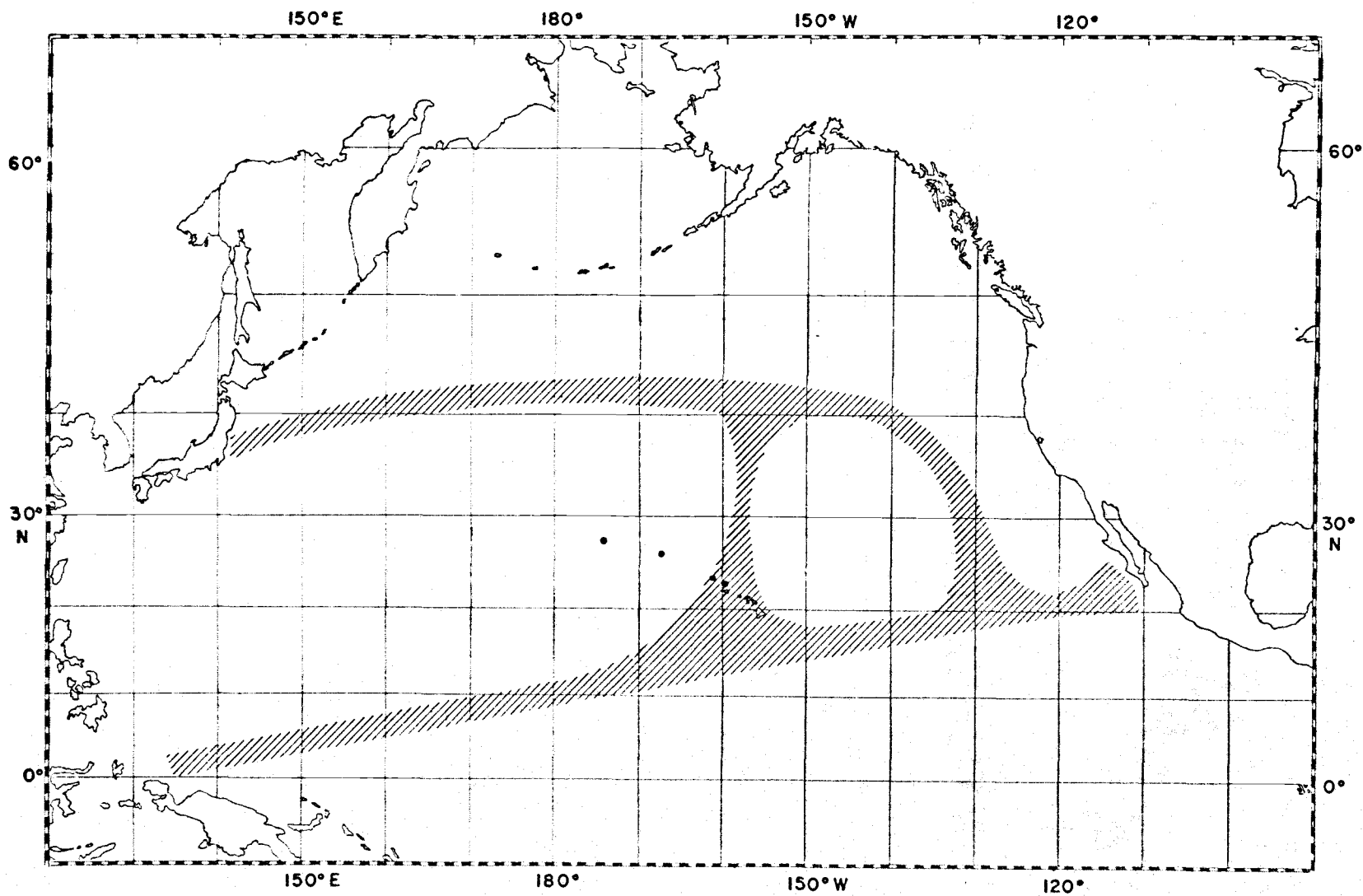


Figure 89. Distribution of *Systellaspis debilis* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

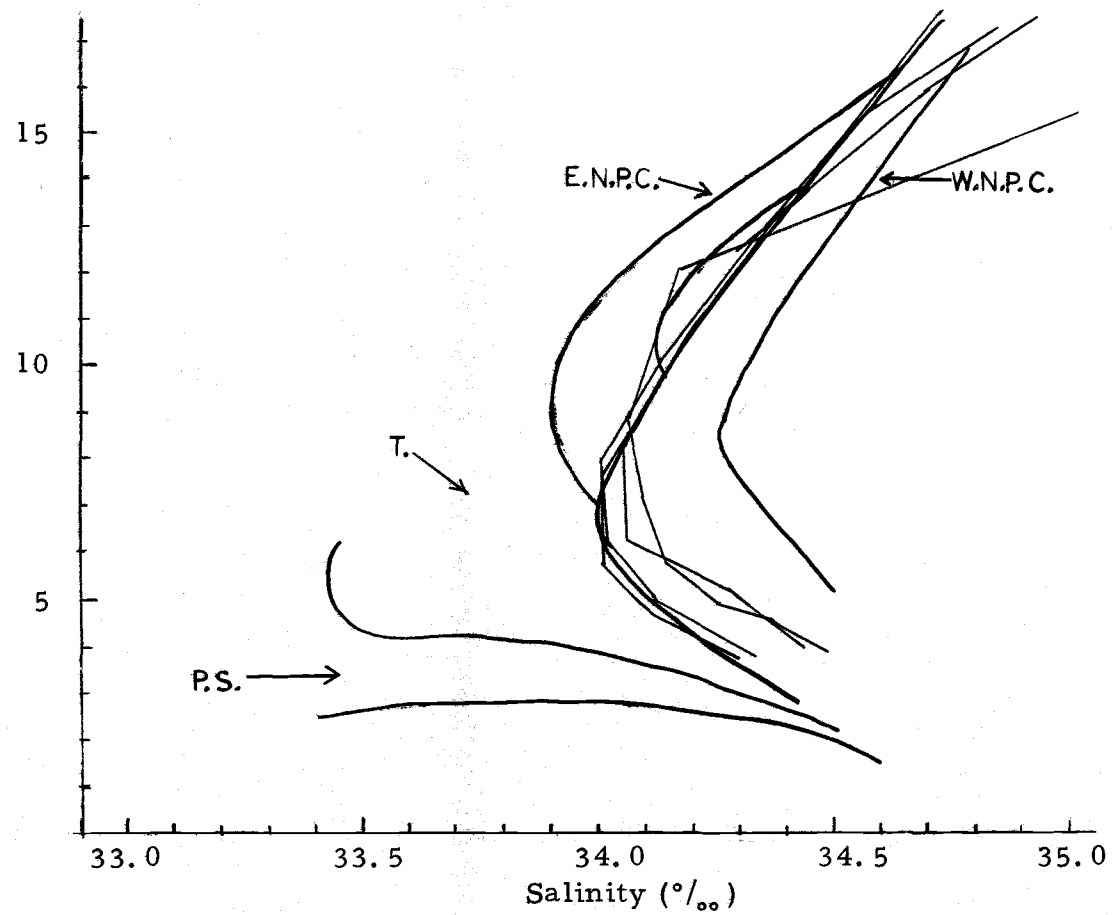


Figure 90. Temperature-salinity capture diagram for Systellaspis debilis. Water masses as in Figure 6.

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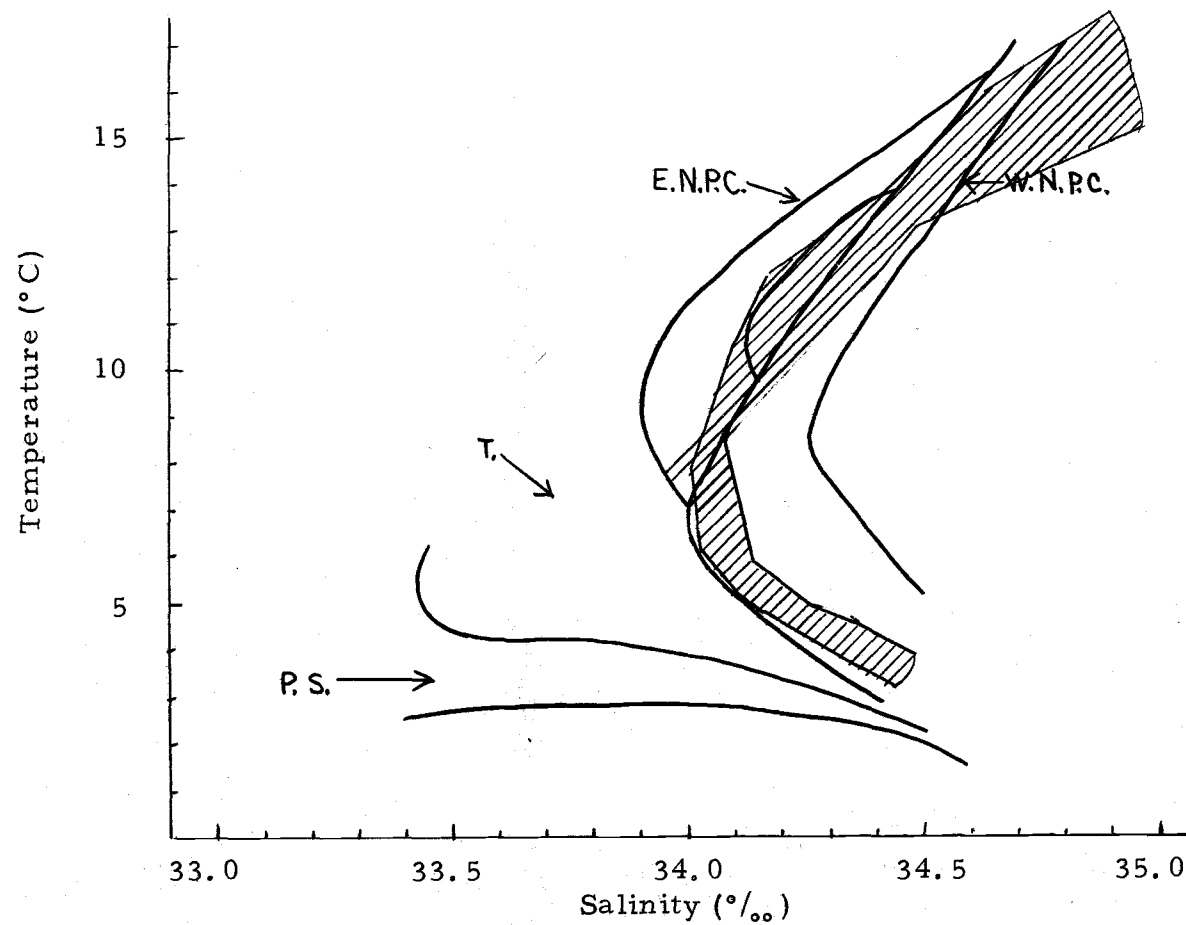


Figure 92. Temperature-salinity capture diagram for Oplophorus spinicauda. Water masses as in Figure 6.

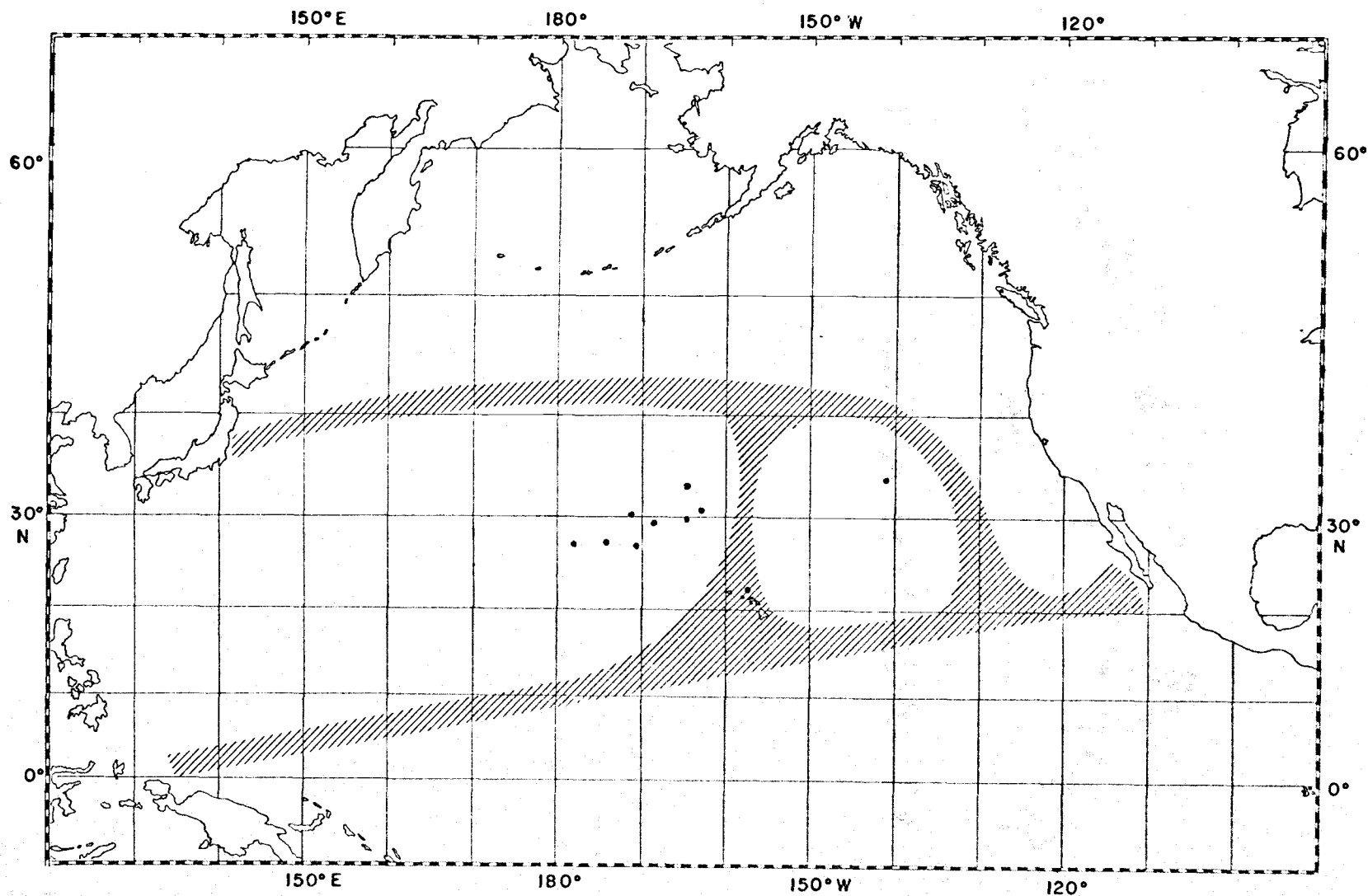


Figure 93. Distribution of *Parapandalus richardi* in the North Pacific Ocean. The hatched bands delimit the relevant water masses (see Figure 5).

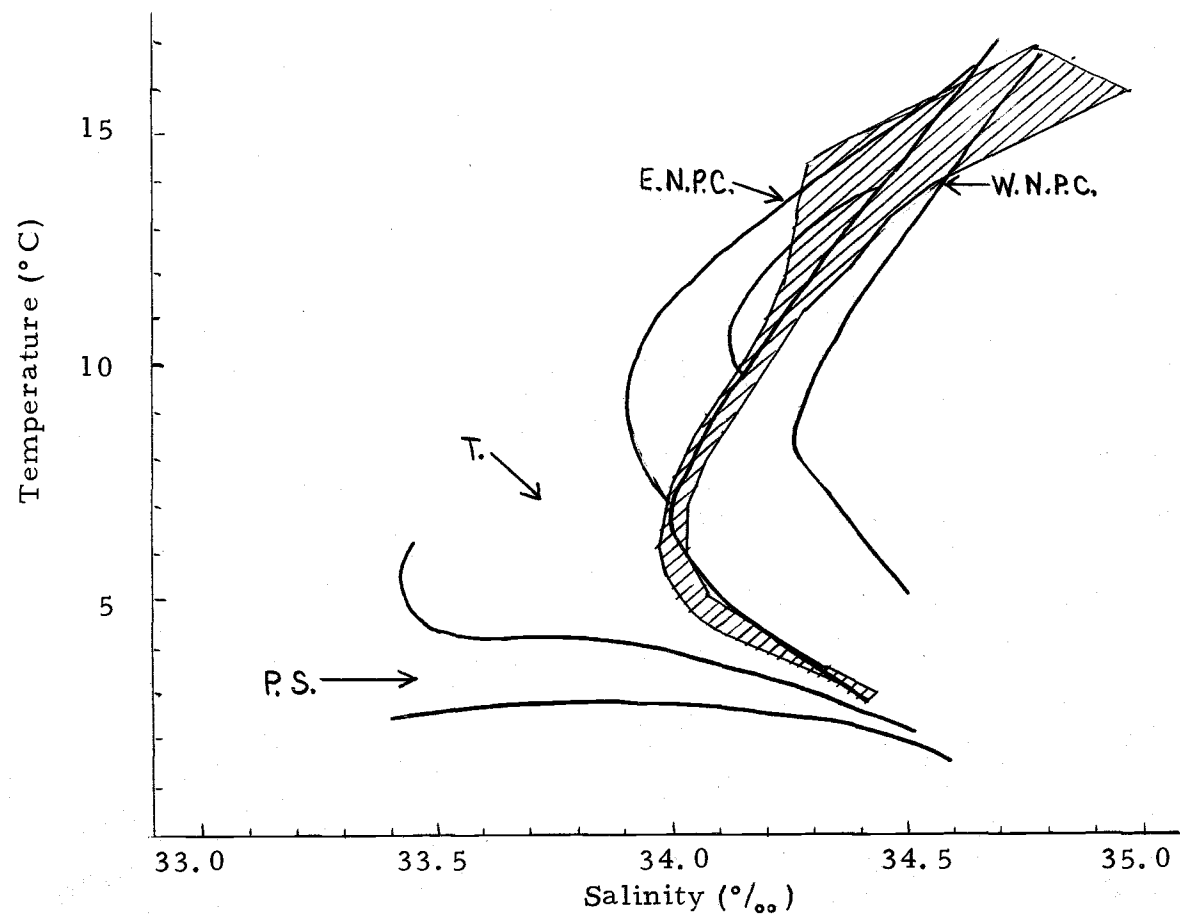


Figure 94. Temperature-salinity capture diagram for Parapandalus richardi. Water masses as in Figure 6.