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**Stock structure and population biology of the Peruvian
jack mackerel, *Trachurus symmetricus murphyi***

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CONTENTS

	Page
Executive summary	5
1. Introduction	6
2. Objectives and scope of the study	8
3. South Pacific stock structure (Objective 1)	8
3.1 Methods	8
3.2 Results	9
3.2.1 Morphology: morphometrics and meristics	10
3.2.2 Parasites	12
3.2.3 Tagging and marking	13
3.2.4 Population genetics	13
3.2.5 Taxonomic papers using biochemical genetic methods	14
3.3 Discussion	14
3.3.1 Morphology	15
3.3.2 Parasites	15
3.3.3 Morphology and genetics	17
3.3.4 Other studies	17
4. Population biology (Objective 2).....	18
4.1 Methods	18
4.1.1 Literature search	18
4.1.2 Length frequencies	18
4.1.3 Sex ratios	19
4.1.4 Examination of fish and plankton collections	19
4.1.5 Reproductive condition and sea surface temperature	19
4.1.6 Distribution of prey species	20
4.1.7 Development of eggs and larvae and their transport in ocean currents	20
4.1.8 Approximating juvenile size at age	20
4.2 Results	20
4.2.1 Literature search	20
Age and growth	21
Reproduction	22
Feeding	25
General papers	30
4.2.2 Length frequencies	34
4.2.3 Sex ratios	35
4.2.4 Examination of fish and plankton collections	35
4.2.5 Reproductive condition and sea surface temperature	35
4.2.6 Distribution of prey species	32
Adult feeding	32
Larval feeding	32
Prey species in New Zealand waters	32
4.2.6 Development of eggs and larvae and their transport in ocean currents	37
4.2.7 Approximating juvenile size at age	38
4.3 Discussion.....	39
4.3.1 Biological features of <i>Trachurus symmetricus murphyi</i>	39
4.3.2 Reproductive condition, sea surface temperature, and prey distributions	39
4.3.3 Fish size: fish collections and length frequencies	40
4.3.4 Sex ratios	41
4.3.5 Summary: Suitability of New Zealand waters for <i>T. s. murphyi</i>	42
5. Conclusions	42
6. Acknowledgments	43
7. References	43

Appendix 1: A list of prey species from gut contents of *Trachurus symmetricus murphyi* sampled in Peruvian waters

Appendix 2: Page numbers of references summarised in this report

EXECUTIVE SUMMARY

Taylor, P.R. (2002). Stock structure and population biology of the Peruvian jack mackerel, *Trachurus symmetricus murphyi*.

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Online literature databases were searched for references on *Trachurus symmetricus*, *T. s. murphyi*, and *T. murphyi*. References were sorted into categories based on methods used in current stock separation research and relevant data were extracted to test the hypothesis of a single trans-oceanic South Pacific stock against that of independent stocks in the southeast and southwest Pacific Ocean.

One morphological study and information on parasite distributions provided evidence for the independent stock hypothesis, but a mitochondrial DNA analysis found no difference between New Zealand and Chilean specimens. The region of DNA tested was conservative, however, and it would be more appropriate to use a faster evolving region in the mitochondrial genome to detect population subdivision.

Genetic studies based on allozymes provided evidence for more than one self-sustaining stock in South American waters, which reflected the results of previous studies based on general biological features that had suggested separate populations in Peru and Chile. The allozyme studies indicated both spatial and temporal variability.

A further allozyme study showed no difference between the Californian and South American jack mackerels, offering evidence that refutes the separation of *T. s. murphyi* from *T. symmetricus*, although the present study supports the continued use of the name "*T. s. murphyi*" because of its wide usage for the South Pacific population. Contrary to the author's conclusion, an examination of the data presented in the same allozyme study shows genetic differences between the small samples, north and south of the Equator.

The literature search provided a wide range of information on the biology of *T. symmetricus* which was used to examine the hypothesis that *T. s. murphyi* has established a self-sustaining stock in New Zealand waters. Based on comparisons of sea surface temperature, distributions of the most preferred prey items of *T. s. murphyi*, and simulations of the effect of coastal transport mechanisms on eggs, larvae, and juveniles, New Zealand waters were shown to be conducive to stock establishment. Spawning adults have been recorded from a number of different areas.

Small juveniles (9.15–12.15 cm) of *T. s. murphyi* from the Te Papa Tongarewa Museum of New Zealand collection had been taken in the South Taranaki Bight. In the East Cape-Mahia area small juveniles (7–28 cm) were taken in the three fishing years 1992–93, 1993–94, and 1995–96, suggesting a possible nursery area in the vicinity. Length frequency distributions from trawl surveys on the east coast of the North Island south of East Cape provided the first evidence of cohorts of young fish in the New Zealand *T. s. murphyi* population from successful local spawning. Small fish are also apparent in length frequency distributions from observer data collected within the west coast fishery.

Sex ratios for a number of years and areas in New Zealand waters showed a predominance (60–70%) of males in most samples. Because of the consistency of these estimates, and their widespread nature in time and space, it is suggested that they may not be related to a particular phase in the reproductive cycle as would normally be expected, but that they are the result of high levels of mortality in females under extreme conditions experienced in oceanic waters.

It is concluded that the New Zealand population of *T. s. murphyi* now consists mostly of individuals that have invaded New Zealand waters, with a small but increasing proportion that are the result of local spawning.

1. INTRODUCTION

Three species of jack mackerel occur in New Zealand waters — the two “New Zealand species”, *Trachurus declivis* and *T. novaezelandiae*, first documented as both being present here by Stephenson & Robertson (1977), and the species known as the Chilean or Peruvian jack mackerel, *T. symmetricus murphyi*, first identified in New Zealand waters during 1987 by Kawahara et al. (1988). The invasion by *T. s. murphyi* in the early to mid 1980s has resulted in a large apparent increase in the jack mackerel biomass, but it is unknown how permanent the presence of this species might be.

In the early 1970s, *T. s. murphyi* was believed to occur only in waters off the west coast of South America (Elizarov et al. 1993). In 1978, Russian fishers made the first commercially significant discovery of this species beyond Peru's fishing ground, within the ocean upwelling over the Peru-Chile counter current. Since then, *T. s. murphyi* has been found in oceanic pelagic water from the Equator to 52 °S, and from Chile to Australia.

Since its appearance in New Zealand waters, *T. s. murphyi* has spread throughout the Exclusive Economic Zone (EEZ), and information from the commercial catch, aerial sightings data, and research voyages indicate that it is now distributed all around New Zealand and is the dominant jack mackerel species in some areas. Whether it has established a reproductive stock is unknown.

Data from research and commercial tows (Figure 1) suggest that *T. s. murphyi* first occurred around the Chatham Islands in 1984–85, and then moved westward. There were small numbers on the west coast of the North Island, the east coast of the South Island from Kaikoura to Mernoo Bank, and the Southland shelf in 1985–86. There was an increase on the west coast of the South Island in the following year, and a gradual increase in all these areas thereafter. The extensive distribution shown in Figure 2 is based on current information from bottom trawl shots in the trawl survey and observer databases.

The implications of the invasion of *T. s. murphyi* are unknown. Concerns have been raised in stock assessment working group meetings about the potential for this species to outcompete endemic species like snapper, kahawai, and the two New Zealand jack mackerel species, but no information is available to determine this. Considering that the management regime is based on a single grouping for jack mackerel species, and that the purse-seine fishery in JMA 1 (Figure 3) has almost exclusively targeted the smaller *T. novaezelandiae* since it began in the mid 1970s (Peter Reid, Tauranga purse-seine skipper, pers. comm.), any increased competition on the New Zealand species of jack mackerel may impart greater pressure on *T. novaezelandiae*, because of the unequal fishing pressure in the past.

Two working hypotheses have been formulated to describe the relationship between *T. s. murphyi* in New Zealand waters and those occurring in the remainder of the South Pacific. The first states that the New Zealand fish are a separate stock established by those migrating from South America, and the second that they are part of a single, extensive trans-Pacific stock. No work has been done to test these hypotheses.

It is possible that a reproductive stock of *T. s. murphyi* has become established in New Zealand waters, especially if one considers the similarity in latitude between northern New Zealand and known spawning grounds in the central South Pacific (Elizarov et al. 1993, Evseenko 1987) (Figure 4). The discovery of specimens of juvenile *T. s. murphyi* (75–100 mm) in the fish collection of the Museum of New Zealand (15 individuals collected in 1995 in January in the South Taranaki Bight; one individual collected in 1988 off Mahia Peninsula) by NIWA staff suggests that at least some local spawning has been successful. It is difficult to understand how individuals of this size could reach this locality from areas of known spawning in the South Pacific against the eastward flowing currents.

Generally, however, juveniles have been difficult to find. For example, *T. s. murphyi* juveniles have been absent from the JMA 1 purse-seine fishery (Figure 5) where the weight of jack mackerel ranges from about 200 g to about 2.5 kg. Most of the small fish (200–600 g) are *T. novaezelandiae* (Figure 6), but occasionally a landing occurs in which *T. declivis* comprises a considerable portion (Figure 7) of this size class. *T. s. murphyi*, however, has never been found as part of the fraction. NIWA has also monitored other possible sources of both larval and juvenile specimens (gut contents of apex predators from tuna troll and longline fisheries, jack mackerel catches from the Northland baitfishery) but none have been found.

Distributions of the positions of bottom trawl shots where immature jack mackerel have been taken have been summarised in an atlas of New Zealand marine fish species (Hurst et al. 2000). The dramatic difference between the number of shots containing *T. s. murphyi* (Figure 8) and the number containing *T. declivis* and *T. novaezelandiae* (Figures 9 and 10) clearly illustrates how seldom they have been found.

In the present context, 'established' means that a stock has formed which is reproductively viable and is therefore self sustaining. The absence of *T. s. murphyi* juveniles from the purse-seine fishery suggests that if there is successful spawning, then their distribution is different from that of *T. declivis* and *T. novaezelandiae*. There are few clues suggesting where they might be found, but recent studies related to features of the east coast circulation and larval retention of the phyllosoma stage of the red rock lobster (*Jasus edwardsii*) (Booth 1994, Booth & Forman 1995, Booth & Stewart 1991, Chiswell & Roemmich 1998, Chiswell & Booth 1999) provide one possible transport mechanism that is worthy of closer examination.

Information is available on the various habitats that *T. s. murphyi* occupies during its life history. In South American waters, Serra (1991) showed that adult *T. s. murphyi* migrate westward off the shelf to spawn, and that the resulting larvae are adapted to an oceanic habitat. The larvae are moved eastward in prevailing currents, onto the shelf, and recruit to the fishery at about age 3 or 4 (Serra 1991).

New Zealand waters present some similarities, but the overall pattern has certain key variations. For adults spawning on the shelf (Table 1), the net water movement is eastward (Heath 1985, Roemmich & Sutton 1998, Stanton et al. 1997), as it is in South America, but represents a transport mechanism that would move eggs and larvae offshore, away from the shelf into oceanic water. The benefit of this sequence is that it would ensure that *T. s. murphyi* larvae reach their preferred oceanic habitat. It may also mean that they become entrained within gyres off the east coast, in much the same way as has been hypothesised for the rock lobster phyllosoma larvae (Booth 1994, Booth & Forman 1995, Booth & Stewart 1991, Chiswell & Roemmich 1998, Chiswell & Booth 1999). For jack mackerel juveniles, which are undoubtedly stronger swimmers than phyllosoma, this may be indirect, resulting from entrainment of appropriate prey species.

The flaw in this hypothesis is that simulations presented by Chiswell & Roemmich (1998) predict a low probability of phyllosoma larvae remaining in the East Coast Gyre system for more than 1 year. The age of recruited individuals of *T. s. murphyi* of about 38 cm is unknown, but it should be similar to the 3–5 years estimated for South American *T. s. murphyi*, and this may be much older than fish would naturally remain within the gyre system. An alternative is that juveniles continue to move east, and Chiswell & Roemmich (1998) discussed the relatively high probability that transported larvae miss entrainment and move to the east well beyond the influence of the gyre system.

A preliminary analysis of length data from fisheries sources has shown that mostly larger fish are present in New Zealand waters. This type of occurrence is usually interpreted as the species being close to the limit of its range (Elizarov et al., 1993). In the present context, however, the situation may be a little more complex. The range of sizes in the New Zealand fishery is quite wide, and it has been suggested that the frequency of large fish may have decreased recently (P. Horn, NIWA, pers. comm.) compared with the frequency during early years of the invasion, a suggestion that is supported to some extent by the work of Elizarov et al. (1993). Such a change in the length data may be indicative of a change in the overall stock

structure, and coincide with the establishment of the stock in the southwest Pacific Ocean (SWPO) (see Fig. 4) described by Kalchugin (1992), or the establishment of a stock within New Zealand waters and the adjacent ocean.

2. OBJECTIVES AND SCOPE OF THE STUDY

Work for this study was funded by MFish as Project JMA9802, "Stock structure and population biology of the Peruvian jack mackerel, *Trachurus murphyi*", which was formulated before the specific name *Trachurus symmetricus murphyi* had been adopted by MFish. This research was directed at obtaining information on the stock structure of *T. s. murphyi* in both New Zealand waters and the greater South Pacific Ocean.

MFish formulated two objectives to cover the two geographical areas. The first was to determine the stock structure of Peruvian jack mackerel in the South Pacific Ocean from existing data which "will have important implications for the management of this species". The second was to determine size composition, sex ratio, and reproductive condition of Peruvian jack mackerel in New Zealand waters from biological data collected by scientific observers, trawl surveys, and other data sources to provide information that "may assist understanding the degree to which *T. s. murphyi* is established in New Zealand waters".

The information presented in this report is aimed at satisfying the objectives of the study in terms of the underlying rationale. Discussion is presented that is specific to each objective, with a summary of the suitability of the New Zealand ecosystem for the establishment of an independent breeding population of *T. s. murphyi*. The conclusions (Section 5) provides an overview of the New Zealand situation within the wider geographical context of the Pacific Ocean.

3. SOUTH PACIFIC STOCK STRUCTURE (OBJECTIVE 1)

3.1 Methods

The stock structure of *T. s. murphyi* within the South Pacific was investigated by summarising and assessing information from the literature and making comparisons of apparently independent groups of *T. s. murphyi* according to standard stock discrimination methodology. A number of sources of existing information are available, but the widest coverage is within the primary literature. The approach to extracting useful and relevant information from this source was to review all papers for their content and sort relevant data according to the broad headings of stock discrimination techniques for marine fishes summarised by Smith (1997) (i.e., morphology and meristics, chemistry, parasites, distribution and biology, tagging and marking, and genetics). The approach was focused on drawing together as much information as possible and assessing it to test the hypothesis that more than one reproductive stock of *T. s. murphyi* exists in the South Pacific Ocean.

A two step search was made of online databases: the search phrases "*Trachurus symmetricus murphyi*" and "jack mackerel" were used to identify databases with relevant information, and summary information for a unique set of references was then extracted using "*Trachurus symmetricus murphyi*" and "jack mackerel Peruvian or Chilean". A similar approach was taken to identify references containing information on "*Trachurus murphyi*".

Copies of these references, and those that were unobtainable from this source were obtained and reference lists were examined for any relevant papers that may have been missed in the original search, and these were then obtained from the NIWA collection or through interloans.

Papers were sorted at two levels: by the area of the South Pacific from which their data were collected (i.e., mostly west or east, though there was a north-south component on the coast of South America), and into the stock discrimination categories of Smith (1997). Data recorded in the category "distribution and biology" are more indicative of variations in local conditions (Peter Smith pers. comm.), so only those studies that make specific statements about stock structure (e.g., information on feeding and spawning centres) were considered further for this part of the study. Papers in foreign languages were examined initially using the online translator at <http://babelfish.altavista.com/cgi-bin/translate?> to determine their content and importance in the present context. Where there was difficulty in translation of a paper that contained useful information, the New Zealand Translation Centre Limited was consulted.

Papers were appraised for their ability to provide either raw data for statistically assessing population differences between areas, based on their particular stock discrimination category, or stand-alone information on differences shown to exist between areas in their results. Although most studies from the morphology category, and many from the genetics category, aimed to compare samples from different areas, the aim of the present study was to re-use their data to investigate differences between the western and eastern South Pacific. The prerequisite for such comparisons was that the data were comparable, either in fish size and measuring method for morphology data, or in method and sample size for the genetics data.

Where allozyme data were available, and in particular the observed numbers of genotypes, the χ^2 test was used to test for differences in allele frequencies between samples. Frequencies, or proportions, of the two alleles in each sample were estimated by counting the number of observed alleles. Each fish has two alleles expressed as either homozygotes with two identical alleles (e.g., BB or CC) or heterozygotes with two dissimilar alleles (e.g., BC). Allele frequencies are estimated as the sum of the B and C alleles, divided by twice the number of fish.

During 1997, Dr Aquiles Sepulveda of the Instituto de Investigacion Pesquera, Talcahuano, Chile, and Dr Ricardo Galleguillos of the Universidad de Concepcion, Chile, compared mitochondrial DNA from samples of *T. s. murphyi* taken from New Zealand and South American waters to determine the similarity in genetic composition of the two "populations". The results are still in draft form and have been provided for use in the present study by Dr Sepulveda.

3.2 Results

About 190 references were identified from the literature search, subsequent examination of reference lists, and requests for relevant references made of contacts in Chile and Peru. Not all these papers were available through library interloans, although difficult requests were sometimes met by contacts in South America or Russia. Sometimes copies of the papers proved that their information was inappropriate for the study, or unsound, or that it was presented elsewhere in a more acceptable form with more acceptable statistical analyses.

In most of the following categories the summaries cover all the papers received, but in the parasites category, papers that provide simple records of infestations are summarised in tabular form — a full summary is presented only for the single paper providing information in the context of stock separation. Because papers assigned to the category "Distribution and biology" have little use in determining stock structure, they are summarised under "Literature search" in the results section of Objective 2. A page index by author of the papers summarised in the literature search is presented in Appendix 2.

3.2.1 Morphology: morphometrics and meristics

Twelve papers containing morphometric and/or meristic data were identified.

Bailey (1989)

This study was based on measurements of juvenile *T. s. murphyi* taken from the Subtropical Convergence Zone of the central South Pacific. The 40 specimens were all small juveniles, measuring 46–83 mm standard length (SL). Measurements of 9 morphometric characters as percentages of the SL, 6 as percentages of the head length (HL), and counts of 10 meristic characters are presented.

Hildebrand (1946)

This paper contains a description with mean measurements of *T. s. murphyi* based on seven specimens (485–497 mm SL) from Callao and San Lorenzo Island, Peru. The sample size is too small for these data to be used in statistical analysis.

Kalchugin (1992)

This paper presents morphometric and meristic data from several regions of the South Pacific which have potential for use in further comparisons with data from other studies. However, sample sizes have been omitted, and it is not clear which body length measurement (FL or TL) has been used to express the morphometric percentages.

The study shows differences between specimens of *T. s. murphyi* from the SWPO and eastern South Pacific (SEPO) (see Figure 4), in 8 out of 14 morphological characters and 2 out of 7 meristic characters. Based on this analysis, the author concludes that there is an independent population of *T. s. murphyi* in the SWPO, and describes a spawning season between August and March for this population, suggesting that it begins in the west and gradually moves towards the east, covering a vast reproductive zone. The timing of this spawning is similar to that described by several authors for the eastern population (Abramov & Kotlyar 1980, Alekseeva & Alekseev 1984, Andrianov 1985).

Kawahara et al. (1988)/Berry & Cohen (1974)

This paper contains a description with mean measurements of *T. s. murphyi* based on 10 specimens (480–556 SL) caught with bottom trawl nets from southern and eastern New Zealand waters. A high level of agreement was found with data from specimens from Chile by Berry & Cohen (1974), suggesting a single South Pacific population. However, the sample sizes of both studies are too small for the data to be used in a statistical analysis.

Kotlyar (1976)

This paper presents extensive morphometric and meristic data collected from five areas off the coast of Peru, with sample sizes of 50 fish in each area. Sexual dimorphism is not evident from the data, so data from both sexes are pooled. Statistical tests (Anon. 1974) were used to examine differences between samples, with comparisons limited to samples containing similar size classes.

Comparisons of meristic data between areas showed statistically significant differences in one to three characters for all but one comparison; the greatest number (three characters) came from "the most widely separated sampling sites". Morphological data are presented as percentages of total length (TL), fork length (FL), and HL; differences were found in only one comparison of two sites, where three characters were statistically different.

These data have the potential to be used in a t-test for comparisons of fish from the western and eastern South Pacific. In addition to mean measurements and counts, both sample size and standard deviation are given.

Machii et al. (1990)

This paper examines body shape and size to determine the optimum mesh size of purse-seine nets, presumably in designing nets to catch *T. s. murphyi*, though this is not stated. Eight body measurements were recorded from specimens sampled from the purse-seine catch off Callao, Peru, between November 1979 and October 1980, including fork length, maximum girth, operculum girth, maximum height, operculum height, maximum breadth, operculum breadth, and weight. These are different characters from those recorded in other studies and are therefore unusable in comparisons, except for maximum height, which might be the same as "body depth" recorded elsewhere, but as this is unclear, none of the data from this paper are used further.

Roedel & Fitch (1952)

This paper contains limited morphometric and meristic data from two specimens of *T. s. murphyi*, making the sample size too small for these data to be used in a statistical analysis.

Salem (1995)

This study uses morphometric and meristic measurements and counts to examine differences between 15 species of *Trachurus*, including *T. s. symmetricus* and *T. s. murphyi*. A total of 26 characters were used, with sample sizes of 156 fish for *T. s. symmetricus* and 46 for *T. s. murphyi*. A key is presented based on results from the study; *T. s. symmetricus* and *T. s. murphyi* are treated as separate species.

The data cannot be used in further statistical analyses — the origin of specimens is unclear, with ranges given instead of means in a number of cases, and standard deviations are omitted.

Shabonev (1980)

This paper presents limited data (6 characters) on 12 *Trachurus* species, but does not include sample sizes, standard deviations, or origin of the specimens. The data cannot be used in the present analysis.

The paper contains a useful interpretation of the origins of *Trachurus* species. It is a good review of the systematic position, taxonomy, and phylogenetic relationships of the members of the genus *Trachurus*, and proposes a classification based on groupings of species related by common origins, and by similarity of morphological and ecological characteristics. A summary of the four groups is as follows.

Mediterranean	Picturatus	Trachurus	Aberrant form
<i>T. trecae</i>	<i>T. symmetricus</i>	<i>T. delagoa</i>	<i>T. declivis</i>
<i>T. lathami</i>	<i>T. murphyi</i>	<i>T. novaezelandiae</i>	
<i>T. indicus</i>	<i>T. picturatus</i>	<i>T. japonicus</i>	
<i>T. mediterraneus</i>		<i>T. trachurus</i>	

The Mediterranean group should be regarded as the most primitive in the genus, the Picturatus group as the most advanced, and the Trachurus group as an independent line containing both primitive and advanced forms. The placement of *T. declivis* in a separate group is based on it displaying characteristics of both the Picturatus (a large number of lateral line scutes and a well developed trunk commissure) and Trachurus (large scutes, a deep body, and relatively few fin rays in the dorsal and anal fins) groups.

Members of the Mediterranean group are coastal species and are most similar morpho-ecologically to the ancestral form akin to the genus *Selar* postulated by Alejev (1957a, 1957b).

Shabonev & Kotlyar (1979)

A total of 250 *T. s. murphyi* (23–48 cm) from the Peruvian shelf were used to derive measurements of 14 morphological and counts of 8 meristic characters. Data were not separated by sex because sexual dimorphism is not observed in *Trachurus* species (Alejev 1957a, Kotlyar 1976). These data are almost certainly the same as those presented by Kotlyar (1976).

The objective of the study was to compare, morphologically, *T. s. murphyi* with the Atlantic species *T. picturatus picturatus*, and similar data are presented for the latter.

Suda et al. (1995)

This study used 279 specimens of *T. s. murphyi* off central Peru (at about 12 °S) to derive morphological and meristic data, but none are presented.

Summary

The use of data from these studies to compare and contrast specimens from different areas is hampered by their not being comparable. Most of the papers either omitted important explanatory data or used sample sizes that were too small to be of use. Only the datasets from Bailey (1989) and Kotlyar (1976) were complete, but difficulties arose from the former recording data from juveniles and the latter from adults.

The Russian authors are usually not specific about their statistical methodology. They often refer to the Anon. (1974) manual as the method they used, although sometimes they briefly discuss whether there has been a correlation between two datasets, and a correlation coefficient is presented.

3.2.2 Parasites

Nine papers were identified as containing information on parasites in *T. s. murphyi*. Six of these simply reported the presence of the following parasites.

	Species	Author	Area
Copepoda	<i>Caligus bonito</i>	Duran (1980)	Peruvian waters
	<i>Lernanthropus</i> sp.	Duran & Oliva (1983)	Peruvian waters
	<i>L. trachuri</i>	Romero & Kuroki (1985)	Northern Chile
Cestoda	<i>Tenticularia coryphaena</i>	Soto & Carvajal (1979)	Northern Chile
	<i>Nybelinia</i> sp.	Soto & Carvajal (1979)	Northern Chile
Myxosporidia	<i>Ceratomyxa meglitschi</i>	Kovaleva & Gaevskaya (1983)	Southeast Pacific*
Nematoda	<i>Anisakis</i> sp.	George-Nascimento et al. (1983)	Central Chile

*Oceanic waters

The following papers provided summaries of their results that were more relevant to stock structure.

Aldana et al. (1995)

This reference was available only as an abstract from the Cambridge Scientific Abstracts database.

The use of parasitic isopod species of the genus *Ceratothoa* as population indicators of the horse mackerel *Trachurus symmetricus murphyi* off Chile was assessed. Eight hundred and one *Ceratothoa* specimens were collected from the oral cavity and gill chamber of 900 *T. s. murphyi* individuals sampled monthly in northern and central Chile from January to October 1990. Another 793 specimens of isopods were collected from 289 individuals of *T. s. murphyi* sampled from July to October of the same year from northern/central Chile. Two isopod species, *Ceratothoa gaudichaudii* (Milne-Edwards, 1840) and *Ceratothoa trigonocephala* (Leach, 1818) were found in similar proportions in all localities.

Avdeyev (1992)

This study postulates the presence of the parasitic isopod *Ceratothoa trigonocephala* in *T. s. murphyi* from the SEPO as evidence of a transoceanic migration by the host from New Zealand waters. The absence of the Southeastern Pacific species *C. gaudichaudii* in *T. s. murphyi* from New Zealand waters is concluded from this study and several others that were cited, and "possible causes of such a pattern of distribution for *C. gaudichaudii* may be restriction of its reproduction to spawning

aggregations of the shelf group [in contrast to an oceanic group] of *murphyi* and subsequent duration of life that is insufficient to complete a transoceanic extension to the west as a parasite of the oceanic group”.

Oliva (1994)

This reference was available only as an abstract from the Cambridge Scientific Abstracts database.

To develop an understanding of the parasite fauna of *Trachurus symmetricus murphyi*, which is poorly known, 78 specimens of *T. s. murphyi* were obtained, with gill nets from Caleta Constitucion (23 ° 24 'S 70 ° 36 'W), during 1986–87. The specimens ranged in size between 25.6 and 47.8 cm (ages 2+ to 5+). The analysis showed that the Chilean jack mackerel is parasitised by at least nine species: *Anisakis* sp. (Nematoda), *Scolex pleuronectis*, *Tentacularia coryphaenae*, and *Nybelinia* sp. (Eucestoda), *Corynosoma australis* (Acanthocephala), an unidentified Opecoelidae (Digenea), *Caligus* sp. and *Lernanthropus trachuri* (Copepoda), and *Ceratothoa gaudichaudi* (Isopoda). The most noticeable characteristic of this parasite fauna is the absence of some parasite groups which have been found in other species of *Trachurus*, such as monogeneans, adult digeneans, and adult acanthocephalans.

3.2.3. Tagging and marking

Gutiérrez (1986)

Between October 1982 and March 1984, 16 082 jack mackerel were tagged with nickel-plated internal tags: 81 tags were recovered. Although the author concludes that there are no latitudinal migrations, the tag return rate is too low at 0.5% to allow a conclusion to be made. One possibility is that tagged fish moved out of the recovery area.

3.2.4. Population genetics

Alay et al. (1982)

This paper reports on electrophoretic analysis of two common proteins (lactate and malate dehydrogenases — LDH and MDH) in carp (*Cyprinus carpio*) and jack mackerel (*T. s. murphyi*), but no population data on the jack mackerel are presented.

Koval (1988a)

This paper examines the geographical variability of the allozyme marker EST-1.

Samples were collected between 7° and 50 °S and tested for one allozyme marker. The author claims that there is a clinal variation south of 30 °S, but presents no statistical analyses to support this conclusion. The tabulated summary data suggest only weak evidence for a cline with Esterase B allele frequencies of 0.59, 0.60, and 0.64.

Koval (1996)

This paper examines allele frequencies at one polymorphic locus.

Esterase allele frequencies were compared north and south of 30 °S over 5 years of sampling. The author concluded that there are differences between samples from the northern and southern areas at the Est-1 locus, but provided no statistical analyses in support. An analysis of the esterase genotype frequencies is presented in Table 2 which shows that only one of the five years of sample pairs show a significant difference between northern and southern samples. The difference between the northern and southern samples in 1982–83 is unlikely to be due to sampling error as samples sizes were over 1000 fish. Clearly there is not a simple spatial regional difference, and the observed genetic

differences may be produced by year class differences and/or north-south movement of stocks along the coast.

Gonzalez et al. (1996)

Analysis of 15 allozyme markers in five populations, each sampled twice in winter and spring, showed no differentiation. The authors do not present raw data, but the genetic distance dendrogram indicates that the largest genetic distances consistently occur between spring and winter samples, indicating the presence of two seasonal groups of mackerel.

Sepulveda & Galleguillos (Unpublished results)

Analysis of mitochondrial DNA haplotypes found no significant differences in haplotype frequencies in three samples of *T. s. murphyi* from South America, one from New Zealand and one from Australia. The authors suggest that the region of DNA tested is conservative and it would be more appropriate to use a faster evolving region in the mitochondrial genome such as the D-loop.

Stepien & Rosenblatt (1996)

Populations of *Trachurus symmetricus* from Pacific North and South America showed little genetic divergence, leading the authors to conclude that there is gene flow across the tropics. However, the data show a significant overall difference in nine loci between Northeast and Southeast Pacific samples (Table 3) which indicates genetic differentiation, although sample sizes are small (12–18). There is no evidence for more than one species of jack mackerel in the genetic data.

3.2.5. Taxonomic papers using biochemical genetic methods

Koval (1988b)

This paper demonstrates that esterase isozymes are a useful taxonomic character. Intraspecific polymorphisms are noted.

Kijima et al. (1988)

This paper describes allozyme markers in 15 species, including 6 species of *Trachurus*. Intraspecific polymorphisms are noted.

3.3 Discussion

A number of studies have commented on the stock structure of *T. s. murphyi* in the South Pacific, but the results do not allow a clear conclusion to be drawn. Most of these studies are not accessible to the western reader and one must rely on the summaries of Evseenko (1987) and Elizarov et al. (1993). Elizarov et al. (1993) have shown that results are highly contradictory, with six studies concluding that there are between two and four populations, and a further four studies suggesting that there is a single population. Evseenko (1987) reviewed the various hypotheses and placed them in three categories.

1. There is a single population in the South Pacific.
2. There are separate populations in coastal and oceanic waters.
3. There is coastal population and an oceanic population that is dependent on it.

This treatment appears useful, but the use of "coastal" and "oceanic" is unclear. The confusion arises from the understanding that the South American populations, and the Californian population of *T. symmetricus*, are known to follow the pattern described by Serra (1991) for the Chilean population, of migrating off the shelf to spawn and back onto the shelf to feed. Thus, they cannot clearly be termed coastal or oceanic. There is evidence that spawning in South American waters occurs in areas of both coastal and oceanic upwelling (Gorbunova et al. 1985), but Serra (1991) concluded, based on a review of work by other authors, that the "intensity of spawning appears to increase as one goes further offshore,

peaking at about 100 to 200 nautical miles" and supporting the hypothesis that "jack mackerel spawns beyond 100 nautical miles."

To clarify the discussion it seems necessary to modify the three categories to focus on the SEPO population(s) and some unknown number of populations in the SWPO, beyond the usual offshelf-onshelf migration of the SEPO population(s). Thus, Evseenko's (1987) category 1 remains the same, and the other two become

2. There are separate populations in the SEPO and SWPO.
3. There is a SEPO population and a SWPO population that is dependent on it.

Evseenko (1987) favours category 3, with the explanation that the first is unlikely because fish will not return to the eastern South Pacific from the central and western regions, and the second is doubtful because there are no stable media or large circulations within which an oceanic population could become confined. He argues that the third is the only choice because western populations would be continually replenished with fish migrating from the east.

In this context the information summarised in the present study is somewhat inconclusive. Because of the current flow in the South Pacific there will always be some level of continual replenishment of eastern populations with fish from more westerly areas, based on the vast areas of spawning and the movements described in the literature (Vinogradov et al. 1991, Elizarov et al. 1993). This does not mean however, that the western population is dependent on the eastern, only that there is gene flow between them, and it is also true that if conditions remain the same, which is likely considering the relationship between El Niño and jack mackerel abundance (Muck & Sanchez 1987, Elizarov et al. 1993), individuals from the east will continue to migrate into western populations. Evseenko's (1987) argument that there is no mid-ocean feature to support a separate western stock does not consider the huge (up to 50 M t), apparently stable though seasonally fluctuating, biomass of zooplankton in the central and western South Pacific described by Vinogradov et al. (1991), and the known behaviour of the closely related (see Shabonev 1980) oceanic horse mackerel, *Trachurus picturatus picturatus*, to form populations on seamounts and submerged rises (Shabonev & Ryazantseva 1977). Given its heterotrophic adaptability (Konchina 1980) it seems reasonable that oceanic *T. s. murphyi* in the western South Pacific could easily employ oceanic seamounts to maintain an independent, oceanic population in the SWPO, particularly when food is limiting as a result of zooplankton populations overwintering at depth (Vinogradov et al. 1991).

3.3.1. Morphology

There is evidence for independent stocks, however. Some comes from the morphological study by Kalchugin (1992) who showed statistically significant differences in morphometric and meristic characters between specimens of *T. s. murphyi* from the western and eastern South Pacific, and concluded that there is an independent population of *T. s. murphyi* in the western South Pacific.

3.3.2. Parasites

Evidence for independent stocks also comes from parasite information. There are sources providing background (Duran & Oliva 1983, Romero & Kuroki 1985) and more explicit information (Avdeyev 1992) on parasite distributions. Avdeyev (1992) concluded that the Southeastern Pacific species of the ectoparasitic isopod *Ceratothoa gaudichaudii*, which is known to infest specimens of *T. s. murphyi* from the South American shelf (see Oliva 1994, Aldana et al. 1995), is absent in *T. s. murphyi* from New Zealand waters. Some 500 specimens of *T. s. murphyi* from New Zealand waters have also been examined for the presence of ectoparasites of the genus *Lernanthropus*, but none were found (Brian Jones, Senior Fish Pathologist, Fisheries Western Australia, pers. comm.). The presence of

Lernanthropus species in *T. s. murphyi* has been shown by Duran & Oliva (1983) for Peruvian waters and Romero & Kuroki (1985) and Oliva (1994) for waters off northern Chile.

Avdeyev (1992) has suggested that these absences in New Zealand fish can be explained in two ways. The first is that the *T. s. murphyi* entering New Zealand waters are second generation fish spawned in mid-oceanic waters by those adults that originally migrated from the SEPO. The alternative is that the period of migration from east to west is longer than the lifespan of the parasite. Testing the probability of either occurring is difficult however, because there was no information on the longevity of these species. The ectoparasitic isopod *Anilocra pomacentri* is known to live on the host for about 12–14 months; it is expected that *Ceratothoa* sp. would have at least the same longevity, perhaps a good deal longer (Robert Adlard, Curator of Protozoa, Queensland Museum, pers. comm.). Given their settlement within gill lamellae of the host, one might expect a low probability for *Ceratothoa* sp. to be dislodged at sampling.

The question is, how long does it take a jack mackerel to swim from South America to New Zealand? Konchina et al. (1996) suggests that fish of 20 cm (1 yr) are capable of migrating 240–840 nautical miles in a month. A very rough approximation, based on about 100 degrees of longitude across the South Pacific, and a travel speed of 6.8 mph (10.9 kph) (determined for *Scomber scombrus* and presented by Lagler et al. 1962), under an assumed constant swimming speed, is about 40 days. It is known that migrations of *T. s. murphyi* are complex and it is very difficult to speculate about the annual migratory pattern of an average fish, but if we assume that the highly stylised spiral migration postulated by Elizarov et al. (1993) increases the migratory distance by up to a factor of 10, then the time of migration becomes 400 days or about 13 months.

This is highly speculative but very conservative in using the factor of 10, and comes within the life span suggested above. Based on this estimate, it is not unreasonable to expect that some proportion of fish arriving in New Zealand could be infested with these parasite species, but none have been found. While this seems to support the hypothesis that individuals invading New Zealand waters are from an intermediate spawning point, one must also consider the age of the invaders. Length distributions of the fish indicate that those arriving in New Zealand are at least 3 years old, based on the summary of Kochkin (1994); if they are spawned at an intermediate point, then their migratory path must be a lot more convoluted than was assumed for those infested with parasites — it takes them a lot longer than 200 days cover the second half of the distance from South America.

A third possible explanation for the absence of these parasite species in New Zealand specimens of *T. s. murphyi* is that their intermediate hosts are absent. However, it is unclear whether an intermediate host is necessary for the infection of *T. s. murphyi* by *C. gaudichaudii*. No detailed information is available on its biology, but Sievers et al. (1996) hypothesised infection of farmed Atlantic salmon (*Salmo salar*) in Chile by infested *T. s. murphyi* feeding around salmon cages, suggesting that although a change of host is known to occur during the free-swimming “manca” life history stage, settlement occurs and “the parasitic life begins once they have found an adequate host”. No information is available for *Lernanthropus* species.

The isopod, *C. gaudichaudii*, was described by Avdeyev (1992) as being, to some degree, cryophilic, and he suggested that *T. s. murphyi* are infested by this species as members of the “oceanic group” migrate south of 40 °S into the colder waters of the South Subtropical Gyre, and mix with members of the “shelf group”. A fourth, perhaps more plausible, explanation of the absence of *C. gaudichaudii* from New Zealand specimens, is that subsequent spawning migrations of members of the so-called oceanic group into warmer waters to the north of 40 °S, results in the death of this cryophilic species. On the other hand, *Lernanthropus* species are presumably not cryophilic in that they have been described from the waters to the north of Chile, at latitudes similar to oceanic spawning grounds and New Zealand waters.

3.3.3. Morphology and genetics

Information collected during the present study adds to our knowledge of the entire Pacific population of *T. s. murphyi*. Nichols (1920) used morphological data to separate the South American jack mackerel from the Californian jack mackerel as an individual species, and a number of other studies using the same approach have supported the separation (Hildebrand 1946, Roedel & Fitch 1952, Santander & Castillo 1971, Berry & Cohen 1974), but where direct comparisons have been made, sample sizes have been small. Other workers support the existence of a single species, including Fowler (1945) who used morphological data, and the recent allozyme work by Stepien & Rosenblatt (1996) who have shown little genetic divergence in populations of jack mackerel from Pacific North and South America, leading them to conclude that *T. s. murphyi* is the same species as *T. symmetricus*. This evidence is definitive (Peter Smith, NIWA, pers. comm.) and supports the use of the name "*Trachurus symmetricus murphyi*", which is commonly used in the primary literature, rather than "*Trachurus murphyi*", which is widely used in New Zealand and is currently used in New Zealand legislation.

The lack of genetic differences between Northeast and Southeast Pacific samples also led Stepien & Rosenblatt (1996) to conclude that there is gene flow across the tropics, but the data show significant differences indicating genetic differentiation between the two populations. Thus we conclude that there is a single species of *T. symmetricus* with a known distribution from British Columbia (Ahlstrom & Ball 1954) to southern Chile (Evseenko 1987), and from South America to New Zealand and Tasmania (Elizarov et al. 1993), but with a low rate of gene flow across the tropics between the Californian and South Pacific populations (Stepien & Rosenblatt 1996). The use of "*T. s. murphyi*" is retained to distinguish the South Pacific population.

The results of a number of studies support population differences on the west coast of South America. Koval (1996) showed a significant difference in esterase allele frequencies in one out of five comparisons of annual samples taken north and south of 30 °S, and Gonzalez et al. (1996) showed consistent differences in allozyme markers between winter and spring at five sites in Chile. Together, these two studies clearly indicate that there is not a simple regional difference, suggesting at least two populations on the South American coast that are separated in time and space by different migratory behaviours.

The mitochondrial DNA study by Sepulveda & Galleguillos (Unpublished results) found no significant differences in haplotype frequencies between samples from South America, New Zealand, and Australia. This says that there is no genetic difference between *T. s. murphyi* from the SWPO and SEPO, based on this method. However, the region of DNA tested is conservative and it would be more appropriate to use a faster evolving region in the mitochondrial genome, such as the D-loop. This region of the mitochondrial DNA does not have a particular function in the cell machinery. Consequently, it is able to undergo mutation without reducing the fitness of the animal and remains in the population for much longer, making it a more sensitive indicator of population change.

3.3.4. Other studies

Other studies have concluded that there are separate stocks between Peru and Chile, based on distribution, abundance, size composition, and reproductive distributions. Serra (1991) suggested two self-sustaining populations, with separation somewhere off southern Peru. Evseenko (1987) proposed a similar structure, but further separated the Chilean population into coastal and oceanic populations. Serra (1991), however, disagreed with this latter subgrouping, at least to a distance of 900 nautical miles. off shore (about 90 °W), suggesting that Evseenko's (1987) proposed oceanic population might occur further to the west but would require verification.

4. POPULATION BIOLOGY (OBJECTIVE 2)

4.1 Methods

The issue of *T. s. murphyi* becoming established in New Zealand waters was examined by testing the hypotheses that New Zealand waters are conducive to its successful spawning and recruitment. Several areas of research, some of which were supported by results from papers selected from the original literature search, were identified as having the potential to provide key information for summarising the degree to which establishment has occurred in New Zealand and adjacent waters. Evidence of spawning was collected and interpreted in terms of the environmental information.

4.1.1. Literature search

Background information on the biology of *T. s. murphyi* for use in this objective was based mainly on those references from the literature search for Objective 1 that were categorised under "Distribution and biology". Searches for information on topics that were poorly represented in the original search because little work has been done using *T. s. murphyi* (e.g., sex ratios) were based on a more general approach and expanded to include other species of *Trachurus*. Other information (e.g., plankton studies) for use in methodology described in the following sections was identified from discussion with NIWA staff working in the field, and expanded from reference lists and database searches. A page index by author of the papers summarised in the literature search is presented in Appendix 2.

4.1.2. Length frequencies

Length data from the Ministry of Fisheries trawl survey database (*trawl*) (Mackay 1998) and the Ministry of Fisheries Scientific Observer Programme (SOP) database (*obs*) (Mackay 1995) were used to develop two series of length frequency distributions of increasing fine scale. Distributions were summarised by fishing year and were not scaled to total catch.

The trawl survey data were used at two levels of scale. The first was a time series of distributions using length records of *T. s. murphyi* from all years and areas. The second used specific data from trawl survey series that are comparable in gear type and the time of year of the survey. The following trawl series were known to satisfy these criteria and were examined for the presence of length data for *T. s. murphyi*:

- Kaharoa west coast South Island (WCSI) and East Coast South Island (ECSI) surveys;
- Kaharoa east coast North Island (ECNI) surveys (south of East Cape);
- Kaharoa Bay of Plenty, ECNI (north of East Cape), and west coast North Island (WCNI) surveys use comparable gear but have very short tow times;
- Tangaroa Stewart-Snares shelf surveys between 1993 and 1996;
- Tangaroa Chatham Rise surveys.

Time series of length frequency distributions were produced for those trawl series containing data.

The SOP data were used at three levels of scale: all length records of *T. s. murphyi* were used to produce an overall time series by fishing year; two different time series were produced by jack mackerel Fishstock (JMA 1, JMA 3, and JMA 7) (see Figure 3) and by season; and, at the third level, time series sets were produced for jack mackerel Fishstock and season combined.

Length data were extracted from the trawl survey and SOP databases by date and area and loaded into a working database. Data for males and females were pooled because *T. s. murphyi* does not exhibit size-based sexual dimorphism (Carrera & Collantes 1978, Kochkin 1994). Jack mackerel Fishstock codes

were substituted for statistical area codes in the SOP data, and a fishing year code was added to both datasets. Functions were written in the New S programming environment to produce histograms of fish numbers in single centimetre size classes. These functions were designed to produce time series by year class, according to the various levels of scale described above.

Scaled length frequency distributions of *T. s. murphyi* in fishing years 1994–95 to 1996–97 were presented by Taylor (1998) based on jack mackerel shed sampling data of the purse-seine jack mackerel target fishery for MFish Projects PJM601 and PJM01. These distributions are presented here in Figure 5.

4.1.2. Sex ratios

Trawl survey data were used to determine sex ratios of *T. s. murphyi*. Proportions of the two sexes were estimated for each voyage where *T. s. murphyi* was recorded, using their numbers in catches aggregated over the voyage. The minimum sample size was arbitrarily chosen as 45, and proportions were rounded to 1 decimal place, which produced three proportion classes for voyages meeting the selection criterion—70:30, 60:40, and 50:50. These were designated a, b, and c.

4.1.3. Examination of fish and plankton collections

Fish and larval collections at NIWA and the Museum of New Zealand were examined to obtain information on the distribution of *T. s. murphyi* juveniles within New Zealand waters and the adjacent ocean. Specimens of *Trachurus* recorded as having been collected since 1983 (an arbitrary year closely preceding the first known appearance of *T. s. murphyi* in New Zealand waters, see Figure 1) were examined for the presence of small juvenile *T. s. murphyi*. Specimens have been collected during SOP trips, and on NIWA and Ministry of Fisheries research voyages.

Larvae of the three jack mackerel species were distinguished by descriptions published by Ahlstrom & Ball (1954), Santander & Castillo (1971), and Neira et al. (1998). The first task was determine the whether the three species could be successfully separated. Based on a successful result, the second task was to examine plankton collections from fine mesh net tows to produce a distribution of *T. s. murphyi* larvae.

4.1.4. Reproductive condition and sea surface temperature

Sea surface temperatures from known areas of spawning in New Zealand waters were compared with those from known spawning grounds in South America (Muck et al. 1987, Bendik 1991) and the open waters of the South Pacific, to determine the potential of the local habitat to provide an optimum thermal regime for eggs and larvae.

A summary of *T. s. murphyi* in maturing, ripe, and spent condition in New Zealand waters was made using data from the trawl survey and SOP databases, and from the jack mackerel shed sampling data. Each of the data sources used a different gonad staging system (a 6 point system in the trawl database, a 5 point system in the observer database, and an 8 point system in the shed sampling data). To minimise confusion, the data from all sources were recoded to fit the system described by Horn (1991) (see Table 1).

Data were summarised by year, month, and area, with an accompanying list of the gonad stages observed, the number of each recorded, and the mean SST (see) in the area during the month of the record. Data were also summarised for all years as positions (latitude and longitude) on a map where observations were recorded; some positions represented more than one record, especially in JMA 1 where shots from several vessels had been assigned the same position in the shed sampling dataset.

Extracts from the trawl and SOP databases included latitude and longitude, which provided precise positions for the map and were replaced with areas for the table.

Records of SST from satellites were extracted from the bulletin board of meteorological analyses operated by the United States National Weather Service's Climate Analysis Center (CAC), as described by Gilbert & Taylor (2001). Relevant data were identified in time and by area according to spawning events based on the distribution of maturing and mature fish, and distributions of juvenile fish. These values were compared with values recorded in the literature for other geographical areas.

4.1.5. Distribution of prey species

Distributions of life history stages of known prey species of *T. s. murphyi* larvae (e.g., calanoid copepods) were compared with areas of known spawning events and the distribution of *T. s. murphyi* juveniles to determine whether food is a limiting factor in the survival of any life history stages. A profile of prey species for all life history stages of *T. s. murphyi*, from first feeding larvae to the adult, was developed using feeding information from the literature search for *T. s. murphyi* and *T. symmetricus* in other regions of the Pacific Ocean. The presence of these or similar prey species in New Zealand waters was determined based on the results of local studies. To summarise existing local feeding information, a list of prey species for *T. s. murphyi* in New Zealand was produced from the trawl survey and market sampling datasets.

4.1.6. Development of eggs and larvae and their transport in ocean currents

A summary of water currents (Heath 1985, Stanton et al. 1997, Roemmich & Sutton 1998) and their geographical relation to the recorded spawning events in New Zealand waters were used to determine possible transport directions for eggs and larvae. Estimation of transport rates from current speeds coupled with larval hatching times and growth rates (Esin 1993) were used to predict distribution summaries of various life history stages. Based on this information, the feasibility of *T. s. murphyi* becoming entrained within the east coast gyre system for some period of its life history before returning to the New Zealand shelf was investigated.

4.1.7. Approximating juvenile size at age

A monthly estimate of size throughout the first year would be useful for determining where any juveniles from fish collections or in the length frequency distributions were spawned. Details of transport mechanisms and information from the literature search were used to develop a series of larval and juvenile lengths for the first year. The methodology is described as a result from the literature search and presented in the results section along with the series of estimated lengths.

4.2. Results

4.2.1. Literature search

The following are papers from the "Distribution and biology" category of the original literature search for Objective 1. They are summarised according to the headings Age and growth, Reproduction, Feeding, and General, and are restricted to the most useful papers received for developing a profile of the biology of *T. s. murphyi*.

The summaries of some papers contain references to other works. Sometimes these papers had been examined as part of the literature search, but often they were unobtainable and are cited in the

summaries of papers only, to show that the result being discussed is from another work. These references are marked with an asterisk in the References.

Age and growth.

A number of workers have investigated the growth of *T. s. murphyi* by several different methods.

Carrera & Collantes (1978)

This paper reported age and growth using otoliths to estimate length-weight parameters ($a = 3.2115 \times 10^{-5}$, $b = 2.7659251$) for fish weight in grams and length in millimetres, and von Bertalanffy parameters ($K = 0.10879$, $L_{\infty} = 1062.82$ mm, $t_0 = -0.8772$) and a best fit for asymptotic weight of 7780 g. There was no evidence of sexual dimorphism.

Cubillos & Arancibia (1995)

These workers estimated von Bertalanffy parameters for specimens from the central-southern area of Chile ($FL_{\infty} = 65.2$ cm, $TL_{\infty} = 65.2$ cm, and $K = 0.138$, where FL and TL are fork length and total length respectively), and concluded that "*Trachurus* stocks inhabiting upwelling systems (e.g., Humbolt and Benguela) grow better than ecological equivalents in temperate waters (e.g., the North Sea)".

Cubillos et al. (1995)

Specimens were collected from the central-southern area of Chile between January 1987 and October 1991, to estimate $K = 0.144 \text{ yr}^{-1}$, $L_{\infty} = 75.3$ cm, and $t_0 = -0.170$.

Chekunova & Naumov (1978)

These workers investigated growth and respiration, and showed a relationship between O_2 consumption and body weight. They estimated respiratory rate as $R = 0.248W^{0.897}$. Their estimate of mean daily increase for juveniles is 0.52% of body weight with a daily ration of 9.5%, and for adults is 0.33% with a daily ration of 13.5%; they concluded that with intensive feeding for 6 months mature *T. s. murphyi* eat 25 times their body weight.

Kaiser (1973b)

This study was based on samples from three areas off the Chilean coast during the 1962–63 and 1963–64 fishing seasons, and growth was investigated using otoliths and length frequencies. The author determined the relationship $nt = 21.5 + 0.85L$ ($n = 92$), where nt is the distance from the nucleus to the border of the otolith in ocular micrometer units, and L is the fork length in centimetres; the correlation coefficient was $r = 0.246$. He found that maximum growth occurred in the area off Valparaiso where individuals reached 65.8 cm at age 12 years, and estimated that 50% of total calculated growth was attained by age 3 years, and 84.3% of total growth by age 7 years. Larger fish were found in colder water.

Kochkin (1994)

This study sampled individuals from both the SWPO and the SEPO between 1983 and 1990 and also investigated growth using otoliths and length frequencies. The author determined the relationship $R = 2.0285 \times L^{0.6334}$ where R is the otolith radius in ocular micrometer units and L is fork length in millimetres; the correlation coefficient $r = 0.958$. His estimated von Bertalanffy relationship is $L_t = 74.2405[1 - e^{-0.1109(t + 0.8113)}]$, and he determined $L_{\max} = 0.943L_{\infty}$. Results of a length-weight analysis ($W_{(g)} = aL_{(cm)}^b$; L is fork length) produced the following values, and led to his conclusion that there is no difference between males and females.

Sex	A	B	n
Males	0.0248	2.7542	350
Females	0.0189	2.8319	310
Both	0.0238	2.7671	660

He observed annulus formation occurring mainly in November and December at times of peak spawning. The data cannot be separated by area.

Reproduction.

Andrianov (1985)

This study investigated reproduction in *T. s. murphyi* from the Peruvian shelf in 1972–73. Andrianov determined a sex ratio close to unity with a slight predominance of males, and 50% maturity at 36–39 cm in males and 39–42 cm in females. Using a six point gonad staging system (i.e., 1 = immature, 2 = resting, 3 and 4 = maturing, 5 = running, 6 = spent) he showed that resting fish are predominant throughout the year, that there are few (3–7%) running fish, that maturing fish represent 29–65% of the total, and that spent fish are present most of the year, with numbers increasing to the end of December followed by a decrease to the end of March, and their total absence in April–May. He concluded that spawning took place over 10 months from June–March and suggested increased intensity in winter–spring (August–November).

Esin (1993)

An ichthyoplankton survey was carried out in the SWPO in January 1990. The author used artificial incubation to determine mass emergence of larvae 40 h after fertilisation at 19.5–21.2 °C (cf. the 82 h at 16 °C presented by Voronina 1987), estimated a coefficient of instantaneous mortality for roe of 0.98, and larval yolk sac resorption at 1.5 days. He established spawning over a wide geographical range from 110 to 170 °W longitude, finding that “larvae and fry 4–14 mm long were caught almost everywhere”, with increased concentrations coinciding with increased concentrations of roe in two areas centred on 39 °S, 132 °W, and 36 °S, 120 °W. Fingerlings 25–80 mm long were noted throughout the area to 170 °W, with a maximum southerly range at 40 °S. In January the frequency of occurrence of this latter fraction was 35% south of 38 ° 30 'S, and 57% to its north. The northern boundary of fingerlings was at a higher latitude than for roe and the author suggested this was the result of either a migration by fingerlings to the north, or “a shift of the subtropical frontal zone, to which the spawning of jack mackerel in the SWPO is confined, to the south in October–November”. The following points were made in conclusion.

- A comparison of the distributions of early ontogenetic stages does not support the hypothesis that generative material is carried from the SWPO into the SEPO.
- The presence of different reproductive centres for the SWPO and the SEPO makes it possible to consider the SWPO as a dependent population (see Evseenko 1987), not a pseudopopulation as previously supposed.

Evseenko (1987)

Ichthyoplankton surveys were carried out in the SWPO (120–160 °W) and the SEPO (two areas, 300 and 600 nautical miles from the South American coast), but most discussion in this paper is concentrated on the latter. The highest egg concentrations were confined to regions of cold water upwelling and gradient zones. Surface water temperatures were 14.5–17.0 °C and salinity 33.98–34.02‰ in areas where eggs and larvae occurred; eggs and larvae were distributed in the upper mixed layer and upper part of the thermocline located between 20 and 50–60 m; maximum egg densities were located at depths between 1–3 m and 19–22 m. He noted that larvae were found as isolated specimens with numbers not exceeding 0.072 m⁻³ in “towed horizontal nets” and 7 m⁻² in Bogorov-Rass net tows. The following conclusions were reached.

- *T. s. murphyi* spawns all along the South American coast from 7 to 41 °S.
- The main spawning grounds are located between 15 ° 40 ' and 18 ° 00 'S off Peru (Santander & Castillo 1971) and between 24 and 40 °S off Chile (Serre 1983).
- In the Peruvian region spawning is in coastal as well as adjacent oceanic waters and is found up to 300 nautical miles offshore (Santander & Castillo 1971); its western border of spawning in this area is probably determined by the position of oceanic upwelling.

- Off Chile the spawning grounds extend at least to 139 °W (3000 nautical miles); precise locations are unknown although they are definitely confined to the relatively narrow zone of the Subtropical Convergence.
- A single population in the South Pacific cannot be justified because it is difficult to accept the possibility of return migrations from central and western regions to the Chilean coast.
- The existence of separate populations in oceanic and coastal waters is doubtful because there are no stable media or large circulation, "to which the main areas of distribution of the oceanic species is usually confined", and the west to east movement of watermasses at about 40 °S will result in the eastern population being "continually replenished by a population from more western regions".
- The hypothesis describing an oceanic population dependent on the coastal population is the most acceptable of these three hypotheses.
- Assuming a similar ecological characteristic in young *T. s. murphyi* to that of young *T. symmetricus*, where adaptation to a shallow water habitat is known (no reference is given in the text), spawning in western regions will be ineffective where fish cannot reach the South American shelf, and they will be "destined to perish".
- Spawning in *T. s. murphyi* occurs at temperatures (15–16 °C) similar to those for *T. symmetricus* (15.5 °C) (see Stepanenko 1980).
- The Peruvian and Californian jack mackerels are ecologically identical forms.
- Movement of this species into the oceanic pelagic zone is assumed to be a consequence of an increase in the coastal populations, leading to expansion of the feeding area in all directions. Because the population peaks sporadically, migrational paths in the open sea are not fixed genetically, and fish groups a long way from the shelf are not in a condition to return to the shelf and form separate populations.

Evseenko et al. (1990)

The authors carried out an ichthyoplankton survey off Callao, Peru, in February 1987, and found very weak spawning which they attributed to high water temperatures on the shelf (23–26 °C), which exceeded the upper limit of *T. s. murphyi*'s spawning temperature range, and a lack of coastal upwelling with which spawning aggregations were usually associated (Gorbunova et al. 1985, Evseenko & Karavaev 1986).

Farris (1961)

Much biological information was available from this study on *T. symmetricus*. The author developed the relationship $\log Y_{(hrs)} = 3.257 - (0.088X_{(C)})$ for estimating the time to hatching of eggs at a given incubation temperature and showed that the time of maximum spawning is midnight, and that spawning occurs throughout a range of water temperatures (10–21 °C) with a peak at 16–16.5 °C. He determined a remarkably constant mean and median temperature (15.5 °C) for 1951–54, thus providing a sharp temperature optimum. He also showed that 60% of spawning occurs within 1 °C of the mean and median, and concluded that because spawning occurred at a particular time during the season, despite the presence of physiologically optimum water temperatures, other factors like fish condition, food availability, and day length are also important.

The author also investigated larval survival and showed that over four years "little more than 1 larva survives for every 1000 eggs spawned, with maximum mortality occurring during the first nine days". He showed that growth during the first three days was about five times as great as that in the next four, and that yolk sac absorption coincided with the eyes becoming pigmented during the sixth day after hatching. He developed the relationship $\log L_{(mm)} = a + (b * X_{(days)})$ to estimate larval size and provided the following parameter values.

Days after hatching	<i>a</i>	<i>b</i>
1-3	0.328	0.486
4-8	0.067	0.013

The author found that almost all larvae were taken at depths shallower than 100 m, with none deeper than 140 m and most in the top 30 m. He referred to Ahlstrom & Ball (1954) who computed a day/night ratio and, based on the assumption that larvae cannot see the net at night, found that the ratio increased with size suggesting better avoidance with size/age. This was interpreted as being related to increased strength and swimming ability, but the author could not repeat this result, and found that there was no age-related difference in net avoidance.

George (1995)

This study was based on monthly sampling, October 1989–September 1990 and July 1991–May 1992, off the northern coast of Chile, to investigate a number of aspects of the reproduction of *T. s. murphyi*. When estimating sex ratios he found mean values of 53.7% (range 39.0–64.3%) and 46.3% (range = 35.7–61.0%) for females and males respectively, which resulted in a total sex ratio of 1:1.107 ($n = 2491$) males:females. This ratio became highly male dominated (73%) during September 1990 when ovarian histology showed a high presence of postovulatory follicles. Atresia was present throughout the year in a few single-yolked oocytes, but increased dramatically when the peak spawning season began to decline. Maturity was estimated using ovarian histology to give 24 cm FL as the first appearance of mature females and 27 cm FL as more than 90% classified mature. The gonosomatic index was used by Grimes (1976) to estimate 50% maturity, and average first maturity was shown to be reached at 24.5–25.0 cm FL.

George disagrees with the classification of this species as a determinate batch spawner, which is based the assumption that the standing stock of yolked oocytes of a female prior to the onset of spawning is equivalent to the potential annual fecundity. He concludes *T. s. murphyi* to be an *indeterminate* batch spawner, based on the oocyte-size-frequency-distribution (OSFD) of reproductively active females, and their “presence over a long temporal extension of seven to nine months per year”. This conclusion is supported by *T. symmetricus* larvae having an almost year-round presence off California as described by MacGregor (1966), and evidence from Evseenko (1987) and Bailey (1989) that supports the assumption that *T. s. murphyi* spawns wherever environmental conditions are suitable, a strategy that is available only to an indeterminate batch spawner.

Gorbunova et al. (1985)

This study investigated spawning aggregations off Peru over a wide range of distances offshore. Groups of eggs were recorded at distances of 25, 80–120, and 200–270 nautical miles from the coast, which coincided with “the rise in the gradient layer to the surface”. He concluded that the temperature requirement for normal embryonic development of *T. s. murphyi* has a wide range and does not act as the factor determining the position of spawning grounds.

Kaiser (1973a)

The author examined the GSI, condition factors, and distribution curves of egg sizes for 309 specimens of *T. s. murphyi* from three fishing localities off Chile between January 1963 and April 1964. He concluded that spawning probably lasts less than a month, and that first spawning for females occurs during the third year at about 36 cm FL and 600 g body weight. A large variation was found in fecundities of individual females of similar size and weight.

Kuroiwa (1997)

The author used data from midwinter trawl surveys off Chile, south of 30 °S during 1983–89, to determine a spawning season over the austral summer (January–March), with spawning occurring in oceanic waters. Sizes of maturation were estimated as 24 cm for males and 26 cm for females.

Lisovenko & Andrianov (1991)

This study was designed to estimate annual fecundity, using as a first premise the suggestion by Oven (1976) that to base an assessment of fecundity in fishes with continuous oocyte maturation and multiple spawnings on the number of trophoplasmic oocytes is incorrect because it does not take into account the number of reserve oocytes maturing during the spawning season. The authors stated — “therefore we avoided the use of the term fecundity in our publications and used the expression *number of vitelline oocytes*”. Individual fish utilising a strategy of continuous oogenesis and multiple spawning can remain in a state of permanent maturity with a constantly replenished stock of vitellogenic oocytes, spawning under favourable environmental conditions and abandoning the behaviour when conditions deteriorate. Thus, fecundity can vary with the conditions.

Where this occurs, total annual fecundity must be based on the multiplicity of spawning and the number of eggs laid by a female in a average spawning event. The data indicated that spawning intensity and its dynamics varied over time from year to year. Based on a batch spawning range of 26 765–187 613 eggs in fish of different lengths and weights, a mean batch fecundity of 60 956 eggs was estimated. The following results were presented.

	1981–82	1982–83	1983–84	1984–85
Spawning multiplicity	7.2	11.1	16.6	19.8
Total fecundity	483 883	676 612	1 011 870	1 206 929

Therefore, Lisovenko & Andrianov concluded a large variation in spawning multiplicity and the magnitude of annual individual fecundity. This was explained as the result of variation between incomplete utilisation of vitelline oocytes in some years, and the release of trophoplasmic and protoplasmic size in others.

Loeb & Rojas (1988)

Winter ichthyoplankton (July–September) was surveyed during 1964–70, 1972–73, and 1983, at two target depths: 0–50 m and 0–100 m. *T. s. murphyi* larvae were 5 times more abundant and 3–6 times more abundant in the shallower category.

Orrego & Machii (1989)

Specimens of *T. s. murphyi* were collected off Callao, Peru, from November 1979 to October 1980. Gonad index and condition factors (girth and fat indices) were used to determine the spawning season from October to March.

Feeding.**Arthur (1976)**

Arthur investigated feeding in the larvae of *T. symmetricus* off California, examining 750 specimens from 65 samples to determine first feeding at 3.25 mm, and noting that no specimen was found with both a yolk sac and ingested food organisms. Copepodite stages of copepods contributed the greatest bulk of its food (about 96% of its diet comprises various species of copepods by the time the larvae are a 7.0 mm long), with copepod eggs much less important and numbers of copepod nauplii significant only in the diet of larvae of the smallest size group. The presence of high numbers of the harpacticoid copepod *Microsetella norvegica* suggested that this was a preferred species because it scored low in counts from plankton tows. This species, and two other groups (*Corycaeus* and *Oncaea* spp.) that were also identified in the diet may be captured easily because they “are among the most brightly coloured or least transparent of copepods”.

In the diet of larger larvae, calanoid copepods become important, perhaps because of increased visual acuity, increased mouth size, or a change in vertical distribution. The gape of larvae increases isometrically with length — a doubling of its length from 3.5 to 7 mm increases the potential size of ingested particles from 225 to 435 μm in cross section. A number of factors from its feeding strategies suggest greater fitness in Californian jack mackerel larvae than competing species: it can ingest particles three times larger than sardine larvae of the same length, which represents a difference in volume of about 27 times; its incidence of feeding increases with length, whereas it decreases with length in anchovy and sardine; its gut is looped, dividing it into functional parts, and is a feature that has been described for larval species containing large food volumes.

Konchina (1978)

The gravimetric method (Anon. 1974) was used to examine the diets of 92 specimens taken from Peruvian coastal waters by pelagic and bottom trawls from depths of 10–150 m in 1972. Most individuals were 32–38 cm in length (adults). He concluded that *T. s. murphyi* is a zoophage with Euphausiacea, young Stomatopoda, and the larvae of Decapoda the main food items, with Copepoda and decapodan larvae the most diversely represented; fish were important in the diets of large adults over 52–58 cm long; species composition changes by month and in different parts of *T. s. murphyi*'s range.

Konchina (1979)

The gravimetric method (Anon. 1974) was used to examine the diets of 280 specimens taken from Peruvian coastal waters by midwater and bottom trawls from depths of 10–280 m in July–December 1973. Euphausiidae (particularly *Nyctiphanes simplex* and *Euphausia mucronata*) were the main food item (51.1% by weight); fish (pelagic and demersal species) were also important (20.3% by weight), as were the larvae of Decapoda (11.4% by weight), particularly the zoea of the family Hippidae (Anomura). Also frequently encountered in *T. s. murphyi* stomachs are Copepoda and Pteropoda (51.4 and 16.6% respectively, by frequency of occurrence), but by weight their presence was low. Overall, *T. s. murphyi* exhibits "great feeding plasticity and is capable of using diverse animals inhabiting both the neritic and the oceanic pelagic zone". Fish prey include groups from the neritic zone (family Engraulidae — anchovy from the pelagic zone of shelf waters and family Normanichthyidae — *Normanichthys crockeri* which forms considerable demersal aggregations on the shelf), and the oceanic pelagic zone (family Gonostomatidae, especially *Vinciguerria lucetia*). Diets also included Siphonora, Mollusca, and Chaetognatha.

There were marked differences in food composition of *T. murphyi* with locality and season. Konchina also concluded that the size of food organisms does not change "substantially with the growth of the fish", because juveniles and adults feed on both small and large food items. This study showed a change in preferred habitat with age, with juveniles feeding in the oceanic epipelagic zone, and sexually mature fish feeding in the neritic zone.

Konchina (1980)

This study appears to have reworked the data presented in Konchina (1978) and Konchina (1979), but concentrates on determining the trophic level of *T. s. murphyi* in the coastal upwelling ecosystem. A parallel is drawn with other *Trachurus* species which have been shown to be more than plankton feeders by the presence of fish in their gut contents (Gail 1955, Kompowski 1976). According to the author, the second of these two papers shows a change in feeding with age in horse mackerel off the coast of northwest Africa, with individuals smaller than 30 cm being typical zooplankters, and larger fish including fish and squid in their diets. Categorising *T. s. murphyi* as a facultative predator (tertiary consumer), compared with zooplankters, which are described here as secondary consumers, the author discusses its feeding adaptations.

- Divergence from its competitors is apparent early in life history — according to Arthur (1976), *T. symmetricus* larvae have a different and higher volume food composition than *Engraulis mordax* and *Sardinops sagax*, and they switch earlier to copepodite stages.

- Its heterotrophic nature (i.e., its ability to inhabit various biotopes) is a feature of its ecology and allows it to vary its behaviour under changing conditions — the present study (i.e., Konchina 1980) shows that in 1972–73 an El Niño event was clearly operating and *T. s. murphyi* foraged in oceanic waters.
- The ability to take lengthy migrations can be directed towards expanding the foraging and geographic range — this ability is apparent in early life history stages of *T. s. murphyi* and *T. symmetricus* whose larvae can inhabit two biotopes (Macgregor 1966, Santander & Castillo 1971).
- Speculation on the possibility of *T. s. murphyi* “to form a number of semidependent populations living on seamounts and submerged rises located beyond the limit of the neritic zone” as has been shown for the oceanic horse mackerel by Shabonev & Ryazantseva (1977).

Konchina (1983)

This study is based on sampling off the coast of Peru in 1972–73, and presumably represents the same data used by Konchina (1978, 1979, 1980). It is a continuation of information presented in those papers, and continues the objective of Konchina (1980) to determine the trophic level of *T. s. murphyi*. The approach here is to compare trophic analyses of *T. s. murphyi* and the hake (*Merluccius gayi*) and develop a description of the trophic chain for the neritic zone of the Peruvian coastal upwelling. The gravimetric method (Anon. 1974) was used to process gut contents of 296 *T. s. murphyi* and 252 hake from aggregations fished during March–December in the shelf zone of Peru, and during August in the oceanic epipelagic zone. Most fish were mature — 35–50 cm (3–5 yr) for hake, and 32–44 cm (3–7 yr) for the jack mackerel. The jack mackerel's biomass is created from five components: squid, Copepoda, Euphausiacea, crab larvae (meroplankton), and fish — squid, Copepoda, and meroplankton are on the third trophic level. In 1983 two trophic chains were known for this zone: a short chain consisting of 1½ levels or links and comprising phytoplankton and anchovy (*E. ringens*), and a second one that is long and complex, referred to here as the facultative predator chain. It consists of four links with its upper level occupied by hake and *T. s. murphyi*. Hake occupies the upper limit of this level, and *T. s. murphyi* is at the lower limit. These two species are characterised by a high level of feeding adaptability and a number of adaptations to maximise potential food sources. It is suggested again that this is advantageous in allowing them to extend their foraging when conditions become unfavourable, and reference is made to both having moved into the oceanic epipelagic zone during the El Niño event of 1972–73.

Konchina (1990)

This study was designed to compare feeding in the mackerel *Scomber japonicus* and the jack mackerel *T. s. murphyi*, and was based on stomach-content data of 41 *S. japonicus* and 69 *T. s. murphyi* collected by bottom trawl in spring (September, November) 1983 on the Ecliptic Bank at 22 °S off Peru. Previously published data from fish taken in the same months from Peruvian shelf zone were also used. The gravimetric method (Anon. 1974) was used to process the stomachs. Feeding rate was determined from the index of fullness and proportions of items in total amount consumed was estimated.

For *T. s. murphyi*, eight taxonomic groups (order and above) of invertebrates, and fishes were consumed. The invertebrates included siphonophores, cephalopods, crustaceans (ostracods, copepods, amphipods, euphausiids, decapods), and tunicates (salps). Fish included larval, juvenile, and adult *Vinciguerria* (Photichthyidae); juvenile Nomeidae, Gempylidae, and Scorpaenidae; adult Myctophidae; and larval Clupeidae. The bulk of food was represented by three items — euphausiids, hyperiids, and fish. In September the feeding rate was low and increased by a factor of 2.5 in November. The main food items switched from euphausiids and hyperiids in September to euphausiids and fish in November.

The spatial niches of *S. japonicus* and *T. s. murphyi* coincide, but they differ in their food niches and the way they hunt for food. In the oceanic epipelagic zone, *S. japonicus* hunts for salps and *T. s. murphyi* captures large hyperiids, including members of the genus *Phrosina*, that live on salps.

During jack mackerel spawning, salps feed on its eggs, thus providing a high energy food for pre-spawning *S. japonicus*; *S. japonicus* also feed on jack mackerel fingerlings about 9 cm long.

An El Niño event occurred in 1983 but this did not affect feeding in these two species, which dominated the open pelagic zone during the spring.

Konchina (1993)

This study was based on individuals of Peruvian sardine (*Sardinops sagax*, $n = 94$), chub mackerel (*Scomber japonicus*, $n = 165$), and the jack mackerel (*T. s. murphyi*, $n = 610$) taken beyond the Peruvian shelf 300–350 nautical miles from shore from 9 to 22 °S during winter and spring 1980–83. A quantitative (by weight) method was used to process stomach contents. Generally, fish were 2–4 years old; i.e., juvenile and adult sardines 18–26 cm, chub mackerel 26–34 cm, and jack mackerel of 22–36 cm.

Konchina et al. (1996)

This paper summarises much of the work that has been done on the feeding of *T. s. murphyi*. However, it is unclear where some of the data are from. Generally, it reads like a review, but there are often large tracts of text seemingly without reference to any specific work. Given that the senior author is responsible for 90% of the 10 or so papers written on the topic, most references would have been to his own previous work. There is reference to Vinogradov et al. (1991), but it is unclear whether similar work was done by Konchina et al. (1996) on distributions of prey species in the oceanic epipelagic zone (i.e., small prey north of 40 °S, larger to the south).

"Based on our own material on ecology of the jack mackerel in the Eastern Pacific (from the Chilean and Peruvian economic zones to 105 °W), including data on spatial distribution, size and age distributions, reproductive status, and feeding, we tried to analyse the peculiarities of temporal and spatial distribution of fish in order to reveal causes and mechanisms of the mackerel migrations, and the role of the species in the oceanic ecosystems in this region."

Most data and material were collected in spring 1989 (September–December), using hydroacoustic equipment to study the oceanic epipelagic zone from the Peruvian and Chilean economic zones to 105 °W, and midwater trawl to sample fish. Biological parameters of the jack mackerel were estimated, including size and age distributions, reproductive status, and feeding from fish trawled in the upper 100 m, mainly at night (89% of all tows).

"We substantiate the thesis that the biomass of the jack mackerel recruitment is formed in the open ocean. Our analysis proves that before reaching sexual maturity (at the age of three years), the young jack mackerel (20–26 cm, two-year-olds) successfully forage and grow in oceanic epipelagic waters, including insular and shallow (thalassic) zones, close to the Chilean and Peruvian shelf zones. ... The ranges of feeding migrations of the mackerel juveniles [may be] extensive because fish at the length of 20 cm (1 yr) can move 280–840 nautical miles in a month."

"Our results confirm that the temporal and spatial characteristics of migrations of the Pacific jack mackerel are determined by the temporal and spatial dynamics of species composition and biomass of its main food, meso- and macro-plankton representing the epipelagic and mesopelagic migrating communities."

Muck & Sanchez (1987)

This study "is an attempt to estimate the consumption of anchoveta (*Engraulis ringens*) by mackerel (*Scomber japonicus*) and horse mackerel (*T. s. murphyi*)". It uses a modelling approach to produce the estimates on a monthly basis for 1953–82. Key factors are the temperature-induced onshore-offshore migrations of the two species, their relationship with El Niño events, and resulting changes in the overlap between anchoveta and mackerel/horse mackerel distributions. Most of the data had been published elsewhere.

Vinogradov et al. (1991)

The aim of this study was to investigate the oceanic ecosystem of the South Pacific and estimate food resources for *T. s. murphyi*. A research cruise was conducted in the southwest Pacific Ocean (SWPO) within the boundaries of 158–126 °W and 30–57 °S. Detailed analysis of the upper 500 m of the water column was conducted at more than 30 stations, including hydrophysical and hydrochemical parameters, and extensive biological samples “from bacteria and picoplankton to macroplankton and micronekton”. An array of gear was used to sample the various fractions: 0.2–0.3 (small mesoplankton), 3–30 mm, and larger macroplankton.

“Although the study areas were distributed over 1500 miles, the latitudinal distribution, community structure, and zones of dominant species concentration was constant at all sites.”

- The first zone at 40 °S is inhabited by a subtropical community. Biomass is quite high (e.g., 16–17 g m⁻² for the 200 m layer) but constituent animals are small with lengths less than 2–3 mm. Small filter feeding nanophages are more important than further south and comprise more than 22% of the mesoplankton. Macroplakton is poorly represented, with a mean biomass of less than 3 g m⁻². These small zooplankton are better suited as food for the larvae and young of jack mackerel than adults, “affording them the possibility of progressing through these most critical development periods.”
- The second zone (43–50 °S) is characterised by aggregations of large calanoid copepods (e.g., *Calanus tonsus*), chaetognaths, and euphausiids above the thermocline. At night they ascend into the upper 100 m layer. Mean mesoplankton biomass is high (36 g m⁻²) and up to 44.2 g m⁻². Large mesoplanktonic euryphages and predators greater than 3 mm represent approximately 50% of the mesoplanktonic biomass. The biomass of macroplankton (mostly euphausiids) was 5–12 g m⁻², representing up to 24% of the overall zooplankton mass. Calanoid copepods exceeded 700 mg m⁻³. Copepods and euphausiids are the principal food of jack mackerel during the growing season (Gorbatenko 1988).
- The third zone is plankton-rich and associated with the Antarctic Current (AC). Mean mesoplankton biomass is 53 g m⁻², increasing to 72 g m⁻² in the region of the AC — euryphages dominate (about 50% of the total biomass) comprising mostly large interzonal copepods and predators (35% of biomass), mostly chaetognaths. Macroplankton biomass was low (4 g m⁻² and 6% of total). Because of its low water temperature (5 °C), this zone is unavailable to jack mackerel.

Spawning aggregations of jack mackerel occur to the north in waters of the subtropical frontal zone (STFZ) at the frontal break at about 40 °S, characterised by small food, warm water (summer SST is 16–18 °C), and less seasonal change in plankton biomass than the more southerly zone. Between 45 and 50 °S is the feeding zone characterised by rich areas of larger food items. “Thus it follows that seasonal migrations are not due to following the shifts of hydrological fronts, but are associated with seasonal changes in feeding area, which are different for the young and adults”.

An estimate of the average abundance of the principal food of *T. s. murphyi* in the areas discussed, for the upper 200 m layer over the grazing area, was approximately 50 million tons (M t). The food coefficient of planktivorous fish is 7–10, indicating that the 50 M t of forage in the area may produce 5–7 M t of planktivorous fish.

Springtime ascent of proportions of this biomass from being sequestered as wintering stocks, at depths greater than 200 m beyond the reach of jack mackerel, is “probably not simultaneous [for all areas] but is stretched over a lengthy period or repeatedly over the course of the spring–summer season. Therefore the high biomass of calanoid copepods remains in the surface layers throughout a large part of the summer [only descending into deeper layers in the autumn]”.

Gorbatenko (1988)

This work aimed to study the diet of *T. s. murphyi* in the SWPO in an attempt to understand its behaviour, "and in particular the reasons for the formation of its accumulations and their stability". A quantitative-weight method was used to examine 101 jack mackerel stomachs, and full biological analysis was performed on more than 500 specimens including a visual examination of their food. Fish were collected from 20 stations in a vast area within 97° 17'–140° 20' W, and 38° 24'–47° 43' S, between 10 January and 31 March 1985, and plankton tows were performed in parallel. Work was split between five sectors, with sectors 3–5 being more southerly and westerly than the first two.

The plankton exhibits distinct latitudinal zonality. In the north coelenterates and salps dominate (more than 60%), with crustaceans (particularly euphausiids) poorly represented (6%). In the southern sectors (3–5) salps were almost absent and crustaceans increased.

Euphausiids are the most preferred item in the diet of *T. s. murphyi*, but in the northern sectors they are poorly represented in the diet, with salps (*Pyrosoma* is specified) representing more than 60% of total food items by weight. In the southern sectors, crustaceans are more important, with salps and pyrosoma present in small numbers. Large jack mackerel at the southern periphery of the habitat range often include the larvae of squid and fish; mainly the families Gonostomidae (*Vinciguera boops* and *V. lucetia*), Myctophidae (*Smybolophorous boops*, *S. barnardi*, and Trichiuridae spp.). A similar diet has been described for *T. s. murphyi* in the Peruvian upwelling region.

Evidence that euphausiids are selected by the mackerel came from the third and fourth sectors in February and March respectively, where their numbers were no more than 20% in the plankton but they were the main component of the diet. Diet composition varies with time.

A drop in feeding intensity was observed during the day, corresponding with the vertical plankton migration. Between 0600 and 1000 h 70% of individuals' stomachs were empty and 30% contained some remains from the nocturnal feeding. Daytime feeding peaked between 1000 and 1400 h, and nighttime feeding occurred between 1800 and 0200 h. Maximum coefficients of fullness were observed at 1400 and 0200 h. Mean daily food intake was 4.7% of jack mackerel body weight.

General papers.

Elizarov et al. (1993)

This paper reviews a considerable amount of information on *T. s. murphyi* with particular reference to its oceanic migration and distribution, and presents a number of results and hypotheses based on the 13 years from 1978 "of study and exploitation of resources in the southeastern Pacific", and "(from 1980) in the southwestern Pacific, more than 200 investigatory and collection expeditions," collecting data "on the biology, distribution, behaviour, and living conditions of the Peruvian jack mackerel in pelagic oceanic waters."

The paper refers to work by Bogorov (1967) who classified the transoceanic zone from South America to New Zealand as being among the most highly productive regions of the Pacific. Using virtual population analysis (VPA) it was determined that in the 5–7 years up to the publication of this paper jack mackerel biomass has remained stable, varying within 12–22 M t in total: 1.3–2.4 M t in the northern SEPO, 10–14 M t in the southern SEPO and eastern part of the SWPO, and 6–8 M t in the central and western SWPO. An acoustic trawl survey in the SWPO in 1987 was used to estimate total biomass in this region as 8 Mt (Nazarov & Nesterov 1990). Based on the biomass of the plankton (about 50 M t), jack mackerel biomass was estimated at about 5–7 M t (Vinogradov et al. 1991). "Work performed between 1979 and 1982 [has] shown that the jack mackerel form[s] commercial concentrations from 78 to 160 °W."

Reference was made to New Zealand catches near the Snares Islands in late March 1990 where large specimens were taken, mostly with a length range of 44–63 cm, an average length of 58.3 cm, and a modal length of 61 cm. It is stated that this is typical of fish living at the extreme of their range. It is concluded that the appearance of *T. s. murphyi* in New Zealand waters in the mid 1980s is a result of the growth of the population in the open waters of the South Pacific and its migration in a generally western direction.

The phrase “jack mackerel belt” is used for the first time to describe the distribution of *T. s. murphyi* across the South Pacific. It is described as having a north-south breadth of “15 degrees or more” across “the southern subregion of the SEPO and SWPO” which varies with season as “winter groups concentrate mainly in the north of 40 °S, [and] in summer farther south than 40 °S”; this is summarised as “more or less spans the southern part of the Pacific Ocean”.

The paper suggests that El Niño events influence the composition of coastal communities, and refers to the “catastrophic event of 1972–73” and its effect on the anchovy population of the SEPO, with the subsequent dramatic increase in abundance of other pelagic planktivores like mackerel (*Scomber japonicus*), sardine (*Sardinops sagax*), and jack mackerel, as described by Zuta et al. (1983). The result was that “these species began to occupy the ecological niche made available by the disappearance of the anchovy,” and “by the end of the 1980s the total catch of the primary pelagic fishes in the region — anchovy, sardine, jack mackerel, and mackerel — had almost reached the level of the anchovy catch during the late 1960s and beginning of the 1970s (12–13 M t).”

Similar fluctuations are suggested for oceanic waters, with the result that during years of El Niño the Peru-Chile countercurrent, which carries nutrient-enriched equatorial waters to the far south (48–52 °S), becomes highly intensified. This intensification is also observed in the upwelling of the subantarctic divergence zone which “leads to the increase in productivity of the water in the jack mackerel belt”, and “favourable conditions [being] created for pelagic fish.” It is assumed that because of the scale of fluctuations in oceanic and atmospheric conditions in this region, changes occur almost simultaneously in coastal and oceanic waters, providing the population of jack mackerel that had begun to increase rapidly in size as it invaded the niche left available by the declining anchovy, with a niche that itself underwent major expansion.

A brief summary of previous attempts at population analysis in the South Pacific is given, showing that results are highly contradictory, from the two to four or more independent populations suggested by Koval (1984), Alekseev (1986), Koval & Gordeev (1987), Nekrasov & Karataeva (1987), Nekrasov & Timokhina (1987), and Kalchugin (1992), to a single population or pseudopopulation suggested by Parin (1984, 1988), Evseenko (1987), and Nazarov & Nesterov (1990). Elizarov et al. hypothesise that two interdependent subpopulations exist within the jack mackerel’s broad range — a coastal and an oceanic — but that their relationship is unclear.

Generally, small fish are found in the warmer peripheries of frontal zones of water masses, and large fish in colder waters. This probably explains the predominance of smaller fish in catches in the north of the SEPO, outside the fishing limits of Peru and Chile, compared with the predominance of larger fish in catches from within Peruvian waters that are essentially cold waters of the Peru current. Fish size increases in the south of the SEPO and SWPO from east to west, with large fish (45–63 cm or more) predominating at the western extent of the range. This was especially true in the SWPO in the early years (1980–81). In later years (1987–90), there was “significant renewal of the oceanic subpopulations in the central and western parts of the range that is connected with the appearance in oceanic water of schools of fish from very abundant generations in the SEPO, particularly those of 1985–86 (Nazarov & Nesterov 1990) and their rapid assimilation into new productive regions in the South Pacific”. This regeneration of oceanic subpopulations tends to occur in anomalously warm years, like the El Niño years of 1982–83, 1987, and the end of 1991. The largest changes in spatial distribution of size groups and size-age structure of aggregations also occur during these years.

By contrast, during years of normal or near-normal oceanographic conditions the size composition of jack mackerel catches was constant over several years, and evidence is presented to support the suggestion of relatively stable annual recruitment in the fishable stocks of the oceanic subpopulation.

The paper presents an extensive description of the distribution of reproduction and early stages of development. Spawning occurs from September–October to February–March in Peruvian and Chilean coastal waters and in almost all oceanic pelagic waters of the jack mackerel belt; it begins 2–3 months earlier in the north and west. The southern boundary of the egg and larvae distribution occurs at about 41–42 °S, with eggs being found in discrete patches of low density to the Equator in the northern region of the SEPO, and to a distance of 300–500 nautical miles from the coast of Peru and northern Chile. Dense spawning aggregations and high densities of eggs (over 250–500 eggs m⁻²) are “encountered mosaically”.

Three main areas of reproduction, where egg concentrations were found to be the most dense, are described for “oceanic subpopulations”, with particular size classes spawning in each area: 3+ and 5+ fish of mean length 31–36 cm at 78–90 °W, 38–42 °S (“the eastern centre for spawning”); fish older than 4+ and larger than 34 cm at 105–125 °W, 35–38 °S (“the central centre”); larger fish at 130–155 °W, 35–40 °S (“the western centre”). Sometimes the central and western centres are combined into one.

Based on encounter data, distributions of jack mackerel in the first year of life are presented. Specimens in the 15–20 cm range were rarely reported, but their frequency increased in 1987–88 “evidently as a result of the redistribution of the fish in the region due to the effects of El Niño, with fish moving into more productive oceanic waters.” This was also observed in the El Niño years of 1982–83 and late 1991. Yearlings and 2-year-olds are present only in small numbers in more western areas, which “may suggest that these fish cannot complete their full life cycle here”.

This paper calls for “strong international collaboration between Ecuador, Peru, Chile, New Zealand, Australia, Russia, and other governments to resolve these questions” related to the population of *T. s. murphyi* in the South Pacific.

Serra (1991)

The scope of this paper is wide ranging, reviewing the “distribution, abundance, fisheries location, landings, size composition and reproductive aspects of jack mackerel [*T. s. murphyi*].” It concludes that there are two sub-populations in the southeast Pacific, one off Peru and the other off Chile, and describes a transoceanic distribution of jack mackerel along the Subtropical Convergence Zone associated with a large increase in abundance over the 20 years to 1991. It also describes a seasonal migration between coastal and oceanic waters for the Chilean subpopulation, and relates this to “reproductive and trophic processes.” “This migration forms a pattern which determines the seasonal availability of the resource in the coastal and oceanic fisheries and establishes an important factor for stock assessment.”

A summary of depths at which aggregations of *T. s. murphyi* have been described are given: Guzman et al. (1983) used hydroacoustic equipment to record it down to 250 m off the coast of northern Chile; in central and southern Chilean waters, Bahamonde (1978) described it to 300 m; and Japanese trawlers have recorded it to depths of 300 m beyond the Chilean EEZ (Anon. 1984 & 1985).

Reference is made to catches off Ecuador (which are described as unusual), the entire coast of Peru with highest concentrations in the central zone, and along most of the coast of Chile, with main fisheries concentrated in the north (from the border with Peru at 18 °S, to Antofagasta at 24 °S), off Coquimbo at 30 °S, and off Talchuano at 35–38 °S. The Chilean fishery is predominantly purse-seine with a very minor component (several thousand tonnes) by bottom trawl. In Chile, 95% of catch is converted into fishmeal and oil; the remainder is canned or frozen for human consumption.

A large fleet fished in the southeast Pacific beyond the Chilean EEZ that consisted mainly of Soviet midwater trawlers (the Soviet fleet has not fished there since 1992 — Alexander Nesterov, Atlantic Scientific Research Institute of Marine Fisheries and Oceanography (AtlantNIRO), Kaliningrad, pers. comm.). At the time of this paper (1991) the location of this fleet's fishery was south of 37 °S, "westward from the limit of the [Chilean] EEZ to about 90 °W." It also operated between Antofagasta and Coquimbo, and at position bounded by 39–45 °S and 100–120 °W.

Although catches occurred year-round, the fishery was seasonal with most being taken in Chile from January–February to June–July. In Peru the fishery occurred "in the first half of the year."

Size compositions of Chilean and Peruvian catches are compared. A conversion factor was used ($FL = 0.3873 + 0.8893 TL$) because Peru uses total length (TL) compared with Chile's use of fork length (FL). The paper references sources of information for the oceanic fisheries off Chile as: research surveys by the Japan Marine Fishery Resource Research Centre (JAMARC); a research survey by JAMARC and the Chilean fisheries research institute, Instituto de Fomento Pasquero (IFOP); and a study in the early 1980s by an East German supertrawler in the fishing area within 39–46 °S, and the EEZ boundary of Chile to 83 °W. Generally, fish from all areas have a similar size composition which roughly reflects the results of Lambert & Sievert (1982): range = 25–50 cm FL, mode between 32 and 35 cm FL. The similarity is remarked upon and the "near absence in the catches of specimens larger than 40 cm and less than 20 cm is noteworthy when we consider that the jack mackerel attain sizes of about 70 cm FL. The bulk of the catch (25–35 cm FL) is 3–7 years old.

A summary of areas of highest concentration is given, with estimated biomass off Peru ranging between 5 and 9 M t during 1980–83. Hydroacoustic surveys were used to identify positions of several large concentrations off Chile which were estimated as having a total biomass of 4.6–8.9 M t during 1978–83.

Spawning occurs along most of the coast and according to Santander & Flores (1983) extends to more than 120 nautical miles offshore; it appears poor compared with results obtained off Chile, but this may be related to annual variation. Gorbunova et al. (1985) recorded Peruvian spawning across a 15 nautical miles coastal belt in 1978, with spawning to 270 nautical miles offshore in 1982. According to Abramov & Kotlyar (1980), spawning off northern Peru in 1972 and 1973 occurred between June and March, peaking in September–October, which compared favourably with evidence compiled by IMARPE (1986). Muck et al. (1987) analysed 81 cruises from between 1964 and 1986 and stated that the main spawning area is located about 200 nautical miles offshore.

Spawning off Chile ranges from the Peruvian border, at about 18 ° 30 'S, to at least 40 °S. The main area is from Antofagasta south with the highest concentrations found between 33–38 ° 30 'S. Eggs and larvae are distributed well beyond 200 nautical miles offshore, and possibly reach 800 nautical miles. Evseenko (1987) found eggs and larvae at 900 nautical miles off the Chilean coast (between 40–42 °S and 80–88 °W).

There is agreement on the timing of spawning in Peruvian waters between July and March, peaking during spring (September–October) by Abramov & Kotlyar (1980), Santander & Flores (1983), and Zuzanaga (1986). A similar time frame has been described in Chilean waters by Rojas & Mujica (1981), but others (Basten & Contreras 1978, Serra et al. 1979, Martinez et al. 1986, 1987, Böhm et al. 1987) described Chilean spawning beginning in spring and continuing to the end of summer.

First spawning has been described at 25 cm FL by Abramov & Kotlyar (1980), 23 cm TL/21 cm FL by Dioses et al. (1989), based on histological examination of ovaries, 22 cm (Marcelo Oliva Morena, Instituto de Investigaciones, Universidad de Antofagasta, Chile, pers. comm.), and 23 cm (Basten & Contreras 1978).

According to Serra & Zuleta (1982), Serra (1983), Tsukayama (1983), and Jordán (1983) there has been an increase in southeast Pacific abundance of *T. s. murphyi* since the early 1970s, which has coincided with an increase in range.

Seasonal changes in availability in both the neritic and oceanic zones are explained by the jack mackerel's spawning and feeding behaviour: it migrates from coastal waters to spawn in oceanic waters, and returns to coastal areas to feed. This has been shown by the distribution of eggs and larvae, hydroacoustic surveys, seasonal variations in landings, and in deeper seas by seasonal changes in the CPUE of midwater trawlers.

Larvae are adapted to oceanic conditions. They are more robust and stronger than earlier stages of sardine and anchovy larvae. The mouth is proportionally larger and they feed selectively on particular planktonic organisms. Copepodite stages of copepods are their main source of particulate food; it is postulated that they detect food by colour, and their larger mouth allows the ingestion of particles about three times larger than sardine larvae of a similar size (Arthur 1976).

This paper suggests that "their greater strength and mouth size, and their ability to select large coloured copepods can be explained by their greater need to search more for their food." Selection of larger particles offers more calories ingested per energy expended (Theilacker & Dorsey 1980), and an increase in particle diameter by a factor of 2.5 increases calorie intake by a factor of 10 (Hunter in Theilacker & Dorsey 1980).

Theilacker (1986) showed that "starvation is a major cause of mortality of first feeding jack mackerel larvae in far offshore waters." At 350 km offshore about 70% of first feeding larvae were starving per day, which contrasts with 12% of larvae collected near islands and banks. This mortality decreases to about 1–3% after a couple of weeks of growth.

4.2.2. Length frequencies

Generally, length frequency distributions do not indicate any gross changes over time in the maximum size of *T. s. murphyi* inhabiting New Zealand waters, either in the trawl survey data (Figure 11) or the observer data (Figure 12). At the other extreme, however, there does seem to have been a change. Small fish (under 35 cm FL) are evident in both series between 1992–93 and 1996–97, with a minimum size of 7 cm FL recorded in the trawl survey data in 1995–96. Minimum size in the observer data is somewhat larger at 24 cm FL in 1996–97. Small fish were also recorded in the observer data in 1990–91 and 1997–98, but not in the trawl survey data.

A finer scale examination of the length data by area shows that small fish in the trawl survey data are mostly from inshore trawl surveys on the southeast coast of the North Island south of East Cape (Figure 13). In 1993–94 (research voyage KAH9402) there is evidence for a cohort of small fish centred at 10 cm. In 1994–95 (research voyage KAH9502) few small fish were taken, but in 1995–96 (research voyage KAH9602), there are at least two, and possibly three, modes of small fish apparent. The smallest is centred at 11 cm, and the second ranges between 16 and 29 cm, with evidence for modes centred at 17–19 cm and 23–25 cm, although the sample sizes are too small to be sure.

Small fish were also recorded in the west coast South Island trawl survey series in 1993–94, 1994–95, and 1996–97 (Figure 14), although the numbers were very low. Small fish in the east coast South Island series (Figure 15) are not significantly smaller than in the main distribution and occur in very small numbers. There are no other instances of small fish from trawl survey data.

Finer scale analysis of the observer data indicates that almost all small fish were taken in JMA 7 (Figure 16) except for one fish in JMA 3 in 1992–93 (Figure 17). Most small fish from JMA 7 were taken in 1994–95 and 1995–96 during January–March (Figure 18), and a little later in 1996–97 during

April–June (Figure 19). These fish fall within a similar range in all years, between about 28 and 37 cm.

A comparison of length frequency distributions from the Chatham Rise (Figure 20) and the Stewart Snares shelf (Figure 21) suggests that there may be a difference in mean fish size between the two areas, but statistical tests on the means in each year were not significant.

4.2.3. Sex ratios

Estimates of sex ratios from trawl survey and purse-seine shed sampling are given in Table 4. In almost all cases there is a high predominance of males, generally between about 60 and 70%. There are two lower values at 50 and 44%.

There appears to be a difference in the mean proportions between area 3 (Chatham Rise) and 4 (the Stewart-Snares shelf). Although this is not clearly significant, possibly because the sample sizes are small particularly in area 4, the difference may become clear with more data.

4.2.4. Examination of fish and plankton collections

The fish collection at Te Papa contained only three records of small juvenile *T. s. murphyi*.

Te Papa code number	Size of specimen(s) mm	Collection date	Locality	Number of specimens	Source
P23607	88	26/2/88	Off Mahia Peninsula	1	RV <i>James Cook</i> survey
P29978	77.5	25/1/93	Waipiro Bay, East Cape	1	National Museum field trip
P31970	91.5–121.5	28/1/95	South Taranaki Bight	15	Scientific observers trip

An examination of jack mackerel larvae with reference to descriptions published by Ahlstrom & Ball (1954) (*T. symmetricus*), Neira et al. (1998) (*T. declivis* and *T. novaezelandiae*), and Santander & Castillo (1971) (*T. s. murphyi*) proved that there were no features by which *T. declivis* and *T. s. murphyi* could be distinguished from one another. Specimens of *T. novaezelandiae* could be distinguished because developmental stages were reached at a smaller size than the other two species.

4.2.5. Reproductive condition and sea surface temperature

Maturing and mature *T. s. murphyi* are widely distributed in New Zealand waters. Positions of sets where adults with gonads at stage 3 or greater are shown in Figure 22. This distribution is not indicative of the numbers, particularly north of East Cape, where all positions are from purse-seine sets and each represents a number of sets, often by different vessels.

Numbers of fish are presented, along with year, month, sex and gonad stage, and SST in Table 1. No strong relationship between gonad stage and SST is evident. Although low gonad stages sometimes occur at low water temperatures (e.g., female stage 3 with SST of 11 °C), there are others where high stages occur at low SST (e.g., female stage 4 and 5 with water around 11 °C). Sometimes larger numbers of mature fish are taken when the SST is 15 °C or more, but large numbers have been taken at the lower lower temperatures of 11.9, 12.5, and 13.8 °C.

There are a number of cases where adults have been collected in late stage maturity, and often both sexes are included. This has occurred particularly in east Northland, the Bay of Plenty, the South Taranaki Bight, and the central west coast of the South Island. Observer sampling is limited to recording female gonad stages only.

4.2.6. Distribution of prey species

Adult feeding. A number of adult feeding studies have concluded that *T. s. murphyi* is highly adaptable in its feeding strategy (Konchina 1979, Andrianov 1985, Gorbatenko 1988). Although there is a preference in adults for euphausiids, which are actively selected (Gorbatenko 1988), they are able to feed on a wide range of prey species. The most extensive list was presented by Konchina (1979) and it is presented here as Appendix 1.

The effectiveness of the feeding strategy of *T. s. murphyi* is further illustrated by the trophic analyses of Konchina (1980, 1983) who identified this species as a tertiary consumer, mainly because it includes a variety of fish in its diet.

Larval feeding. Arthur (1976) discovered that in first feeding larvae of about 3.25 mm, copepodite stages of copepods contribute the greatest bulk of food (Table 5), and that the harpacticoid copepod *Microsetella norvegica* is actively selected. He suggested that its bright colouration or low level of transparency may be important in this selection. In larger larvae, calanoid copepods become important. The high feeding fitness of *T. s. murphyi* compared with its main competitors (the anchovy and sardine), resulting from its much larger mouth size and looped gut, was suggested as an important reason for its success.

Prey species in New Zealand waters. Generally, zooplankton studies indicate widespread dominance of a range of copepod species, including studies in Hawke Bay during September 1976 by Bradford et al. (1980), at East Cape in 1978 by Bradford & Chapman (1988), off Westland in 1979 and 1982 by Bradford (1985), off the west coast of the South Island in August 1987 by Bradford-Grieve et al. (1996), and in the Subtropical Convergence region near New Zealand in spring 1993 by Grieve et al. (1996).

Some information is available on the distribution of euphausiids. The work of Bary (1956) showed an extensive assemblage of the species *Euphausia lucens*, *Nyctiphanes australis*, *Thysanoessa gregaria*, and *Nematoscelis megalops* between Cook and Foveaux Straits. *N. australis* has a distribution restricted to coastal waters of New Zealand and South Australia (Sheard 1953) and was listed as one of the most common species in a study of the zooplankton distribution off the west coast of the South Island by Bradford (1985) in June 1979 and February 1982 where it was measured in large numbers (i.e., more than 100 m⁻³ at one or more station) during both trips. It was absent from a study off East Cape in 1978, where sampling was beyond its coastal range, but other species were present in this latter study, including *N. megalops*, *T. gregaria*, *E. recurva*, *E. similis*, and *E. spinifera*. Although the *Euphausia* spp. were listed as secondary species (i.e., present at less than 50% of stations) in areas where they occurred, *T. gregaria* was a "subdominant" species in three assemblages with occurrences ranging between 50 and 80%, and *N. megalops* was dominant in one of the four assemblages (i.e., 100% occurrence). *Euphausia lucens*, *E. similis*, and *N. australis* were described by Bradford-Grieve et al. (1998) as being dominant in the over 1000 µm size fraction during spring in the Subtropical Convergence region near New Zealand.

Shed sampling data from the purse-seine catch of jack mackerels in Fishstock JMA 1 between 1994 and 1996 (Table 6) shows a predominance of euphausiids in *T. s. murphyi* gut contents. In 1994 and 1995 most of the stomachs that were opened (94 and 87% respectively) were at least 50% full of euphausiids. This was also true in 1996, although there was a wide variety of prey items found. Of the 648 fish sampled over the three years, 636 contained euphausiids.

A summary of prey items for all three jack mackerel species in New Zealand waters showed that *T. s. murphyi* (JMM) includes a greater variety than does *T. declivis* (JMD). Data are from trawl surveys. Gut contents are not available for *T. novaezelandiae*.

	APH	COP	CRU	EUP	Crustacean sp.		Squid sp.		Salps	Fish sp.	
					MUN	PAS	ESQ	SQX	SAL	LAN	FIS
JMD	✓			✓					✓		
JMM	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓

Codes from left to right represent amphipods, copepods, crustaceans, Euphausiids, *Munida gregaria*, *Pasiphaea* sp., *Enoplateuthis* sp., squid, salps, lantern fish or Myctophidae, and fish.

Information is also available for other prey items. For example, salps are known to be widespread in New Zealand waters. They were described by Bradford & Chapman (1988) as "visually the most conspicuous constituent of the zooplankton assemblage at a number of stations" during a study of epipelagic zooplankton assemblages off East Cape in January 1978. Their distribution was patchy on the west coast of the South Island in June 1979, but at some stations *Salpa fusiformis* was taken in large numbers, and comprised the main part of the large quantity of zooplankton taken (over 1000 mg m⁻³).

4.2.7. Development of eggs and larvae and their transport in ocean currents

Eggs of *T. s. murphyi* are positively buoyant and are found in the upper 60 m of the water column (Evseenko 1987, Loeb & Rojas 1988), corresponding to the upper mixed layer and upper part of the thermocline (Evseenko 1987). They would be moved by prevailing winds and surface currents. From the work of Farris (1961) we know that the development time for eggs of *T. symmetricus* can be expressed by the relationship $\log Y = a + bX$, where Y is hours of development, X is temperature in °C, $a = 3.257$, and $b = -0.088$. He showed that growth rate of larvae can be expressed with a similar relationship, where Y is the length in millimetres and X is days after hatching. He estimated two values for each of the regression parameters, one for the early period of larval development from days 1 to 3, and a second for days 4 to 8: the values for a are 0.328 and 0.486, and b are 0.067 and 0.013, respectively.

The method of Farris (1961) is chosen in preference to results presented by Esin (1993) because his model provides a flexible methodology that can easily be applied. The exercise is not to be precise but to provide approximations for interpretation of the New Zealand data. Esin's (1993) estimates differ from those of Farris (1961), suggesting that there are factors operating in development that have not been accounted for here.

A summary of the current knowledge about transport rates in New Zealand waters provided by Stephen Chiswell (NIWA, Greta Point, pers. comm.) indicates a value of 10–20 cm s⁻¹ in coastal waters around New Zealand. In determining approximate destinations of *T. s. murphyi* larvae spawned in the various areas shown in Figure 17, the information given above can be used, coupled with SST values at the time of spawning (see Table 1), and the direction of currents. Based on the summary of currents presented by Heath (1985), and the additional movement of the D'Urville Current up the Wairarapa Coast suggested by Stephen Chiswell (pers. comm.), it seems that net flow from most possible spawning sites in New Zealand waters is toward the Wairarapa coast.

Usually, eggs spawned off east Northland will be transported quite quickly into the East Auckland current by prevailing northwest winds, where they will be transported to the southeast and eventually into either the East Cape Gyre or the Wairarapa Gyre (S. Chiswell, pers. comm.). At an SST of 21 °C, and assuming a transport rate of 15 cm sec⁻¹, it will take 26 h for hatching to occur, at which time the larvae will be about 14 km from their point of being spawned; at 15 °C the distance covered before hatching will be about 47 km.

Given that East Cape is about 300 nautical miles (or 555 km) from North Cape, the larvae now have about $555 - 47 = 508$ km to complete the distance. Assuming an initial temperature of 15°C , which is consistent with that obtained for Cape Brett in August 1995 (see Table 1), this will take about 39 days. Using the growth relationship of Farris (1961), larvae will attain a length of 9.84 mm at the end of 39 days.

Eggs spawned in the South Taranaki Bight will be transported through Cook Strait and up the Wairarapa Coast by the D'Urville current (S. Chiswell, pers. comm.). Estimating this distance as about 400 km, the distance will be completed in about 30 days. Temperatures associated with spawning in the South Taranaki Bight are 14°C in June and 19.3°C in February, resulting in hatch times of 105.9 and 36.19 h respectively. At hatching, larvae will be 57 and about 20 km from their point of being spawned. At the time of arrival at the Wairarapa coast destination, larvae will be 6.76 or 7.36 mm, for eggs spawned in June and February respectively.

An SST of 13.8°C coincided with the presence of mature fish off the central west coast of the South Island in July 1998. Based on the summary of Heath (1985), the transport direction would be northward in the Westland current with probable continuation in the D'Urville current and subsequent movement towards the Wairarapa coast. Based on a distance of 400–450 km from the central west coast to the South Taranaki Bight, larvae from these spawning areas would be about 7 mm long by the time they arrived there, and 19 mm upon reaching the Wairarapa coast.

4.2.8. Approximating juvenile size at age

According to Ahlstrom & Ball (1954), the larval phase ends at the completion of fin formation, at which point the young jack mackerel are classed as juveniles. This stage approximates to a length of 16 mm in *T. symmetricus*, although Ahlstrom & Ball (1954) warn that the metamorphosis is not well defined in this species. If we assume that Farris's (1961) growth relationship holds throughout the larval phase, then we can estimate the time at which the early juvenile stage occurs as

$$X_{\text{days}} = \frac{\log l_{\text{mm}} - a}{b} = \frac{\log 16 - 0.486}{0.013} = 55 \text{ days}.$$

Kaiser (1973b) used otoliths and length frequencies to estimate growth in *T. s. murphyi*. He back-calculated to estimate the mean length at the end of year one as 17.5 cm, which agreed with a number of other studies (see summary by Kochkin 1994). Based on this information and assuming linear growth throughout the juvenile stage in the first year, we can approximate the mean juvenile size at the end of each month.

At the beginning of the juvenile phase there are $365 - 55 = 310$ days remaining in the year, and $175 - 16 = 159$ mm still to be grown by the average larva. Thus, we estimate the mean monthly increment as 15.9 mm based on $310 \text{ days} = 310/31 = 10$ months. A monthly increment of about 16 mm seems reasonable, given that the first two months of larval growth have produced a total length of about 16 mm, and that growth throughout the first year will accelerate within the overall sigmoidal growth curve, and possibly level off a little based on Kaiser's (1973b) suggestion that the highest growth occurs during the first year. The final result is a series of lengths.

	Larval phase		Juvenile phase (to end of first year)									
Days	28	55	86	117	148	179	210	241	272	303	333	365
Months	1	2	3	4	5	6	7	8	9	10	11	12
Length (mm)	7.08	16	32	48	64	80	96	112	128	144	160	176

This can be used to determine the approximate ages and spawning dates of small juveniles from the Te Papa fish collection. Possible spawning areas can be inferred from upstream locations.

Te Papa code	Approximate age (months)	Approximate spawning date	Possible spawning area
P23607	6.5	12 August 1987	East Northland-BOP*
P29978	6	25 July 1992	East Northland-BOP*
P31970	7-9	28 May 1994	Westland-South Taranaki Bight

* Bay of Plenty

4.3 Discussion

4.3.1. Biological features of *Trachurus symmetricus murphyi*

A number of features of the biology of *T. symmetricus*/*T. s. murphyi* have been identified as important in its dramatic increase in abundance in the SEPO and subsequent range expansion into oceanic water far beyond the South American shelf. Serra (1991) has postulated that the larvae are adapted to oceanic conditions and Arthur (1976) has shown that they are more robust and stronger than larvae of their main competitors in Californian waters, and that their mouths are larger, providing more than a ten-fold potential advantage in calorific content of food particles. Adults employ an extremely adaptable feeding strategy (Konchina 1979, Gorbatenko 1988, Vinogradov et al. 1991) with the ability to feed on a wide range of prey items (see Appendix 1) and the advantage over sardine and anchovy and other zooplankters of being tertiary consumers. Their spawning strategy as indeterminate batch spawners ensures that they are able to spawn immediately conditions become favourable (Lisovenko & Andrianov 1991, George 1995).

Konchina (1980) summarised these advantages of the jack mackerel's fitness as evidence that: from its earliest life history stage it displays divergence from two of its main competitors, based on its larval and later-stage feeding strategies; that its heterotrophic nature (i.e., ability to inhabit various biotopes) allows it to vary its behaviour as conditions change; and that the larva's ability to inhabit two biotopes allows it to expand its foraging and geographic range. These features are important in discussing the potential for *T. s. murphyi* to establish a self-sustaining population in New Zealand waters.

4.3.2. Reproductive condition, SST, and prey distributions

The results of the present study indicate that New Zealand waters should support establishment of a population of *T. s. murphyi*. SSTs range from 11–21.1 °C, which is similar to the 10–21 °C range described by Farris (1961). Based on egg and larval distributions, Gorbunova et al. (1995) concluded that the temperature requirement of normal embryonic development of *T. s. murphyi* has a wide range. The lower limit of viability is unclear, but there is evidence from Evseenko et al. (1990) that temperatures higher than 22 °C can reduce spawning strength. Conditions in New Zealand are close to the optimum 15.5 °C shown by Farris (1961).

Prey distributions generally comprise the types preferred by *T. s. murphyi* (Bradford et al. 1980, Bradford & Chapman 1988, Bradford 1985, Bradford et al. 1996) but there is little information for some areas where spawning is known to occur, including the South Taranaki Bight, the southeast coast of the South Island, the Bay of Plenty, and general information on the east Northland coast. Information from Bradford et al. (1996) shows that species preferred by first feeding larvae are abundant, including the harpacticoid copepod *Microsetella norvegica* which Arthur (1961) showed to be actively selected from an assemblage in which its numbers were low relative to other species.

Unpublished results from a NIWA research programme examining the ecosystem of the inner and outer Hauraki Gulf provides some insight into this area. Production during spring is based on the

processing of mineralised nitrogen brought into the photic zone by local upwelling, and the plankton is dominated by autotrophic organisms like large diatoms, blooms of dinoflagellates like *Noctiluca* spp., and salps. This assemblage largely dissipates by December when the copepod population begins to grow. During December the system is dominated by microzooplankton, like ciliates and larval copepods, and the abundance of adult copepods increases throughout the summer. Summer production is mostly the result of the regeneration of nitrogen in the form of ammonia (John Zeldis, NIWA, pers. comm.).

Whether this system extends into a region that would benefit developing *T. s. murphyi* is unknown, but the dominant assemblage in December is ideal for early larval feeding, and the summer plankton would support later stage larvae, juveniles, and adults. The transient nature of the system indicates that only the progeny of spawning events occurring within a relatively short time span would be able to take advantage of the forage. Nevertheless, when the timing was right, the change from larval to adult copepods would suit development from early feeding to older stages of *T. s. murphyi* larvae, according to the sequence described by Arthur (1976) and Vinogradov et al. (1991). But if the timing was wrong spawning could easily fail, given the high egg and/or larval mortality under favourable conditions shown by Farris (1961) and Esin (1993).

4.3.3. Fish size: fish collections and length frequencies

The two small juveniles from the Te Papa collection found in the East Cape-Mahia area are about 6–7 months old, with approximate spawning dates of late July–early August. Assigning a spawning area somewhere between East Northland and the Bay of Plenty is reasonable, given its upstream position, but it is impossible to be more precise. Their estimated ages are much greater than the time of 42 days estimated as the transport time from North Cape to East Cape for larvae in the East Auckland current. A similar level of uncertainty is evident for the 15 small juveniles collected in the South Taranaki Bight.

Small specimens taken in research trawl surveys are mainly from the East Cape-Mahia area. Most of these are from around Waipiro Bay about 25 nautical miles south of East Cape, and one of the Te Papa specimens was also from Waipiro Bay. This suggests that there may be quite well defined nursery areas in this area, with specimens taken at Waipiro Bay in three years: 1992–93 (Te Papa specimen), 1993–94 (KAH9402), and 1995–96 (KAH9602). The distribution of trawl survey tows might explain why small fish were not seen on voyage KAH9502.

The cohorts of small fish in the east coast North Island trawl survey data in 1993–94 and 1995–96 are the first evidence of potential recruitment from spawning in New Zealand waters. That the fish are the result of local spawning is based on the observations of Elizarov et al., (1993) who described the eastwards passive movement of larvae and small juveniles in the currents of the South Pacific. This result reflected the eastward movements of larvae and juveniles in the SEPO described by Serra (1991). If the small fish found off East Cape-Mahia had been spawned offshore, they would have spent some time drifting east away from New Zealand, almost certainly preventing the chance of their arriving near East Cape by the age of 6 months.

The Te Papa fish collection contains most samples from the phyllosoma voyages using fine mesh midwater sampling east of New Zealand. All these samples were examined and no specimens of any of the three jack mackerel species were present. However, it is possible that there was bias in the selection of specimens for the Te Papa collection and jack mackerels were not included. There is also some doubt about whether *T. s. murphyi* would have been taken in midwater trawls. Bailey (1989) found juveniles at the surface in the mid South Pacific where he used a dip-net to capture them at night. Our inability to distinguish larvae of *T. s. murphyi* from those of *T. declivis* prevented meaningful data being recorded from the large amount of small-fraction material from these voyages and surveys in the outer Hauraki Gulf.

Together, these factors prevented testing of the hypothesis that early life history stages of *T. s. murphyi* become entrained in the gyre system off the East Coast of the North Island. However, the high concentration of small juveniles in the East Cape-Mahia area and their almost exclusive appearance as 6 month old individuals indicates that this hypothesis may still offer a possible explanation for their earlier whereabouts, although the presence of similar aged juveniles in the South Taranaki Bight is more difficult to explain.

Small fish are represented in the JMA 7 observer length frequency distributions by what appears to be a similar size fraction for three years. This similarity in size between years suggests that sample sizes are too small for modal information to become expressed, causing the distribution to be smeared out and requiring measurements from a lot more fish before peaks become established.

Small fish in the JMA 7 observer data do not appear in the same months in all years. This could be an indication of annual variations in the timing of spawning events, but is more likely to be caused by variations in the timing of observer effort. Highest levels of observer coverage are evident in the January-March quarter (Table 7) since 1992-93 but not for the April-June quarter in 1996-97 when highest levels of small fish were recorded for the year. In 1996-97, observers covered 283 and 26 observed tows for January-March and April-June respectively (see Table 7). It seems clear that the numbers recorded in this case are more likely to be biased downwards, compared with the bias upwards for the earlier years.

There appears to be a difference in the size of the distributions from length data collected on the Chatham Rise and Stewart-Snares shelf by *Tangaroa*. The peaks of the distributions consistently lie at about 48-50 cm in the Stewart-Snares shelf data, compared with 44-47 cm in most years since 1993-94 in the Chatham Rise data. Sample sizes are small in the latter dataset, however, and the distribution for TAN9801 suggests a peak at 49 cm. These discrepancies may be a result of an area effect in the sampling. A t-test determines no significant difference between the two series, but this is probably due to a lack of sensitivity in the test caused by the spread of the data in each series and the degree of overlap in each annual pair.

Length distributions do not simply support the proposal by Elizarov et al. (1993) that the New Zealand population comprises large fish. They reported a modal length of 61 cm for samples taken near the Snares Islands. The ranges of length frequency distributions presented in the present study are usually similar to their results of 44-63 cm (ignoring the small fish), but the modal lengths all lie within 44-50 cm, which is considerably lower. This contrast with their data suggests a larger mean size in the south, a result which reflects the apparent difference in the modal peaks for the two areas (Chatham Rise and Stewart-Snares shelf) in the *Tangaroa* length frequencies distributions.

4.3.4. Sex ratios

Investigation of sex ratios might provide some information on the reproductive status of *T. s. murphyi* in New Zealand waters. Other studies have shown a ratio of about 1:1 male to female (Andrianov 1985, George 1995), which changed in the latter study to one where males were markedly predominant (about 73%). This predominance was coincident with high rates of postovulatory follicles in female ovaries, based on histological examination.

The situation in New Zealand waters is different. The estimated sex ratios are from all areas at different times of the year and almost always result in a high predominance of males. This seems to suggest that the result is not related to spawning condition. Discussion surrounding the interpretation of sex ratios in the literature indicates that a predominance of males can result from higher mortality of larger females when a population is exposed to extreme conditions, because a relatively higher amount of a female's energy is channelled into reproductive fitness (Kerstan 1995).

4.4 Summary: suitability of New Zealand waters for *T. s. murphyi*

Information presented in this study suggests it unlikely that *T. s. murphyi* is under biological stress in New Zealand waters — there is no evidence that food is limiting, and gut contents from individuals taken by purse-seine off east Northland and in the Bay of Plenty consistently contain high numbers of euphausiids. The feeding strategy of *T. s. murphyi* is highly flexible and it has the ability to target a wide range of prey items (Konchina 1979, Gorbatenko 1988, Vinogradov et al. 1991). Other aspects of New Zealand conditions, like the range of SST, also appear to be similar to those on the South American shelf. Kerstan's (1995) suggestion about higher mortality in larger females than males because of their channelling more energy into reproductive fitness is compelling when one considers the degree of physiological stress individuals are likely to undergo while migrating through oceanic waters, particularly during periods when major parts of the oceanic zooplankton assemblage overwinter at depth, beyond the reach of jack mackerel (Vinogradov et al., 1991).

5. CONCLUSIONS

The present study has summarised information to determine the stock structure of *T. s. murphyi* and develop an understanding of the degree to which it has become established in New Zealand waters.

1. A single species of *Trachurus symmetricus* ranges from British Columbia to Southern Chile and from South America to New Zealand and Tasmania. This species includes the Peruvian or Chilean jack mackerel from the South Pacific, widely known as *Trachurus symmetricus murphyi*.
2. Up to four separate stocks are suggested by the data throughout the range of this species: separation is apparent between North and South America, based primarily on the work of Stepien & Rosenblatt (1996); in South America there is evidence for at least two stocks based on results of genetic (Koval 1996, Gonzalez et al. 1996), and generalised studies using distribution, abundance, size composition, and reproductive distributions (Evseenko 1987, Serra 1991); there is evidence for a stock in the SWPO that is independent of SEPO stocks, based on morphological (Kalchugin 1992) and parasite information (Duran & Oliva 1983, Romero & Kuroki 1985, Avdeyev 1992).
3. New Zealand waters are conducive to the establishment of a self-sustaining stock of *T. s. murphyi*: the widespread distribution of prey species and the highly adaptable feeding strategy largely eliminates the possibility of food being limiting; the reproductive condition of specimens sampled here indicates a wide geographical range of fish in maturing and spawning condition; sea surface temperatures are close to the optimum for spawning shown by Farris (1961).
4. Based on length frequency distributions and small juveniles from fish collections there is evidence of successful spawning over three years in New Zealand waters; length frequencies do not indicate any change in the maximum size of *T. s. murphyi* in New Zealand waters since they first appeared in the mid 1980s.
5. Sex ratios indicate that the population is dominated by males in all areas, at all times of the year, possibly as a result of a higher mortality in females as the invading portion migrates through extreme conditions in oceanic water. Based on this line of reasoning, the greater portion of the New Zealand population is recruited from invading individuals.
6. The New Zealand population appears to now be made up of a major portion recruited from invading individuals, and a smaller portion recruited from locally spawned fish.
7. There is some evidence that the east coast of the North Island is an important nursery area for early life history stages of *T. s. murphyi*.

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8. REFERENCES

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Appendix 1: A list of prey species from gut contents of *Trachurus symmetricus murphyi* sampled in Peruvian waters (after Konchina 1979)

The range of food organisms taken by *T. s. murphyi* is very wide, including various planktonic invertebrates — Siphonophora; molluscs, worms, crustaceans, and Chaetognatha — and eggs and larvae of fishes. Off the coast of Peru invertebrates such as molluscs (Gastropoda and Cephalopoda) and Decapoda are represented mainly by larvae.

A list of the food organisms recorded for *T. s. murphyi* is given below.

Amphipoda, Hyperiididae;

Bivalvia;

Cephalopoda: Decapoda (juv.) was stated, but is systematically incorrect — possibly Octopoda was intended; Cephalopoda (larvae);

Chaetognatha;

Copepoda — *Calanus* sp., *Eucalanus attenuatus*, *E. subtenui*, *Eucalanus* sp., *Calausocalanus* sp., *Aetideus bradyi*, *Actideus* sp., *Euchirella bella*, *Euchirella* sp., *Nannocalanus minor*, *Euchaeta media*, *E. rimana*, *Euchacta* sp., *Scolecithrix danae*, *Scolecithrix* sp., *Pleuromamma piseki*, *Pleuromamma* sp., *Lucicutia* sp., *Candacia pachdactyla*, *C. bipinnata*, *Candacia* sp., *Sapphirina* sp., *Corycaeus* sp., *Cirripedia* (larvae);

Decapoda (larvae). Also — *Macrura*, Sergestidae (larvae, juv.), *Macrura* (larvae); Anomura, Thalassinidae (zoea), Galatheididae (zoea, juv.), Paguridae (zoea, glaucothoe), Porcellanidae (zoea), Hippidae, *Emerita* sp. (zoea), Hippidae (zoea), Albuneidae (zoea); Brachyura, Pinotheridae (zoea), Brachyura (zoea, magalopa);

Euphausiacea — *Nyctiphanes simplex*, *Euphausia mucronata*, *Euphausia* sp., *Nematoscelis* sp. (juv.), Euphausiacea (juv.);

Gastropoda (larvae, juv.);

Mysidacea (juv.);

Ostracoda;

Pisces: Engraulidae, Gonostomatidae, *Vinciguerria lucetia*, Gonostomatidae (juv.), Myctophidae (larvae), Scomberesocidae, Perciformes, Normanichthyidae, *Normanichthys crockeri* Pisces (eggs), Pisces (larvae);

Polychaeta;

Pteropoda;

Siphonophora;

Stomatopoda (larvae, juv.).

The two most diverse orders of planktonic crustaceans were Copepoda and Decapoda.

Thirteen genera of Copepoda were recorded: *Calanus*, *Candacia*, *Clausocalanus*, *Corycaeus*, *Eucalanus*, *Euchaeta*, *Euchirella*, *Lucicutia*, *Nannocalanus*, *Pleuromamma*, *Sapphirina*, and *Scolecithrix*.

The following Decapoda were recorded:

1. the larvae and young of the shrimp (*Macrura*), particularly from the family Sergestidae;
2. the larvae (in various stages of development) of Anomura from 6 families: Thalassinidae, Galatheididae, Paguridae, Porcellanidae, Hippidae and Albuneidae;
3. the larvae of crabs (*Brachyura*), including larvae from the family Pinnotheridae.

Euphausiidae were considerably less diversity than the two preceding groups of crustaceans — only three genera were noted: *Nyctiphanes*, *Euphausia* and *Nematoscelis*.

The fish represented five families, Engraulidae, Gonostromatidae, Myctophidae, Scomberesocidae and Normanichthyidae.

Appendix 2: Page index of references summarised in this report

	<i>Page</i>
Alay et al. (1982)	11
Aldana et al. (1995)	10
Andrianov (1985)	20
Arthur (1976)	23
Avdeyev (1992)	10
Bailey (1989)	8
Carrera & Collantes (1978)	19
Chekunova & Naimov (1978)	19
Cubillos & Arancibia (1995)	19
Cubillos et al. (1995)	19
Duran (1980)	10
Duran & Oliva (1983).....	10
Elizarov et al. (1993)	28
Esin (1993)	20
Evseenko (1987)	20
Evseenko et al. (1990)	21
Farris (1961)	21
George (1995)	22
George-Nascimento et al. (1983)	10
Gonzalez et al., (1996)	12
Gorbatenko (1988)	28
Gorbulnova et al. (1985)	22
Gutiérrez (1986)	11
Hildebrand (1946)	8
Kaiser (1973a)	22
Kaiser (1973b)	19
Kalchugin (1992)	8
Kawahara (1988)/Berry & Cohen (1974)	8
Kijima et al., (1988)	12
Kochkin (1994)	19
Konchina (1978)	24
Konchina (1979)	24
Konchina (1980)	24
Konchina (1983)	25
Konchina (1990)	25
Konchina (1993)	26
Konchina et al. (1996)	26
Kotlyar (1976)	8
Koval (1988a)	11
Koval (1988b)	12
Koval (1996)	11
Kovaleva & Gaevskaya (1983)	10
Kuroiwa (1997)	23
Lisovenko & Andrianov (1991)	23
Loeb & Rojas (1988)	23
Machii et al. (1990)	9
Muck & Sanchez (1987)	26
Oliva (1994)	11
Orrego & Machii (1989)	23
Roedel & Fitch (1952)	9
Romero & Kuroki (1985)	10
Salem (1995)	9
Sepulveda & Galleguillos (unpublished results).....	12
Serra (1991)	30
Shaboneyev (1980)	9
Shaboneyev & Kotlyar 1980)	9
Soto & Carvajal (1979)	10
Stepien & Rosenblatt (1996)	12
Suda et al. (1995)	10
Vinogradov et al. (1991).....	27

Table 1: Areas where mature *Trachurus murphyi* have been taken; for sex and gonad stage, M is male, F is female, 3 is developing gonad, 4 is ripe gonad, 5 is running ripe, 6 is partially spent, and 7 is spent. (Sources: Scientific observer data, trawl survey data, purse-seine shed sampling data).

Year	Month	Area	Sex & gonad stage	N	SST °C	Data source
1989	11	Southland Shelf	M4	3	12.3	Trawl survey
1989	12	Mernoo Bank	M3,4; F3	4, 7; 10	14.5	Trawl survey
1990	2	Central West Coast	M3; F7	1; 1	20.5	Trawl survey
1992	7	Challenger Plateau	F5	8	17.8	Scientific observer
1993	6	Challenger Plateau	F3	1	12.8	Scientific observer
1993	11	East Coast South Is.	F3,4,5	31,2,12	11.9	Scientific observer
1994	1	Sth Taranaki Bight	F3,5	3,1	17.5	Scientific observer
1994	2	Sth Taranaki Bight	F3,4,5	29,5,26	19.3	Scientific observer
1994	4	Southland Shelf	F5	1	10.9	Scientific observer
1994	6	Sth Taranaki Bight	F5	2	14.0	Scientific observer
1994	1	Mernoo Bank	M7	1	14.4	Trawl survey
1994	3	Southland Shelf	M7	1	13.2	Trawl survey
1994	12	Cape Brett East Northland	F3,4,5,7	11,20,6,21	19.3	Purse-seine shed sampling
1995	1	Chatham Islands	M3	3	15.3	Trawl survey
1995	2	Southland Shelf	M6,7; F3,7	1,12; 5,7	12.5	Trawl survey
1995	2	Puysegur	M7; F3	4; 1	13.5	Trawl survey
1995	2	East of Catlins	M7; F7	1; 1	12.9	Trawl survey
1995	2	Stewart Island	M6,7; F3,7	1,12; 5,6	12.5	Trawl survey
1995	3	Stewart Island	F3	1	11.6	Trawl survey
1995	2	Cavalli Is. East Northland	M3; F3,4,7	2; 14,1,4	21.1	Purse-seine shed sampling
1995	8	Cape Brett-Mokohinaus	M3,4,5,6; F3,4,5,6,7	5,4,14,62; 4,8,21,1,30	15.0	Purse-seine shed sampling
1995	10	Bay of Plenty	M5,6;F4,5,6	35,37;7,4,2	15.5	Purse-seine shed sampling
1995	12	Mernoo Bank	F3	2	14.1	Scientific observer
1996	1	Southland Shelf	F3	1	12.1	Scientific observer
1996	2	Stewart Island	M7	2	14.3	Trawl survey
1996	3	Southland Shelf	M7	8	11.9	Trawl survey
1996	8	Alderman Is.	M4,5; F3,4,6,7	3,5; 1,1,1,6	15.4	Purse-seine shed sampling
1996	8	Central West Coast South Island	F3	4	12.5	Scientific observer
1996	9	White Island	M5; F4,5,7	11; 1,1,1	15.7	Trawl shed sampling
1996	9	Alderman Is.	M3,4,5; F4,5,7	3,1,33; 4,9,10	15.7	Purse-seine shed sampling
1997	3	Southern Islands	F3	1	11.0	Scientific observer
1998	3	Southland Shelf	F3	3	11.1	Scientific observer
1998	7	Central West Coast South Island	F3,4,5	51,2,38	13.8	Scientific observer
1999	1	Chatham Rise	M7; F3	1, 1	16.8	Trawl survey

Table 2: Esterase genotypes in Peruvian horse mackerel, from two areas, north and south of 30°S. Genetic differences between each pair of samples were tested with χ^2 on allele frequencies. N.B. Rare genotypes have been lumped with the "BC" genotype, as 5/6 rare genotypes were heterozygotes (After Table 1, Koval 1996).

Year	Area	Genotypes			Number of fish	χ^2 1 d.f.	P statistic
		BB	"BC"	CC			
1979-80	1	531	647	253	1431	0.95	0.331
	2	2265	3238	896	6399		
1980-81	1	823	1099	308	2230	2.32	0.128
	2	1215	1546	395	3156		
1981-82	1	819	857	303	1979	3.12	0.077
	2						
1982-83	1	431	450	160	1041	7.59	0.006*
	2	1596	2289	702	4587		
1984-85	1	918	1149	420	2487	0.616	0.433
	2	1754	2688	778	5220		

* significant at the 5% level with a Bonferroni-modified P for multiple tests.

Table 3: Contingency chi-square analysis for 9 loci in two population samples of *T. s. murphyi*. Data from Stepien & Rosenblatt (1996). Bonferroni modified $P = 0.0055$ ($\alpha = 0.05$).

Locus	No. of alleles	Chi-square	D.F.	P
sAH-1	2	0.226	1	0.63477
sAH-2	3	1.163	2	0.55896
ACP-1	2	0.356	1	0.55099
G6PDH-1	3	3.243	2	0.19758
G6PDH-2	3	6.429	2	0.04018
GLUDH	2	4.701	1	0.03015
sIDHP	2	6.571	1	0.01036
MPI-1	2	0.059	1	0.80792
PEP-B	2	5.072	1	0.02431
Total		27.82	12	*0.00588

*Significant difference overall

Table 4: Sex ratios from trawl survey data and purse-seine shed sampling. (Sources: Trawl survey and market sampling databases).

Source*	Number of males	Number of females	Totals	Proportion male	Proportion female	Month†	Area
AEX8903	257	131	388	0.66	0.34	11	3
KAH9105	36	23	59	0.61	0.39	5	1
KAH9205	158	100	258	0.61	0.39	5	1
KAH9306	134	64	198	0.68	0.32	5	1
KAH9406	72	36	108	0.67	0.33	5	1
KAH9618	62	29	91	0.68	0.32	12	1
KAH9701	31	14	45	0.69	0.31	3	2
KAH9809	112	94	206	0.54	0.46	8	1
TAN9106	206	143	349	0.59	0.41	12	3
TAN9212	598	434	1032	0.58	0.42	12	3
TAN9301	421	157	578	0.73	0.27	2	4
TAN9401	194	121	315	0.62	0.38	1	3
TAN9402	971	494	1465	0.66	0.34	2	4
TAN9501	41	17	58	0.71	0.29	1	3
TAN9502	870	433	1303	0.67	0.33	2	4
TAN9601	140	106	246	0.57	0.43	12	3
TAN9604	1499	837	2336	0.64	0.36	2	4
TAN9701	108	59	167	0.65	0.35	1	3
TAN9801	85	86	171	0.50	0.50	1	3
TAN9901	119	71	190	0.63	0.37	1	3
Purse-seine 1994	100	49	149	0.67	0.33	8	5
Purse-seine 1994	26	19	45	0.58	0.42	11	5
Purse-seine 1994	52	66	118	0.44	0.56	12	5
Purse-seine 1995	38	19	57	0.67	0.33	2	5
Purse-seine 1995	91	65	156	0.58	0.42	8	5
Purse-seine 1995	72	13	85	0.85	0.15	10	6
Purse-seine 1996	38	23	61	0.62	0.38	9	7

*Apart from purse-seine shed sampling data sources are research trawl surveys

†For trawl survey data month is from start date of voyage

Area:

1. East coast South Island
2. West coast South Island & Golden Bay–Tasman Bay
3. Chatham Rise, Chatham Rise–Mernoo Bank, Chatham Rise–Mernoo Bank–ECHR–WCHR
4. Puysegur–Stewart–Snares, Puysegur–Stewart–Snares–East Coast South Island
5. West coast South Island–West Coast North Island, West Coast South Island–North Taranaki Bight–South Taranaki Bight–Tasman Bay
6. East coast South Island–East Coast North Island
7. East coast North Island, including Bay of Plenty, East Cape, Tolaga Bay, Wairarapa Coast and Madden Banks

Table 5: Food of larval *Trachurus symmetricus*. (After Arthur 1976, Table 3).

Food items	Size group					
	End of yolk-sac stage to 4.5 mm		5.0 to 6.5 mm		7.0 to 10.5 mm	
	No.	%	No.	%	No.	%
Copepod eggs:						
Single eggs	5	4.3	9	4.4		
Egg sacs	1	0.9	4	2.0	1	0.6
Copepod nauplii:						
Calanoid	3		3			
Cyclopoid	5		2		1	
Harpacticoid	7		2			
Total nauplii	15	12.8	7	3.4	1	0.6
Copepod adults:						
Calanoid:						
Calanoid spp.	7		15		60	
Metridia sp.	1					
Candacia sp.					1	
Cyclopoid:						
Oithona sp.	1				3	
Corycaeus sp.	3		3		5	
Onacaea sp.	6		29		39	
Harpacticoid:						
Microstella norvegica	46		130		56	
Microstella rosea	1					
Clytemnestra rostrata					1	
Unidentified					4	
Total copepods	65	55.6	117	86.3	169	96.0
Euphausiid:						
Nauplii	1	0.9			2	1.1
Calyptopi			2	1.0	1	0.6
Cladocera			1	0.5		
Unrecognisable crustacean remains	10	8.5				
Pteropods	3	2.6	4	2.0	2	1.1
Tintinnids	16	13.7	1	0.5		
Foraminifera	1	0.9				
Total number of food particles	117		205		176	

Table 6: Gut contents of *Trachurus symmetricus murphyi* from shed sampling of purse-seine landings in JMA 1 during 1994, 1995, and 1996: numbers of fish containing particular prey items at three levels of gut fullness — trace amount, partially full*, and full. (Source: Market sampling database).

Prey item and % represented	1994			1995			1996			*Row total
	Trace	Part*	Full	Trace	Part*	Full	Trace	Part*	Full	
% Euphausiid										
100	18	117	175	37	76	174	1	18	3	
95							1	3		
90			1					2		
85									2	
80								1	1	
75								1		
60								2		
50							1			
30								1		
10								1		
Total with Euphausiids	18	117	176	37	76	174	3	29	6	636
% Other crustaceans										
90								1		
70								1		
50							1			
40								1		
25										
20								1		
15									1	
10								1		
5								1		
Total with other crustaceans							1	6	1	
% Cephalapods										
40								1		
25								1		
5							1	2		
2							1	4		
Total with cephalapods							2	8		
% Munida										
5								1		
100							1			
% Salps										
100								1		
% Unidentified										
100				1						
20									1	
15									1	
10			1							
5								1		
Total number of fish	18	117	176	38	76	174	12	31	6	648

*Partially full = about 50%

†Totals do not reflect number of fish in the columns; fish appear more than once if contents are less than 100%

‡Row columns compare number of fish containing Euphausiids with total number of fish

Table 7: Number of observed tows by year and quarter in the jack mackerel fishery in JMA 7. (Source: Scientific Observer Database).

Fishing year	Quarter				Totals
	October–December	January–March	April–June	July–September	
1985–86	–	–	–	7	7
1986–87	281	64	30	2	377
1987–88	24	–	–	–	24
1988–89	33	1	17	154	205
1989–90	21	20	–	–	41
1990–91	9	130	217	41	397
1991–92	143	46	12	28	229
1992–93	142	378	71	1	592
1993–94	73	150	134	47	404
1994–95	47	358	6	2	413
1995–96	15	209	71	7	302
1996–97	24	283	26	36	369

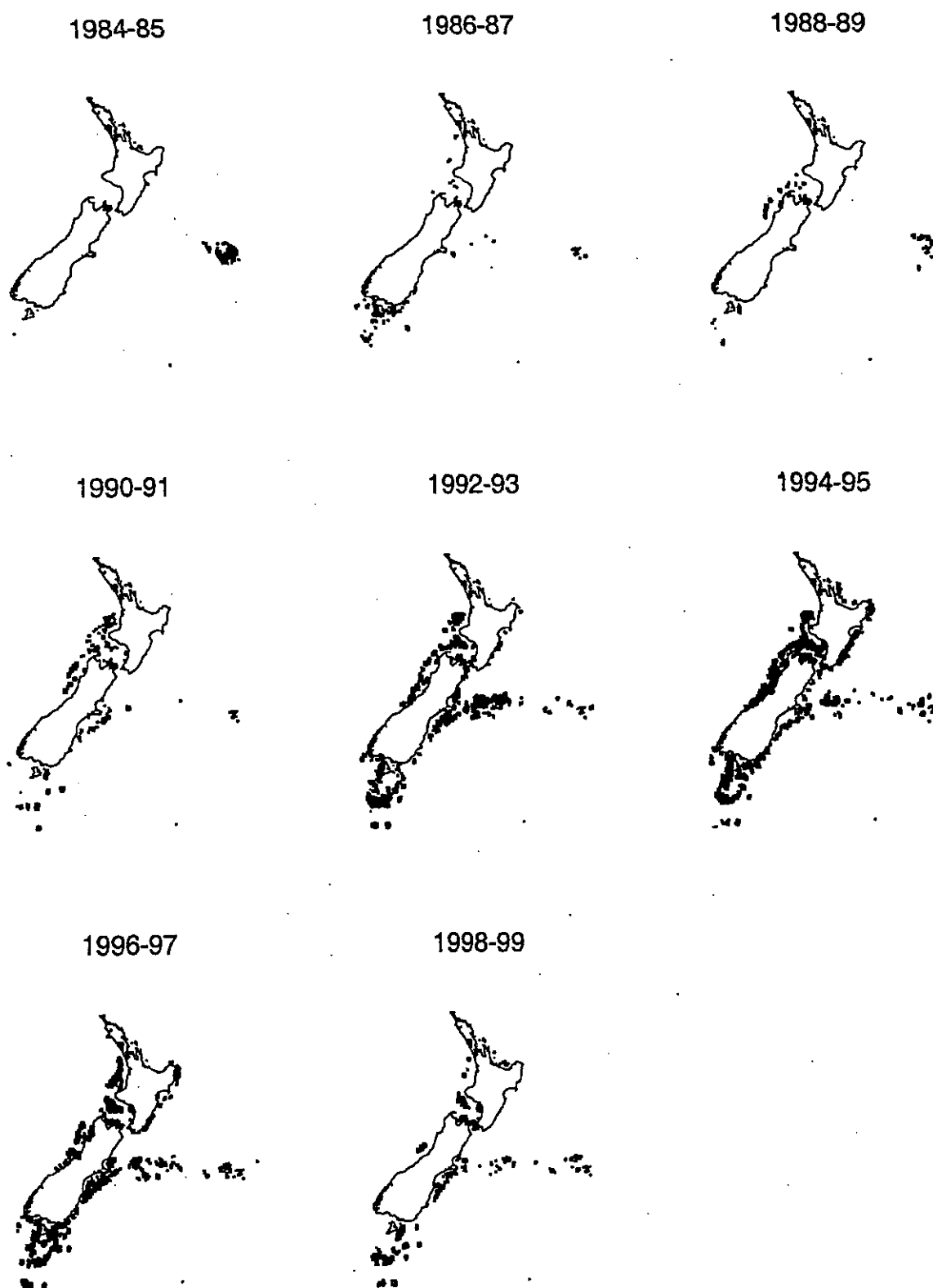


Figure 1: Positions of research and observed commercial trawl shots landing *Trachurus symmetricus murphyi* since 1984; data are all jack mackerel larger than the maximum size of *T. declivis* (57 cm) (which provides data for the earliest years) and positively identified *T. s. murphyi*. Data for 1998–99 are incomplete (Source: Trawl survey and Scientific Observer databases).

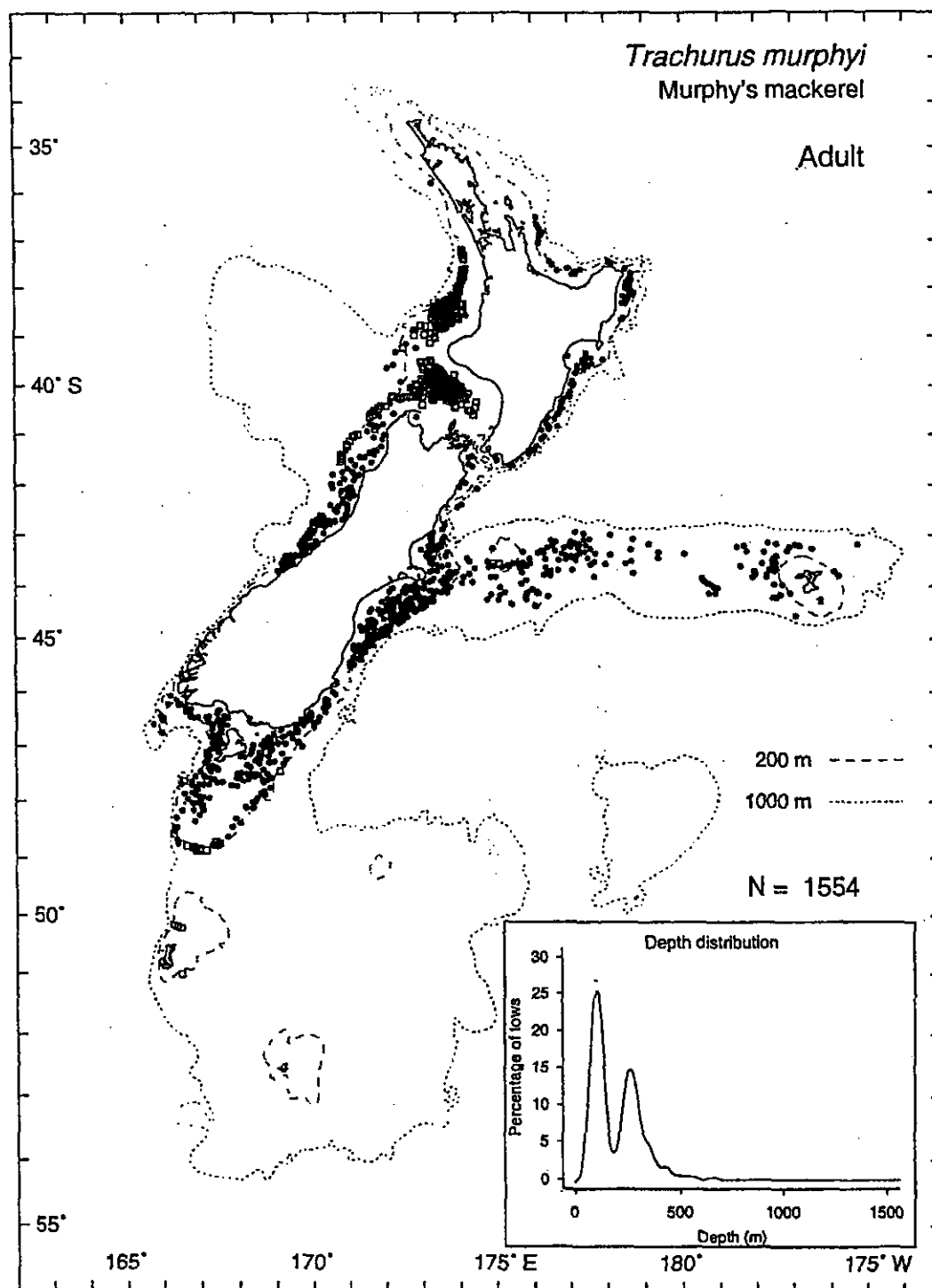


Figure 2: Distribution of bottom trawl shots landing adult (larger than 32 cm) *Trachurus symmetricus murphyi* (Sources: Trawl survey database — closed circles, and Scientific Observer database — open squares) (After Hurst *et al.* 2000).

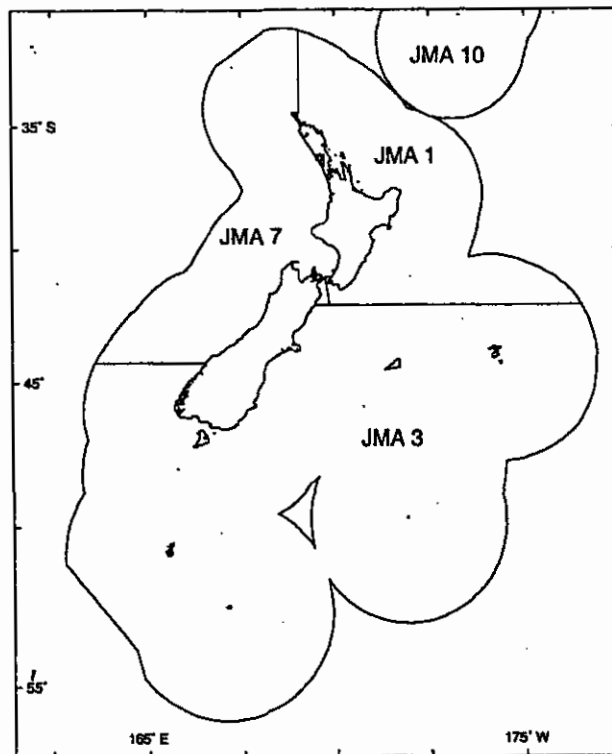


Figure 3: Jack mackerel Fishstocks.

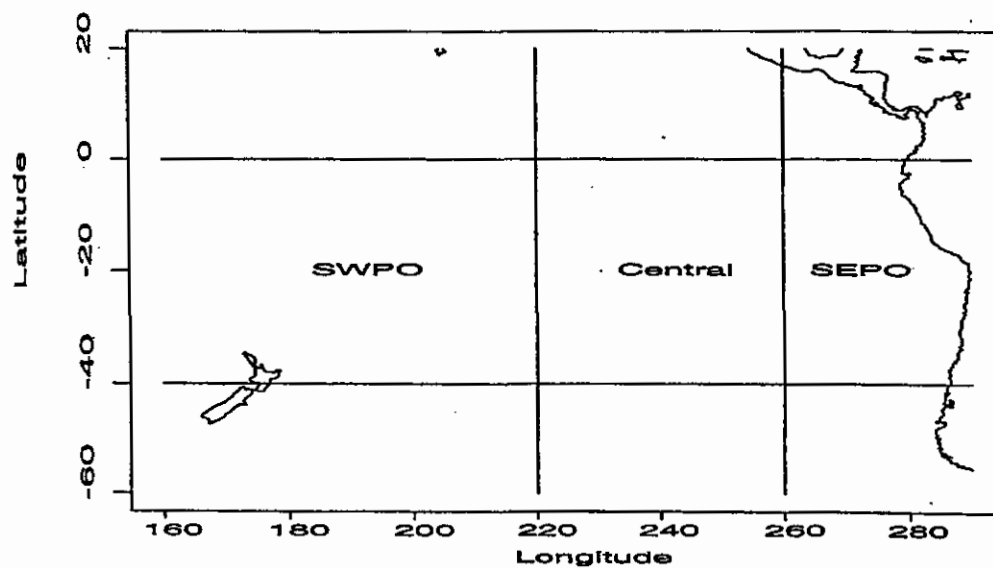


Figure 4: South Pacific Ocean divided into zones frequently used in describing various aspects of the migration, biology, and stock structure of *Trachurus symmetricus murphyi*; SWPO is southwest Pacific Ocean, Central is central South Pacific Ocean, and SEPO is southeast Pacific Ocean. Map plotting function courtesy of Steve Wofsy (scw@io.harvard.edu).

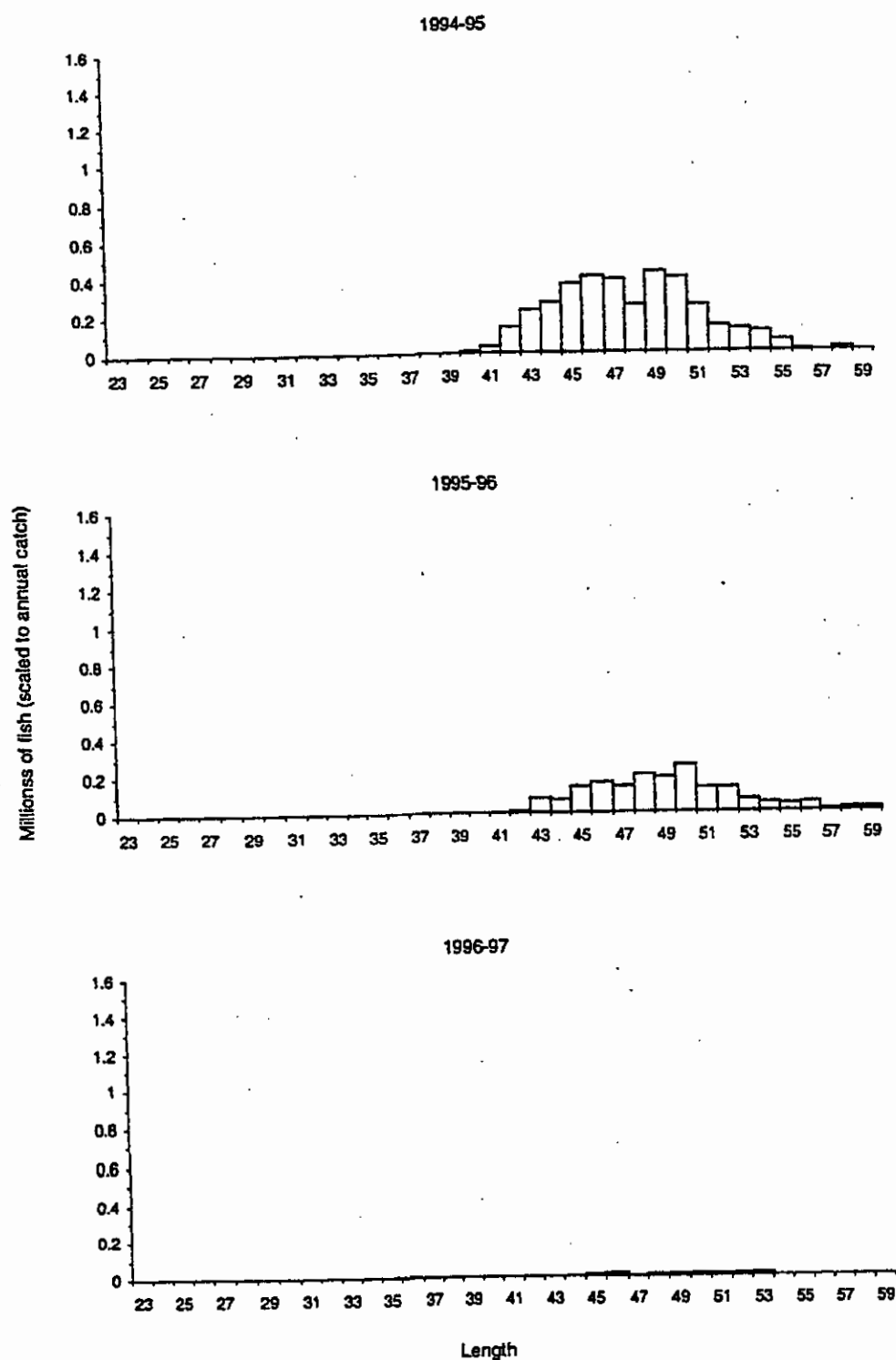


Figure 5: Length frequencies (by centimetre class) of *Trachurus symmetricus murphyi* from shed samples of the purse-seine target fishery for jack mackerel in JMA 1 between 1994-95 and 1995-96. (Source: Market sampling database).

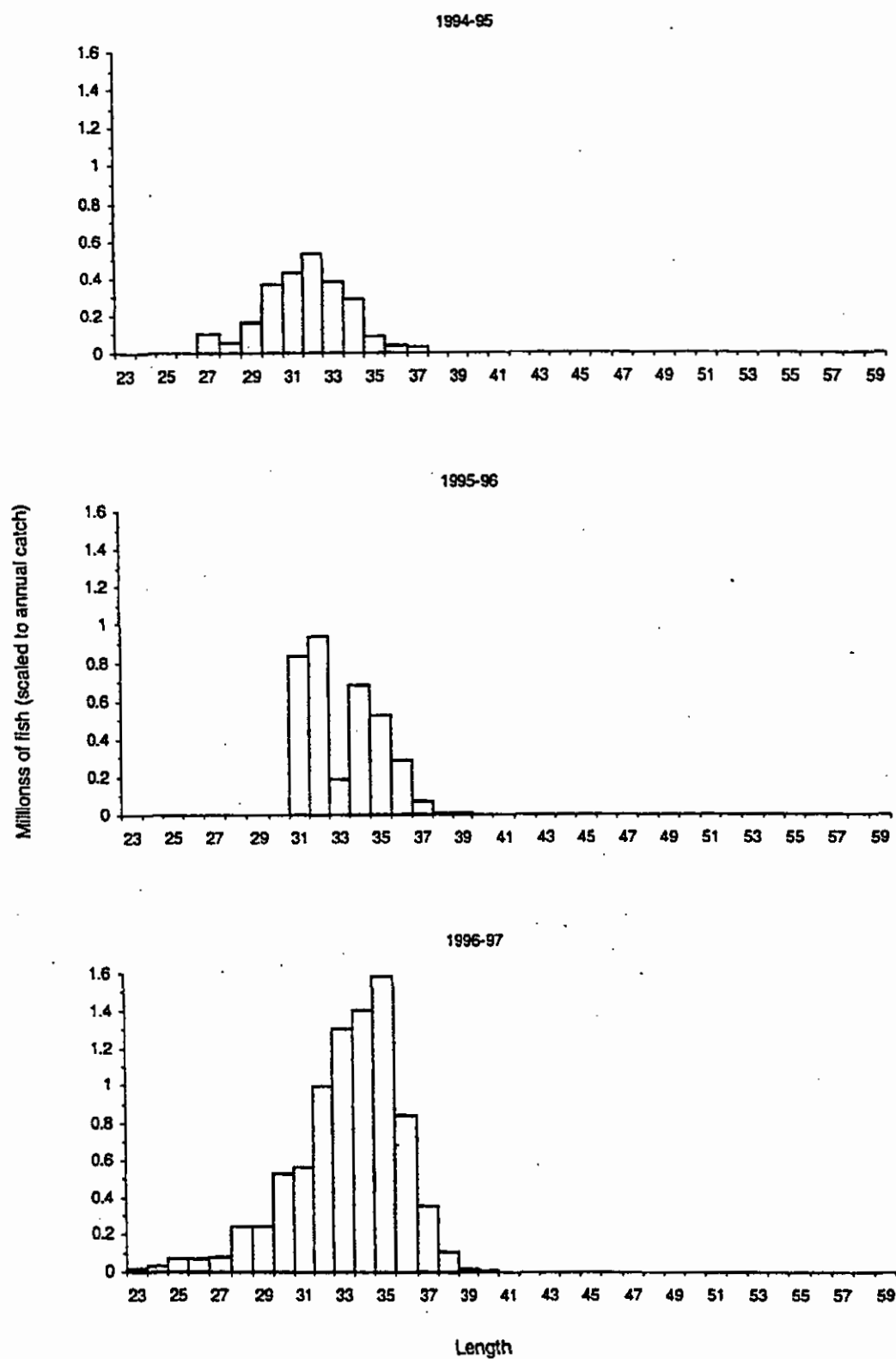


Figure 6: Length frequencies (by centimetre class) of *Trachurus novaezelandiae* from shed samples of the purse-seine target fishery for jack mackerel in JMA 1 between 1994-95 and 1995-96. (Source: Market sampling database).

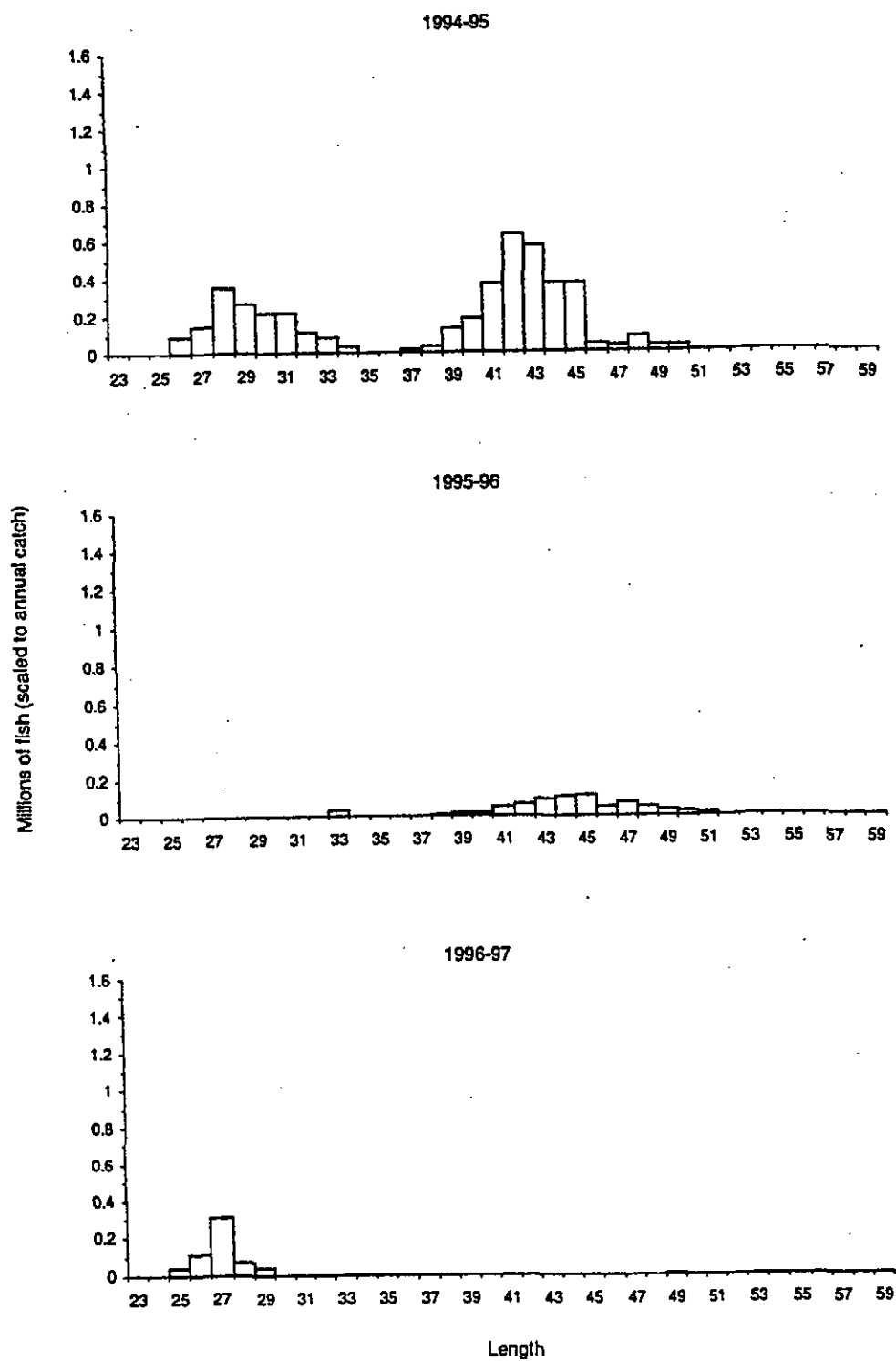


Figure 7: Length frequencies (by centimetre class) of *Trachurus declivis* from shed samples of the purseseine target fishery for jack mackerel in JMA 1 between 1994-95 and 1995-96. (Source: Market sampling database).

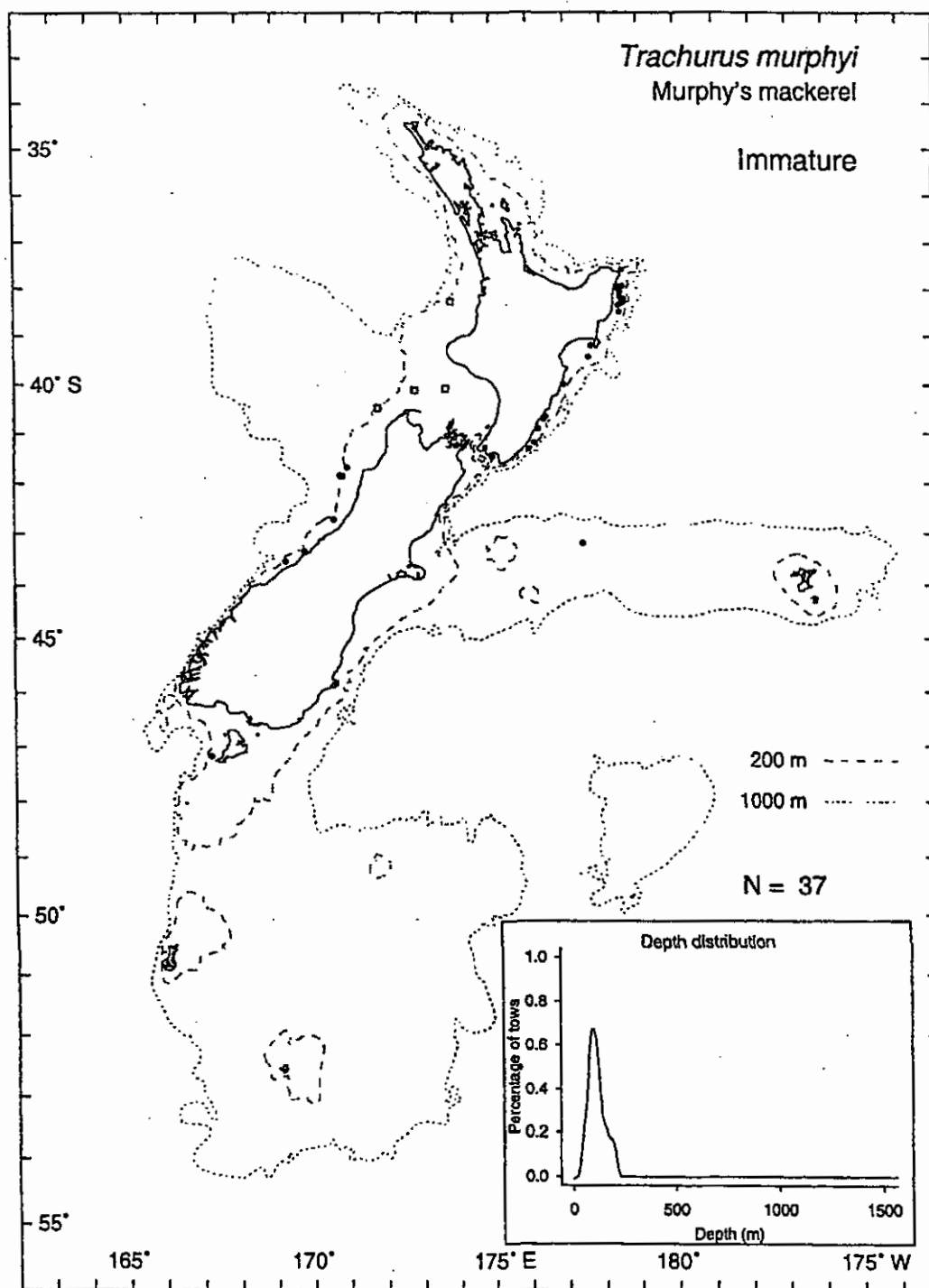


Figure 8: Distribution of bottom trawl shots landing immature (smaller than 33 cm) *Trachurus symmetricus murphyi* (Sources: Trawl survey database — closed circles, and Scientific Observer database — open squares) (after Hurst et al. 2000).

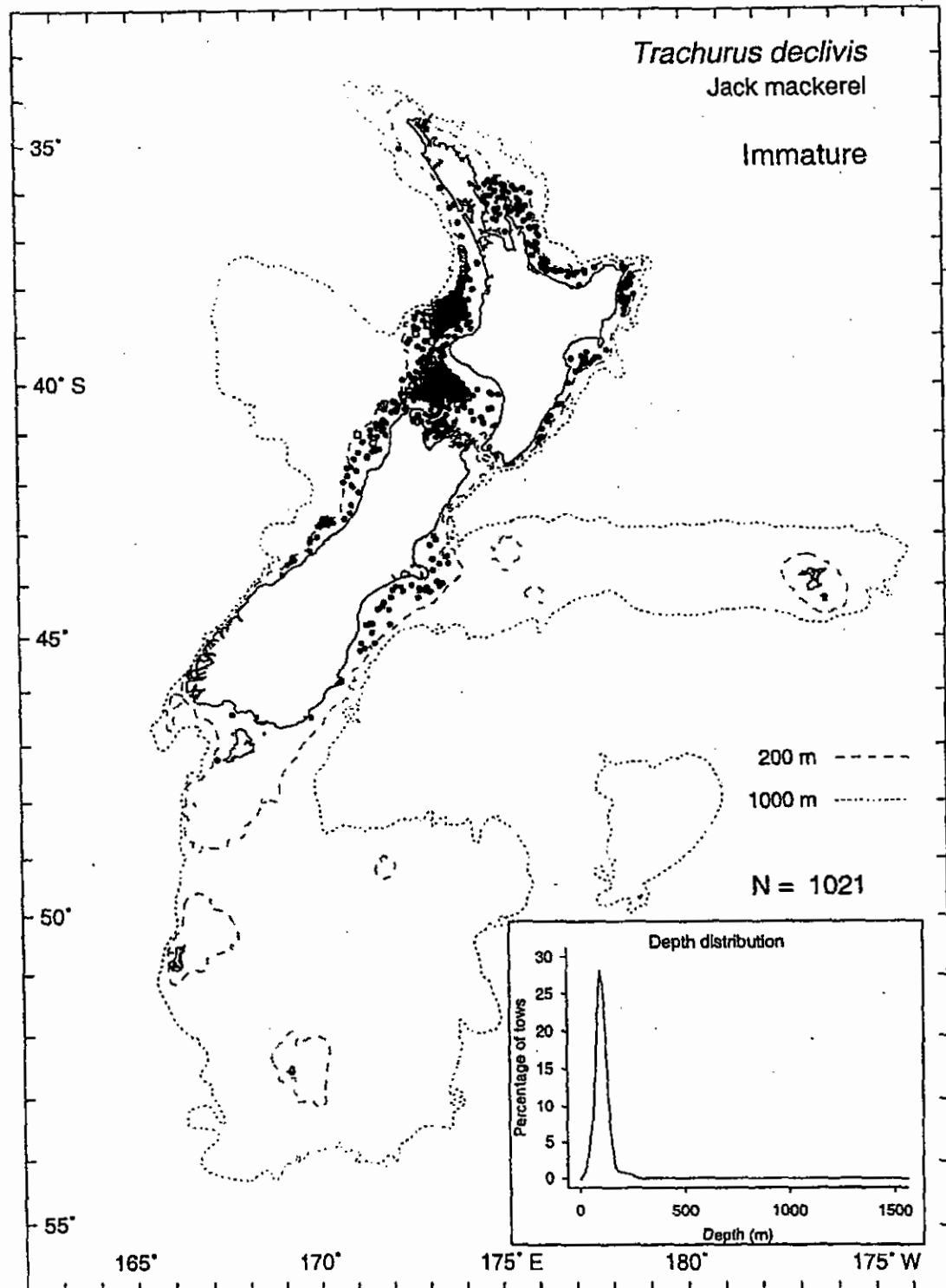


Figure 9: Distribution of bottom trawl shots landing immature *Trachurus declivis* (Sources: Trawl survey database — closed circles, and Scientific Observer database — open squares) (after Hurst et al. 2000).

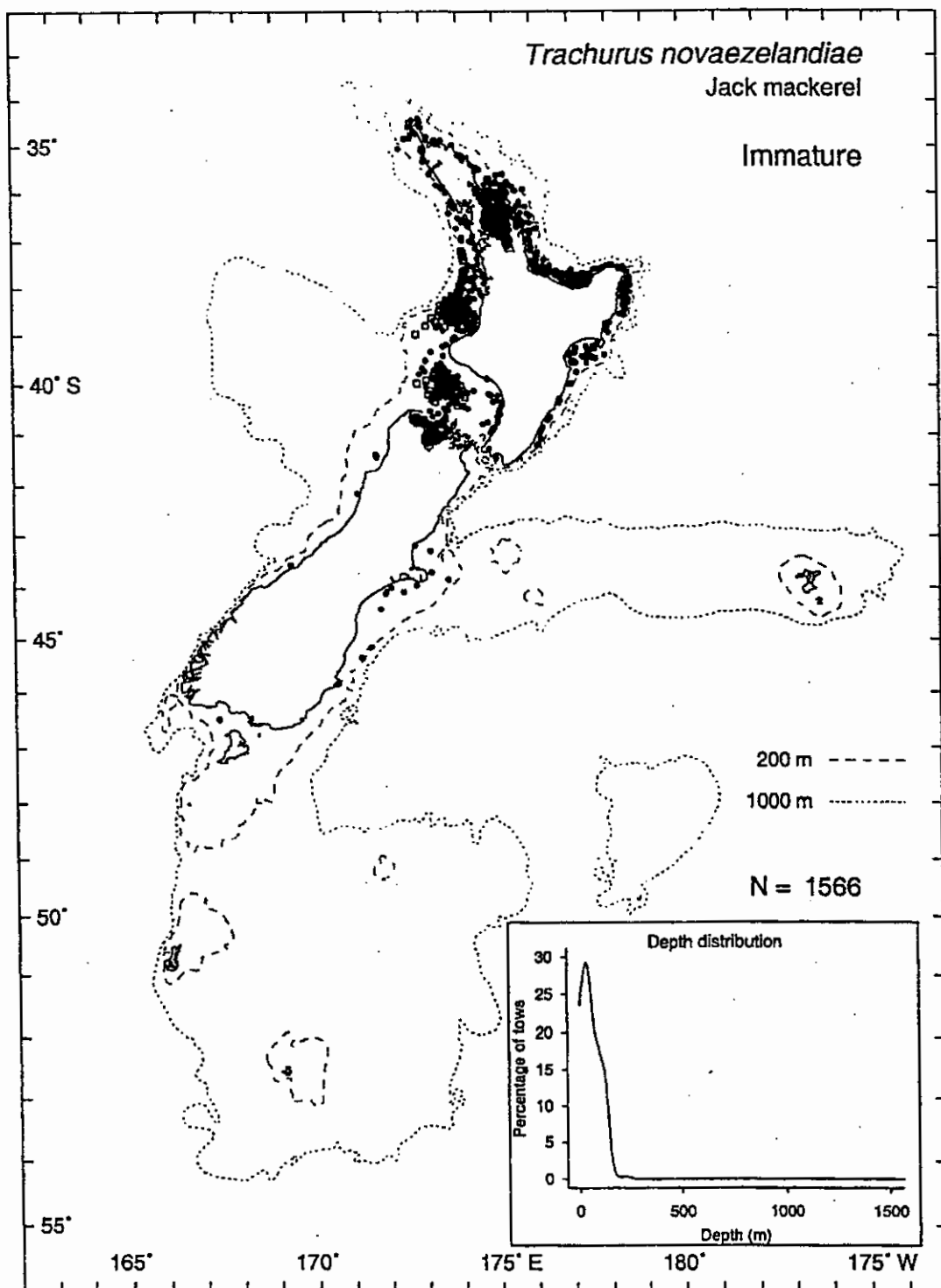


Figure 10: Distribution of bottom trawl shots landing immature *Trachurus novaezelandiae* (Sources: Trawl survey database — closed circles, and Scientific Observer database — open squares) (after Hurst et al. 2000).

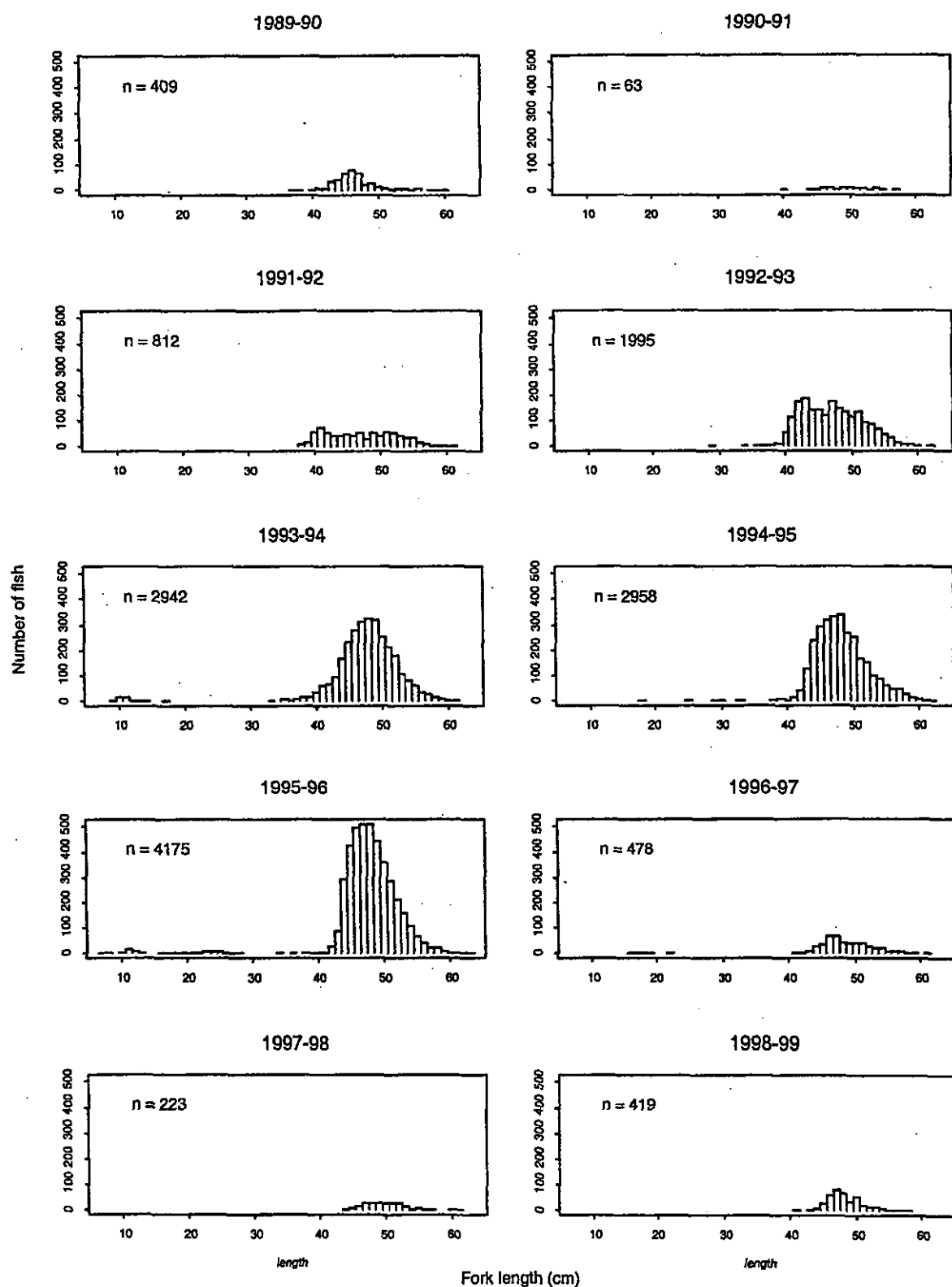


Figure 11: Annual length frequency distributions of *Trachurus symmetricus murphyi* from trawl survey data (Source: Trawl survey database).

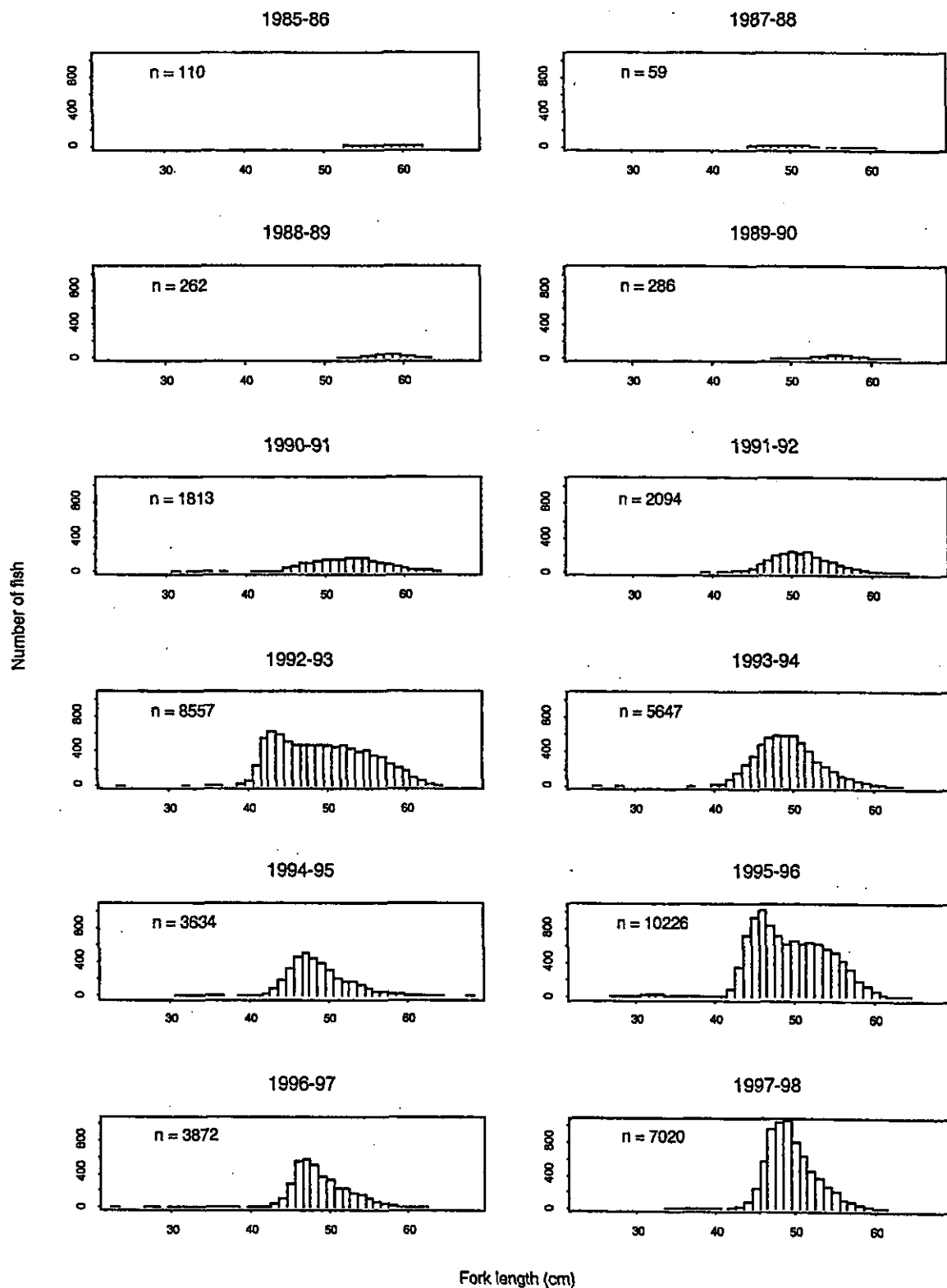


Figure 12: Annual length frequency distributions of *Trachurus symmetricus murphyi* from observer data. (Source: Scientific Observer database).

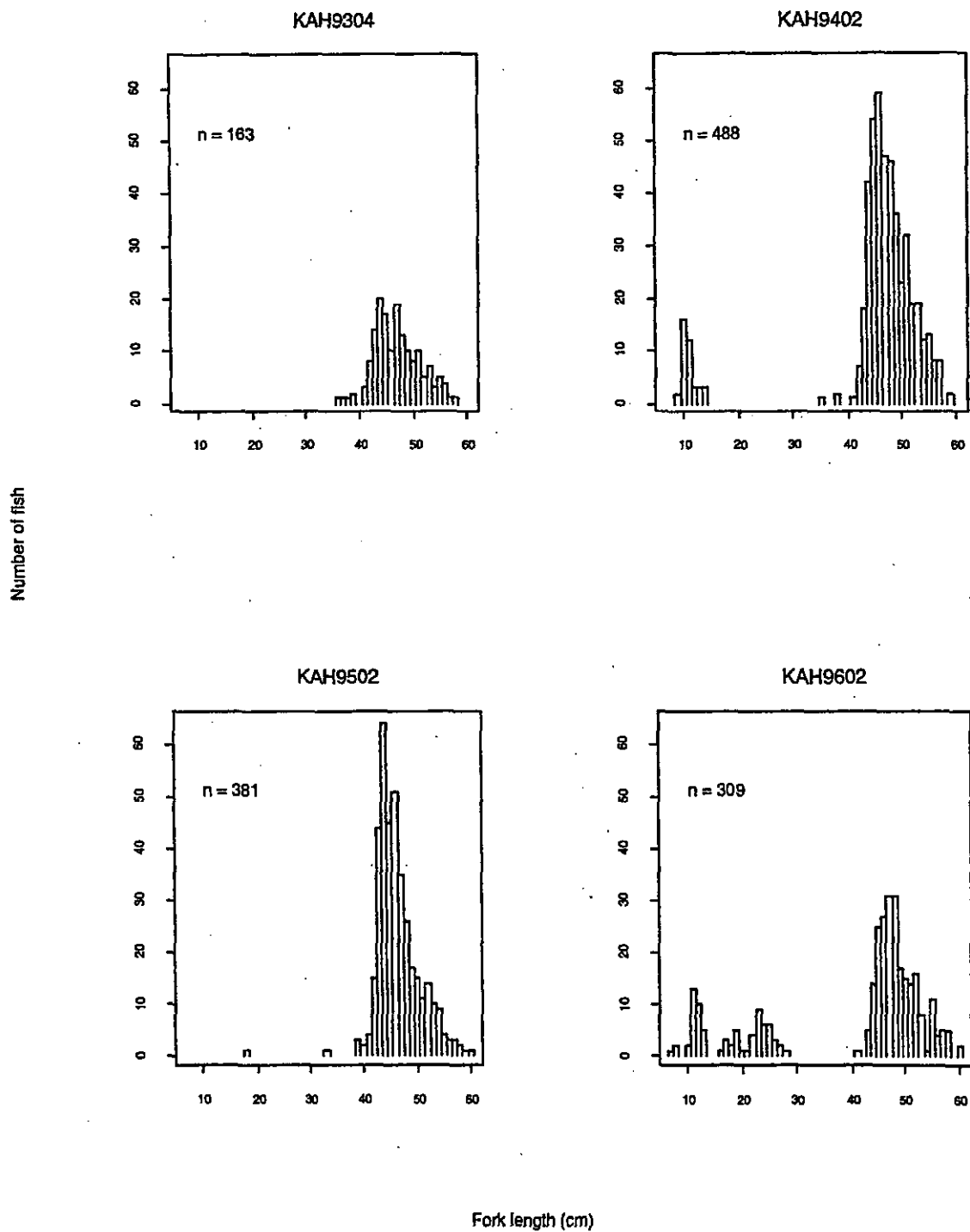


Figure 13: Length frequency distributions of *Trachurus symmetricus murphyi* from the Kaharoa east coast North Island trawl survey series; all surveys were during February except KAH9304 which was in March. (Source: Trawl Survey Database).

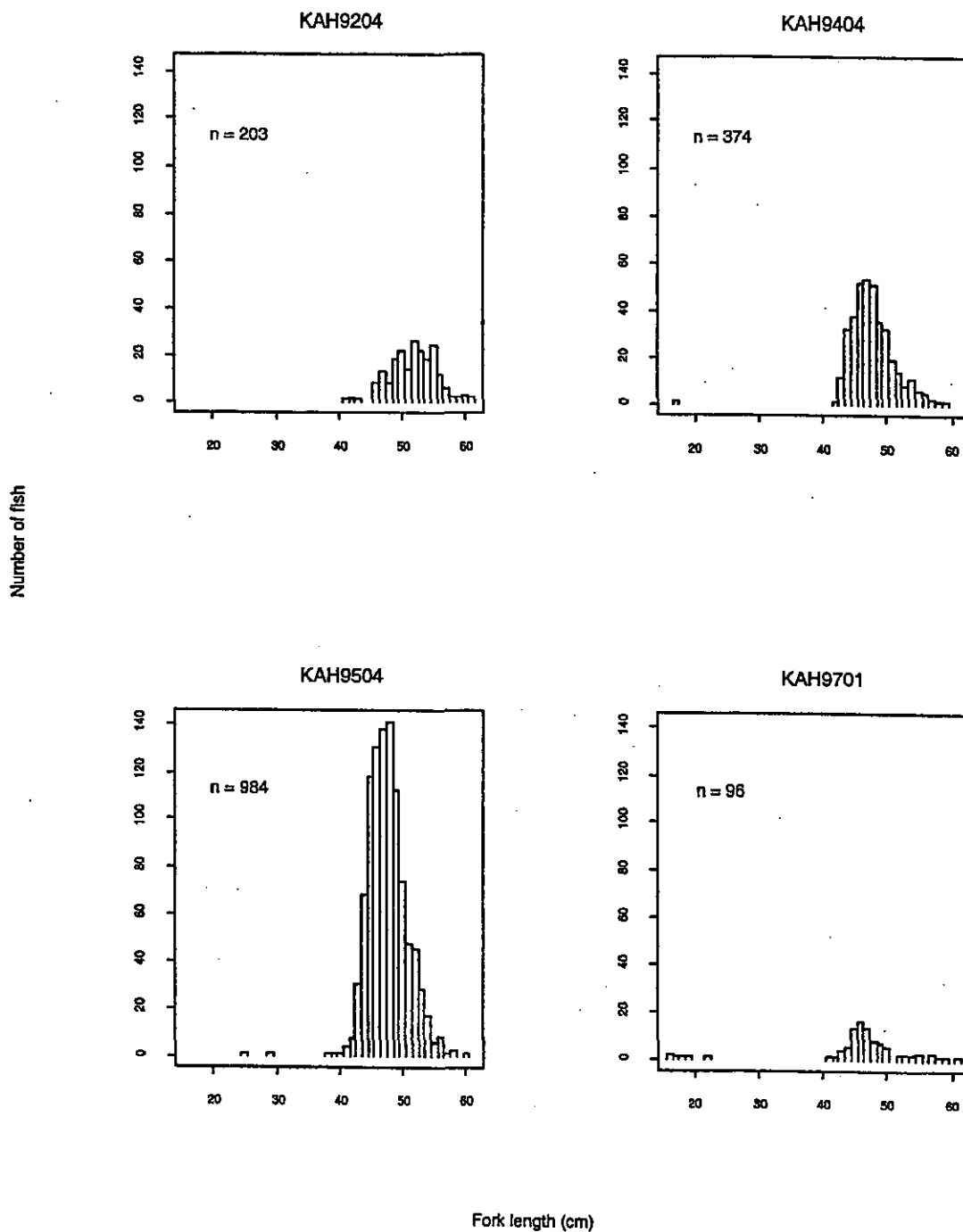


Figure 14: Length frequency distributions of *Trachurus symmetricus murphyi* from the Kaharoa west coast South Island trawl survey series; all surveys were during March. (Source: Trawl Survey Database).

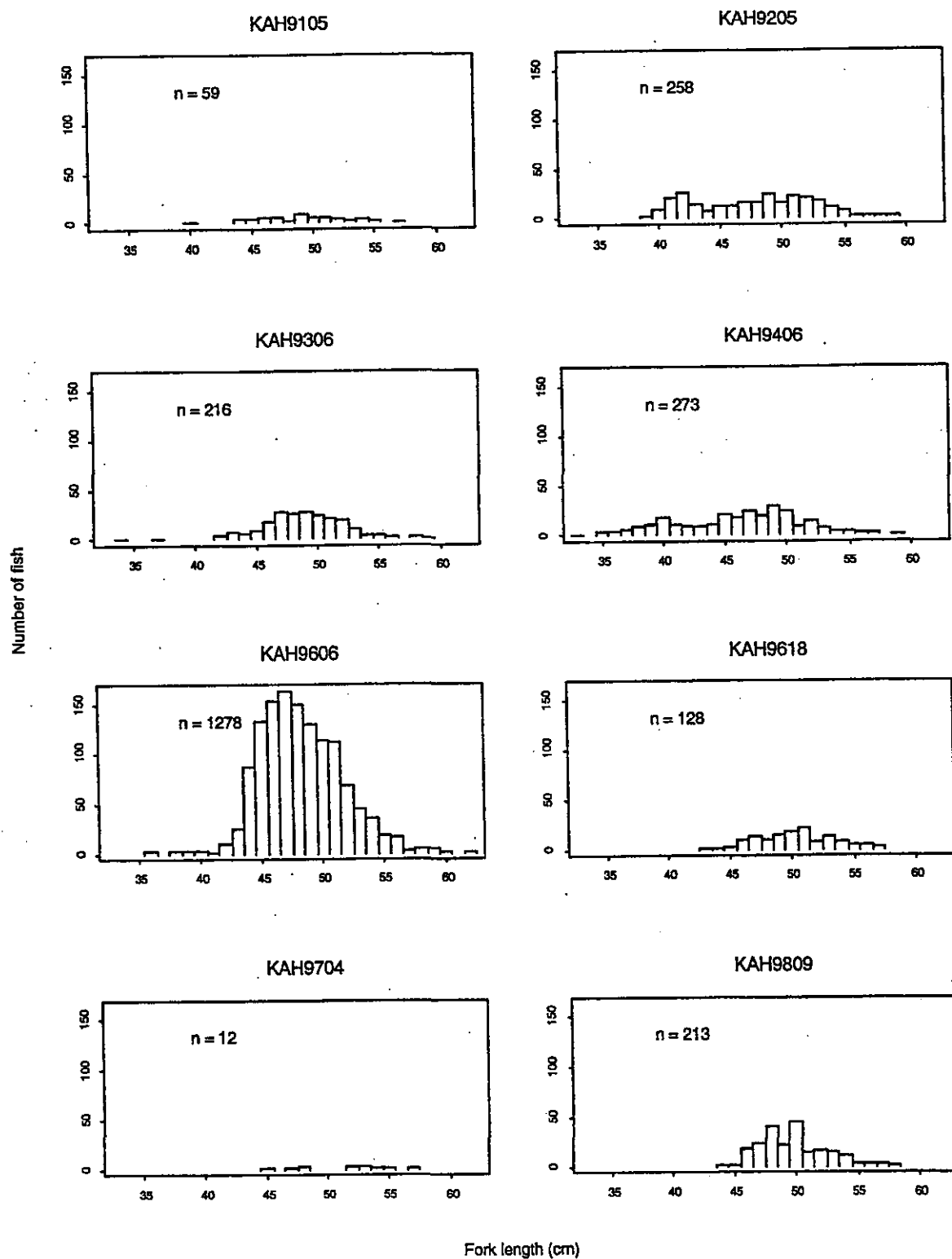


Figure 15: Length frequency distributions of *Trachurus symmetricus murphyi* from the Kaharoa east coast South Island trawl survey series; surveys from KAH9105 to KAH9606 were during June and the remainder were during December–January. (Source: Trawl Survey Database).

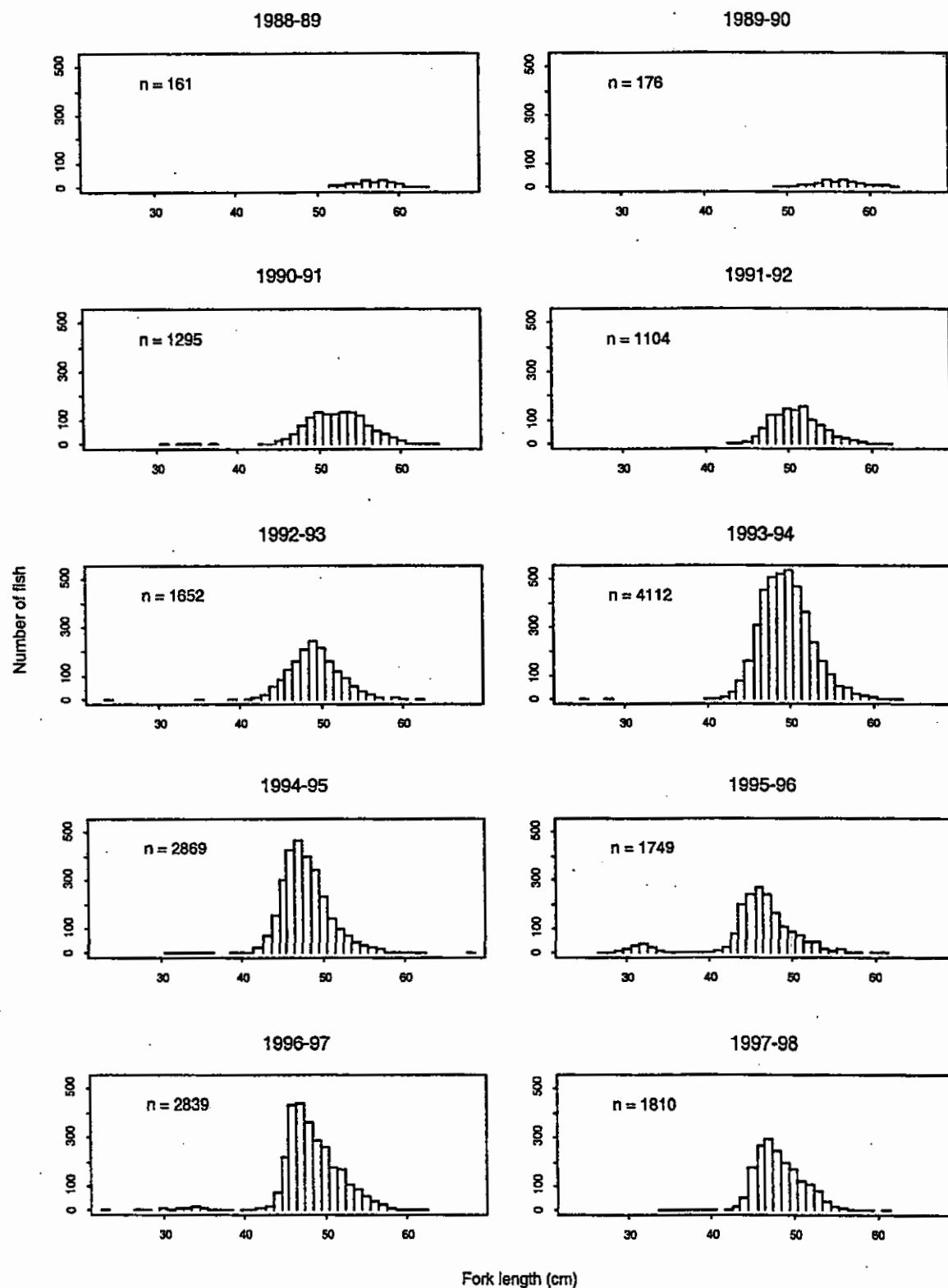


Figure 16: Length frequency distributions by fishing year for *Trachurus symmetricus murphyi* using observer data from JMA 7; data aggregated for all months. (Source: Scientific Observer Database).

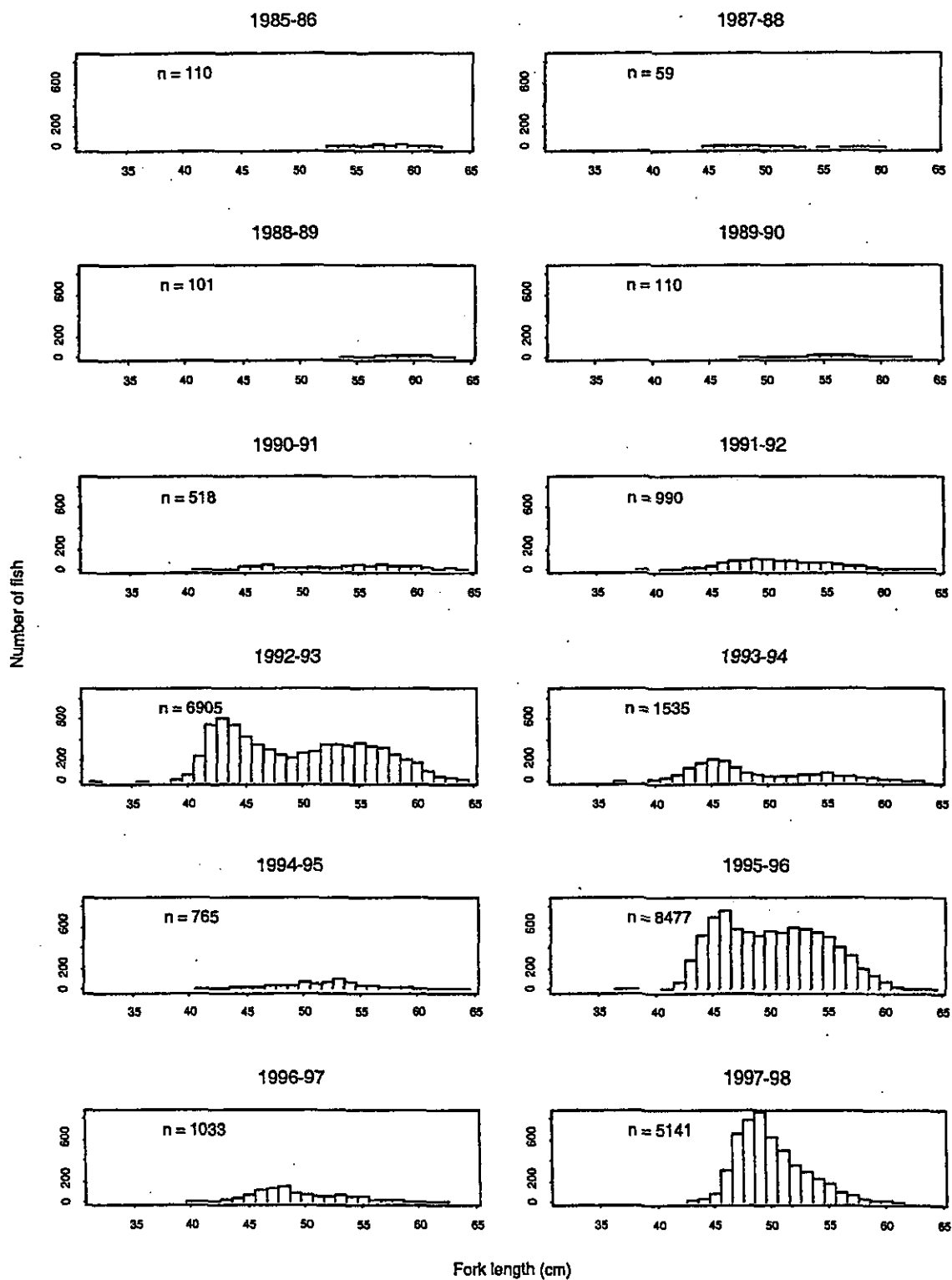


Figure 17: Length frequency distributions by fishing year for *Trachurus symmetricus murphyi* using observer data from JMA 3; data aggregated for all months. (Source: Scientific Observer Database).

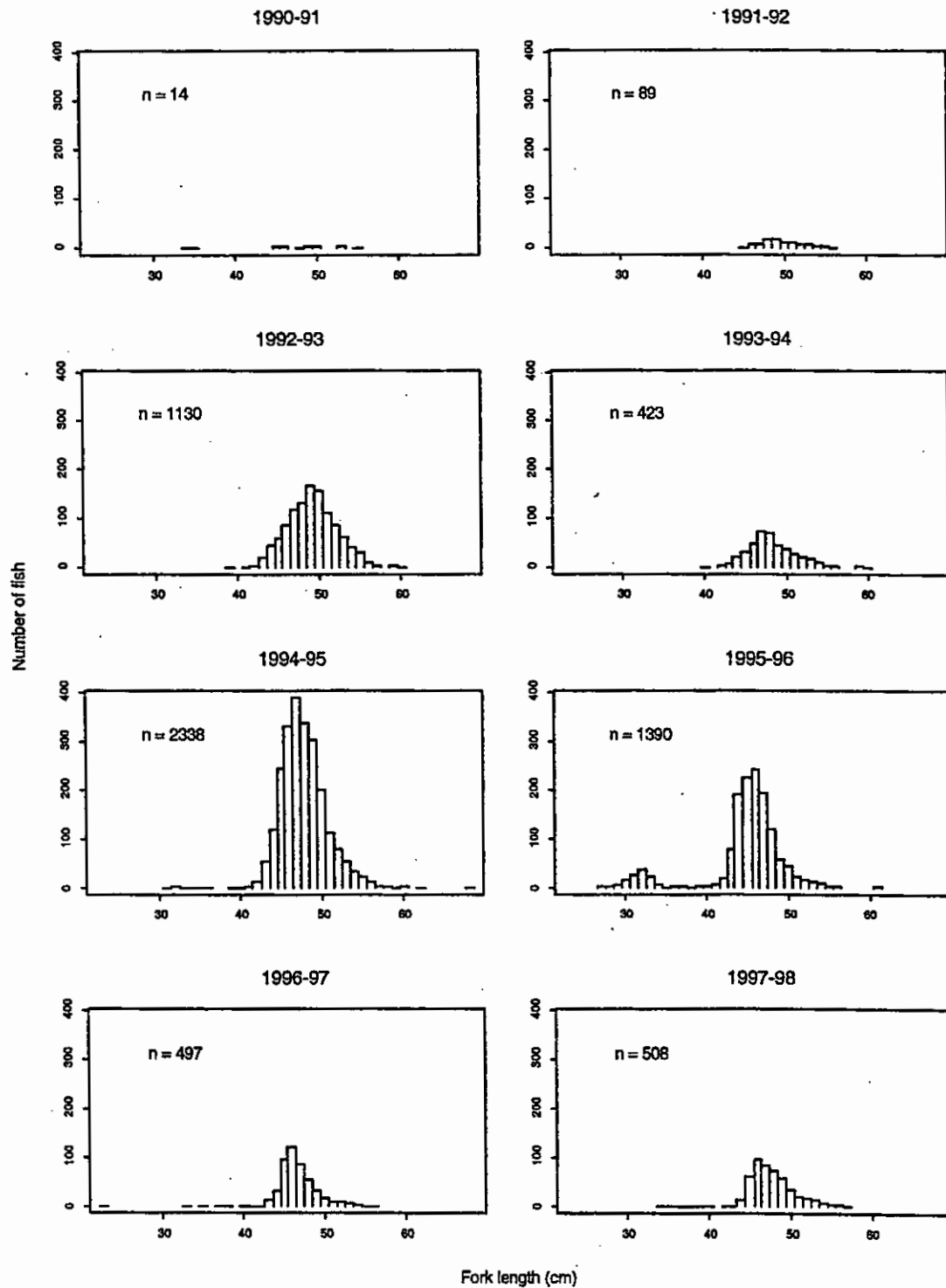


Figure 18: Length frequency distributions by fishing year for *Trachurus symmetricus murphyi* using observer data from JMA 7 during the quarter January–March. (Source: Scientific Observer Database).

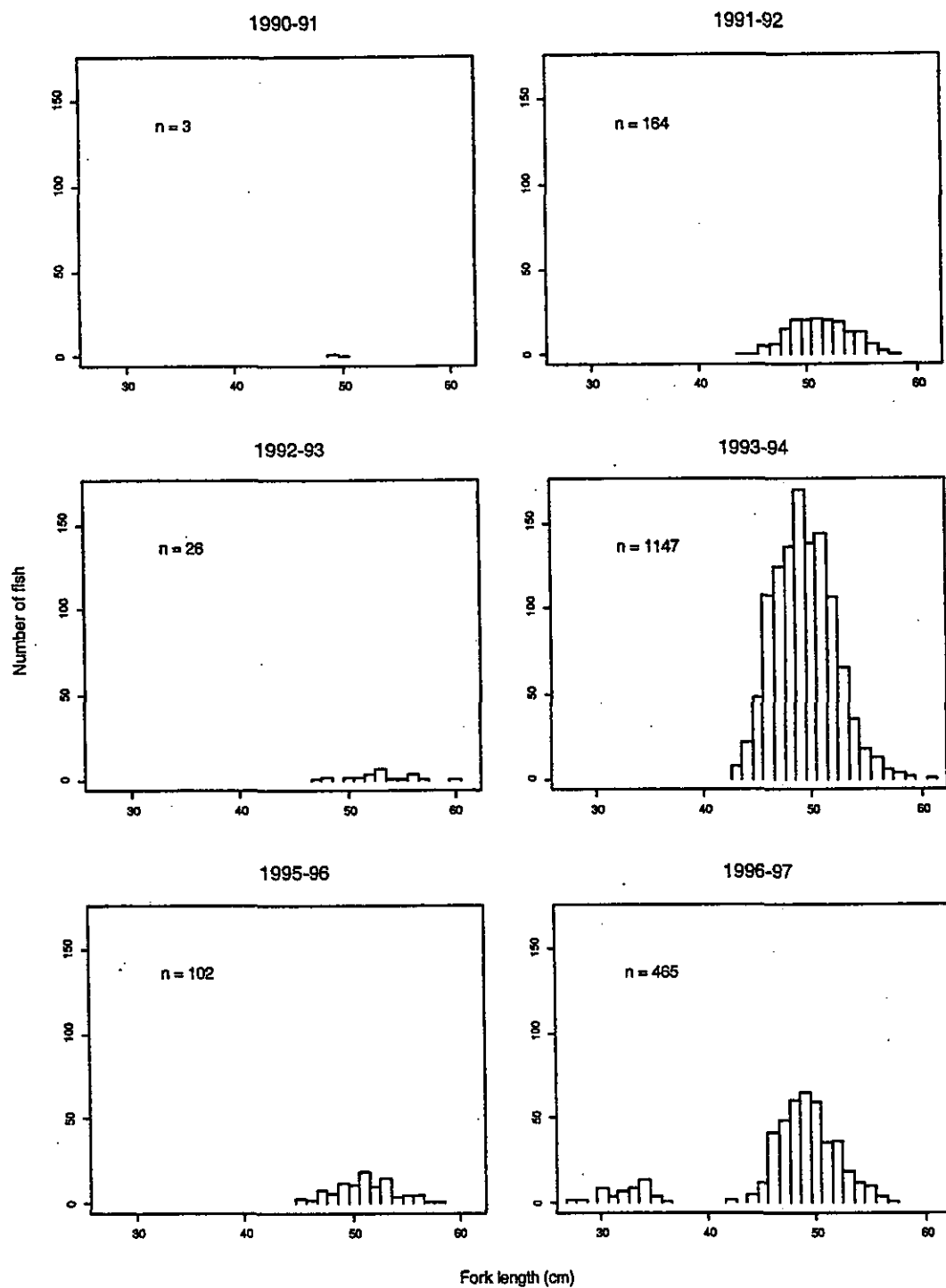


Figure 19: Length frequency distributions by fishing year for *Trachurus symmetricus murphyi* using observer data from JMA 7 during the quarter April–June. (Source: Scientific Observer Database).

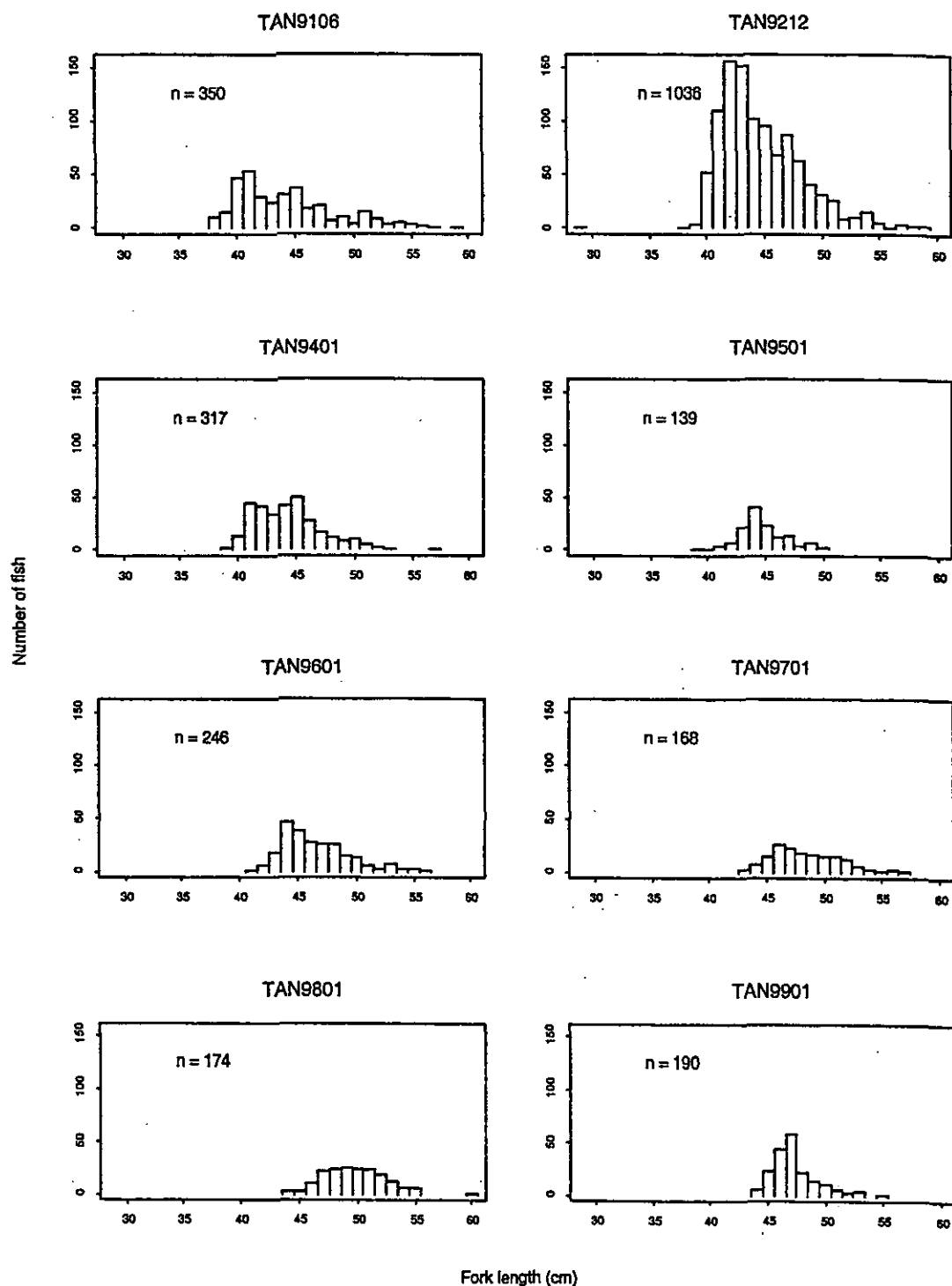


Figure 20: Length frequency distributions of *Trachurus symmetricus murphyi* from the Tangaroa Chatham Rise trawl survey series; TAN9106, TAN9212, and TAN9601 were carried out in December and the remainder in January. (Source: Trawl Survey Database).

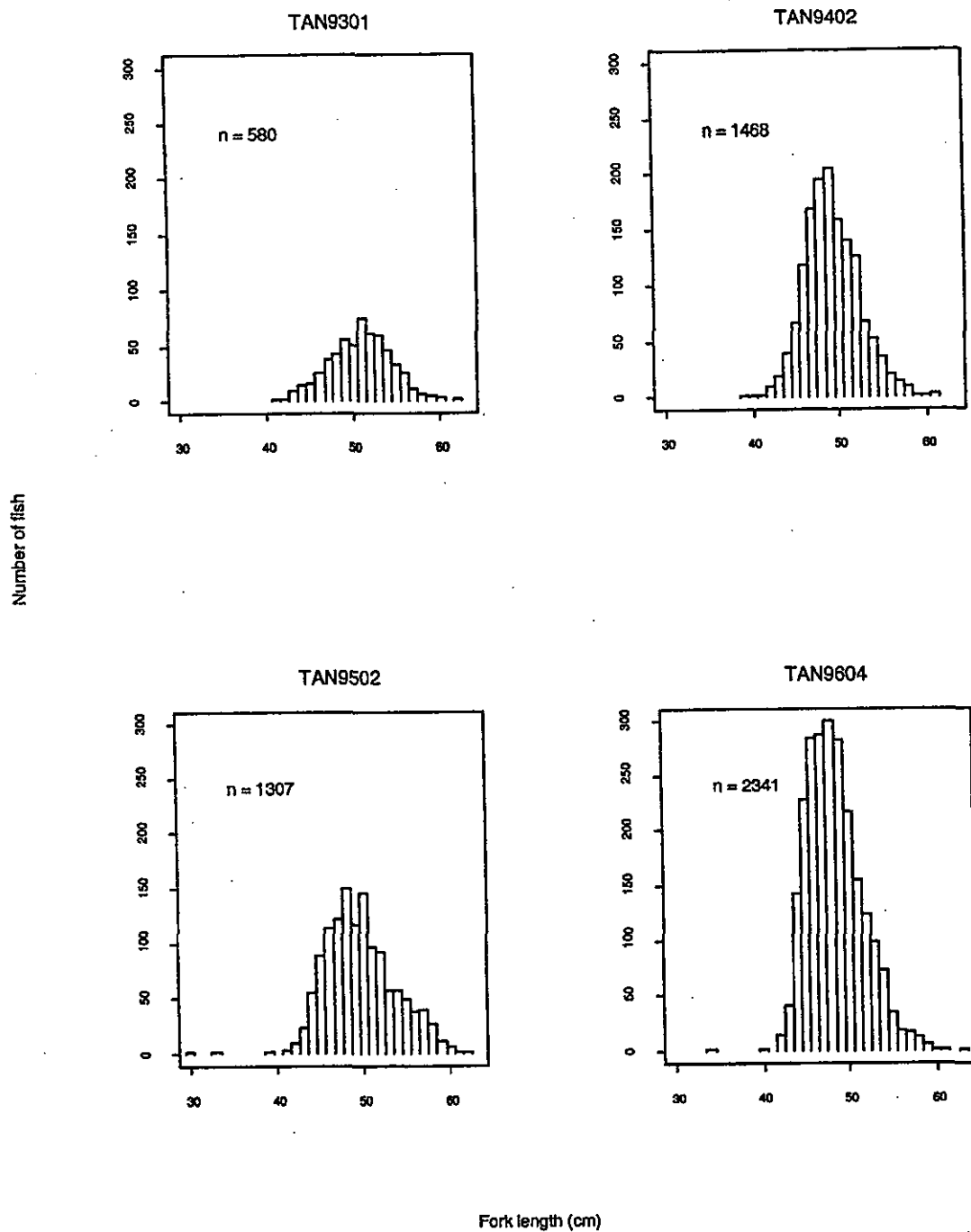


Figure 21: Length frequency distributions of *Trachurus symmetricus murphyi* from the *Tangaroa* Stewart-Snares Shelf trawl survey series; all surveys were during February. (Source: Trawl Survey Database).

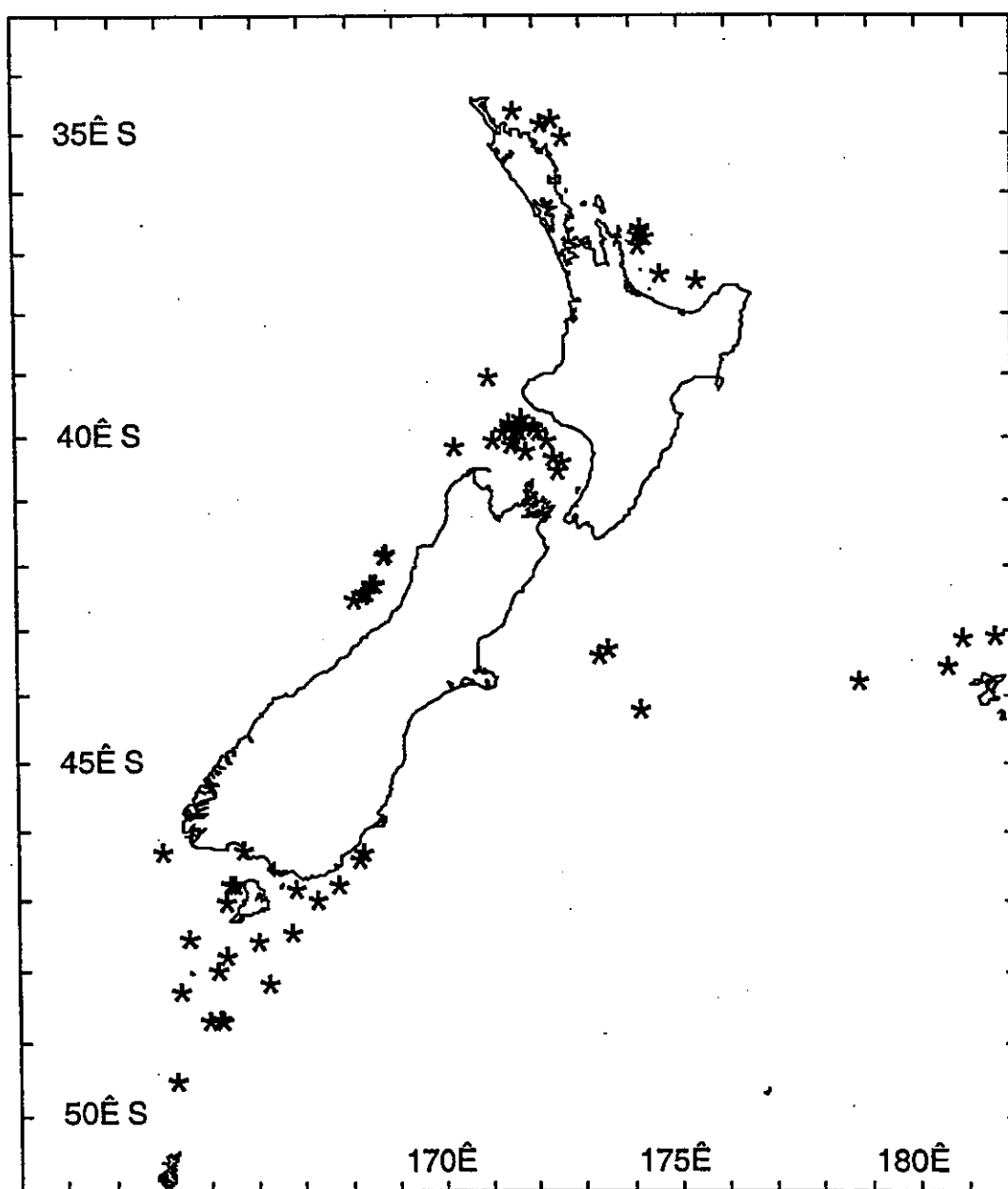


Figure 22: Positions of sets containing individuals of *Trachurus symmetricus murphyi* in maturing and spawning condition. (Sources: Trawl survey, Scientific Observer, and Market sampling databases).