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No 1984/163

- ☐ NEW PROPOSAL
- ☐ CONTINUING PROJECT
- ☒ FINAL REPORT
- ☐ PROGRESS REPORT

FIRC 37

FISHING INDUSTRY RESEARCH TRUST ACCOUNT

TITLE OF PROPOSAL/PROJECT: THE BIOLOGY AND ECOLOGY OF BLUE GRENADIER WITH PARTICULAR REFERENCE TO STOCK RECRUITMENT, STOCK IDENTITY AND ITS ROLE IN A MULTISPECIES FISHERY.

ORGANISATION: CSIRO

PERSON(S) RESPONSIBLE: DR FR HARDEN JONES

FUNDS SOUGHT/GRANTED

YEAR	SOUGHT	GRANTED
1984/85		$145,195
1985/86		$151,537

RELATED APPLICATIONS:

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Secretary
Fishing Industry Research Committee

F139—12/84

FINAL REPORT TO FIRC

PROJECT: 84/63

TITLE: THE BIOLOGY AND ECOLOGY OF BLUE GRENADIER WITH PARTICULAR REFERENCE TO STOCK RECRUITMENT, STOCK IDENTITY AND ITS ROLE IN A MULTISPECIES FISHERY.

CONTENTS

6. Feeding ecology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia.
7. Reproductive biology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia.
8. Larval development and caudal osteology of Blue Grenadier.

FISHING INDUSTRY RESEARCH TRUST ACCOUNT

APPLICATION FOR GRANT AND FUNDING

1. Title of Proposal:

The biology and ecology of Blue Grenadier with particular reference to stock recruitment, stock identity and its role in a multispecies fishery.

2. Name of Applicant: CSIRO

3. Division: Fisheries Research

4. Proposal:

It is proposed to study aspects of the biology of blue grenadier relevant to the developing slope fishery of south east Australia with particular regard to stock recruitment parameters, the number of different stocks in the area, and the relationship between adult Blue Grenadier and other species in the fishery.

5. Name of Person Responsible for Programme:

S.W. Jeffrey. PhD. Acting Chief, Division of Fisheries Research (1984/85)
F.R. Harden Jones. PhD. Chief, Division of Fisheries Research (1985/86)

6. Qualifications of Staff Employed on the Programme:

		% of time on this project
S.J.M. Blaber	PhD DSc - Project Leader	(15)
R. Thresher	MSc PhD	(25)
J.B. Shaklee	MSc PhD	(15)
T.J. Kenchington	MSc PhD	(50)
C. Stanley	MSc PhD	(15)

J.W. Young	BSc	(5)
J. May	BSc	(15)

The following staff were employed on the FIRTA grant and the funds for these positions formed a vital part of this application.

D. Milton	BSc Hons	(Experimental Scientist)
C. Bulman	BSc Hons	(Experimental Scientist)
B. Bruce	BSc	(Experimental Scientist)
D. Furlani	BSc	(Experimental Scientist)
S. Kent		(Technical Assistant)

7. Objectives:

The objectives of the proposed study are to investigate:

(a) recruitment patterns to the stocks using larval and adult fish,
(b) the number of separate stocks in the area using biochemical genetic techniques and,
(c) the relationship between adult Blue Grenadier and other species in the fishery, with particular regard to mortality from predation and the influence of food supply on the populations.

Work on the stock sizes, spawning areas, inshore juveniles and potential yields of Blue Grenadier in Tasmanian waters are presently undertaken by the Tasmanian Fisheries Development Authority. Their work is limited, however, by lack of a suitable research vessel and shortage of manpower. The study proposed here is designed to complement the ongoing TFDA program and provide much extra urgently needed data for future management of the stocks.

8. Justification:

The initial results from TFDA surveys indicate that Blue Grenadier are relatively abundant in Tasmanian waters and it is likely that a substantial fishery may develop in the region. During 1980/81 about 1000 tonnes were landed in the whole south east region but present

TFDA estimates suggest that this could be increased sixfold. Although the TFDA results provide a basis for yield estimates, further biological research is urgently required as the fishery develops. The fishery has national importance as the resource occurs in Victoria and New South Wales as well as Tasmania. Management of the Blue Grenadier fishery is likely to become a matter of controversy between States particularly with regard to total allowable catch. Little is known of stock recruitment patterns or even whether the fishery is based on a single stock. The effects of increased fishing pressure on a long-lived deep sea species such as Blue Grenadier are unknown, as are the indirect effects on other commercial species of large scale removal of the species. As part of a broader southern program, CSIRO research on Blue Grenadier will be of assistance to the fishing industry in the following ways:

(a) Because larvae provide recruits to the juvenile and subsequently, adult populations, a thorough understanding of the factors affecting larval abundance and distribution are essential if we are to understand the life cycle of the Blue Grenadier and, ultimately, predict annual fluctuations in stock size.

(b) The determination of the number of individual stocks making up the fishery is a basic requirement for future fisheries management. Treating several stocks as a single unit or vice versa could prove disastrous to the long term future of the fishery. This area is of considerable significance since the fishery extends over more than one State.

(c) Adult Blue Grenadier are both predators and prey in a multispecies fishery. Hence the undoubted effect of changes in stock structure of Blue Grenadier, caused by fishing, on other important species, is vital for management of a multispecies fishery, particularly with regard to conservation of stocks. The sensitivity of Blue Grenadier to a sustained fishery is presently unknown.

(d) The program would have valuable spin-offs for other fisheries besides Blue Grenadier. A great deal of data will be generated on

other potentially commercial species such as the Dories, gurnard perches, sharks and possibly gemfish. This is not to mention the enormous amount of material on non-commercial species e.g., plankton and forage species.

9. Location of Operations

The base for the program will be the CSIRO Marine Laboratories in Hobart. Work will take place around Tasmania and in the eastern Bass Strait. Areas of operation may be extended depending on availability of ship time, manpower and finance. Samples for analysis will be obtained from throughout southern Australia.

10. The Proposal in Detail, Including Procedures

(a) Plan of Operation

(i) Methods of Procedure

General Procedure: 1 year of sampling using 'Soela' plus smaller vessel in Hobart area. 'Soela' is only suitable vessel for regular work in the Tasmanian area. Second year will consist mainly of laboratory based analyses of data although sampling will continue.

Larval work:

1. Hobart transect - in conjunction with detailed studies of the adults in adjacent areas, an extensive series of depth-specific plankton tows on a transect from immediately near shore to the edge of the continental slope will be undertaken on a regular basis. Samples will be taken near the surface and, using a remotely operated opening and closing RMT net, at specified depths between the surface and bottom to sample effectively the entire water column. This extensive sampling program will be supplemented by surface and oblique tows in a grid patter

throughout the Hobart area, both to ensure that larvae will be caught when they occur in the area and to permit an intensive collecting effort in periods of peak larval abundance. The Hobart-based operation will not only provide information on local spawning, if any, but also indicate larval depth preferences, diurnal changes in larval distribution and a comprehensive data base for evaluating inshore-offshore distribution. The supplemental sampling program will continue into the second year of the overall program, and consequently will involve a second spawning season.

2. Circum-Tasmanian and Victorian trawl grounds sampling. Because we are, as yet, uncertain of where and how often Blue Grenadier spawn off Tasmania, we will conduct a regular series of plankton tows at eight sites roughly equally spaced around the island and in the Victorian trawl grounds. At each site, surface and oblique plankton tows will be made near shore, at mid-shelf, at the shelf edge and on the slope, to cover all possible areas where larvae may be found. The objective is to get as thorough a coverage of the area as possible consistent with ship availability and weather limitations.

3. Specimen handling and analysis - Samples will be divided into two equal portions, half to be preserved in formalin for purposes of identification and half in ethanol. The latter will be used in otolithic studies, that is, the otoliths will be extracted from the larvae and, by means of growth increments in otolith microstrucutre, each larva will be aged to the nearest day. Since we will know the size of each larva we can calculate their growth rates; since we know the date on which each larvae was collected, we can back-calculate to the date on which each was spawned. The latter is a particularly powerful means of determining spawning dates and spawning cycles for the species. By combining information on current patterns

with knowledge of how long larvae have been in the water column, we will be able to pinpoint spawning areas. The otolithic ageing work might also be extended to juvenile specimens.

Stock Identification

A biochemical genetic analysis of stock strucutre will be performed using electrophoretic techniques. It is envisaged that samples (each containing 100-200 frozen fish) will need to be obtained from the following localities:

Sydney	New South Wales*
Port Hicks	Victoria
Cape Liptrap	Victoria*
Portland	Victoria
Adelaide	South Australia
Great Australian Bight	S.A.*
Launceston	Tasmania
Freycinet Peninsula	Tasmania*
Cape Sorell	Tasmania
South East Cape	Tasmania
Cascade Plateau	

*Two samples taken 6 months apart from these locations.

These samples will probably not all be collected directly by CSIRO although Tasmanian and Victorian samples will be generated by CSIRO programs.

Adult Blue Grenadier in a Multi-species Fishery

The following parameters will be investigated:

(a) Determination of the important food items, particularly with regard to euphausiids (krill) and juveniles of other commercial fish species. This will be done on a quantitative basis using Bomb Calorimetry. Euphausiids

and small fish will be collected using a rectangular midwater trawl and fine mesh trawl liners.

(b) Determination of major predators of Blue Grenadier at all stages of the life cycle. This will be achieved by stomach analyses of predators from throughout the water column. It is vital for stock assessment purposes to know at which stage of the life-cycle significant mortality takes place and how this affects adult populations.

(c) Movement and migration patterns of adults, both vertically in the water column (there is some evidence that they feed in the water column) and horizontally on the slope. Also in relation to prevailing hydrological conditions. These parameters will be determined by stratified and 24 hour sampling.

Capture of fish will be by means of Engel High Lift trawls, midwater trawls and Frank and Bryce trawls fitted with heavy bobbin gear thus allowing relatively rough grounds to be worked. Basic biological parameters will be measured on board but detailed dietary analyses will be performed using calorimetric techniques in the laboratory.

Fish will be collected from east and west Tasmania and the south east trawl grounds in east Bass Strait on a bimonthly basis. Actual sampling sites will be selected after trial sampling to establish the location of suitable grounds in the different areas.

(ii) Facilities available

(a) At sea: F.R.V. 'Soela' - 52 m stern trawler fitted with deep sea trawling gear and providing accommodation for 11 scientists as well as laboratory facilities. In addition a smaller vessel will be used in the Hobart area and funds to pay for this are requested in this application.

On land: CSIRO Marine Laboratories, Hobart, Cleveland and (initially) Cronulla provide office and laboratory facilities and a full back up of computing, technical and library services.

(b) Supporting Data: CSIRO Division of Fisheries Research has a longstanding record of fisheries research in areas of direct importance to the fishing industry and has a commitment to research which will be of long-term value to Australia.

11. Proposed Commencement Date and Anticipated Completion Date:

1 July 1984 - 30 June 1987

The work on adult blue grenadier will be completed during 1985/86 but larval work will continue in 1986/87.

12. Total funds granted:

1984/85	$145,195
1985/86	$151,537
Total	$296,732

STOCK STRUCTURE OF BLUE GRENADIER

(Detailed information available in Appendix 1)

1.0 OBJECTIVES:

The major objective of the stock structure component of the southern program was to determine the number and boundar(ies) of the stock(s) of blue grenadier in Australian waters, using starch gel electrophoresis. A secondary objective was to see whether Australian blue grenadier comprised a separate stock from New Zealand fish.

2.0 METHODS:

Tissue samples of heart, muscle and liver were collected from fish from eastern, western and south-eastern Australia aboard R.V.Soela by CSIRO personnel. Tissues were frozen immediately and stored at -25^{0}_{c} until required.

In the laboratory, tissues were homogenised and centrifuged at 13,000 rpm. for 45 min. and the liquid supernatants removed and stored at -70°c. (see Appendix 1 for details). Samples were subject to horizontal starch gel electrophoresis and then stained for specific enzymes. Enzyme banding patterns which conformed to the known subunit structure of the enzyme were scored as genotypes.

Data were analysed for temporal and spatial variation between samples using Chi-square and Wright's Fst index. Analyses were performed using a modified version of the BIOSYS-1 computer package.

3.0 RESULTS:

Thirty-eight specific enzymes encoding fifty-three presumed loci were screened initially for genetic variation. Of these, ten loci were found to be variable and polymorphic at the 99% level and useful for examining stock stucture. These enzymes were adenosine deaminase, aconitate dehydrogenase-1, esterase-1, glycerol-3-phosphate

dehydrogenase, idditol dehydrogenase, mannose phosphate isomerase, phosphoglucomutase 1 and 2, superoxide dismutase and tripeptide aminopeptidase. Details of the genetic variation detected are shown in Appendix 1.

Little genetic variation was detected between the three major regions examined. Most of the detectable genetic variation was found within samples and between samples in the same region. Significant differences were detected for two of ten loci compared between samples taken 30 minutes apart at Maria Id. Differences were also detected between multiple samples from western Tasmania and south-eastern Australia.

Fish aged by Kenchington and Augustine (see Appendix 2) were also typed for genetic variation. Over 700 fish of known age were examined electrophoretically. There was no evidence of any age effect, which may account for the observed pattern of genetic variation.

Significant differences were detected between males and females at the Est-1 locus (see Appendix 1). This was due to a significant excess of males homozygous for a rare allele (104) in the August 1984 sample off eastern Tasmania. A significant change in allele frequency at the SOD locus was also found in this sample. During 1984, blue grenadier had a peak spawning period during August, off the west coast of Tasmania (see Appendix 3). These data may indicate differential movement of some fish to the west coast spawning ground from eastern Tasmania.

Australian regional samples were pooled and compared with a sample from New Zealand. There were highly significant differences ($P<0.01$) at six of eleven loci polymorphic in the two areas. This strongly suggests that Australian and New Zealand blue grenadier represent separate stocks.

5.0 CONCLUSIONS:

The stock structure subprogram of the blue grenadier biological study

examined almost 1800 fish from Australian and New Zealand waters using electrophoresis. Ten polymorphic loci were detected and compared between locations. Most genetic variation was detected within, rather than between regions for the Australian samples. These data do not support the hypothesis that there are more than one stock of blue grenadier in Australian waters.

Comparison between Australian and New Zealand samples found highly significant gene frequency differences at six of eleven polymorphic loci. This data indicates that Australian and New Zealand blue grenadier are genetically isolated and form separate stocks.

6.0 IMPLICATION AND RECOMMENDATIONS:

The management implications of this study are: (1) there is no evidence of more than one stock of blue grenadier in Australian waters. (2) there is evidence of differential distribution and non-random mixing of fish within small geographic areas. The implication of this for fisheries management are unclear and could require further research. (3) There is strong evidence that Australian and New Zealand blue grenadier form separate stocks.

LARVAL BIOLOGY

(Detailed information available in Appendix 3)

Just over 500 plankton samples have been collected from southern Australian coastal waters during this program, and examined for the presence of larval Blue Grenadier. These samples were predominantly collected in coastal regions of Tasmania, as outlined in the proposal and in the 1985 progress report to FIRTA. However, samples were also taken from points along the coasts of southern NSW, Victoria and western South Australia, in an attempt to locate spawning areas for Blue Grenadier outside of the Tasmanian region.

The principal results of this program are summarized as follows.

1. Blue Grenadier larvae have been positively identified from Australian waters, and a complete growth series of the larvae, from egg to small juvenile, have been established (Figure 1). Blue Grenadier larvae have not been described previously in the scientific literature, and much of the initial efforts of the program was devoted to determining which of the myriad larvae collected were the species of interest. A technical description of the larvae will be published in the scientific literature.

2. The overwhelming majority of spawning by Blue Grenadier in Australia occurs on the west coast of Tasmania, in a broad area between Sandy Cape and Cape Sorell. Newly spawned eggs have been collected at mid-shelf stations along this coast, although it is still unclear exactly where in the water column Blue Grenadier spawn. We have never seen a mark on our echo sounders that would indicate a recognizable aggregation of large fish in the spawning area; this parallels the experience of New Zealand fisheries biologists.

3. There is no evidence Blue Grenadier spawn anywhere in the Australian Fishing Zone other than in Tasmanian coastal regions. In both years of the field program (1984 and 1985) we collected a small number of very young larvae off the northeastern coast of Tasmania; in

1985, similarly young larvae were also caught close to SW Cape, which is further south than they were collected in 1984. A detailed ichthyoplankton survey of the north-western region was conducted in August 1986, but failed to locate any Blue Grenadier larvae, although large numbers of these larvae were caught on the same cruise on the already documented west coast spawning grounds (see Final Report FIRTA Grant 86/86). We conclude that spawning by Blue Grenadier at sites other than the Tasmanian west coast is sporadic in occurence, and of minor significance to the population or the fishery.

4. Based on ages of larvae collected, spawning by Blue Grenadier in 1984 began on approximately 6 May and ended on 10 September. The peak spawning period was in July and August. In 1985, spawning started later in the year, with the earliest larvae caught estimated to have been spawned on 5 September. Again spawning peaked in activity in July and August. There is a weak indication of a lunar cycle to spawning activity in the 1985 spawning season. Differences in spawning periods between 1984 and 1985 appear to relate to broad-scale differences between years in oceanographic features in southern Australian waters, principally the relative strengths of the East Australian Current on the east coast of Tasmania and the Leeuwin Current Extension on the west coast. It may be possible to predict spawning periods for Blue Grenadier each year on the basis of oceanographic features preceding the winter spawning period.

5. Larval Blue Grenadier occur in a depth zone of roughly 20 m to at least 90 m; few occur near the surface. There is some indication, based on depth stratified sampling conducted over a 24-hour period, of movement of larvae upwards in the water column at night. Larvae occur almost entirely over the continental shelf, and were generally most abundant at mid-shelf stations.

6. After being spawned, larvae remain in the water column for approximately 40 days. The overwhelming majority of larvae less the 5 days post-hatching are found on the west coast of Tasmania; larvae increase in size and age as distance from this region increases (Figure 2). Approximately a quarter of the larvae spawned remain on

the west coast of Tasmania; the remainder are carried by currents around the southern end of the island, to recruit into adult habitats on the east coast (Figure 3). Based on the ages of larvae collected (determined by examination of daily growth increments in the otoliths), transport of larvae from the west coast spawning grounds to Bruny Island, on the southeastern corner of Tasmania, takes about 20 days. That current patterns would carry a passively drifting larva from the west to the east coast was tested by releasing drift cards in the spawning area during spawning periods; these cards were subsequently found at sites along the western (in-shore of release points), southern and southeastern coasts of Tasmania, matching the distribution of larvae collected (Figure 4). The estimated transit time of larvae around southern Tasmania agrees closely with that predicted based on independently obtained estimates of long-shore current speeds of the Leeuwin Current Extension.

7. Larvae grow relatively slowly, at an average rate of approximately 0.4 mm/day. In both 1984 and 1985, however, growth rates of larvae were significantly higher late in the spawning season (Figure 5), presumably due to the occurence of a spring plankton bloom. If rates of larval growth correlate with rates of survival, these late season larvae may contribute disproportionately to year-class strength, a hypothesis which we are testing by examining the otolith microstructure of recruited individuals.

8. Data are also being collated on larvae of fishes other than Blue Grenadier, which were also caught during the larval program. A detailed report on the seasonal and spatial distribution of these larvae, in most cases identified only to the family level, is in preparation.

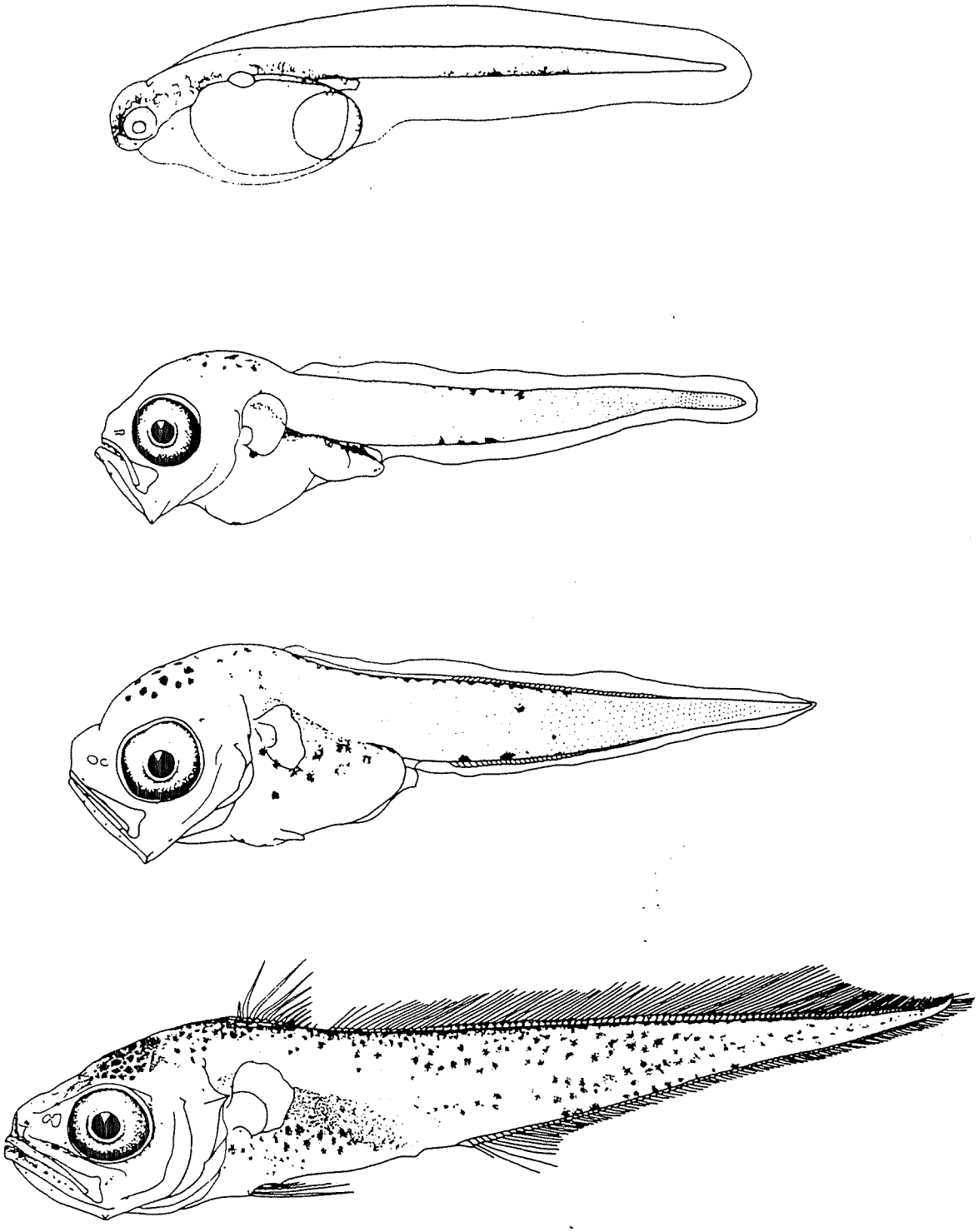


Figure 1. Developmental series of larval Blue Grenadier, from immediate post-hatch (top figure) through planktonic juvenile.

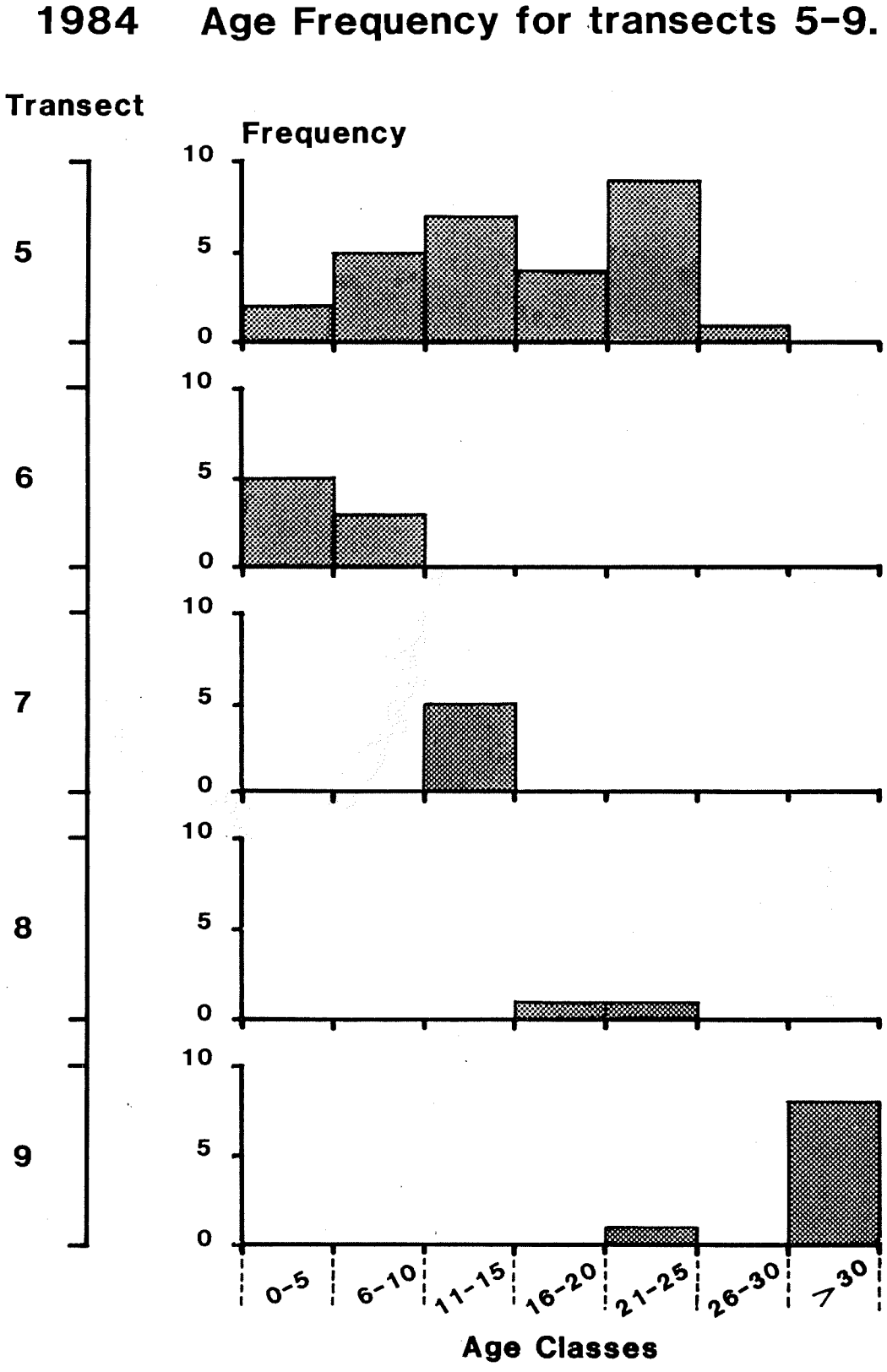


Figure 2. The distribution from west (transect 5) to east (transect 9) coasts of larval Blue Grenadier of different ages (days after hatching) during 1984 sampling.

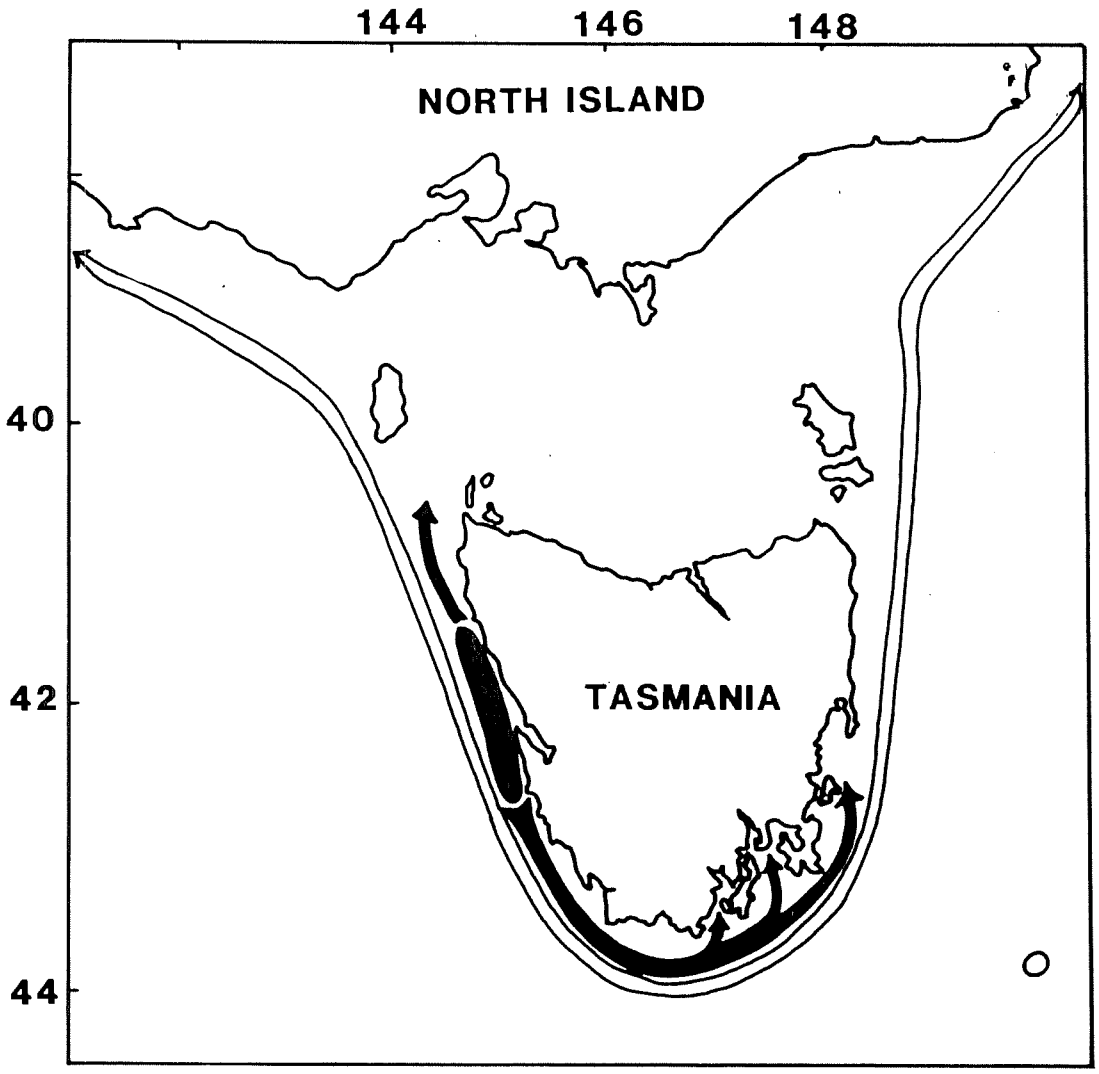
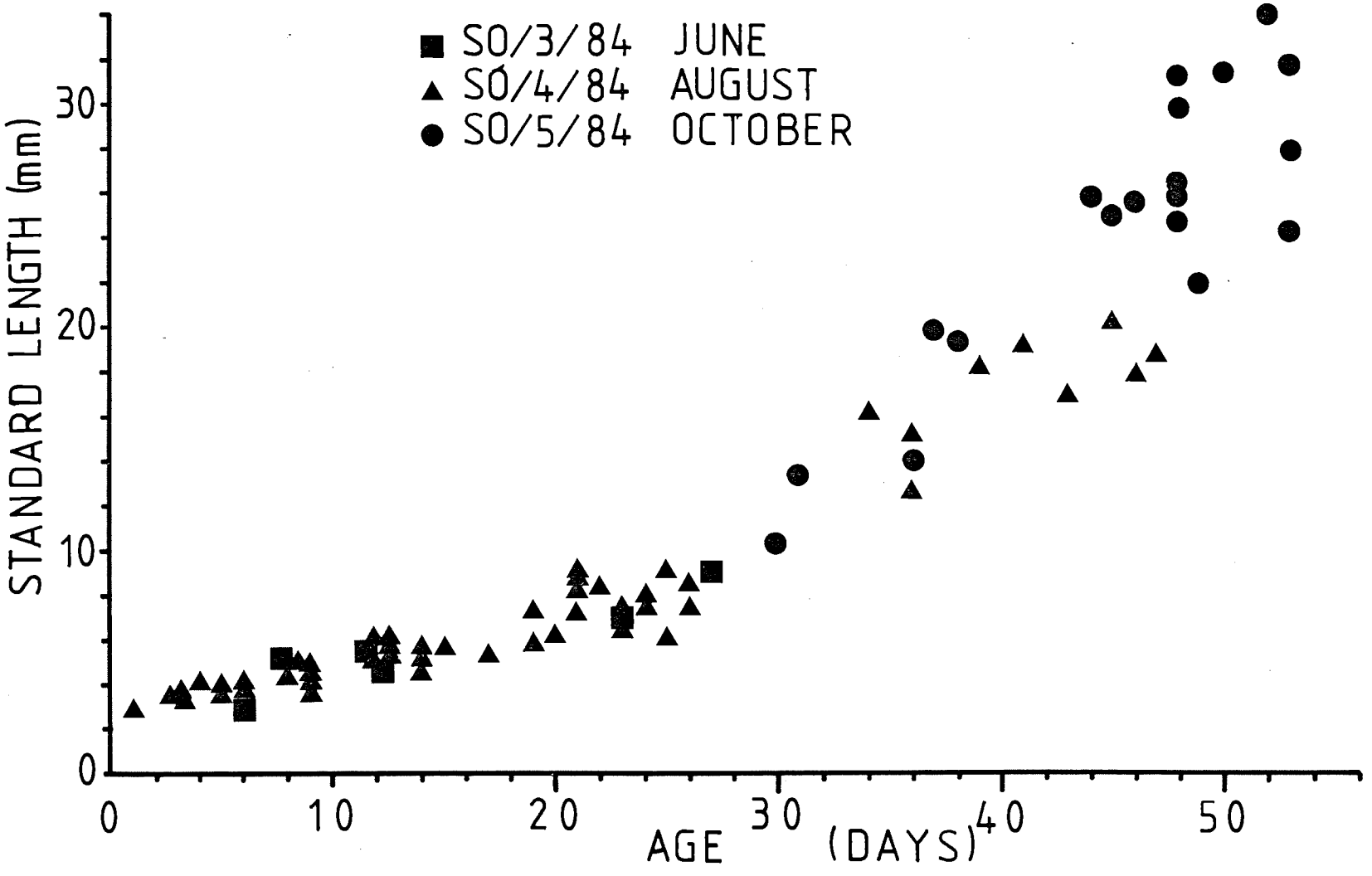


Figure 3. Summary figure of primary spawning grounds for Blue Grenadier in Australian coastal waters and the major routes of larval drift.

Figure 5. Length at age curves for Blue Grenadier larvae collected on three cruises during the 1984 spawning season.



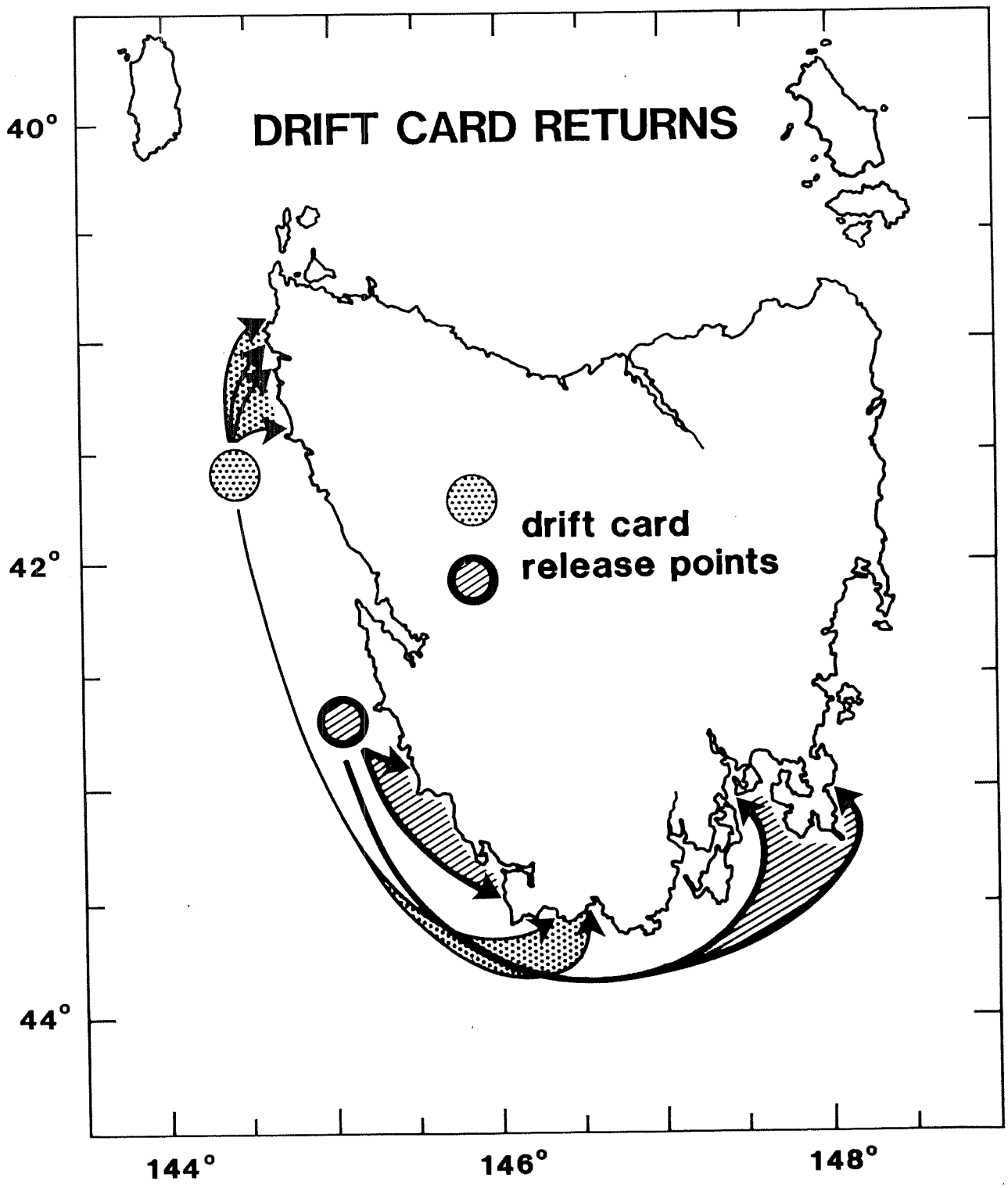


Figure 4. Drift patterns of surface drift cards released in the Blue Grenadier spawning grounds in June 1985.

REPRODUCTIVE BIOLOGY

(Detailed information available in Appendix 3)

Gonads were collected bimonthly from fish caught in the Core Area, with less regular sampling in the east Bass Strait and north west Tasmania regions. A gonosomatic index (GSI) has been calculated for these fish as:

$$GSI = \frac{GW}{BW - GW} \times 100$$

GW = gonad weight
BW = body weight

Inspection of the data showed that GSI values were high during cruises SO3/84 and SO4/84 (mid-June to mid-September). Plotting GSI against standard length for these cruises shows that length-at-first-maturity is slightly less than 70 cm for either sex.

GSI for fish of 70 cm or more standard length was plotted against time for each sex and each of the three study regions. This showed that GSI was low, with the exception of a few individuals, from October to April. The gonads of both sexes then enlarged rapidly, reaching mean sizes of nearly 8% and 12% of somatic weight, in males and females respectively, by July. Thus, mass spawning seems to occur in the June to September period.

Ripe fish were not found in the east Bass Strait. Mean GSIs there in July were under 3 and the highest individual value was only 7.62, while in September no fish over 70 cm were caught in that region and none of the small fish taken had precociously-high GSIs. Off Maria Island, mean GSIs reached 3.23 and one individual had a value of 10.32. However, these are low when compared to the west coast means of up to 11.77 and individual GSIs up to 25.51. Thus, the gonad data suggest that the only major spawning area is west of Tasmania, with only migrating pre- or post-spawners being found on the east coast.

No running ripe female grenadier were taken. Thus, either Soela did not fish on a spawning ground at spawning time or the females rise off

bottom to spawn.

Analyses are now complete for:

(1) Seasonal changes in gonosomatic index
(2) Histological sectioning of male and female gonads and seasonal changes in gonad histology
(3) Fecundity and egg size
(4) Gross morphology of the gonads

Histological work has confirmed the GSI data showing that histological staging of the gonads correlates with GSI valus, and indicates that the species has a single spawning period in winter off the west coast of Tasmania. The mean fecundity of ripe fish is close to one million eggs, which have a mean (pre-hyaline) diameter of 1.00 mm. Sperm and egg development follow a typical teleost pattern.

AGE AND GROWTH

(Detailed information available in Appendix 2)

The work on age and growth of blue grenadier has been completed and a manuscript is currently in preparation (Appendix 2). The fish are moderately long lived (greatest recorded ages: male, 20 years; females, 25 years), and have a growth pattern which is closely approximated by the von Bertalanffy function. Parameter values and their standard errors for lengths in centimetres, weights in kilograms and ages in years from a "birthday" on 1 August are:

	L_∞/W_∞	K	t_o
Males by length	90.7 ± 0.6	0.256 ± 0.009	-1.21 ± 0.11
Males by weight	2.62 ± 0.00	0.277 ± 0.014	-1.39 ± 0.21
Females by length	99.3 ± 0.7	0.203 ± 0.007	-1.48 ± 0.11
Females by weight	4.16 ± 0.00	0.157 ± 0.009	-2.93 ± 0.34

The growth curves for the two sexes are significantly different, but differences between the fish caught off the east and west coasts of Tasmania are thought to be artifacts.

Pauly's (1980) equations suggest natural mortality rates of 0.28 to 0.39 for males and 0.22 to 0.28 for females.

ADULT BIOLOGY AND INTERRELATIONSHIPS

(Detailed information available in Appendices 4, 5, 6 & 7)

Detailed work in the Core Area on the upper continental slope off eastern Tasmania has established the following important points:

1) Blue grenadier are a dominant component of the demersal fish fauna. In terms of biomass this varies according to season but they form not less than 12% and not more than 25% of total fish weight.

2) Adult blue grenadier undergo extensive diel vertical migration to within 100 m of the surface. At this time they are dispersed and feeding. This migration is closely linked with their feeding ecology and the movements of their main prey. They school on the bottom during the day, at which time they are vulnerable to bottom trawling.

3) The diet of adult blue grenadier consists almost entirely of fish with the lantern fish Lampanyctodes hectoris consistently forming about 75% of food throughout the year. The remainder of the diet consists of other fish such as Maurolicus muelleri, Diaphus danae and Lepidorhynchus denticulatus. Small quantities of pelagic Crustacea are consumed.

The cycle of feeding is such that Blue Grenadier attain maximum stomach fullness by early morning (about 6 am) after which feeding continues at a much reduced level during the benthic phase. Juvenile blue grenadier (15-25cm) feed primarily on Crustacea, particularly euphausiids.

4) Large numbers of juvenile blue grenadier (15-25cm) occur in the water column off eastern Tasmania. They appear to be leading a pelagic existence at this stage but in view of their reported occurrence in inshore waters, the relative importance of inshore and offshore waters to the juvenile phase remains to be resolved.

5) No major predators of adult blue grenadier have been found but

juvenile blue grenadier in offshore waters are extensively preyed on by adult blue grenadier.

6) Very large quantities of the lantern fish Lampanyctodes hectoris occur in Tasmanian waters, probably at commercially significant levels. However, apart from being the main food of blue grenadier, they are also the basis of the diet of jack mackerel, king dory, ocean perch, Ray's bream and a number of other species. Thus it is to be expected that any major changes in the population levels of the lantern fish may alter the community structure of the fishes of the slope. This could occur by either fishing down of blue grenadier or lantern fish.

Additional Observations

Length-Frequencies

Length-frequencies of blue grenadier caught by Soela have been drawn up. These are the only set of frequencies from uniform patterns of fishing with small-mesh gear yet prepared for blue grenadier, and serve to illustrate several aspects of blue grenadier distribution.

The length-frequencies are shown in figures 6 to 9. Several of these are based on too few fish to be meaningful. However, taken together they indicate that:

(1) Adult fish (over 70 cm) are present off the west coast of Tasmania throughout the year. They are also found in the eastern areas in some seasons, but not in late winter which is the spawning season. This lends support to the hypothesis that the major population of blue grenadier spawns west of Tasmania, but disperses around south east Australia to feed in spring and summer.

(2) 0-Group fish appeared in the pelagic catches in December at a modal length of 19 cm. During the following cruise, they were caught by the demersal net off both the east and west coasts of Tasmania as well as by the pelagic one. These young fish were not taken off the

eastern Victorian coast until the following June. These observations are consistent with the pattern of larval distribution: some larvae are retained near the spawning ground while others drift to the east coast of Tasmania. By December (age 3 - 6 months) some are large enough to be caught in the trawls, but they do not descend to the bottom until a few weeks later. A continuing drift of some larvae or small juvenile fish (20 - 30 cm) carries them into the east Bass Strait and (presumably) beyond, while others remain in the south and west.

(3) In all areas and cruises, the females reach greater maximum lengths than do the males. This is consistent with the von Bertalanffy parameters reported and with expectations for these fish.

(4) Apart from 0-Group fish, the west coast frequencies show few individuals of less than 70 cm standard length, yet the gear was fine-meshed and was not directed towards any particular size class. This may have been an artifact of the depths fished (approx. 550 m, in contrast to 450 m off Maria Island and both 450 m and 650 m off Flinders Island and eastern Victoria). However, it suggests that adult fish are over-represented off the west coast and that commercial catch length-frequencies from that area (Evans, 1985) are controlled by fish availability rather than net selectivitiy.

Offshore Occurrence of Juveniles

Wilson (1981 a,b) reported juvenile blue grenadier from Storm Bay and the Derwent. They have also been taken in Macquarie Harbour. This has led to the hypothesis that, in common with many continental shelf species, blue grenadier utilize inshore areas as nursery grounds. However, as noted above, 0-Group fish have now been taken offshore and this hypothesis must be re-examined.

The estimated density of blue grenadier juveniles in the pelagic zone off Maria Island in December, based on stratified-random trawl catches, was 0.076 fish per square metre (without allowing for any catchability factor). If these juveniles are distributed only above

the adult habitat (a conservative assumption), they occupy a band about 1000m wide. Assuming that the Maria Island estimate is applicable to the whole continental slope from north east Tasmania to King Island (approx. 1000 km, this gives 76×10^6 pelagic juveniles. No catchability coefficient has been estimated for juvenile grenadier, but for other pelagic species of similar size, in the same survey trawls, it has been taken as 0.25. If this were correct for the juveniles, their total pelagic abundance, at six months of age, would become approximately 300×10^6.

Such estimates are clearly crude and unreliable but do serve to illustrate the importance of the offshore environment to juvenile blue grenadier. The relative importance of this and the inshore areas as nursery grounds cannot be determined until more precise information is available not only on the numbers in each environment but also on their survival rates. In the meanwhile, it is possible to set up a second hypothesis, in contrast to the "inshore nursery grounds" one : blue grenadier are a shelf-break/upper slope species at all life stages and those few individuals which stray inshore contribute little to the future fishable population.

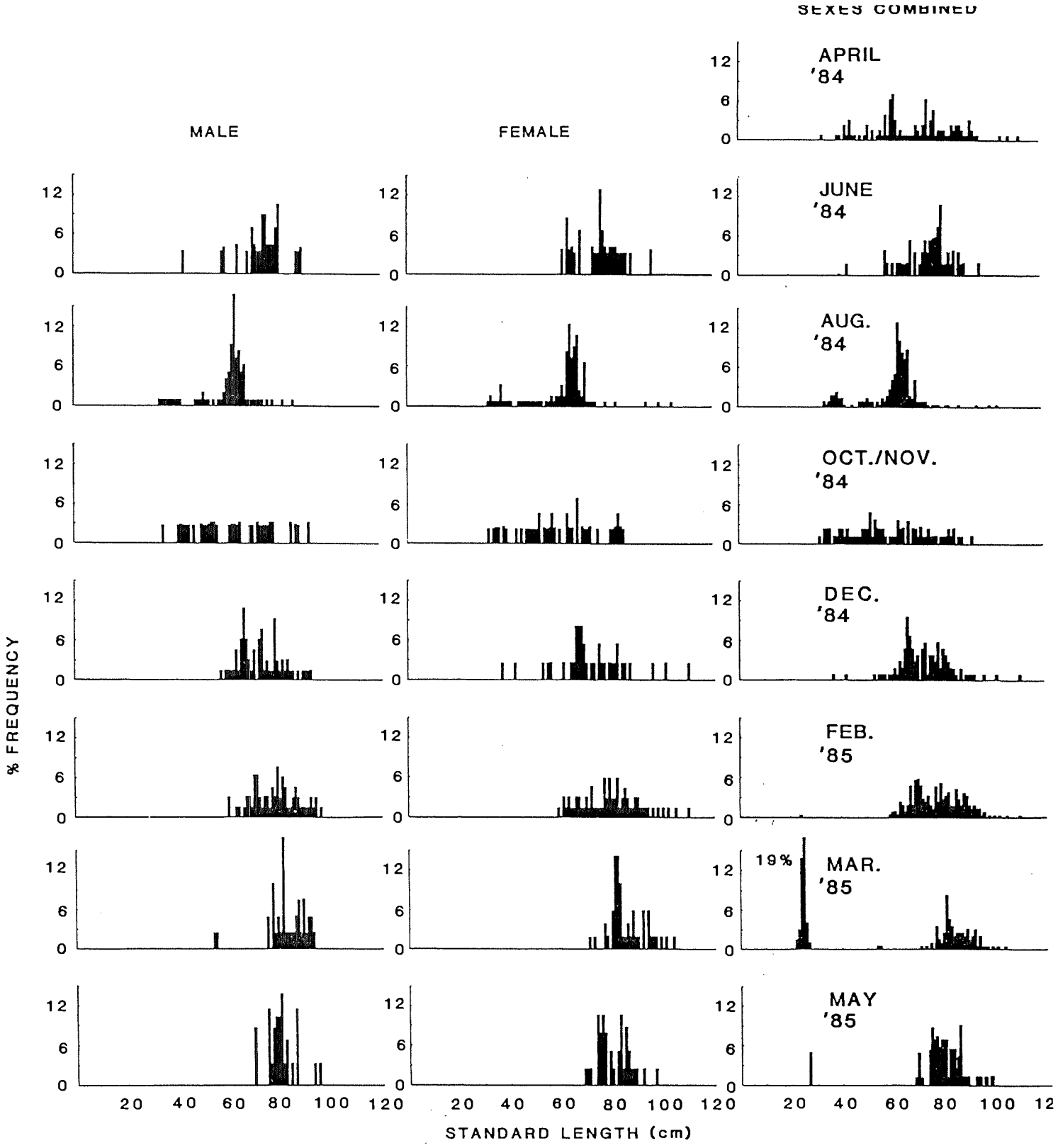


Fig.6. Length frequencies of blue grenadier caught by demersal trawling off Maria Island, Tasmania

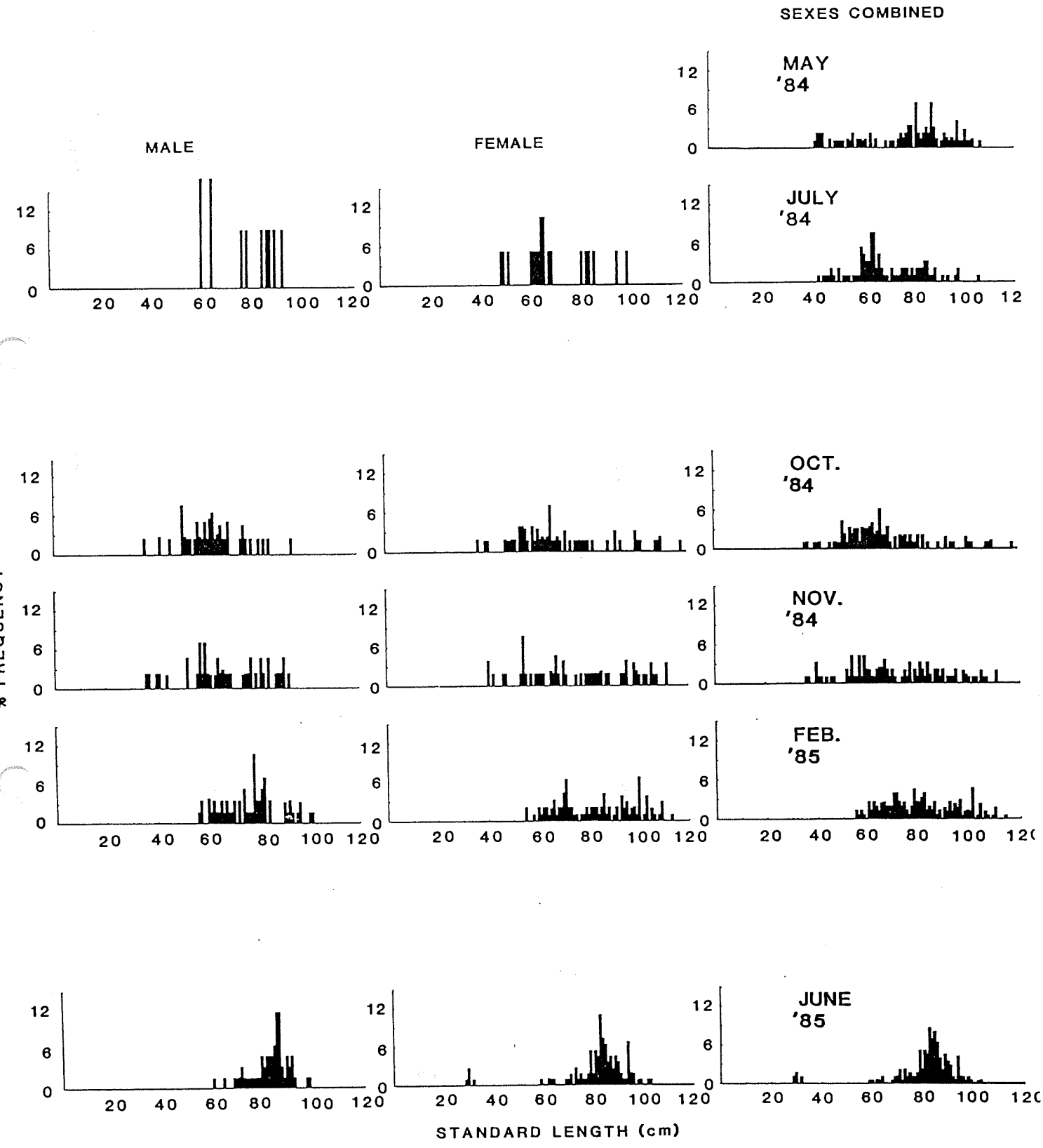


Fig.7. Length frequencies of blue grenadier caught by demersal trawling off Flinders Island and eastern Victoria

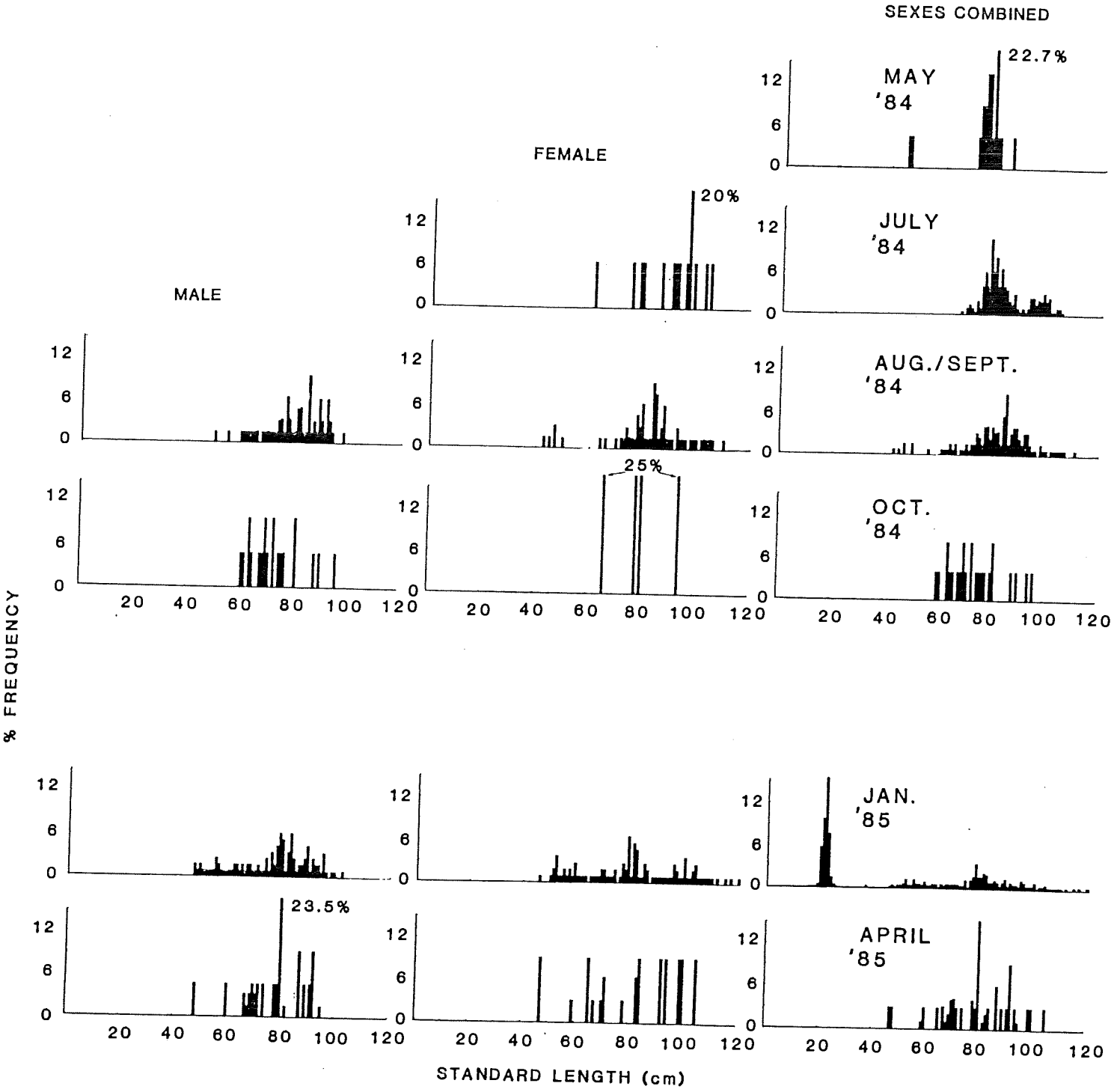


Fig.8. Length frequencies of blue grenadier caught by demersal trawling off the west coast of Tasmania

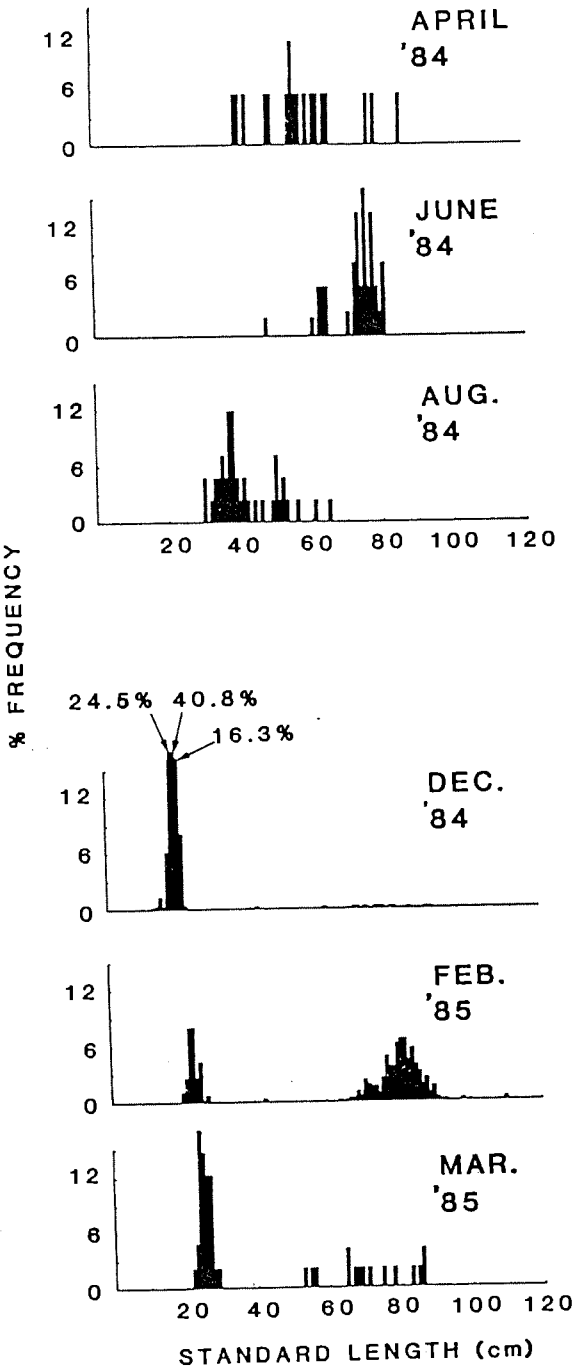


Fig.9. Length frequencies of blue grenadier caught by pelagic trawling off Maria Island, Tasmania

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OVERALL SUMMARY

The most significant findings of the project were:

1. There is only one major stock of Blue Grenadier in Australian waters.

2. Almost all spawning of Blue Grenadier takes place in winter off the west coast of Tasmania.

3. Larvae are dispersed by current patterns from the west coast of Tasmania.

4. Blue Grenadier of both sexes mature at 70 cm.

5. Each fish can spawn once a year and mean fecundity is one million eggs.

6. Maximum ages are 20 years for males and 25 years for females.

7. The growth curves for the sexes are significantly different.

8. Blue Grenadier form 12-25% of demersal fish biomass on the upper continental slope of Tasmania.

9. Adult Blue Grenadier undergo diel vertical migration and are in the mesopelagic region during the night.

10. The lantern fish, Lampanyctodes hectoris, is the most important item in the diet of Blue Grenadier.

11. Large numbers of juvenile Blue Grenadier inhabit the pelagic zone in the vicinity of the shelf-break.

APPENDIX 1

Submitted for publication

BIOCHEMICAL GENETICS AND POPULATION STRUCTURE OF BLUE GRENADIER, *Macruronus novaezelandiae* (PISCES : MERLUCCIIDAE), FROM AUSTRALIA

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ABSTRACT

Spatial and temporal variation in allele frequencies at ten polymorphic loci were investigated in blue grenadier from Australian waters. Little geographic variation was found among three major regions. Nearly all of the detectable variation (> 99 %) was found within samples, while variation between samples taken at the same locality accounted for most of the remaining variation (0.8 %). Blue grenadier were polymorphic at 22% of the forty-six loci initially screened ($P_{.99} = 0.22$). Overall mean heterozygosity was 0.068 ± 0.018. This value is considerably higher than has previously been reported for this species.

Over 700 fish were aged and typed for genetic variation. Fourteen age classes (2 - 14+ yr old) were compared. Little difference was observed among age classes within regions, or in the overall sample. Significant differences were found between sexes at one locus:Est-1; they were due to an increase in males homozygous for the 104 allele in eastern Tasmania during August 1984.This corresponded with a significant shift in allele frequency at Sod in the same sample. The sample was taken during the spawning season on the west coast of Tasmania and may provide circumstantial evidence of differential spawning migration by fish with particular genotypes from eastern Tasmania to the west coast.

Comparisons of samples from the Australian localities with a sample of fish from New Zealand showed significant heterogeneity at six of the eleven loci polymorphic in the two areas. The observed differentiation indicates that the New Zealand populations of blue grenadier are genetically isolated from those of Australia. However, the apparent genetic homogeneity observed for the Australian samples suggests that, for management purposes, blue grenadier throughout southeastern Australia can be treated as a single, unit stock in the absence of indications to the contrary.

INTRODUCTION

Knowledge of stock structure is an important consideration when developing and implementing an effective management strategy for a fishery. Wilson (1984) estimated a biomass of 70,000 t of blue grenadier Macruronus novaezelandiae in the waters off the west coast of Tasmania, and indicated that the commercial fishery had the potential for expansion.

Blue grenadier already support a major commercial fishery in New Zealand : annual catches exceed 100,000 t (Smith et al., 1981). Although little is known about other Macruronus species that support commercial fisheries (e.g. M. magellanicus off South America) they appear to have similar life cycles (Torno and Tomo 1980).

New Zealand blue grenadier were reported by Kuo and Tanaka (1984 a, b, c) to be opportunistic carnivores, living over a variety of substrates on the continental shelf at depths between 200 and 700 m. The fish spawned in late winter and spring in three major areas around New Zealand, to which they migrated during winter from their feeding areas (Kuo and Tanaka 1984a). The survival and growth of larvae have been shown to be positively related to temperature (Blagoderov 1978); survival is reportedly enhanced by warmer water temperatures in the spawning areas (Blagoderov and Shurunov 1980). The stock structure of blue grenadier in New Zealand waters was examined by Smith et.al

(1981) who found no evidence for the existence of more than one stock . However, significant morphological and meristic heterogeneity has been found within small areas (Blagoderov 1977).

Australian populations of blue grenadier have received little attention until recently (e.g. Bulmer and Blaber 1986), when the prospect of an expansion of the commercial fishery necessitated greater understanding of the stock structure, trophic relations, and larval life history (Blaber et al. 1985).

Stocks can be defined as temporally or spatially isolated subpopulations (Shaklee and Salini 1985) within the species range. To delimit stocks, information about the genetic structure of the species is required. Since stocks are assumed to be at least partially isolated reproductively (Grant and Utter 1984), they are, hence believed to be genetically unique (Booke 1981, Kutkuhn 1981). Electrophoresis is a powerful tool for defining stock structure as it allows a direct examination of the expression of the genome of the organism (Shaklee 1983).

The aim of the present study was to examine the stock structure of blue grenadier in Australian waters, using starch gel electrophoretic analyses of isozyme variation. Information on the magnitude and pattern of population subdivision would then enable management to be advised on the biological management of

the emerging fisheries.

METHODS AND MATERIALS

Fish were collected from demersal trawls aboard the RV Soela between April 1984 and April 1985 (samples 1-19), two trawls in July 1984 aboard the RV Kapala (samples 20,21), and by gillnetting off New Zealand (sample 22) (see Table 1; Figure 1) Trawl catches of more than thirty fish, were used in the electrophoretic analysis and each such trawl catch was treated as an individual sample. The length, weight and sex of each fish were recorded and otoliths were removed from most of the fish for age determination.

Muscle, heart and liver tissue were removed and stored at -20° C until processed. Eye tissue was also used until it was found it did not contribute polymorphic loci not already obtainable from other tissues.

To screen for the ten polymorphic loci (Table 2),tissue homogenates were prepared and subjected to horizontal starch gel electrophoresis according to the methods described by Shaklee and Keenan (1986). Patterns of enzyme variation consistent with the subunit structure of the enzyme (where known) and simple models of Mendelian inheritance were scored and recorded as genotypes.

Enzyme and isozyme homology, allelic designation and data analyses follow Shaklee and Salini (1985). Loci were considered polymorphic ($P_{.99}$) when the frequency of the most common allele was not more than 0.99.

Contingency chi square analyses were conducted at two levels. Temporal variation was examined among samples from each location (Table 1). Geographic variation was investigated by comparing pooled samples from each location. A modified version of the BIOSYS-1 computer program of Swofford and Selander (1981) was used throughout the data analyses. The significance of Fst values (Wright 1978) was determined using the test of Workman and Niswinder (1970): $X^2 = 2NFst$, where N is the total number of individuals compared, and the degrees of freedom = number of samples - 1.

RESULTS

Genetic Variation

Thirty-eight specific enzymes encoded by 53 presumed gene loci were initially surveyed for genetic variation. Of these, 7 loci were unscorable due to inadequate, uninterpretable or inconsistent staining: asparate aminotransferase-1, acid phosphatase, fructose bisphosphate aldolase, creatine kinase-B,

glyceraldehyde-3-phosphate dehydrogenase, hexokinase, and fructose bisphosphatase-1. These enzyme loci were not included in any of the further analyses.

Thirty-six loci were either monomorphic or showed only rare variation in the first 300 animals analyzed (100 each from eastern and western Tasmania, and southeastern Australia): aconitate hydratase-2, asparate aminotransferase-2, adenylate kinase, alanine aminotransferase, creatine kinase-A, diaphorase (NADH+), enolase-1 and 2, esterases (3 loci), esterase-D (3 loci), fumarate hydratase-1 and 2, glutamate dehydrogenase, alpha-glucosidase, glucose-6-phosphate isomerase-A and B, glycerol-3-phosphate dehydrogenase-B, fructose bisphosphatase-2, isocitrate dehydrogenase (liver form),lactate dehydrogenase-A, B, and C, malate dehydrogenase-1 and 2, malate dehydrogenase (NADP+), peptidases (4 loci), phosphoglycerate kinase, purine nucleoside phosphorylase, and xanthine dehydrogenase.

Ten loci were polymorphic and the conditions used for their analysis are detailed in Table 2. Allele frequencies for each of the polymorphic loci and the actual number of genes scored in each sample are given in Table 3. To allow statistical tests of the data, each of the rare alleles observed for Ada (7), Ah-1 (2), G-3-pdh-A (1), Iddh (5), Pgm-2 (2) Tapep (2) was pooled with the allele having the closest electrophoretic mobility . Typical patterns of observed electrophoretic variation at five of the variable loci are shown in Figure 2. The proportion of

polymorphic loci ($P._{99}$) was 0.22 (at the $P._{95}$ level, this was 0.17). The mean heterozygosity of individual samples, calculated for all 46 loci, varied between 0.064 and 0.072 with a mean ± standard error of 0.068 ± 0.018 in the Australian samples. The mean heterozygosity of our New Zealand sample was 0.058 ± 0.018 for the 46 loci screened and 0.038 ± 0.013 for the 12 enzyme loci previously examined by Smith et al. (1981).

Heterogeneity chi square tests of agreement of observed allele frequencies with Hardy Weinberg expectations resulted in 10 (out of a total of 210) tests differing significantly from expectation. Since an alpha level of 0.05 was used in the testing, this number of significant deviations is not greater than that expected by chance alone. The greatest number of significant deviations were in the loci EST-1, MPI and IDDH; the often poorer staining of their heterozygotes may have partly contributed to the excess of homozygotes detected in these loci. On the basis of this, we conclude that allele frequencies in blue grenadier conform with Hardy Weinberg expectations and that the observed variation in isozyme banding patterns is consistent with the simple genetic models used for their interpretation.

Population structure

The results of the F-statistic and contingency chi square analyses are shown in tables 4 and 5. Fst values were generally low (>0.01). When all 21 Australian samples were tested without

pooling, the variation was significant. When samples within regions were pooled, there was very little variation between regions; however, samples within regions varied significantly. The Fst values associated with the multiple samples from the west and east coasts of Tasmania were among the highest observed in this study. Short-term temporal variation within a region was examined in eastern Tasmania. Two samples were taken at the same site 30 minutes apart (collections 10 and 11; Table 3). The samples were significantly different at two individual loci (Ada and Iddh) and, in an overall test, at all loci simultaneously : X^2 4df = 9.95, P <0.05; X^2 2df = 6.33, P <0.05; and X^2 20df = 32.35, P <0.05, respectively. Juveniles and adults from the same trawl on the west coast (collections 4 and 5) were also compared; there were no significant differences at any loci between these two samples.

Age

Over 700 fish from eastern and western Tasmania (see Table 1) that were typed for genetic variation were also aged by T. Kenchington and O. Augustine (see Kenchington and Augustine, 1987). Twelve age-classes (2-14+), had sufficient data for statistical comparisons. Although there were no significant differences between age classes in the overall X^2 test (Tables 4 and 5), there were significant differences at three individual loci: Est-1, Mpi and Pgm-2. Sign tests of trends on all loci did not reveal any significant trends in allele frequencies in

any sample. Juveniles and immature fish (0+ and 2-4 yr old) were compared (from all samples combined), since these are age-classes with high mortality and thus, presumably of intense selection. No significant differences were found at any loci between these age-classes in samples from eastern or western Tasmania.

Sex

Comparisons between males and females pooled across all the collections showed significant differences only at Est-1 (Tables 4 and 5). Males eastern Tasmania, especially those in the August 1984 sample, had a significantly higher frequency of the 104 allele of Est-1 (X^2 1df = 6.78; P <0.01)(Table 3). All of the seven fish from eastern Tasmania that were homozygous for the two rarer alleles (104 and 95) at Est-1 were male (Table 6). Three fish whose sex was not determined and two females from other areas also had the 95/95 genotype. There was no difference in the incidence of the 95 allele between eastern Tasmania and the rest of the Australian sample (X^2 1df = 0.47; n.s.). However, within the overall sample there was a significant excess of male 95/95 homozygotes (X^2 1df = 5.17; P <0.02).

Seasonal variation

The seasonal pattern of allele frequencies was examined in eastern Tasmania, the only region for which we had a full year of

samples. There was a significant shift in allele frequencies at Est-1 and Sod (Tables 4 and 5). The differences among samples from the spawning (July-September) and non-spawning periods were highly significant ($P < 0.005$). A reduction in the 225 allele at Sod during the spawning period coincided with an increase in the 104 allele in Est-1 (Table 7).

Australia vs. New Zealand

The allele frequencies of the pooled Australian regional samples and the New Zealand sample at eleven polymorphic loci are given in Table 8. There were highly significant differences ($P < 0.01$) at six of the eleven loci considered. Furthermore, there were unique alleles in the New Zealand sample for Ada, Gpi-B and Mpi. Gpi-B was polymorphic in the New Zealand sample and not in the Australian sample. It is also of interest that the New Zealand sample analyzed in the present study was significantly different from the Cape Campbell samples analysed by Smith et al. (1981) at two (G-3-pdh-A and Pgm-2) of the three polymorphic loci common to the two studies (Table 9).

DISCUSSION

The results of this study do not provide any clear evidence of geographically isolated stocks of Australian blue grenadier.

In fact, there was much greater genetic diversity in the Australian samples, within regions than between regions. This pattern of gene variability, which has been observed in several other groups of marine fishes (reviewed by Gyllensten 1985), presumably results from substantial gene flow between populations due to passive dispersal of eggs and/or embryos, to active migration of juveniles and/or adults, to similiar selection pressures on isolated populations, or a combination of all of these.

Blaber et al. (1985) have found strong evidence of a major spawning aggregation off western Tasmania during winter-spring (July - September). Large numbers of young larvae have been collected in this region in two consecutive seasons (Blaber et al., 1986). It has been suggested that these larvae drift passively in circum-Tasmanian currents around southern Tasmania to the Maria Island region. If this is correct, there would be considerable gene exchange between these two regions.

No data are available on the seasonal movement of adult fish in Australian waters. Non-ripe adults can be found across the Australian distribution of the species throughout the year (Blaber et al., 1985). Underwater videos of blue grenadier have shown that this species is a solitary predator (Bulman and Blaber pers comm), but it is unclear whether fish from throughout the species' range school and migrate to the west coast for spawning or whether only fish resident off the west coast participate in

spawning. Blue grenadier in New Zealand waters did migrate to the spawning ground from their feeding areas (Kuo and Tanaka 1984a, b). Preliminary data from Lester et.al.'s (1986) examination of long-lived endoparasites in blue grenadier did not indicate large-scale movement of fish between eastern and western Tasmania; however, seasonal distribution patterns of parasite load are not yet available (Lester pers comm)

Our genetic data does not rule out the possibility that fish from eastern Tasmania (Maria Island) are contributing to the spawning aggregation off the west coast. Indeed, the data suggest that these region are genetically similiar.

Genetic similarity over long distances is characteristic of many marine species (e.g., Gadus morhua (Mork et al., 1985), Clupea spp. (Grant 1984, Grant and Utter 1984, Ryman et al., 1984), Cheilodactylus macropterus (Richardson 1982a), Engraulis capensis (Grant 1985), Stegastes fasciolatus (Shaklee 1984) Hoplostethus atlanticus (Smith 1986) and Katsuwonus pelamis (Richardson 1983)), and seasonal shifts in allele frequency have been found in other species (e.g. Clupea harengus, Kornfield et al., 1982 , Polyprion oxygeneiosis, Smith and Johnston, 1985). However, heterogeneity in allele frequencies between two samples taken off eastern Tasmania thirty minutes apart suggests that there may be in this species, significant microspatial heterogeneity in eastern Tasmania. Data from other regions and the studies of Blagoderov (1977) support this possibility. In

our own data, some samples taken hours or days apart show significant allele frequency differences for atleast one locus (Tables 1 and 3). Whatever the explanation may be, the data suggest either that the fish are not randomly distributed or that all genotypes are not equally catchable.

The levels of polymorphism ($P_{.99}$ = 0.22) and mean heterozygosity (H = 0.068 $\pm$ 0.018) for blue grenadier are comparable to values found for other marine fishes (Nevo 1978, Winans 1980, Smith and Fujio 1982, Gyllensten 1985). However, the level of heterozygosity found in this study is significantly higher ($P < 0.01$) than was previously reported for blue grenadier (based on liver enzymes) from New Zealand (H = 0.016; Smith *et al.*, 1981). Smith and Fujio (1982) reviewed heterozygosity in deep-sea fishes, including blue grenadier. They found a mean heterozygosity of 0.044 $\pm$ 0.019 for nine species, and interpreted these data, especially in the Gadiformes, as support for the habitat generalist/low heterozygosity hypothesis. As these values were calculated from an average of 19 $\pm$ 1.5 loci per species, they may have underestimated the level of heterozygosity in these species. By basing the calculations on 30 or more loci, the variance associated with calculations of H is reduced (see Nei 1978, Gorman and Renzi 1979). The problem of estimating H for comparative purposes is aggravated by investigators in different laboratories using different sets of loci, which themselves may have very different average levels of variability, as noted by Smith and Fujio (1982).

In contrast to the general pattern of genetic homogeneity among Australian samples of blue grenadier, there is clear evidence of substantial genetic differentiation between Australian and New Zealand populations, as indicated by the significant chi square tests between these two major regions and by the existence of "private" alleles in one of the two regions. At the same time, Nei's (1978) genetic distance between these populations is small: D = 0.003. This relatively low value is comparable to that obtained in several other studies of marine fishes that show little genetic divergence over long distances (e.g. Grant et al., 1983, Grant 1984, Wilson and Waples 1984).

A comparison of our data on New Zealand blue grenadier with that of Smith et al. (1981) also suggests that the New Zealand population may be heterogeneous (cf. Table 9), they found only three alleles for the enzyme IDDH. Whereas we found four alleles in the Paliser Bay sample at this locus. Pooling all our alleles into three allele classes ("fast", 100, "slow") generated allele frequencies that were not statistically distinguishable from the frequencies reported by Smith and coworkers. Statistically significant different differences at two of the three loci polymorphic in both studies does provide further evidence of within-region heterogeneity in blue grenadier.

The observed pattern of allele frequencies might be attributable to natural selection favouring particular genotypes

in certain age-classes (cf. Gauldie 1984) or one of the sexes (assuming that some of the loci screened are sex-linked). Johnson (1971), Hjorth and Simonsen (1975), Gauldie and Johnston (1980), Hoffmann (1981), Philipp et al. (1981) and others have found evidence that temperature may be an important selective agent for particular alleles of several enzymes. Blagoderov (1978) and Blagoderov and Shurunov (1980) have reported higher rates of survival and growth of larval blue grenadier in years with higher water temperatures. If natural selection were operating on particular loci in response to temperature, blue grenadier spawned in warmer years would have enhanced survival and their genotype(s) would be selectively favoured. Hence, differences in the frequencies of alleles at some loci might be expected in fish of different ages in response to annual fluctuations in water temperatures. Although insufficient data restricted our analyses to comparisons of age-classes within regions, we have no evidence to suggest that natural selection is favouring particular genotypes for the enzyme loci and age classes examined. Therefore, differences in the age composition of the samples do not appear to explain the observed allele frequency pattern.

The pattern of allele frequencies at Est-1 shows an interesting trend. The distribution of the alleles of Est-1 between samples appears clumped. The 104 allele is extremely rare throughout the Australian sample (frequency = 0.006). The increase in frequency of this allele to 0.036 in the August 1984

sample from eastern Tasmania occurred concomitantly with a reduction in the 225 allele at Sod. Blaber et al.'s (1985) data on larval aging showed that this sample was collected during the peak spawning period. These data may provide circumstantial evidence of possible differential migration by fish with particular genotypes. Further sampling would be required to test this hypothesis. The shifts in allele frequency at these loci are responsible for most of the within-region heterogeneity observed in the eastern Tasmanian samples. They do not, however, explain similar heterogeneity at other loci in other regions.

To manage any commercial fishery effectively, it is important to know which stocks contribute to the fishery and where their boundaries are. We found no evidence for the existence of geographically isolated stocks in Australian waters; the statistically significant variation observed was largely within rather than between regions. Possibly, as Richardson (1982b) suggested for Trachurus declivis, the observed genetic heterogeneity is due to the existence of two or more stocks of blue grenadier in Australia overlapping in time and space. However, in that case one would expect a significant homozygote excess at several loci; this did not occur in our study.

The genetic data on blue grenadier presented in this report, together with biological data available in Blaber et al.(1985), suggest that there is significant gene flow between regions within Australian waters. Using the simplified island model

(Wright 1978) where $Fst = (4Nm+1)^{-1}$ and substituting 35,000,000 for N (the effective population size) - calculated from the estimated biomass for blue grenadier of 70,000 tonnes (Wilson, 1984) and an average fish weight of 2.0 kg - gives an estimate for the number of migrants between regions of 250 for an Fst = 0.001 (Table 4). This figure is an absolute value and is independent of population size (Allendorf and Phelps 1981). Grant (1985) found a similar pattern of high within-region heterogeneity in the South African anchovy Engraulis capensis, and, as his genetic data conflicted with other biological information about the stock structure of the species, he concluded that the "genetic stock" concept may not be appropriate for Engraulis . In the case of blue grenadier, however, genetic and biological data are congruent. Both types of data suggest that, for effective management purposes, blue grenadier populations in southeastern Australia can be treated as belonging to a single stock.

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Table 1: Data for all Australian collections and the New Zealand sample of blue grenadier (see Figure 1 for locations; S.E.= standard error).

Area	Collection number	Collection date	Sample size	Mean length ± S.E. (cm)	Sex ratio M:F	Mean age ± S.E. (yr)	fish aged (n)
W.Tasmania	1	April 1984	30	84.8±2.9	7:13	7.3±1.2	9
	2	Jan. 1985	104	80.0±1.1	53:32	8.1±0.5	84
	3	Jan. 1985	119	75.7±1.2	83:36	7.2±0.4	97
	4	Jan. 1985	104	86.0±1.2	57:46	11.1±0.8	46
	5	Jan. 1985	91	21.3±0.2	n.d.	n.d.	-
	6	April 1985	61	32.8±2.6	11:7	n.d.	-
	7	Jan. 1985	61	71.9±2.3	23:21	n.d.	-
E.Tasmania	8	April 1984	108	73.4±1.0	34:38	5.1±0.4	32
	9	Aug. 1984	140	73.1±1.0	91:49	6.2±0.6	48
	10	Feb. 1985	101	74.9±0.7	24:26	5.2±0.2	96
	11	Feb. 1985	101	79.8±0.9	45:53	7.0±0.4	84
	12	Mar. 1985	115	84.5±0.5	47:53	11.4±1.2	50
	13	Feb. 1985	91	22.3±0.1	n.d.	n.d.	-
	14	Feb. 1985	49	23.2±0.2	n.d.	n.d.	-
	15	Oct./Nov.1984	38	76.6±2.0	8:3	8.8±0.9	10
E.Bass	16	Oct. 1984	84	71.6±2.0	32:47	n.d.	-
Strait	17	Jan. 1985	81	72.0±0.8	43:38	n.d.	-
Gabo I.	18	Jan. 1985	97	82.8±2.3	30:44	11.8±0.6	53
	19	Sept. 1984	40	61.7±0.9	19:20	n.d.	-
Eden	20	July 1984	55	69.2±1.7	9:40	5.0±0.9	15
	21	Aug. 1984	65	55.4±0.9	26:39	n.d.	-
Puliser Bay (New Zealand)	22	Dec. 1985	53	63.8±0.9	9:4	n.d	-
Total			1787	67.0±1.1	651:609	7.8±0.5	624

Table 2: Characteristics and conditions for analysis of polymorphic enzymes in Macruronus novaezelandiae.

Enzyme (E.C.Number)	Locus	Subunit structure	Tissue	Buffer[1]
Adenosine deaminase (3.5.4.4)	Ada	monomer	muscle/heart	CAAPM
Aconitate hydratase (4.2.1.3)	Ah-1	monomer	liver	TRIC
Esterase (3.1.1._)	Est-1	monomer	muscle/liver	LIOH
Glycerol-3-phosphate dehydrogenase (1.1.1.8)	G-3-pdh-A	dimer	muscle	TC-1
L-iditol dehydrogenase (1.1.1.14)	Iddh	tetramer	liver	LIOH
Mannose-6-phosphate isomerase (5.3.1.8)	Mpi	monomer	heart	EBT
Phosphoglucomutase (5.4.2.2)	Pgm-1	monomer	muscle	TRIC
	Pgm-2	monomer	muscle	TRIC
Superoxide dismutase (1.15.1.1)	Sod	dimer	liver	TC-2
Tripeptide aminopeptidase (3.4.11.4)	Tapep	dimer	muscle	TC-4

[1] = CAAPM = citric acid-aminopropylmorpholine pH 6.0 (Clayton and Tretiak 1972)
TRIC = triethanolamine-citric acid pH 7.2 (Clayton and Tretiak 1972)
LIOH = lithium hydroxide-boric acid pH 8.1 (modified from Selander et al., 1971)
TC-1 = Tris-citric acid pH 7.0 (Shaw and Prasad 1970)
EBT = EDTA-boric acid-Tris pH 8.6 (Boyer et al., 1963)
TC-2 = Tris-citric acid pH 8.0 (Selander et al., 1971)
(see Shaklee and Keenan, 1986 for detailed buffer recipes)

Table 3: The allele frequencies for all Australian samples of blue grenadier and the number of genes scored. (Numbers correspond to the sample numbers shown in Figure 1). N.D.= no data, (+) denotes that rare allele(s) have been pooled with this allele, H = mean heterozygosity.

Allele	Sample number																				
N	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
124(+)	0.267	0.245	0.231	0.269	0.280	0.213	0.205	0.222	0.255	0.300	0.208	0.226	0.286	0.214	0.224	0.202	0.222	0.206	0.237	0.245	0.323
116	0.180	0.245	0.269	0.240	0.236	0.320	0.180	0.204	0.255	0.220	0.238	0.265	0.220	0.224	0.237	0.226	0.253	0.258	0.262	0.218	0.177
100	0.300	0.279	0.235	0.269	0.264	0.238	0.344	0.301	0.273	0.200	0.272	0.296	0.269	0.224	0.276	0.268	0.228	0.294	0.338	0.245	0.238
88(+)	0.233	0.207	0.210	0.173	0.170	0.172	0.213	0.227	0.176	0.245	0.203	0.213	0.187	0.276	0.171	0.256	0.241	0.206	0.125	0.255	0.223
80(+)	0.017	0.024	0.055	0.048	0.049	0.057	0.057	0.046	0.040	0.035	0.079	0.026	0.038	0.061	0.092	0.048	0.056	0.036	0.038	0.036	0.038
N	60	208	238	208	182	122	122	216	278	200	202	230	182	98	76	168	162	194	80	110	130
105(+)	0.067	0.131	0.101	0.173	0.154	0.117	0.133	0.144	0.118	0.120	0.149	0.162	0.110	0.143	0.132	0.128	0.148	0.163	0.138	0.155	0.146
100	0.650	0.728	0.748	0.635	0.670	0.758	0.658	0.704	0.757	0.760	0.678	0.667	0.764	0.714	0.697	0.677	0.667	0.597	0.713	0.709	0.746
94(+)	0.283	0.141	0.151	0.188	0.176	0.125	0.158	0.153	0.125	0.120	0.173	0.171	0.126	0.143	0.171	0.195	0.185	0.240	0.150	0.136	0.108
N	60	206	238	208	182	120	120	216	280	200	202	228	182	98	76	164	162	196	80	110	130
104	0.000	0.005	0.004	0.010	0.005	0.008	0.000	0.000	0.036	0.000	0.005	0.004	0.000	0.010	0.000	0.006	0.000	0.006	0.000	0.000	0.000
100	1.000	0.947	0.905	0.937	0.923	0.967	0.943	0.948	0.904	0.968	0.970	0.952	0.962	0.939	0.961	0.968	0.951	0.950	0.973	0.945	0.984
95	0.000	0.049	0.091	0.053	0.071	0.033	0.057	0.052	0.061	0.032	0.025	0.044	0.038	0.051	0.039	0.028	0.049	0.044	0.027	0.055	0.016
N	58	206	232	206	182	122	122	212	280	188	202	228	182	98	76	158	162	180	74	110	124
118(+)	0.100	0.106	0.122	0.125	0.143	0.156	0.139	0.117	0.146	0.119	0.158	0.096	0.126	0.082	0.079	0.107	0.111	0.120	0.075	0.100	0.108
100	0.900	0.894	0.878	0.875	0.852	0.844	0.861	0.883	0.854	0.881	0.842	0.904	0.874	0.918	0.921	0.893	0.889	0.880	0.925	0.900	0.892
N	60	208	238	208	182	122	122	214	280	202	202	230	182	98	76	168	162	192	80	110	130
122(+)	0.037	0.105	0.100	0.103	0.076	0.156	0.133	0.086	0.139	0.077	0.104	0.143	0.143	0.122	0.143	0.107	0.123	0.153	0.091	0.100	0.141
100	0.889	0.820	0.859	0.858	0.890	0.820	0.833	0.864	0.821	0.842	0.856	0.839	0.802	0.857	0.839	0.843	0.846	0.779	0.909	0.836	0.781
76(+)	0.056	0.070	0.014	0.025	0.011	0.017	0.025	0.015	0.011	0.046	0.005	0.013	0.011	0.010	0.018	0.036	0.019	0.021	0.000	0.000	0.024
48(+)	0.019	0.005	0.027	0.015	0.022	0.008	0.008	0.035	0.029	0.036	0.025	0.004	0.033	0.010	0.000	0.014	0.011	0.047	0.000	0.064	0.055
N	54	200	220	204	182	122	120	198	274	196	202	230	182	98	56	140	162	190	22	110	130
108	0.150	0.188	0.122	0.083	N.D.	0.084	0.080	0.105	0.132	0.129	0.094	0.097	N.D	N.D.	0.076	0.134	0.125	0.113	0.141	0.200	0.074
100	0.850	0.808	0.866	0.909		0.875	0.902	0.880	0.861	0.851	0.891	0.899			0.924	0.860	0.856	0.866	0.833	0.773	0.926
87(+)	0.000	0.005	0.012	0.008		0.041	0.018	0.015	0.007	0.020	0.015	0.004			0.000	0.006	0.019	0.021	0.026	0.027	0.000
N	40	208	238	132		24	112	200	280	202	202	228			66	164	160	194	78	110	94
114	0.038	0.035	0.029	0.059	0.044	0.074	0.025	0.079	0.061	0.054	0.050	0.057	0.044	0.051	0.053	0.048	0.068	0.051	0.038	0.055	0.038
110	0.212	0.248	0.324	0.213	0.214	0.246	0.221	0.188	0.196	0.188	0.228	0.283	0.283	0.235	0.276	0.232	0.204	0.219	0.262	0.236	0.223
105	0.058	0.099	0.080	0.069	0.121	0.115	0.090	0.089	0.089	0.054	0.069	0.061	0.094	0.041	0.105	0.089	0.093	0.077	0.050	0.082	0.085
100	0.538	0.520	0.450	0.550	0.522	0.467	0.549	0.525	0.532	0.574	0.545	0.513	0.444	0.571	0.500	0.494	0.525	0.551	0.538	0.545	0.585
93(+)	0.154	0.099	0.118	0.109	0.099	0.098	0.115	0.119	0.121	0.129	0.109	0.087	0.133	0.102	0.066	0.137	0.111	0.102	0.122	0.082	0.069
N	26	202	238	202	182	122	122	202	280	202	202	230	182	98	78	168	162	196	80	110	130
132(+)	0.017	0.029	0.025	0.014	0.033	0.025	0.041	0.018	0.007	0.015	0.030	0.017	0.027	0.041	0.013	0.012	0.013	0.010	0.025	0.027	0.015
100	0.983	0.971	0.975	0.986	0.956	0.967	0.943	0.963	0.986	0.980	0.950	0.970	0.973	0.959	0.947	0.976	0.975	0.990	0.975	0.964	0.985
75(+)	0.000	0.000	0.000	0.000	0.010	0.008	0.016	0.019	0.008	0.005	0.020	0.013	0.000	0.000	0.040	0.012	0.012	0.000	0.000	0.009	0.000
N	30	208	238	208	182	122	122	216	280	202	202	230	182	98	78	168	162	196	80	110	130
225	0.000	0.034	0.047	0.058	0.038	0.033	0.025	0.060	0.007	0.079	0.036	0.057	0.038	0.061	0.039	0.048	0.062	0.020	0.012	0.036	0.023
100	1.000	0.966	0.953	0.942	0.962	0.902	0.975	0.940	0.993	0.921	0.964	0.943	0.962	0.939	0.961	0.952	0.938	0.980	0.988	0.964	0.977
N	60	208	234	208	182	122	122	216	278	202	194	230	182	98	78	168	162	196	80	110	130
117(+)	0.050	0.025	0.042	0.019	0.022	0.033	0.033	0.028	0.014	0.040	0.035	0.017	0.022	0.020	0.013	0.012	0.019	0.026	0.039	0.027	0.015
107	0.017	0.010	0.004	0.029	0.066	0.025	0.041	0.028	0.021	0.005	0.030	0.057	0.010	0.041	0.039	0.024	0.037	0.026	0.000	0.009	0.038
200	0.833	0.874	0.870	0.861	0.819	0.885	0.877	0.796	0.857	0.840	0.820	0.843	0.857	0.816	0.868	0.863	0.846	0.878	0.842	0.927	0.815
155(+)	0.000	0.086	0.076	0.082	0.093	0.049	0.049	0.069	0.083	0.110	0.115	0.074	0.088	0.122	0.079	0.083	0.099	0.066	0.105	0.027	0.108
192(+)	0.100	0.005	0.008	0.000	0.000	0.008	0.000	0.078	0.0	0.005	0.000	0.009	0.022	0.000	0.000	0.018	0.000	0.0	0.013	0.009	0.023
N	60	198	238	208	182	122	122	216	2	200	200	230	182	98	76	168	162	19	76	110	130
		0.07	59	0.	.067		0.0	071		0.06		0.		064		0.06	164	0		045	

Table 4: Fst values for comparisons of various components of the blue grenadier collections.
(* = P<0.05 , ** = P<0.01, *** = P<0.001).

COMPARISON	Ada	Ah-1	Est-1	G3pdh-A	Iddh	Mpi	Pgm-1	Pgm-2	Sod	Tapep	TOTAL
BETWEEN AREAS	0.000	0.001	0.002*	0.001	0.001	0.001	0.000	0.001	0.001	0.001	0.001*
WITHIN AREAS											
E. Tasmania	0.005	0.004	0.009*	0.007	0.005	0.007	0.007	0.005	0.009*	0.004	0.006
W. Tasmania	0.006	0.013*	0.016**	0.003	0.009	0.006	0.006	0.007	0.020***	0.005	0.008**
S.E. Australia	0.007	0.011	0.009	0.003	0.014	0.012	0.004	0.003	0.017*	0.008	0.008
BETWEEN SEXES	0.001	0.000	0.003**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
BETWEEN AGES											
E. Tasmania	0.025	0.026	0.023	0.024	0.027	0.046	0.024	0.061*	0.025	0.047	0.030
W. Tasmania	0.021	0.035	0.045*	0.023	0.037	0.040*	0.028	0.020	0.020	0.022	0.029*
OVERALL	0.011	0.012	0.011	0.011	0.011	0.015*	0.009	0.014	0.012	0.012	0.011
BETWEEN YEARS	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000
WITHIN 1984	0.005	0.007	0.008*	0.006	0.010	0.012	0.006	0.012*	0.008*	0.007	0.007*
1985	0.000	0.000	0.001	0.000	0.002	0.002	0.001	0.000	0.004**	0.001	0.001
Regions vs N.Z.	0.013***	0.001	0.016***	0.008***	0.001	0.002	0.001	0.004**	0.003*	0.012***	0.006***
21-way Aust.	0.005	0.00[illegible]*	0.009*	0.003	0.006	0.006	0.007	0.005	0.012***	0.005	0.007***

Table 5: Results of the contingency chi square analyses of various components of the blue grenadier samples. (Exact probabilities are given; significant values P <0.05 are italicised).

COMPARISON	Ada	Ah-1	Est-1	G3pdh-A	Iddh	Mpi	Pgm-1	Pgm-2	Sod	Tapep	TOTAL
BETWEEN AREAS	0.68	0.22	0.10	0.40	0.30	0.17	0.56	0.18	0.37	0.36	0.27
WITHIN AREAS											
E. Tasmania	0.31	0.67	0.03	0.29	0.06	0.62	0.40	0.37	0.72	0.61	0.17
W. Tasmania	0.66	*0.04*	0.10	0.80	0.20	0.06	0.49	0.37	*0.04*	0.59	*0.03*
S.E.Australia	0.68	0.13	0.40	0.92	0.42	0.17	0.97	0.83	0.06	0.61	0.67
BETWEEN SEXES	0.13	0.88	*0.01*	0.41	0.79	0.76	0.29	0.47	0.76	0.64	0.32
BETWEEN AGES											
E. Tasmania	0.65	0.61	0.65	0.80	0.72	0.24	0.82	*0.01*	0.65	0.09	0.55
W. Tasmania	0.66	0.16	0.07	0.38	0.18	0.16	0.11	0.54	0.57	0.30	0.08
OVERALL	0.14	0.60	0.23	0.39	0.81	0.13	0.91	0.26	0.19	0.63	0.43
BETWEEN YEARS	0.74	0.59	0.57	0.53	0.66	0.39	0.61	0.97	*0.02*	0.32	0.60
WITHIN 1984	0.43	0.41	*0.04*	0.36	0.10	0.51	0.93	0.20	*0.03*	0.53	0.17
1985	0.59	0.38	0.49	0.31	0.06	0.55	0.39	0.91	*0.02*	0.43	0.19
Regions vs. N.Z.	*0.01*	0.41	*0.01*	0.13	0.47	0.20	0.09	0.20	0.08	0.48	*0.003*
21-way Aust.	0.36	0.07	*0.001*	0.72	0.07	0.19	*0.001*	0.31	*0.002*	0.35	*0.000*

Table 6: The number of male and female blue grenadier from eastern Tasmania and the rest of the Australian sample that expressed 104 or 95 alleles for Est-1.

SAMPLE	104/104	104/100	100/95	95/95
E. Tasmania males	3	5	23	4
females	0	1	17	0
Other Areas males	0	2	29	8
females	0	4	28	2
Total	3	12	96	14

Table 7: Comparison of allele frequencies of fish from spawning and non-spawning periods off eastern Tasmania between April 1984 and March 1985. Significant loci only; *** = P<0.001. (EST-1 104 and 95 alleles are pooled for statistical purposes).

Loci	Allele	Spawning	Non-spawning	Fst	Chi Square
EST-1	100	0.904	0.958	0.011***	***
	95*	0.096	0.042		
	N	140	591		
SOD	225	0.011	0.054	0.015***	***
	100	0.986	0.946		
	N	140	601		

Table 8: Allele frequencies of blue grenadier from the three Australian regions and the New Zealand sample. Multiple samples within each region have been pooled.

Locus	Allele	E.Tas	W.Tas	S.E.Aust	N.Z.
ADA	150	0.001	-	0.001	-
	133	0.01	0.019	0.012	0.009
	129	-	-	-	0.066
	124	0.235	0.236	0.225	0.160
	116	0.225	0.251	0.236	0.151
	100	0.276	0.259	0.264	0.453
	96	0.005	0.003	0.003	-
	88	0.201	0.189	0.219	0.113
	80	0.033	0.028	0.025	0.047
	68	0.014	0.015	-	-
	48	-	0.001	-	-
	32	-	0.001	-	-
	N	828	509	377	53
AH-1	110	0.005	0.006	0.005	0.009
	105	0.135	0.126	0.143	0.151
	100	0.712	0.703	0.671	0.689
	94	0.138	0.153	0.172	0.113
	89	0.010	0.012	0.009	0.028
	84	-	-	-	0.009
	N	825	507	378	53
EST-1	104	0.008	0.006	0.003	-
	100	0.951	0.934	0.957	1.000
	95	0.041	0.060	0.040	-
	N	818	503	362	53
G3PDH-A	138	-	0.001	-	-
	118	0.121	0.128	0.106	0.058
	100	0.878	0.871	0.892	0.942
	89	0.001	-	0.001	-
	N	827	509	376	53

Locus	Allele	E.Tas	W.Tas	S.E.Aust	N.Z.
IDDH	129	0.002	0.002	-	0.009
	122	0.08	0.068	0.078	0.104
	110	0.039	0.03	0.047	-
	104	0.001	-	-	-
	100	0.836	0.854	0.822	0.858
	95	0.002	0.006	0.009	-
	76	0.017	0.023	0.007	-
	68	0.023	0.017	0.037	0.028
	47	0.001	-	-	-
	N	802	496	340	53
MPI	108	0.109	0.131	0.132	0.104
	100	0.879	0.859	0.851	0.830
	94	-	-	-	0.047
	87	0.012	0.008	0.015	0.019
	80	-	0.001	0.001	-
	N	669	355	367	53
TAPEP	124	-	0.002	-	-
	117	0.024	0.029	0.023	-
	107	0.030	0.025	0.024	0.029
	100	0.841	0.858	0.867	0.875
	90	0.001	0.002	-	-
	85	0.085	0.075	0.078	0.087
	79	0.017	0.008	0.008	0.010
	70	0.003	0.001	-	-
	62	-	0.001	-	-
	N	826	506	377	52
PGM-1	114	0.055	0.043	0.050	0.010
	110	0.228	0.247	0.230	0.192
	105	0.076	0.096	0.086	0.163
	100	0.529	0.510	0.534	0.510

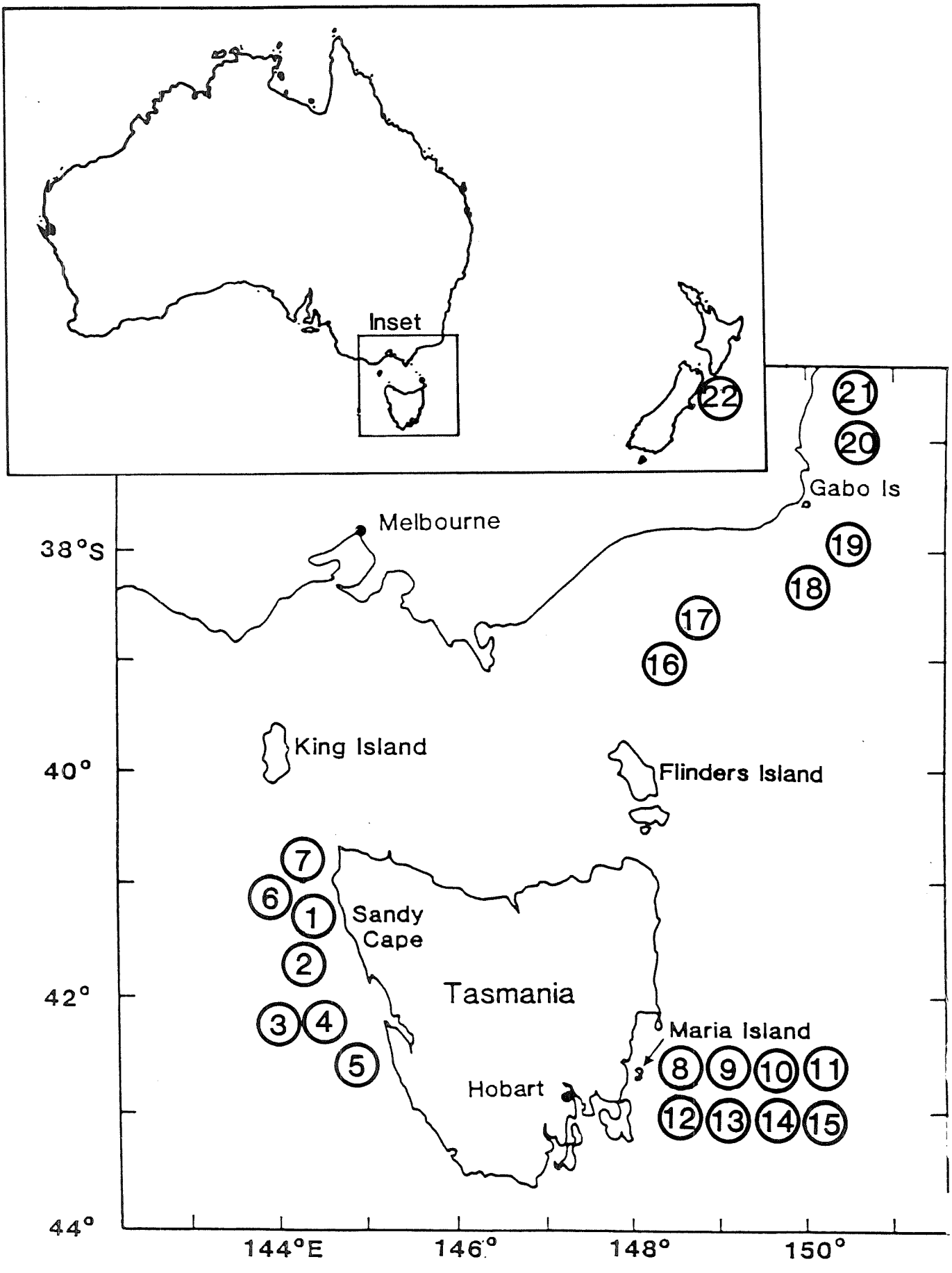
Table 9: Comparison of allele frequencies at polymorphic loci common to two studies of blue grenadier Macruronus novaezelandiae from New Zealand. Twelve enzyme loci compared. (* = P<0.05; ** = P<0.01; *** = P<0.001; d.f.= degrees of freedom; H = mean heterozygosity).

Loci	Allele	Cape Campbell	Paliser Bay	Fst	Chi Square	d.f.
G3PDH-A	118	0.000	0.058	0.026**	10.40**	1
	100	0.996	0.942			
	89	0.004	0.000			
	N	120	52			
IDDH	122	0.079	0.113	0.004	1.34	2
	100	0.879	0.858			
	68	0.042	0.026			
	N	120	53			
PGM-2	122	0.000	0.038	0.021**	11.73***	1
	100	1.000	0.952			
	75	0.000	0.010			
	N	120	52			
OVERALL	H	0.019	0.038	0.010*	23.47***	4
SOURCE		Smith et al. 1981	this study			

CAPTIONS TO FIGURES:

Figure 1. The location of blue grenadier samples from southeastern Australian and New Zealand waters. (sample numbers are those used in Table 1.)

Figure 2. Typical isozyme banding patterns for five variable enzymes in blue grenadier.The enzymes are: ADA, adenosine deaminase; AH-1, aconitate hydratase-1; IDDH, L-idditol dehydrogenase; PGM-1 and 2 phosphoglucomutase-1 and 2. The anode is towards the top of each gel and the sample origin is at the bottom of the gel. The allelic classes for each enzyme are shown at the side. The presumed genotype of each individual is shown at the bottom.


Inset
22
21
20
Gabo Is
Melbourne
38°S
19
18
17
16
King Island
Flinders Island
40°
7
6
1
Sandy
Cape
2
Tasmania
42°
3
4
5
Maria Island
8
9
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11
Hobart
12
13
14
15
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144°E
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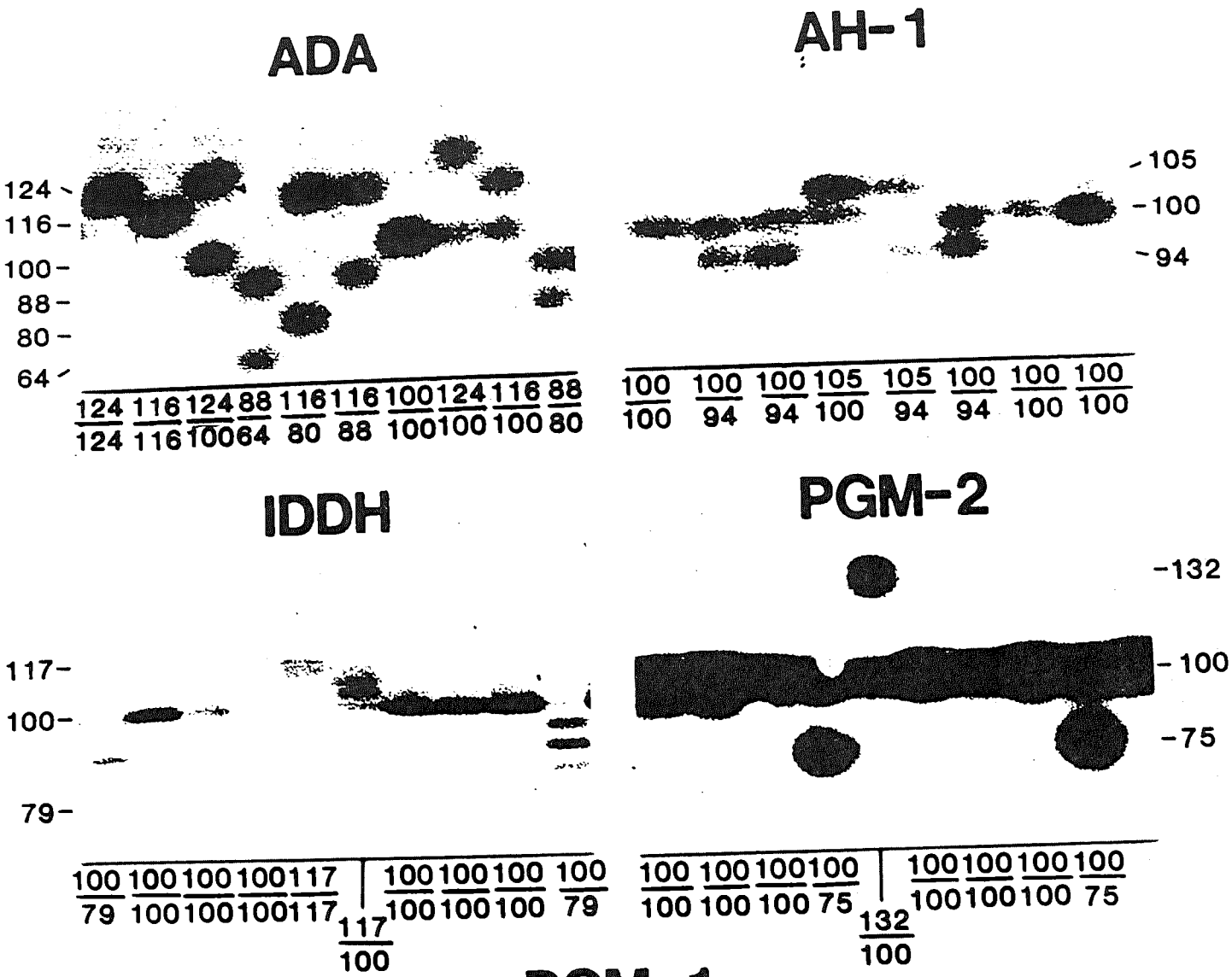
150°


ADA
AH-1
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124 116 124 88 116 116 100 124 116 88
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IDDH
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100 93 100 100 93 93 100 100 100 110 100

APPENDIX 2

Approved by CSIRO for publication

Age and growth of blue grenadier, *Macruronus novaezelandiae* (Hector), in south-eastern Australian waters

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Running head: Age and growth of blue grenadier

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Abstract

Blue grenadier, Macruronus novaezelandiae, from south-eastern Australian waters were aged, using their otoliths (whole and in transverse thin sections). The greatest recorded age was 25 years. A comparison with length-frequency modes validated the ages of immature fish, but no validation was possible for the adults. However, a blind test showed that their recorded ages were reasonably reproducible. Von Bertalanffy growth curves were fitted to both length and weight data:

For males:

$$L_t = 90.7\ (1 - e^{-0.256(t + 1.21)})\ \text{cm}$$

$$W_t = 2.62\ (1 - e^{-0.277(t + 1.39)})^3\ \text{kg}$$

For females:

$$L_t = 99.3\ (1 - e^{-0.203(t + 1.48)})\ \text{cm}$$

$$W_t = 4.16\ (1 - e^{-0.157(t + 2.93)})^3\ \text{kg}$$

The sexes have significantly different growth patterns. Their growth parameters are typical of those of commercially exploited, temperate gadoid fishes and show no modification for the deepwater zone inhabited by blue grenadier.

Introduction

Blue grenadier, Macruronus novaezelandiae, is a large merluccid fish of the upper continental slopes off southern Australia and around New Zealand. In recent years, it has become the target of a considerable, and still growing, commercial trawl fishery. However, most aspects of its population biology, particularly its age structure and growth rate, remain poorly known despite their importance to management of that fishery.

Blue grenadier from New Zealand waters have been aged by Kuo and Tanaka (1984a, b), who used otoliths ground on their proximal and distal faces. They reported moderate growth rates and ages of up to 12 years. Other studies of New Zealand grenadier have found similar growth patterns (reviewed by Kuo and Tanaka 1984b). However, as with other merluccids (e.g. Wysokiński 1983), the otoliths of blue grenadier contain many false checks and their true annuli are often not clear. Thus, age readings of this species are more than normally subjective and it is particularly important for them to be validated (cf. Beamish and McFarlane 1983). Unfortunately, there is no simple way to validate blue grenadier adult ages. Kuo and Tanaka (1984b) were confined, by the lack of other data, to showing that length-frequency modes progressed from 30 cm to 65 cm total length at about the same rate as their growth curve suggested.

In this paper, following a summary of the biology of Australian blue grenadier, we report ages of these fish for the first time and provide length, age and weight relationships for them. The ages are validated against length-frequency modes, to age 3, while the major population dynamic parameters for this species are shown to be similar to those of other exploited gadoid fishes. We present full details of our age reading criteria in an appendix.

Biology of Australian Blue Grenadier and the Grenadier Fishery

In Australian waters, blue grenadier have been found as far north as 33°30'S off Broken Bay, N.S.W. (Gorman and Graham 1979) and westwards across the Great Australian Bight to beyond 130°E (K. Evans, Dept. Sea Fisheries, Tasmania, pers. comm.), but they are most abundant off Tasmania. By day, the adults are demersal and live on the Continental Slope at about 500 m depth (Last et al. 1983). At night, they disperse and rise into the water column (Bulman and Blaber, 1986). The juveniles also occur near the edge of the continental shelf but they are found, in addition, in the inshore waters of southern and western Tasmania (Last et al. 1983).

Ichthyoplankton surveys have located a major blue grenadier spawning ground off north-western Tasmania and a minor one off eastern Victoria (R. E. Thresher, CSIRO Division of Fisheries Research, pers. comm.). Neither those surveys nor a study of adult gonad maturation stage (Blaber et al. 1985) has yet demonstrated spawning elsewhere. Both types of data suggest that spawning occurs between mid-May and late September. The adult fish are assumed to migrate to the spawning areas in early winter and to disperse again throughout their range in spring. The pattern of juvenile movements is unclear at present. Blue grenadier mature at about 70 cm standard length (Blaber et al. 1985).

Australian catches of blue grenadier were very small before 1983. Wilson's (1982) discovery of their spawning aggregations then led to the development of a winter bottom-trawl fishery off north-western Tasmania,

which currently lands about 1500 t of blue grenadier each year. The present estimate of annual "Maximum Prudent Yield" is 3600 ± 1200 t.

Materials and Methods

Field Sampling

Blue grenadier otoliths (sagittae), length frequencies and weight data were collected on cruises of FRV Soela, as part of the CSIRO Southern Programme. Collections were made off the east and west coasts of Tasmania (Fig. 1) by bottom trawling and off the east coast only by pelagic trawling. Both bottom and pelagic nets were fitted with fine-mesh cod-end liners to retain small fish. Length and weight data were also gathered by bottom trawling by FRV Soela off Flinders Island and eastern Victoria, carried out for the Marine Science Laboratories, Queenscliff. Otoliths from those areas were not available to us. In general, each area was sampled every two months from April 1984 to June 1985 (Table 1). Most of the fishing was at pre-selected stations. However, the west coast fishing on cruises S04/84 (August-September 1984) and S01/85 (January 1985) included shots directed towards blue grenadier.

The sampling design adopted called for every blue grenadier caught to be sexed and measured for standard length (to the nearest centimetre, using an offset measuring board), except that very large catches were to be randomly subsampled before measurement. One fish per sex per centimetre length increment from each shot was to be weighed (entire live weight) and its otoliths taken. Additional otoliths and weights were to

be obtained from fish used in other biological studies. Unfortunately, this sampling design was rarely achieved in full. The length-frequencies were generally representative of the fish caught, but the sexing and otolith extraction were sporadic. Fin rays were collected from some fish but did not prove useful for ageing. Fish were rarely caught with scales in place, so these could not be used in age studies either.

Length-Frequencies

The recorded length-frequencies for each shot were raised by the appropriate factor to compensate for subsampling. They were then summed across shots to give frequencies for each of the demersal and pelagic catches from each of the eight cruises. The resulting histograms may serve to illustrate length modes but they are not adequate representations of the overall population length-frequency, since the fishing was unevenly distributed across the range of blue grenadier.

Ageing Methods

The otoliths were collected and stored dry in envelopes and subsequently transferred to glass vials. A number of otolith preparation methods were tried, including cutting, breaking, burning and staining. These were all rejected in favour of a two-stage ageing technique, using both whole otoliths and transverse thin sections of otoliths. The whole otoliths were cleared in water and then examined, under reflected light, while immersed in water. The hyaline zones (terminology follows Jensen 1965) were counted to provide an initial age estimate (Fig. 2; see Appendix for details of age reading criteria). If these zones were unclear or if the estimated age was higher than about eight years, the

otolith was subsequently sectioned using an adaption of Bedford's (1983) method. The sections were about 0.4 mm thick and, without further treatment, were of adequate quality for age reading. These sections revealed not only the annuli visible before sectioning but also, in older fish, a series of regular opaque and hyaline zones near the otolith's proximal face (Fig. 3). Following Beamish (1979) and Chilton and Beamish (1982), these zones were counted as true annuli.

The hyaline zones appeared to be completed in late winter, though the timing was variable. For convenience with our data, 1 August was selected as the arbitrary "birthday" of the blue grenadier, being between cruises S03/84 and S04/84.

Length, Weight and Age Relationships

A length-weight relationship was calculated, using all available data, by regressing the natural logarithm of weight on that of length. Similar curves were fitted to all data from each of male and female fish. Possible differences between these latter curves were examined by fitting curves of constant exponent to the data for each sex and then comparing the resulting residual sums-of-squares with that from the independent sexed curves using the "extra sum of squares" principle (Draper and Smith 1981).

Von Bertalanffy growth curves were fitted to both the length-at-age and weight-at-age data. Several authors (e.g. Roff 1980) have discussed the inadequacies of the von Bertalanffy function while others (e.g. Schnute 1981) have provided substitutes for it. However, assessments of

the blue grenadier resource are presently limited by a lack of data and must use such generalized methods as Pauly's (1980) equation for natural mortality estimation and Beddington and Cooke's (1983) model for yield prediction. These need estimates of the L_∞ and K parameters of the von Bertalanffy function. For similar reasons, the growth curves for weight followed Beverton and Holt's (1957) adaptation of the von Bertalanffy function:

$$W_t = W_\infty \ (1-e^{-K(t-to)})3$$

even though exact isometric growth was not expected.

The von Bertalanffy function was fitted using Kirkwood's (1983) technique, which permits data on individuals to be used and also avoids some of the statistical weaknesses of more conventional methods. Iterative maximization was performed by LMM (Miller 1981). The age data were calculated to the nearest 0.01 years, assuming the "birthday" of 1 August and a capture date at the mid-point of each cruise. This allowed due account to be taken of the seasonal distribution of the catches and the rapid growth of young blue grenadier.

Differences between various growth curves were tested using the "extra sum of squares" principle (Draper and Smith 1981) and a variety of models, in which one or more of the von Bertalanffy parameters were constrained to be equal in each curve. For non-linear relationships, the results of such tests are only approximate (Ratkowsky 1983) and, in the present application, they assume that the ages are measured without

error. Thus, these tests are, strictly, invalid but they may nevertheless be indicative.

Replicability and Validation of Ages

The ageing technique was developed by repeated re-ageing of the otoliths and comparison of the resulting ages with length data. Thus, the ages could be artifacts of this development process. To test this, 120 otoliths were chosen from the collection by an independent assistant so as to include in the sample a range of ages, both sexes, all cruises and both easily-readable and unclear otoliths. The chosen otoliths were assigned new serial numbers and presented to each of the authors in turn, accompanied only by the date of capture of the fish. Each of us read the 120 otoliths, providing, with the original age readings, replicate age determinations by one reader and a set of age readings by a second reader. The level of precision in these readings was calculated using Beamish and Fournier's (1981) Index of Average Percent Error.

The age data are primarily of value in fitting growth curves. Thus, the differences between these replicate readings were tested by first fitting von Bertalanffy curves to each of the three sets of 120 age and length data points and then testing the differences between these curves. The statistical methods described above were employed.

Such tests can only prove that the growth curves were reproducible, not that they were accurate. Validation of the ages and growth curve, to a maximum of three years of age, was based on a comparison with length mode progression from hatching to 60 cm standard length. This involved

length-frequency data from the present study, larval lengths and daily age estimates from recent ichthyoplankton work (J. Gunn, CSIRO Division of Fisheries Research, pers. comm.) and length data from inshore trawling in 1980 by the former Tasmanian Fisheries Development Authority. The Authority had made regular survey trawls with fine-mesh gear in the Derwent Estuary near Hobart (M. A. Wilson and K. Evans, Department of Sea Fisheries, Tasmania, pers. comm.).

Other validation methods cannot be applied to blue grenadier at present: they cannot be tagged because (having soft flesh and deciduous scales) they are too delicate to be caught alive, the fishery has not been in progress for long enough to trace the progress of strong year-classes, and the annual marginal increment (for fish older that about three years) is too narrow and diffuse for edge-type or increment analyses.

Results

Otolith Form

The sagittal otoliths of blue grenadier are much like those of other merluccid fishes (e.g. Hunt 1980, Wysokiński 1983): They are somewhat elongated on the anterior-posterior axis, proximally-distally flattened, concave towards their distal faces and toothed on their dorsal and ventral margins (Fig. 2). Their general shape and particularly their degree of toothing is quite variable.

Early in life, blue grenadier otoliths seem to develop evenly and so retain their overall shape. After an age of about eight years, however,

further growth seems fastest on the proximal face of the otolith, on either side of the sulcus acousticus (Fig. 3). This causes the otolith to thicken, without markedly increasing in length or width. Because of this growth pattern, ages derived from transverse thin sections tended to be higher than those from reading whole otoliths, except in young fish.

Many, but not all, of the fish showed a prominent check within the first true annulus.

Ages

In all, 1631 blue grenadier were aged, including several 0-group individuals and several over 20 years old. The highest ages recorded for each sex were 25 years (Fig. 3) for a female and 20 years for a male.

Length-Weight Relationships

The overall length-weight relationship was:

$$W = 0.743 \times 10^{-5} L^{2.852} \qquad N = 2562,\ r^2 = 0.96$$

for weights in kilograms and lengths in centimetres (Fig. 4). The equivalent relationships for each sex were:

$$\text{Males: } W = 1.3402 \times 10^{-5} L^{2.712}$$

$$\text{Females: } W = 0.7528 \times 10^{-5} L^{2.8498}$$

The slopes of these two curves were very significantly different from the sexes-combined curve ($F = 19.88$; df 1,2276; $P<0.001$) and hence from each other.

Growth Curves

The parameters of the von Bertalanffy growth curves and their standard errors are given in Table 2, and the curves themselves in Figures 5 to 7. The females grow towards larger asymptotic sizes than do the males. However, their relative growth rates, K, are lower and the growth curves for each sex indicate similar sizes-at-age for fish younger than about 6 years.

The von Bertalanffy curves were effective summaries of the length-at-age data, with only moderate variability around the fitted lines and values of asymptotic length, well within the observed lengths of old fish. The weight-at-age data showed greater variability, but part of this was due to errors in weighing at sea and part to fluctuations in stomach and gonad weights. The fitted von Bertalanffy curves are thus reasonable first approximations to the measured pattern of growth in blue grenadier.

The statistical tests indicated that the growth curves for length of the two sexes were very significantly different ($F = 44.72$; df 3,1465; $P<0.001$). This difference occurred in both the asymptotic length ($F = 75.31$; df 1,465; $P<0.001$) and K ($F = 18.05$; df 1,465; $P<0.001$), but the values of t_o were not significantly different ($F = 2.58$; df 1,465; $P>0.05$). Since the data did not fulfill all of the assumptions of these tests, these results are only idicative.

The measured growth patterns also differed between fish caught east and west of Tasmania. For males this effect was only marginally significant ($F = 2.88$; df 3,603; $P<0.05$), but for females it was very

marked ($F = 17.55$; df 3,764; $P<0.001$). However, the sizes of blue grenadier caught off the two coasts were different and the differences in the fitted von Bertalanffy curves may reflect this distributional feature rather than the presence of distinct populations in the two areas.

The growth curves for weight also differ markedly between the sexes ($F = 105.09$; df 3, 1411; $P<0.001$). In these, all three parameters showed very significant differences (W_∞: $F = 106.93$; K: $F = 34.63$; t_o: $F = 11.26$; df 1, 1411; $P<0.001$), though once again these tests are merely indicative. Since the maturation stages, and hence gonad weights, of blue grenadier caught off the east and west coasts of Tasmania were markedly different, a comparison of growth curves by weight between these areas would be spurious.

Tests of Age Replication

The results of the age replication tests are illustrated in Figure 8. The original age readings are the most reliable (having been made by repeated readings over several months, with access to length data and a preliminary growth curve), but may contain some errors. The primary otolith reader's replicate counts were fully in agreement with the original readings in 40% of cases, while 72% of them had a maximum deviation of 1 year and 91% a deviation of 3 years or less. Counts by the alternate reader were markedly less precise (27% "correct"; 85% with a deviation of 3 years or less) and showed a downward bias relative to the original ages. Each otolith reader made one "error" of 8 years, but none greater than this. Since the original ages may have been in error also, the maximum imprecision was between 4 and 8 years.

Beamish and Fournier's (1981) Index of Average Percent Error was 7.98% for replicate age readings by the primary ager and 11.20% for alternative readings by the two of us. These values compare favourably with Beamish and Fournier's (1981) data set of walleye pollock ages, Sikstrom's (1983) calculated indices for arctic grayling and Daniels' (1983) ones for Antarctic plunderfish, but are worse than Prince et al.'s (1985) 0.30% to 6.30% for bluefin tuna and Johnson and Saloman's (1984) 0.72% for gray triggerfish. Clearly, our blue grenadier ages are rather imprecise and quite inadequate for assigning ages to individuals with any useful degree of confidence, but may be sufficiently precise for fitting growth curves.

Von Bertalanffy curves fitted to these three sets of ages (Table 3) were significantly different ($F = 3.03$; df 6,351; $P<0.01$). However, this was caused by the alternate otolith reader's downward bias. The original age readings and the primary otolith reader's replicate readings gave growth curves that were not significantly different ($F = 0.42$; df 3,234; $P>0.05$). Thus, the primary reader's age readings had at least sufficient reproducibility for the preparation of growth curves.

Length-Frequencies

The summed demersal length-frequencies are shown in Figure 9, with the progression of modes from an age of 6 months to 37 months identified. The pelagic catches were insufficient to give meaningful frequencies, except for juvenile fish which were taken in December (Cruise SO6/84) at lengths of 13 to 22 cm and in subsequent cruises at similar

sizes to those caught demersally.

Age Validation

Ichthyoplankton surveys off Tasmania have taken blue grenadier larvae of lengths up to 3.5 cm and estimated ages (from otolith diurnal increment counts) up to 50 days (J. Gunn, CSIRO Division of Fisheries Research, pers. comm.). The routine trawling, in the Derwent Estuary in 1980, first detected small blue grenadier in late September, at a few centimetres length. Subsequent fishing traced the growth of this year-class to lengths of 13-25 cm in early December of that year (M. A. Wilson and K. Evans, Department of Sea Fisheries, Tasmania, pers. comm.). The length frequencies obtained offshore by the present study show progression of a mode from 19 cm in December (pelagic catches) to perhaps 30 cm by the following June. Thereafter, the modes are less clear but are tentatively identified in Figure 9.

Part of the von Bertalanffy curve for length (sexes combined) is shown in Figure 10. On it are superimposed the modes read from Figure 9, those from the inshore trawling in 1980 and the larval growth curve to 50 days of age. It clearly shows that the fitted curve is consistent with blue grenadier growth between one and three years of age. The von Bertalanffy function is unrealistic for younger fish, since it has non-zero values of t_o, while the length data are also distorted at these ages by the compression of a prolonged spawning season into one arbitrary "birthday". However, the Figure does confirm that 40 cm fish in winter are one year old, as found by ageing, and that the ages of the length modes in Figure 9 are correctly assigned.

Discussion

The techniques for ageing blue grenadier set out in the Appendix have been shown to be sufficiently reproducible for use in fitting growth curves, but not necessarily so for assigning ages to particular individuals. The resulting growth curves have been validated against length-frequency modes for young fish. However, this technique cannot be extended beyond about 3 years of age, since distinct modes for older fish are not visible in the length-frequencies.

Beamish and McFarlane (1983) have recently pointed out the inadequacy of such partial validation, and their warnings are particularly relevant to our ageing methods, since we have not validated the ages derived from otolith sections, which include all of the older recorded ages. Unfortunately, none of the conventional methods of age validation can be applied to a fish population that, like blue grenadier, cannot be tagged, grows too slowly for modal analysis, has narrow and complex otolith annuli that will not support marginal increment or edge-type analysis, and has not been fished for long enough to follow the growth of strong year-classes. Even back-calculation of lengths-at-age for comparison with lengths and ages at capture cannot be used if otolith growth is asymetrical in older fish, since the relevant increments will follow a poorly defined curved trajectory rather than a straight radius. Thus, until some new technique can be applied, such as the radioisotope ageing of Bennet et al. (1982), the "ages" of adult blue grenadier reported here must remain no more than unvalidated ring counts. The resulting growth curves are, nevertheless, first estimates of the growth pattern of

Australian blue grenadier and may be useful to management of the fishery pending their verification or rejection.

The von Bertalanffy curves from the present study are quite unlike those Kuo and Tanaka (1984b) reported for New Zealand blue grenadier. The Australian fish grow very much faster early in life, attaining 30 cm standard length when less than one year old and approaching 50 cm by their second "birthday", while Kuo and Tanaka's (1984b) growth curve suggests that the New Zealand blue grenadier are less than 20 cm standard length at age one and do not reach 50 cm until nearly four years old. The growth of Australian fish seems to slow considerably near sexual maturity (about 70 cm length, age about 4 years) and they only gradually approach their asymptotic length of about 95 cm. The New Zealand fish, in contrast, appear to continue to grow rapidly towards an asymptote of about 130 cm, but as they seem relatively short-lived (greatest recorded age 12 years [Kuo and Tanaka 1984b] in contrast to the 25 years reported here for Australian fish), they do not achieve this asymptote. As in the Australian population, very few New Zealand blue grenadier exceed 110 cm length.

The markedly different growth patterns of the Australian and New Zealand fish might be a genuine biological difference; it is, however, more likely to be an artifact of different ageing techniques. Kuo and Tanaka's (1984a) method of grinding the proximal and distal surfaces of their otoliths will have clarified the early annuli but destroyed any late annuli near the proximal faces of the otoliths. Had we used their method with our material, our greatest age reading would probably have been about

16 years; the largest whole-otolith reading that we made. Since, in uncut otoliths, the annuli of slower-growing fish cease to be distinguishable at younger ages than do those of faster growing ones, Kuo and Tanaka's (1984a, b) method would particularly tend to underestimate the ages of slower-growing fish. When coupled to the moderate spread in length-at-age of adult blue grenadier, this could easily produce the appearance of continuing "growth" of large fish reported by Kuo and Tanaka (1984b) and hence the unattained asymptotic lengths. Thus the differences, at older ages, between Kuo and Tanaka's (1984b) growth curves and the ones presented here may well be an artifact. In the absence of age validation, it is not possible to say with certainty which curve is correct for adult fish, though our ageing method, which reveals rather than destroys otolith structure, seems inherently more reliable.

At younger ages, the rapid growth of Australian blue grenadier has been validated against length data from larval and juvenile fish. The New Zealand growth curve certainly is incorrect for these ages in Australian waters. Kuo and Tanaka (1984b) did not have access to young fish and they may have been misled by false checks within the first true hyaline ring, which were common in our otoliths, so over-ageing their young fish by one year. Certainly, deducting one year from their published ages brings their data for pre-adult fish into close agreement with the validated growth curve presented here.

If our growth curve is correct, it suggests that blue grenadier, despite their deepwater habitat, are similar in their population dynamic parameters to typical commercially exploited temperate continental shelf

gadoid fishes. Our estimates of the growth coefficient, K, for blue grenadier are between 0.20 and 0.25, which is comparable to the 0.10 to 0.35 reported for a range of cod (Gadus morhua), haddock (Melanogrammus aeglefinus), pollock (Pollachius virens) and hake (Merluccius spp.) populations (Pauly 1980). Since water temperatures on the bottom within the Australian blue grenadier range vary from 7° to 10°C (unpublished data, CSIRO Division of Fisheries Research), the natural mortality rates implied by Pauly's (1980) equations are between 0.28 and 0.39 for males and between 0.22 and 0.28 for females. These values are typical of exploited gadid fishes (0.10-0.44; Pauly 1980) but rather low for Merluccids (0.37-0.84; Pauly 1980). The similarities in these important parameters between Australian blue grenadier and other exploited gadoids suggest that those forms of fisheries management which have proven successful with their northern relatives may be effective with grenadier.

Pending future developments in fish age-validation procedures, we recommend ageing blue grenadier by the methods set out in the Appendix and the use of the von Bertalanffy curves given above in the management of the grenadier fishery. As the growth patterns of the sexes are different, if not greatly so, separate von Bertalanffy parameters should be used for assessments of males and females. However, the evidence for growth differences between fish caught off the east and west coasts of Tasmania is presently insufficient to justify distinct growth curves for the two areas.

Acknowledgements

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APPENDIX: Criteria for Age Determination

Blue grenadier are of commercial importance to the fisheries of several nations and states. The fishery laboratories of at least five of these are currently ageing blue grenadier or considering doing so. To assist those who wish either to follow our ageing methods or to compare them with their own, we here present full details of our criteria for "reading" blue grenadier otoliths.

Whole Otoliths

The otoliths must first be examined whole. Following dry storage, they should be cleaned and soaked in tap water for a few hours or days to clear. Their distal faces can then be examined while the otolith is immersed in water on a dark background and illuminated by reflected light. Low magnification (usually 5 to 10 X but sometimes as low as 2X) and dim light make the major bands in the otolith most clearly distinguishable from the minor ones.

The outer margin of the first hyaline annulus is 5 to 10 mm long; any hyaline checks within this should be disregarded. The second annulus is usually much larger than the first, but otolith growth then slows and the third and fourth annuli can be close together. These early annuli are often most clearly seen near the ventral margin of the otolith, about one third of its length from the posterior tip.

Once the third or fourth hyaline zone is found, it can be followed towards the posterior or anterior tips of the otolith, where subsequent

annuli are more clearly visible. The posterior tip is usually the better one. By rotating the otolith, such that the reader's view remains perpendicular to the otolith's distal face, the annuli can be counted. Higher magnification (15 to 25X) may be required. Ages of up to 16 years have been read in this way, but many old fish have thick and almost opaque otoliths in which few annuli are visible.

Some otoliths can be read easily by this method; others have a profusion of minor bands that obscure the true annuli. This is a particular problem with early annuli where it can only be solved by experience. The later annuli often show a faint double-structure. Where this is especially prominent, one year's growth may be mistaken for two annuli. Once again, only experience and a comparison of several replicate readings can resolve such doubts. Identifying the first true hyaline zone can also be difficult. In young fish, a false inner check is sometimes found, while in old ones the true first hyaline zone may be obscured. Measurement of this zone's expected major diameter can help.

The age, in years, is equal to the count of hyaline zones. For fish captured during early winter before the chosen arbitrary "birthday" (here 1 August, but for general use preferably 1 September), a hyaline zone that forms the otolith edge is not counted. After the "birthday", such a zone is counted.

Otolith Sections

Otolith sections do not help in the ageing of fish younger than about 5 years, since the annuli are obscured by many false checks. Thus, sectioning must always be preceded by whole otolith examination. On the other hand, where the whole otolith reading suggests an age above about 8 years, a section can reveal additional annuli. In some cases, the section age-reading exceeds the whole otolith one by more than 10 years. The additional annuli in a section, if any, will be visible across the otolith's proximal face, on either side of the sulcus acousticus. If a section age-reading exceeds the whole otolith age estimate for an otolith lacking these distinctive additional annuli it usually indicates that the reader has counted false checks in the section.

In practice, the first hyaline zone can be identified by comparing its width in the section and in the whole otolith (its major diameter is often half that of the entire section). The second to fourth or fifth hyaline zones are then located by following the major axis of the section towards its ventral margin. Either the fourth or fifth zone can then be traced towards the sulcus acousticus. From any point along this hyaline zone, the reader then begins counting the regular annuli, which lie between it and the otolith's proximal face.

The later annuli are usually easily countable, though some have a prominent double structure, which can cause counting errors, while others may be faint. The true annuli seem to be very regular, and an assumption of regular spacing can help to resolve uncertainties.

It is usually best to count both from the nucleus outwards and from the edge inwards. These counts often differ if some hyaline zones are being incorrectly identified. Replicate counts should be made in each direction until the reader is satisfied with the consistency of his age estimate.

Otolith Photographs

Photographs of a range of whole otoliths and sections follow (Fig. 11 to 13). These include a variety of ages and degrees of clarity. Details of the fish from which these otoliths were taken are given in Table 4, with points of note in each, while our interpretations of their annuli are indicated on the photographs.

Table 1: Periods of field sampling in each area

Cruise	East Coast Area	West Coast Area	Flinders Island and Eastern Victorian Areas
SO2/84	April	May	May
SO3/84	June	July	July
SO4/84	August	August-September	-
SO5/84	October-November	October	October
SO6/84	December	December	November
SO1/85	February	January	February
SO2/85	March	April	-
SO3/85	May	-	June

Table 2: Estimated parameters of von Bertalanffy growth curves for blue grenadier (lengths in cm; weights in Kg; ages in years; confidence limits are standard errors)

BY LENGTH

	L_∞	K	t_o	N
All Data	95.6 ± 0.4	0.226 ± 0.005	-1.22 ± 0.07	1631
Males	90.7 ± 0.6	0.256 ± 0.009	-1.21 ± 0.11	634
Females	99.3 ± 0.7	0.203 ± 0.007	-1.48 ± 0.11	837
East Coast only				
Males	89.5 ± 0.7	0.276 ± 0.028	-1.03 ± 0.11	403
Females	93.5 ± 0.7	0.268 ± 0.009	-0.93 ± 0.09	469
West Coast Only				
Males	93.0 ± 1.4	0.196 ± 0.023	-2.48 ± 0.65	206
Females	101.2 ± 1.2	0.181 ± 0.014	-1.71 ± 0.35	301

BY WEIGHT

	W_∞	K	t_o	N
All Data	3.62 ± 0.00	0.173 ± 0.007	-2.71 ± 0.23	1593
Males	2.62 ± 0.00	0.277 ± 0.014	-1.39 ± 0.21	609
Females	4.16 ± 0.00	0.157 ± 0.009	-2.93 ± 0.34	808

Table 3: Parameters of von Bertalanffy curves fitted to age-replicability test data (lenghts in cm; ages in years)

	L_∞	K	t_o
Original Reading	97.2	0.231	-1.34
Primary Ager	96.4	0.228	-1.36
Second Ager	95.5	0.287	-1.05

Table 4: Details of otoliths and otolith sections illustrated in Appendix

Otolith number	Month of capture	Fish length (cm)	Age (years)	Comment
1	February	22	0	
2	October	40	1	
3	October	42	1	"Double" structure of hyaline zone, forming false check.
4	May	53	2	
5	June	43	2	Both hyaline zones "double".
6	March	54	3	
7	December	62	3	
8	June	58	4	
9	February	69	4	Second hyaline zone very weak.
10	December	72	5	
11	December	64	6	
12	September	79	7	First hyaline zone obscured.
13	September	75	8	First hyaline zone obscured.
14	January	99	25	This is the pair of the otolith shown in Figure 3. Note that few annuli can be distinguished.

Table 5 cont.

Otolith number	Month of capture	Fish length (cm)	Age (years)	Comment
15	September	74	5	Section of young otolith, showing confusion of checks.
16	February	76	6	
17	September	78	8	
18	February	87	10	Annuli clearly visible near proximal face.
19	February	89	12	Proximal face missing from photograph.
20	February	94	16	
21	February	104	19	Proximal face missing from photograph.
22	September	110	20	
23	February	103	22	

Figure Captions

Figure 1: Chart of southeastern Australian waters showing the areas sampled for blue grenadier (Macruronus novaezelandiae); 1: west coast, 2: east coast, 3: Flinders Island, 4: eastern Victorian areas

Figure 2: Whole otolith of three-year-old blue grenadier (distal view). Scale bar is 1 cm

Figure 3: Transverse thin section of otolith of 25-year-old blue grenadier. Annuli indicated by black dot, ringed in white when necessary for clarity)

Figure 4: Length-weight relationship for blue grenadier (o: single data point; ● : overlapping data points)

Figure 5: Von Bertalanffy growth curves by length for blue grenadier, areas combined (o: single data point; ● : overlapping data points)

Figure 6: Von Bertalanffy growth curves by length for blue grenadier from off the east and west coasts of Tasmania

Figure 7: Von Bertalanffy growth curves by weight for blue grenadier, areas combined (o: single data point; ● : overlapping data points)

Figure 8: Plot of errors in age replication tests (● : replicate age reading or readings by primary otolith reader; ▲: replicate age reading or readings by second age reader; ◆: overpal of replicate age readings by both readers; dashed line indicates agreement between original and replicate readings)

Figure 9: Length-frequencies of blue grenadier caught by demersal trawling: summation of frequencies for east, west, Flinders Island and eastern Victorian areas

Figure 10: Von Bertalanffy growth curve by length for young blue grenadier (sexes and areas combined), with length modes of captured fish superimposed. (Solid bars: range of mode from offshore trawling; Dashed bars: range from inshore trawling; Dots: larval growth curve; ↑ : upper limit of mode indeterminate)

Figure 11: Representative examples of otoliths of young blue grenadier, at constant magnification. (Completed hyaline zones indicated by white-ringed dots; see Table 4 for details of these fish)

Figure 12: Representative examples of otoliths of older blue grenadier and an otolith section from a young fish. Magnification of whole otoliths as in Figure 11. That of section as in Figure 13. (Completed hyaline zones indicated by white-

ringed dots in otoliths 11, 12 and 13; see Table 4 for details of these fish)

Figure 13: Representative sections of otoliths of older blue grenadier, showing areas between their nuclei and proximal faces. Magnification constant. (Completed hyaline zones indicated by black dots, ringed in white when necessary for clarity; see Table 4 for details of these fish)

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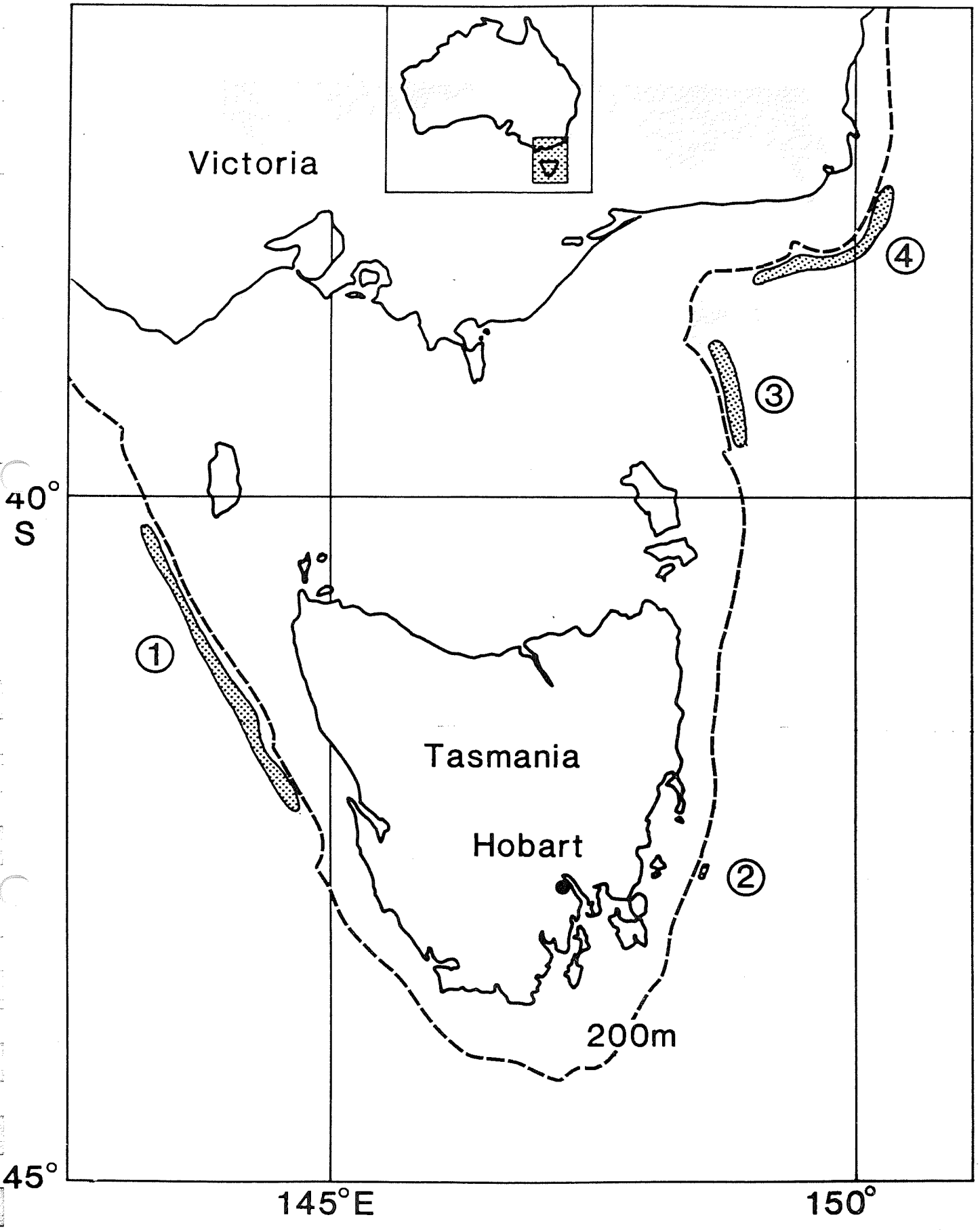
Fig 1



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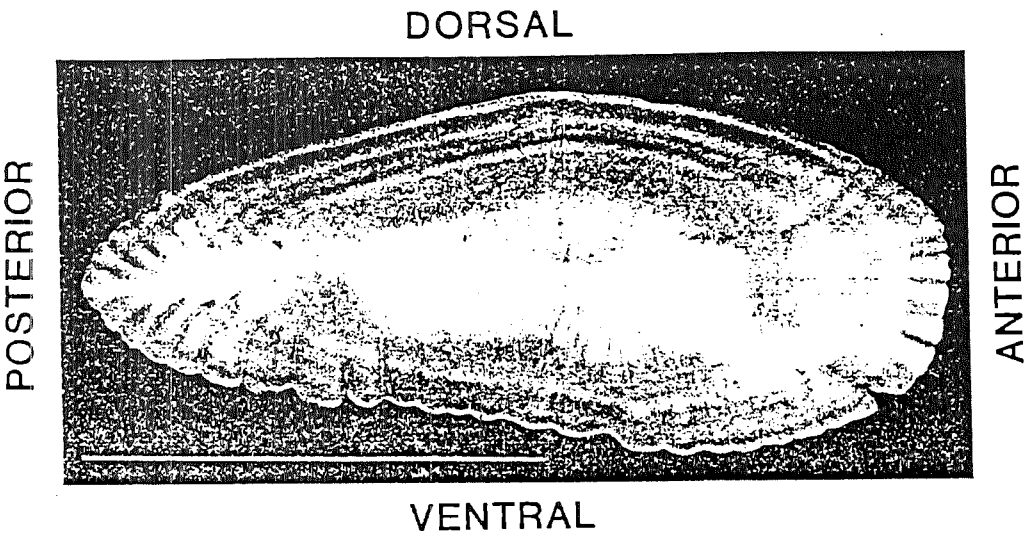

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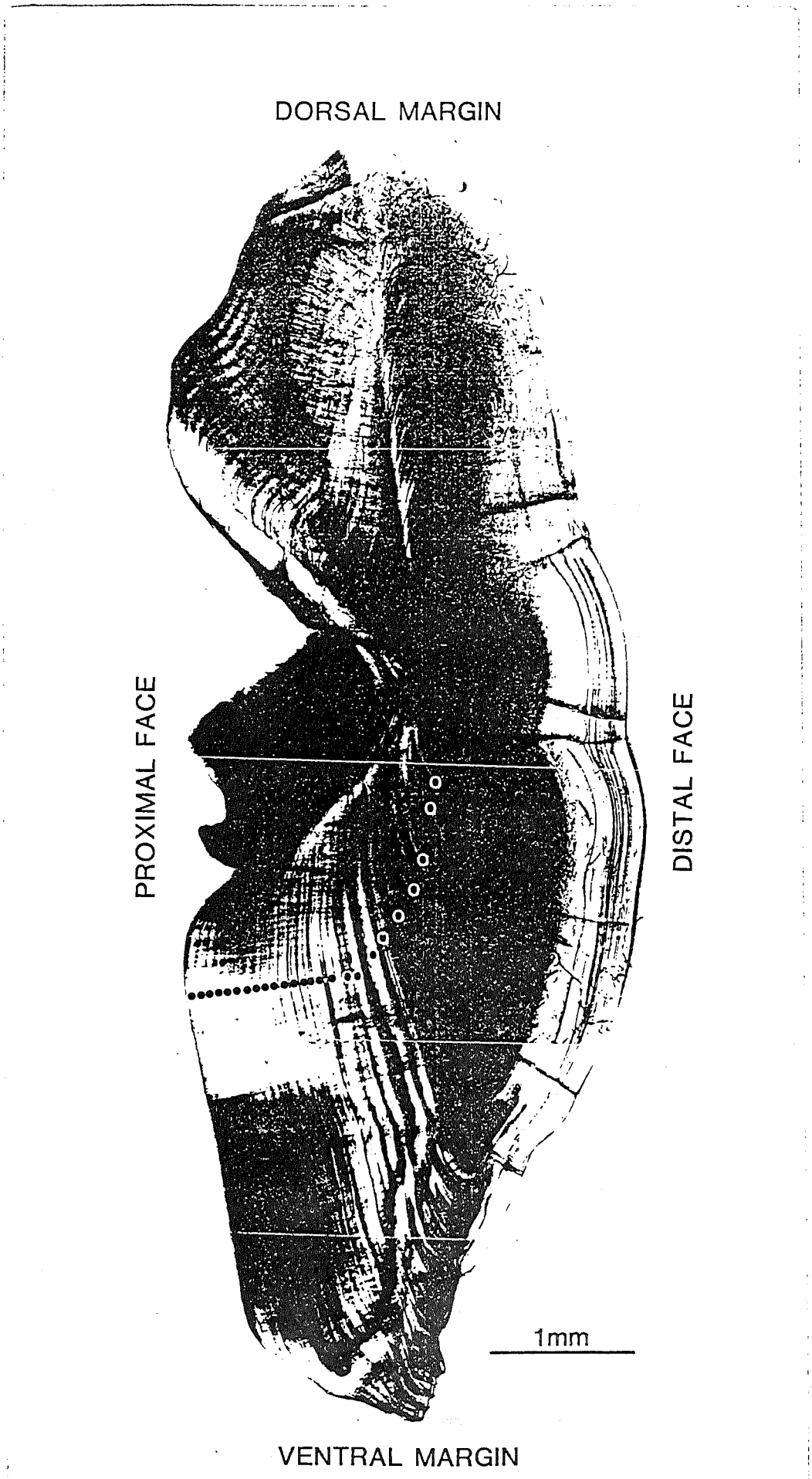
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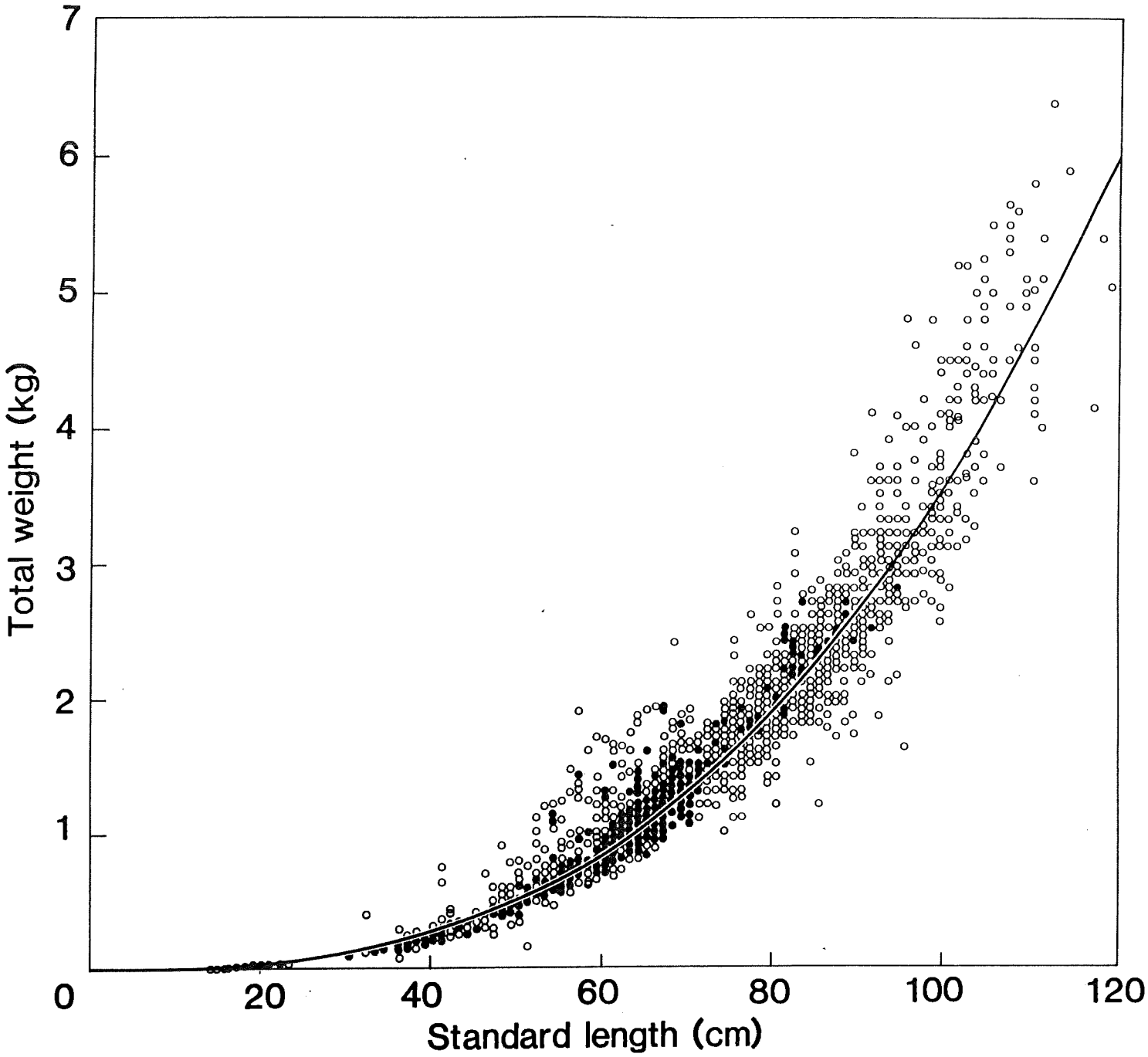
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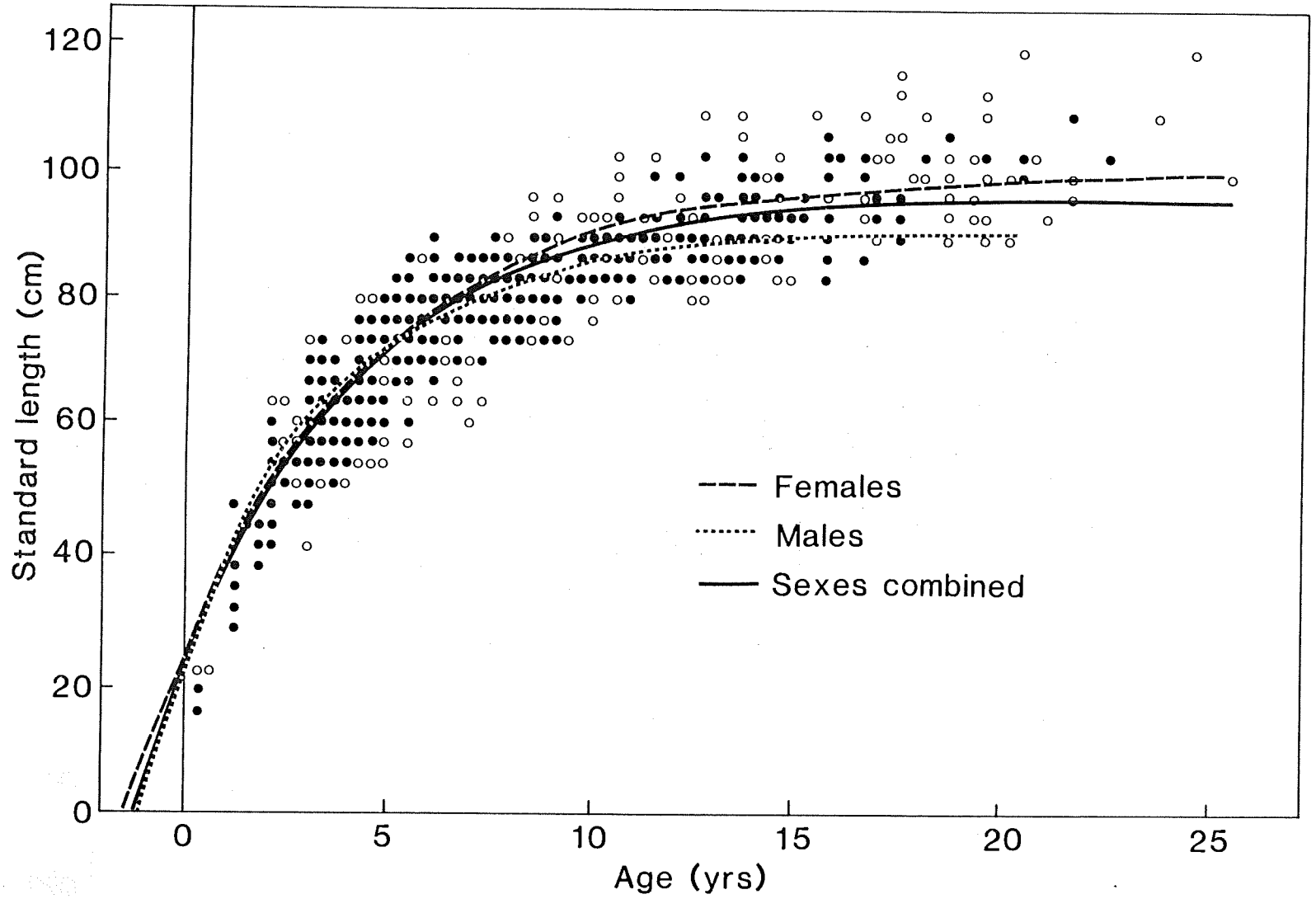
7
20
40
60
80
100
120
Standard length (cm)

Fig 4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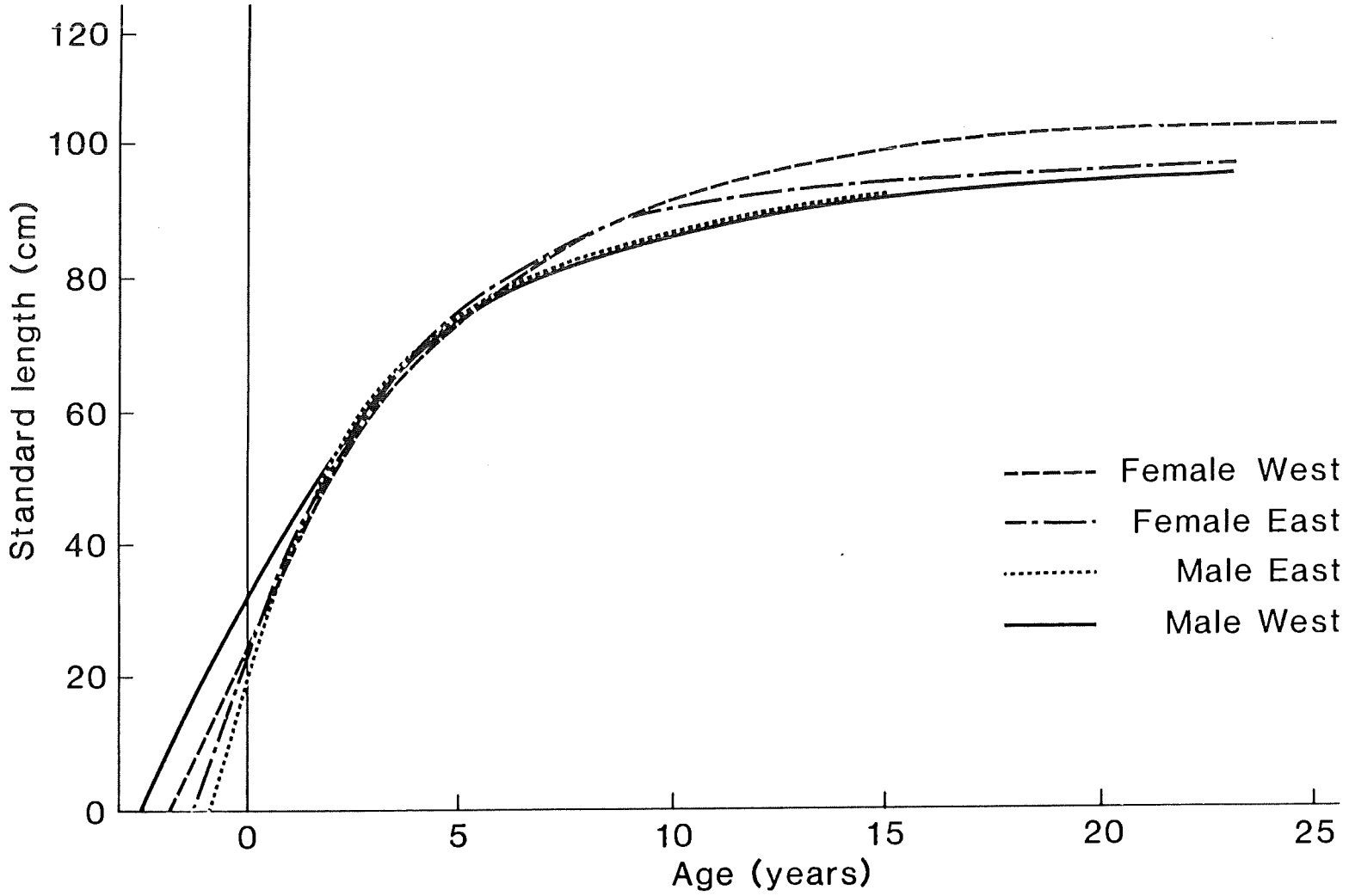
Age (yrs)
Females
Males
Sexes combined

Fig 5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Age (years)
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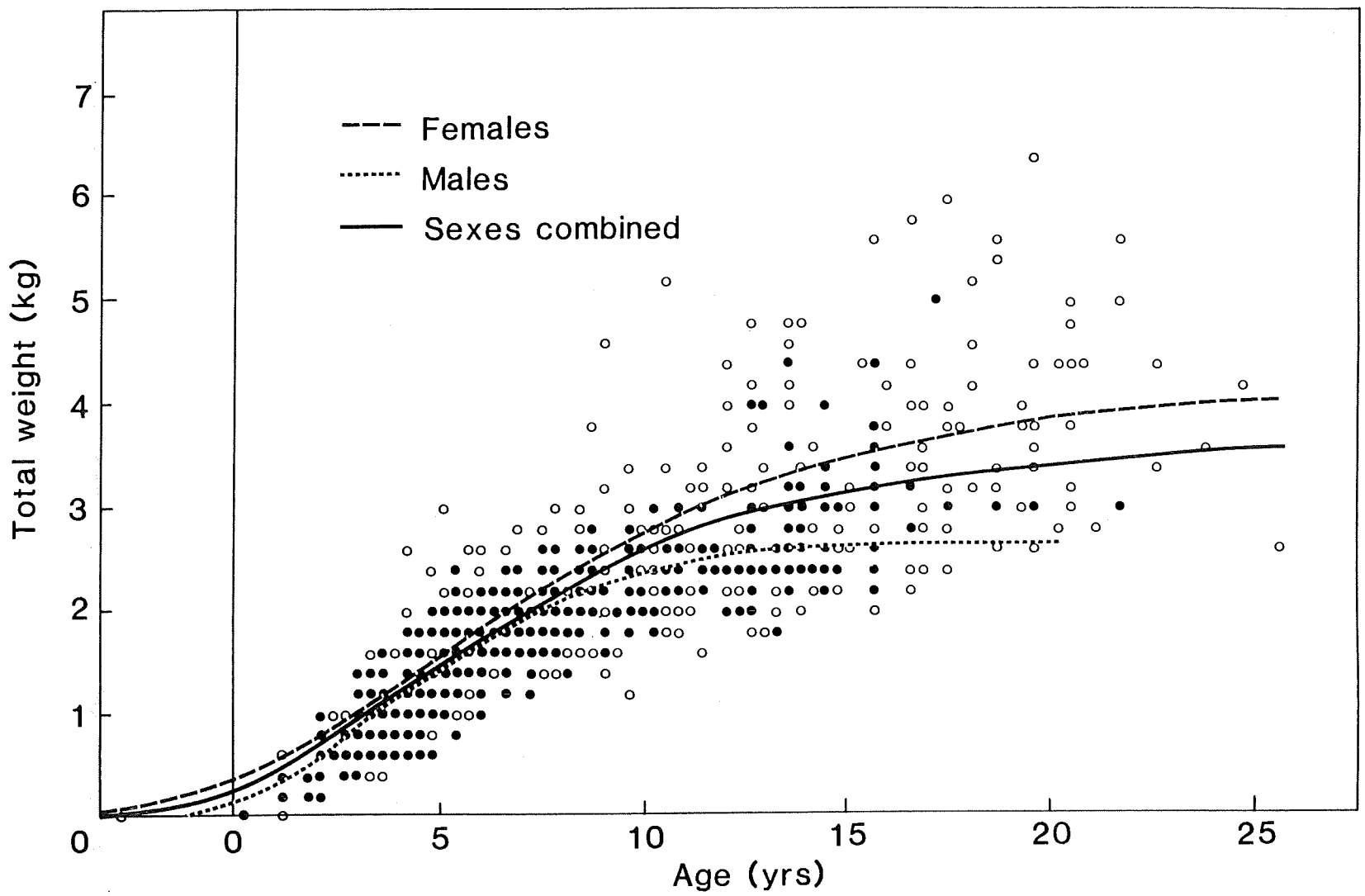
Female East
Male East
Male West

Fig 6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Males
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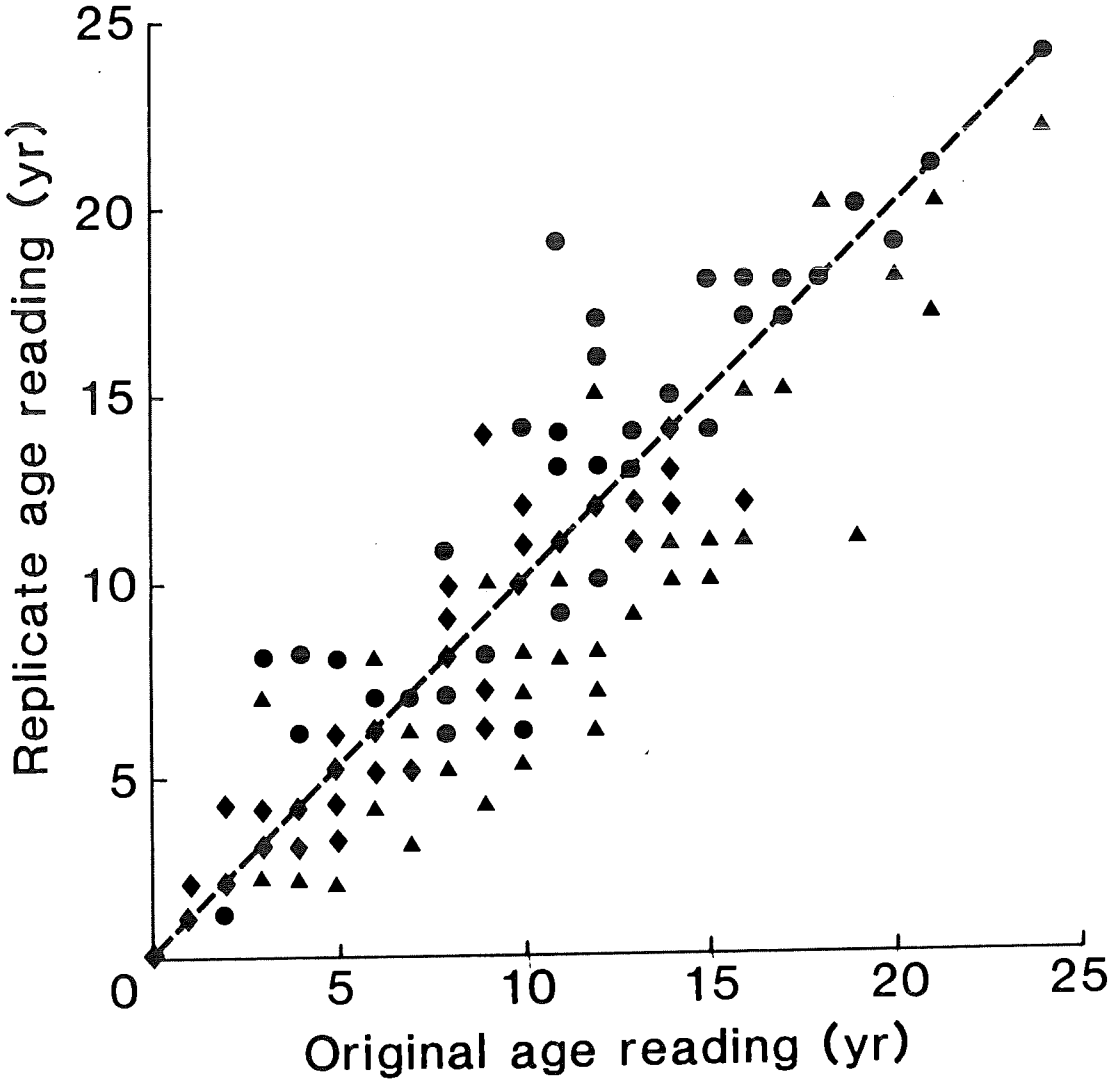
Age (yrs)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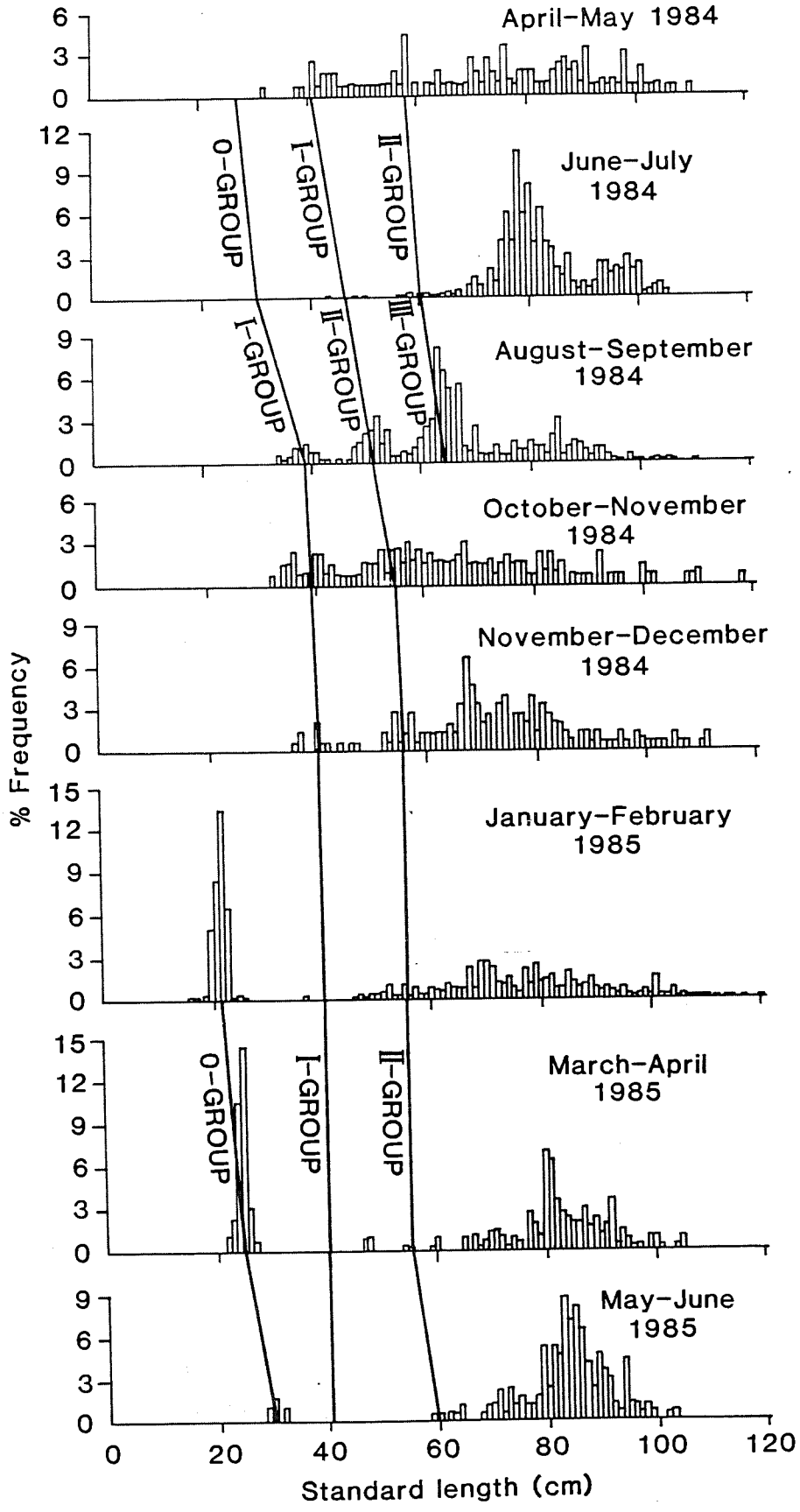
10
15
20
25

8 of 8

Fig 9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II-GROUP
III-GROUP
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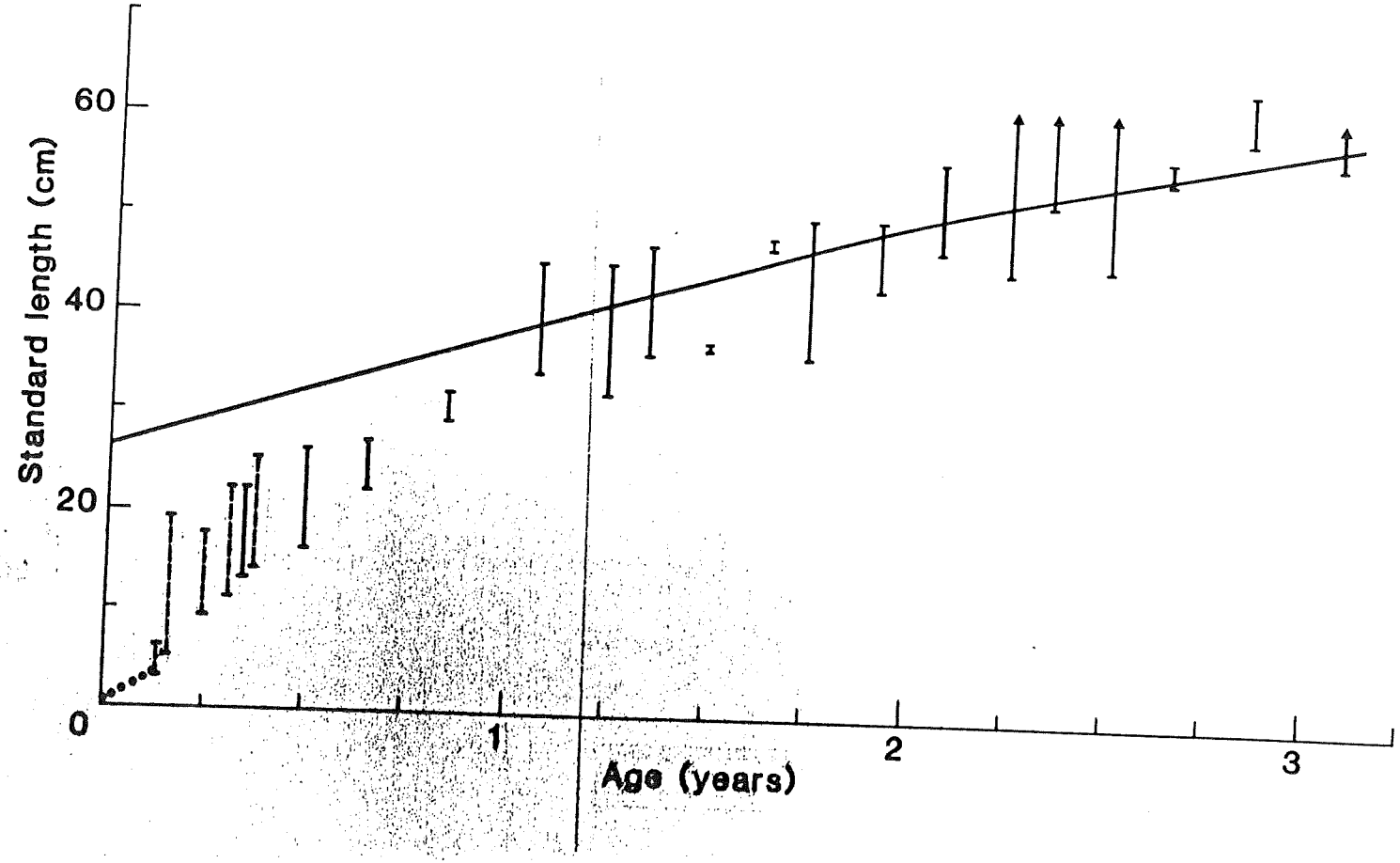
60
80
100
120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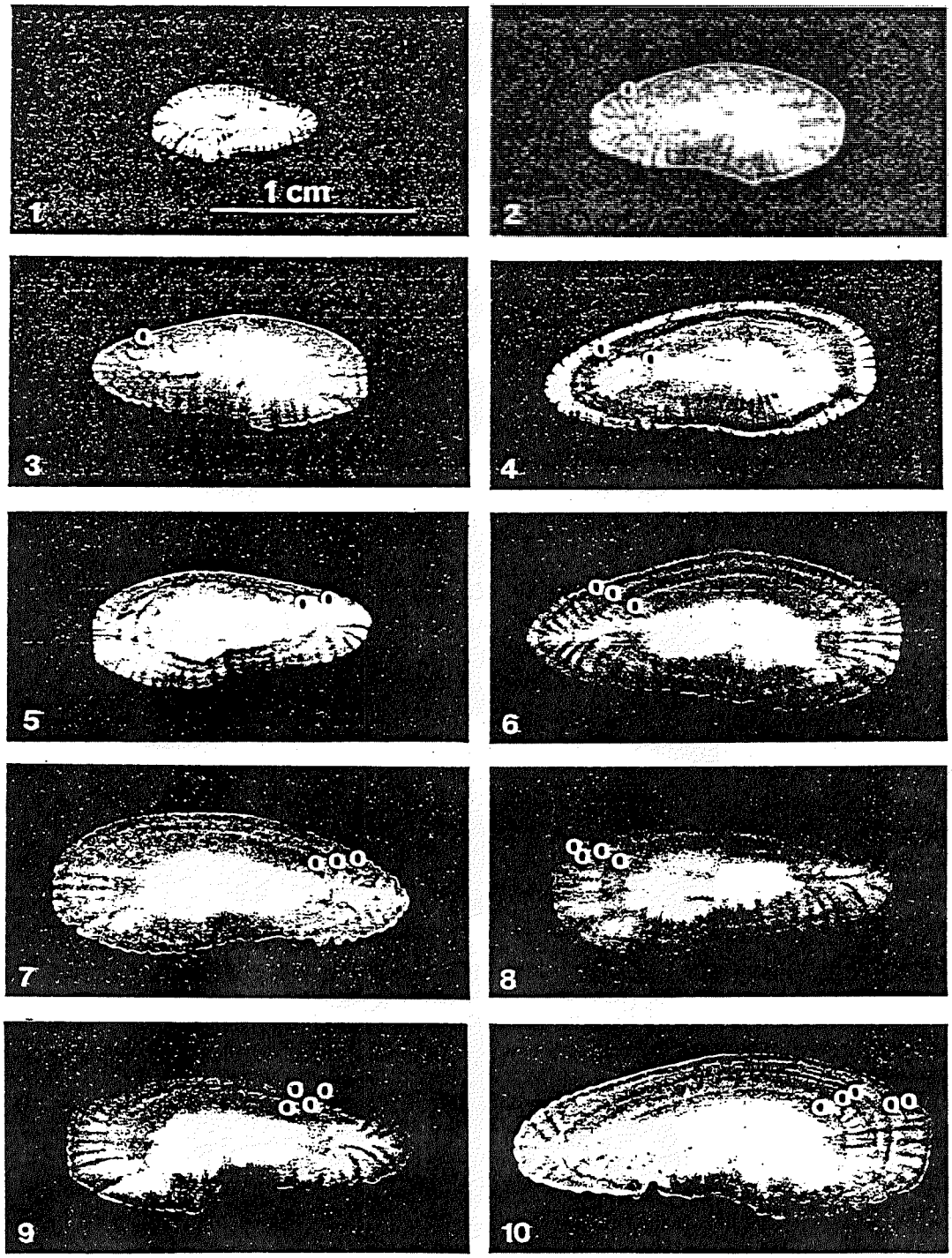
0
1
2
3
Age (years)

Fig 11

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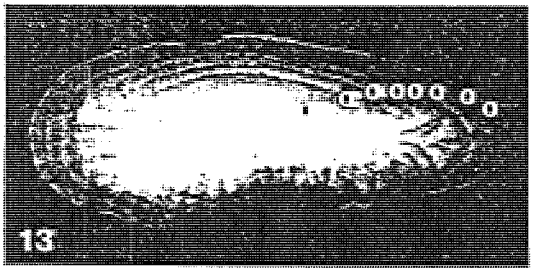
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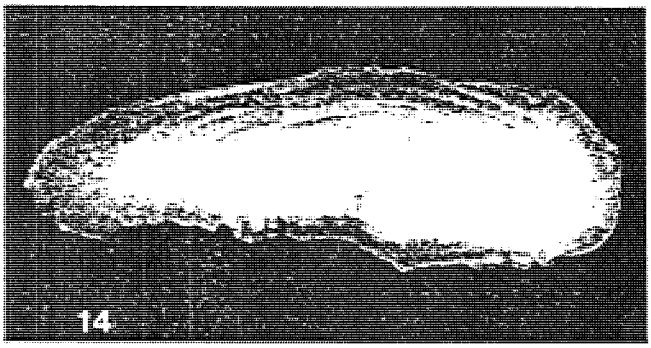
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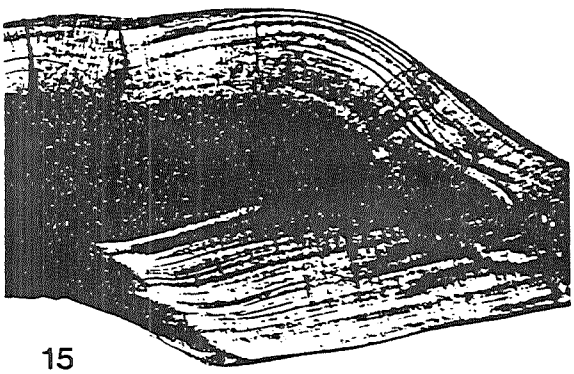
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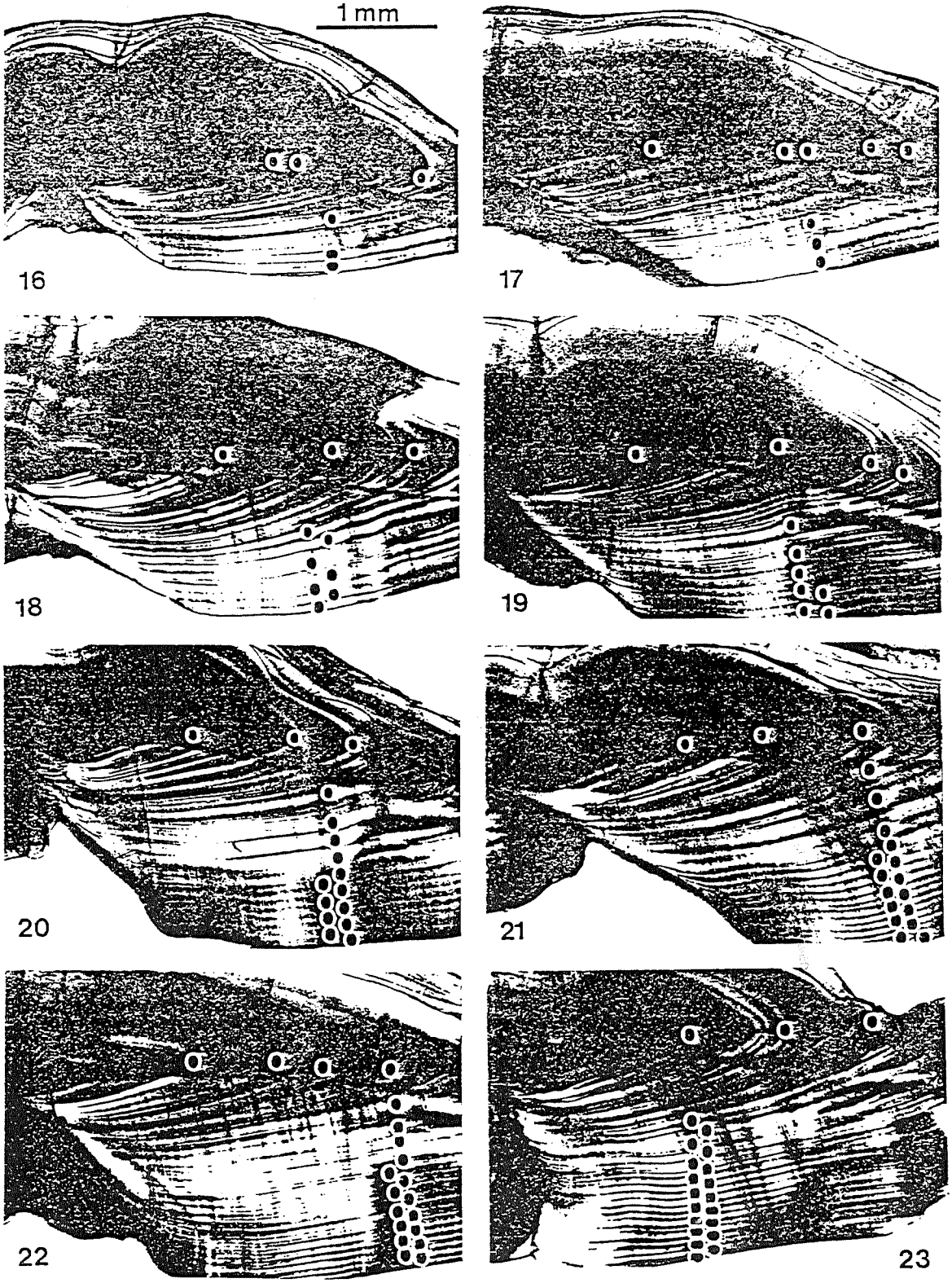
Fig 13



APPENDIX 3

TIMING AND LOCATION OF SPAWNING BY THE BLUE GRENADIER, *MACRURONUS NOVAEZELANDIAE* (TELEOSTEI : MERLUCCIIDAE) IN AUSTRALIAN COASTAL WATERS

BY

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ABSTRACT

The distribution and ages of larvae of the blue grenadier, Macruronus novaezelandiae, based on ichthyoplankton surveys in southern Australian waters in 1984 and 1985, indicate the species spawns primarily off the west coast of Tasmania in winter, and may spawn on a lunar cycle. Winter spawning off Tasmania is also suggested by adult gonad morphology: GSI's peak in winter, and mature and spent individuals were collected only off the west coast of Tasmania. A few larval blue grenadier were also collected off northeastern Tasmania, suggesting the occurrence of small scale and sporadic spawning in that area. Date of first spawning differed by a month between 1984 and 1985, which was apparently related to broad scale differences between years in the oceanography of southern Australian coastal waters. Use of oceanographic features to retrocast spawning dates for blue grenadier suggests that shifts in date of first spawning of approximately a month occur commonly in the species.

INTRODUCTION

The blue grenadier, Macruronus novaezelandiae, is a large, southern temperature gadoid that supports a major fishery in Australia and New Zealand. Despite its commercial importance, little is known of the reproductive biology of the species. JAMARC (1976, 1979) and Blagodyorov and Nosov (1978) describe seasonal patterns of reproduction of New Zealand populations, which have since been shown to migrate each winter to spawning grounds on the west coast of the South Island (Patchell 1982, Kuo and Tanaka 1984a, 1984b). Wilson (1981, 1982) suggested that the species reproduces in a similar fashion in Australian waters, though data to support the hypothesis have been sparse. Wilson (1981, 1982) noted that ripe and spent blue grenadier had been caught off the west coast of Tasmania in winter (August), 1982 and that small juveniles could be collected later in the year (October) along the south coast of Tasmania. These observations led Wilson to suggest tht blue grenadier spawn somewhere between South Cape and Cape Sorell, on the west coast of Tasmania, during the winter. Currently, the Australian fishery for blue grenadier concentrates on the west coast of Tasmania, and is believed to be taking mature fish either migrating to or at the spawning grounds.

This hypothesis has not been tested. There are no compelling data on the location(s) or timing of spawning by blue grenadier in Australian waters, nor even on the general reproductive ecology of the species. Hence, the aims of this study wer (1) to determine the basic reproductive morphology and histology of the species, (2) to establish where blue grenadier spawn in Australian waters and (3) to determine the duration of the spawning season.

MATERIALS AND METHODS

Two complementary techniques were used to document elements of the reproductive biology of blue grenadier: analysis of larval ecology and exmaination of adult reproductive morphology.

Detailed information on the location of spawning areas and duration of reproductive seasons was obtained by determining the temporal and spatial distribution of eggs and early larval stages. As noted above, preliminary data suggested that blue grenadier spawn in Tasmanian coastal waters. The precise location of spawning was determined by sampling ichthyoplankton at approximately two month intervals along nine transects spaced around Tasmania (Figure 1). Most transects consisted of four stations (depending on shelf width), designated as nearshore, midshelf, shelf edge and offshore. Sampling procedures are detailed in Thresher, et al. (ms). On all transects except number 9, samples were collected using a standard configuration, 1 m diameter ring net fitted with 500 μm mesh, a 333 μm cod end and a Rigosha 2536B flowmeter. At each station, a stepped oblique tow was made to a maximum depth of 200 m - bottom depth permitting. The volume of water filtered during each tow was calculated from flowmeter readings. Reported catch rates have been standardized to values per 5000 cubic meters of water. On transect 9, sampling procedures were altered in an attempt to obtain data on depth distributions of larvae. Sampling was done using an RMT 8+1, fitted as above, which was towed each time at a fixed depth, with several set depths sampled at each station.

Samples were collected in Tasmanian waters from April 1984 to September 1985, and again in August 1986. In July/August 1985, an additional cruise was carried out in waters off New South Wales, Victoria

and South Australia to determine whether spawning occurred in other Australian waters. This cruise also included additional sampling of western Tasmanian coastal waters, thus providing a finer scale temporal and spatial coverage of the known spawning grounds than was possible in 1984. Partly for this reason, much of the biological work in this study focuses on the 1985 cohort.

After collection, samples were divided equally into two portions, one of which was preserved in buffered formalin (10% in seawater) and the other in 95% ethanol. The former were used to identify the larvae collected; larvae in the ethanol-preserved sample were used for otolith-based ageing. Details of the features used to identify blue grenadier larvae are provided in Bruce (ms). Ages of larval blue grenadier were determined by examination of otolith microstructure, following procedures outlined in Brothers, et al. (1976) and Campana & Neilson (1985). Whole otoliths were extracted from the larvae and viewed at 750-2500x using a Leitz Orthoplan microscope and a high-resolution, closed circuit television. Growth increments in the otoliths were almost invariably well developed and unambiguous (Fig. 2). Details of the procedures used and limits of the ageing technique are discussed in Thresher, et al. (ms).

Information on reproduction obtained from larval distributions was supplemented by gonad data from adults. Samples of adult fishes were obtained from demersal trawls made at approximate two month intervals from April 1984 to April 1985, at three sites along the Tasmanian shelf slope (400-700 m) (Figure 1), using an Engel High Lift Trawl. The trawl sampling procedures are described in Bulman and Blaber (1986). Specimens collected were weighed and measured and their gonads were fixed at sea in Bouin's solution; smaller numbers of female gonads were stored in Gilson's

Fluid to allow fecundity estimates. In the laboratory, gonads were weighed to the nearest 0.1 g and the data used to calculate a gonadosomatic index (GSI), as (gonald weight/body weight) x 100. A selection of 200 gonads of different sizes and sexes were processed histologically to determine stage of ovarian maturity and to confirm the validity of the GSI data.

Histological sections (7 μm) were cut from the material fixed in Bouin's and stained with hematoxylin and eosin using standard techniques (Baker 1966). The assignment of maturity stages to histological sections followed Cyrus & Blaber (1984). Fecundity of gonads stored in Gilson's Fluid was estimated using a gravimetric sub-sampling technique (Bagenal and Braun 1968). Oocyte size-frequency distributions were based on histologically processed gonads.

RESULTS

In both years of the field study, blue grenadier larvae aged less than 5 days post-hatching were collected only off the west and south coasts of Tasmania (Fig. 3). The overwhelming majority of these larvae (100% in 1984, 95% in 1985) were collected at transects 5 and 6, located off the coast slightly south of Sandy Cape (41°30'S., 144°30'E) and south of Cape Sorell (42°40'S, 145°10'E), respectively (Fig. 1). They were most abundant at the mid-shelf and near shore stations (Fig. 4). Larvae of this age were also present along the central west coast in 1986, though limited ship time prevented delimitation of spawning grounds. In general, the number of blue grenadier larvae collected decreased, and the age of those larvae increased, with increasing distance from the mid-west coast of Tasmania (Thresher et al. ms). Both early and late in the 1985

spawning season, however, some young larvae were also collected at transects on the southwest and south coast of Tasmania (transects 7 and 8) (Fig. 5).

No larval blue grenadier, of any age, were caught either in Bass Strait or at any station off southern New South Wales, Victoria or South Australia. However, a few larvae (1 in 1984 and 32 in 1985) less than 15 days post-hatching were collected at transect 1, off the north east coast of Tasmania near St. Helens. The age of these larvae was less than half the minimum time estimated for larval drift from the west coast spawning ground either through Bass Strait (C. Fandry, personal communication) or around the southern end of Tasmania, the usual advection route (Thresher, et al., ms). The presence of these larvae, therefore, suggested some spawning by blue grenadier in the vicinity of northeastern Tasmania and eastern Bass Strait. To test this hypothesis, detailed sampling continental shelf waters along the east coast of Tasmania between 40°S. and 42°S was carried out in 1986. Five transects of three stations, each composed were sampled between August 12 and August 27, 1986. On the same cruise, samples were also collected at 27 stations in the previously documented spawning area on the west coast. Despite the effort expended, no larval blue grenadier were caught off the northeastern coast in 1986. By comparison, approximately 10,000 larvae were collected during the same time period off the west coast of Tasmania.

Spawning dates of blue grenadier were determined by ageing all larvae collected in 1984 and a random sub-sample of the much greater number of larvae collected in 1985. In both years, spawning occurred predominantly in the winter (Fig. 6). In 1984, the earliest estimated hatching date was 13 May and the latest was 16 September; in 1985, first recording hatching

was on 13 June and the last on 12 September (Figs. 6a and 6b, respectively). Differences between years (i.e., spawning commencing one month later in 1985) coincided with major differences in the oceanography of southern Australian waters (Fig. 7). In April, sea surface temperatures in Bass Strait, as determined by thermosalinograph readings made during cruises, were 2C° higher in 1985 than in 1984 and temperatures on the east coast of Tasmania averaged 4C° higher, due to the presence of a tongue of warm water extending southwards along the coast. Differences in surface temperatures were least on the west coast spawning ground, and generally declined during the course of the two spawning seasons.

Hatching was recorded on 45 of the 127 days spanned by the 1984 spawning season, and on 71 of the 82 days spanned by the 1985 season. Data on hatching dates for 410 larvae, caught on four cruises in 1985, indicate spawning to have been essentially continuous throughout the spawning season (Fig. 6b). The possibility of patterning within the data was tested by periodic analysis using fitted sine functions. Analysis was based on ageing of all larvae from small samples, and of 20 randomly selected larvae from each of the large samples of newly hatched larvae. Limiting sample sizes of newly hatched larvae compensates in part for the unknown effects of larval mortality on estimating spawning cycles. Results indicated spawning occurred most frequently on dates close to the full moon (Fig. 8a), although some spawning occurs throughout the lunar month. Periodic analysis also suggested a lunar component to spawning with the best fit (most variance accounted for) between a sine function and the distribution of hatching dates being a period of 27.8 days (Fig. 8b).

Data on reproductive condition of adult blue grenadier are sparse,

but generally support the results of the ichthyoplankton surveys. Histological examination of male and female gonads revealed no indication of hermaphroditism, suggesting the species is a gonochore. This suggestion is also supported by the broad overlap in size-ranges of males and females (Kenchington & Augustine, ms). Both testes and ovaries are paired and undergo seasonal development simultaneously. The seasonal pattern of GSI's (Figure 9) indicates the species has a relatively protracted spawning season. GSI's for specimens collected off south-eastern Tasmania and in eastern Bass Strait were uniformly low throughut the year, with the only indication of an increase being a minor peak for south-eastern fish in June. In contrast, individuals collected on the west coast had high GSI's in both June and August. In addition all running ripe and spent fish caught in this study were collected off the west coast during the period June to August. These dates coincide with the dates of the spawning season determined from patterns of larval abundance.

Despite the relatively protracted spawning season, oocyte size-frequency distributions of ovaries at maturity stages II (pre-vitellogenic), III (yolk precursor) and IV (primary yolk) reveal a clear size separation of pre- and post-vitellogenic stage oocytes as development takes place (Figure 10). Stage IV ovaries characteristically had a unimodal batch of primary yolk oocytes, varying in diameter from 0.33 to 0.76 mm, clearly separated from their reserve of oogonia, which were less than 0.05 mm diameter. Spent (Stage VII) ovaries contained no yolked oocytes. Estimated fecundity ranged from 321,000 eggs in an 81 cm, 2.0 kg female to 1,592,000 eggs in a 92 cm, 3.7 kg individual. The smallest female with yolk precursor or developing ovaries was 73 cm, a length which

would be obtained between ages of 4 and 7 years for the Tasmanian population (Kenchington & Augustin, ms).

DISCUSSION

The general features of the reproductive biology of Macruronus novaezelandiae are similar to those of other gadoid fishes (Breder and Rosen, 1966, Hislop, 1984). It is a gonochore and has a generally normal teleostean reproductive system, with paired gonads that undergo simultaneous development. Oocyte size frequency data for maturity stages II, III and IV indicate that females develop single batches of oocytes, a process usually associated with isochronal or total spawning (Hickling and Rutenberg, 1936). Spent female gonads contained no yolked oocytes, a further indication of total spawning. Also like other gadoids, spawning by blue grenadier takes place at a particular spawning ground, used each year. Adult blue grenadier are widely distributed along the slope and shelf edge of southern Australia, from the Great Australian Bight to the coast of New South Wales (Iast, et al., 1983). All adults ready to spawn apparently migrate from throughout this broad area to the spawning grounds. Similar migrations are well documented in a variety of North Atlantic gadoids, e.g., cod (Gadus morhua (reviewed by Harden Jones, 1968), have been implied for other species of Macruronus (Bezzi, 1984), and have previously been reported for M. novaezelandiae off New Zealand (Patchell, 1982).

The distribution of Macruronus novaezelandiae larvae indicates that the primary spawning ground in Australian waters is off the west coast of Tasmania. The scattered distribution of larvae less than five days post-hatching suggests that some spawning occurs along most of this coast. As

over 90% of immediate post-hatching larvae were caught at stations off Cape Sorell, however, we believe this area to be the centre of spawning activity for the species in Australia. Electrophoretic data (Milton and Shaklee, in prep.) indicate a single Australian population, suggesting that additional major spawning areas for the species in Australian waters are unlikely.

Nonetheless, a few relatively young larvae, between 6 and 15 days post-hatching, were also caught during this study off the north east coast of Tasmania. It is unlikely these larvae derived from the known spawning ground off the west coast: transport of larvae during the winter around the southern end of Tasmania, the normal advection route, or through Bass Strait would require in excess of 30 days (C. Fandry, pers. comm.). These anomolous larvae, therefore, appear to indicate small scale spawning events occurring somewhere off the east coast of Tasmania or in eastern Bass Strait. The sporadic nature of this spawning ground is indicated by the failure to collect M. novaezelandiae larvae off this coast in August, 1986, despite an intensive ichthyoplankton survey of the area. Consequently, we suspect this spawning ground to be of only slight significance to either the population or the fishery.

The spatial patterning of spawning by M. novaezelandiae in Australia is strikingly similar to that off New Zealand. Patchell (1982) reported a migration of M. novaezealandiae from feeding grounds off both the east and west coasts of New Zealand to a single spawning ground off the west coast of South Island, between 41°S and 44°S latitude. By comparison, the Australian spawning ground, also on a west coast, lies between 41°S and 43°30'S. The Australian pattern is also paralleled by recent work that indicates occasional small scale spawning by the New Zealand stock off the

east coast of South Island (D. Robertson, pers. comm).

Spawning by blue grenadier occurs only during winter and early spring. Winter spawnings are not typical of gadoids (Breder & Rosen, 1966), but have been reported both for other species of Macruronus (Torno & Tomo, 1980; Bezzi, 1984) and for M. novaezelandiae off New Zealand (Patchell 1982). The two years data on hand further indicate that duration of the spawning season varies between years; in 1984, spawning commenced in mid-May, whereas in 1985 it began in mid-June, ending in September in both years. On the basis of only two years data, it is not possible to determine what factor(s) drive inter-annual differences in spawning periods. However, it is unlikely to be coincidental that these differences coincided with significant differences between years in the hydrography of coastal waters off south-eastern Australia. In the autumn of 1985, prior to spawning and during what is presumably the period when mature blue grenadier migrate to the spawning ground, sea surface temperatures along the east coast of Tasmania averaged approximately 4C° higher than for the corresponding period in 1984. This temperature difference was linked to the variable presence of a tongue of warm water, an extension of the East Australian Current (Harris, et al., in press), that flows south down the east coast of Tasmania during spring and summer. The southern limits and persistence of this extension vary from year to year, reflecting differences in the balance between it and two other currents, a seasonally present south-flowing current on the west coast (the Zeehan Current of Baines, et al., 1983, described by Nillsen, et al., ms., as an extension of the Leeuwin Current), and a general northerly wash of sub-Anarctic waters along the southern end of the island.

We hypothesize that mature blue grenadier respond to differences in water column characteristics, and particularly water temperature, each year as they begin their spawning migrations. Although the cues for migration by blue grenadier are not known, water temperature has been widely reported in the literature as a factor synchronizing gonadal recrudescence and stimulating spawning migrations in marine fishes (see review by McKeown 1984). As blue grenadier spawn in winter, when water temperatures are at a seasonal low, a "delay" in the seasonal decline in temperatures, brought about by a southerly extension of the East Australian Current that persists into autumn, could lead to a delay in the onset of adult migration.

If this hypothesis is true, then it should be possible to develop methods to use sea surface temperatures as predictors of the timing and duration of the spawning period of blue grenadier. In the interim, two long-term data sets are available which permit retrocasting of spawning periods in the recent past, and assessment of the relative frequency of "early" and "late" spawning by the species. These data sets are the GOSSTCOMP plots of sea surface temperature, based on satellite imagery and provided by NOAA since 1975, and the hydrographic data for a station off Maria Island (east coast Tasmania) occupied monthly by CSIRO since 1944. Both data sets are consistent with the results of the two years of this field study; GOSSTCOMP plots indicate the stronger development and greater persistence of the east coast extension of the East Australian Current in 1985 than in 1984, and the seasonal decline in sub-surface water temperatures at the Maria Island station occurred later in 1985 than 1984 (fig. 11). The latter data also suggest a close relationship between temperatures at Maria Island and the onset of spawning by blue grenadier

(fig. 11); in both years, first recorded spawning occurred when sub-surface water temperatures at Maria Island were approximately 13.5°C. If one assumes this to be a reliable index of first spawning, then the approximate date of first spawning each year can be calculated for the last four decades (Fig. 12).

Unfortunately, GOSSTCOMP data are not wholly consistent with the pattern of inter-annual variation suggested by the Maria Island station, and suggest a different pattern of first spawning dates (Fig. 12). The two data sets are in good agreement for the last five years, but for the full eleven year GOSSTCOMP data set, the correlation between the estimated date at which sub-surface temperatures at Maria Island reach 13.5°C and maximum latitudinal penetration of the warm water extension during autumn is not significant (r_s = 0.27, N.S.). Why the data sets differ is not clear, since Harris, et al. (in press) suggest that the Maria Island hydrographic data reflect oceanographic processes on the shelf and shelf edge. Determination of the relative accuracy of the two long-term data sets in retrocasting spawning periods is not possible without further information on the timing and duration of spawning each year. Both data sets, however, suggest that shifts in the onset of migration and spawning of blue grenadier of up to a month occur frequently, and that relatively late spawning (beginning in June) is likely to occur at least as often as early (May) spawning.

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FIGURE CAPTIONS

Figure 1. Locations of regular ichthyoplankton and demersal trawl stations.

Figure 2. Photomicrograph of otolith from larval blue grenadier, estimated to be 8 days post-hatching.

Figure 3. Distribution of catches during 1984 and 1985 of larval blue grenadier estimated to be aged less than 5 days post-hatching.

Figure 4. Cross-shelf distribution of blue grenadier larvae for three cruises in 1985.

Figure 5. Proportional distribution across transects of blue grenadier larvae aged 0-5 days and 6-10 day post-hatching larvae during three sampling periods in 1985.

Figure 6. Spawning dates for larvae collected during 1984 (6a) and 1985 (6b) cruises, based on back-calculating spawning date from date of capture, apparent age of larvae as indicated by otolith microstructure, and a 4 day interval between hatching and the development of the first daily growth increment. Arrows indicate dates of the full moon.

Figure 7. Plots of sea surface temperatures around Tasmania during autumn and early winter of 1984 and 1985. Plots are based on thermosalinograph data obtained during research curises.

Figure 8. a. Mean number of larvae from 1985 samples spawned on each day of the lunar month. Based on data in Figure 6b. One outlier not shown. Fit between sine function and observed data is significant at $P<0.01$ (X^2 goodness of fit = 49.07, d.f. = 28). b. Results of periodic analysis seeking best fit between distribution of spawning days in Figure 6b and sine function of unknown period. Plot shows amount of variance in the distribution accounted for by a fitted functions varying in period from 8 to 40 days. The greater the amount of variance accounted for, the better the fit between observed data and the sine function.

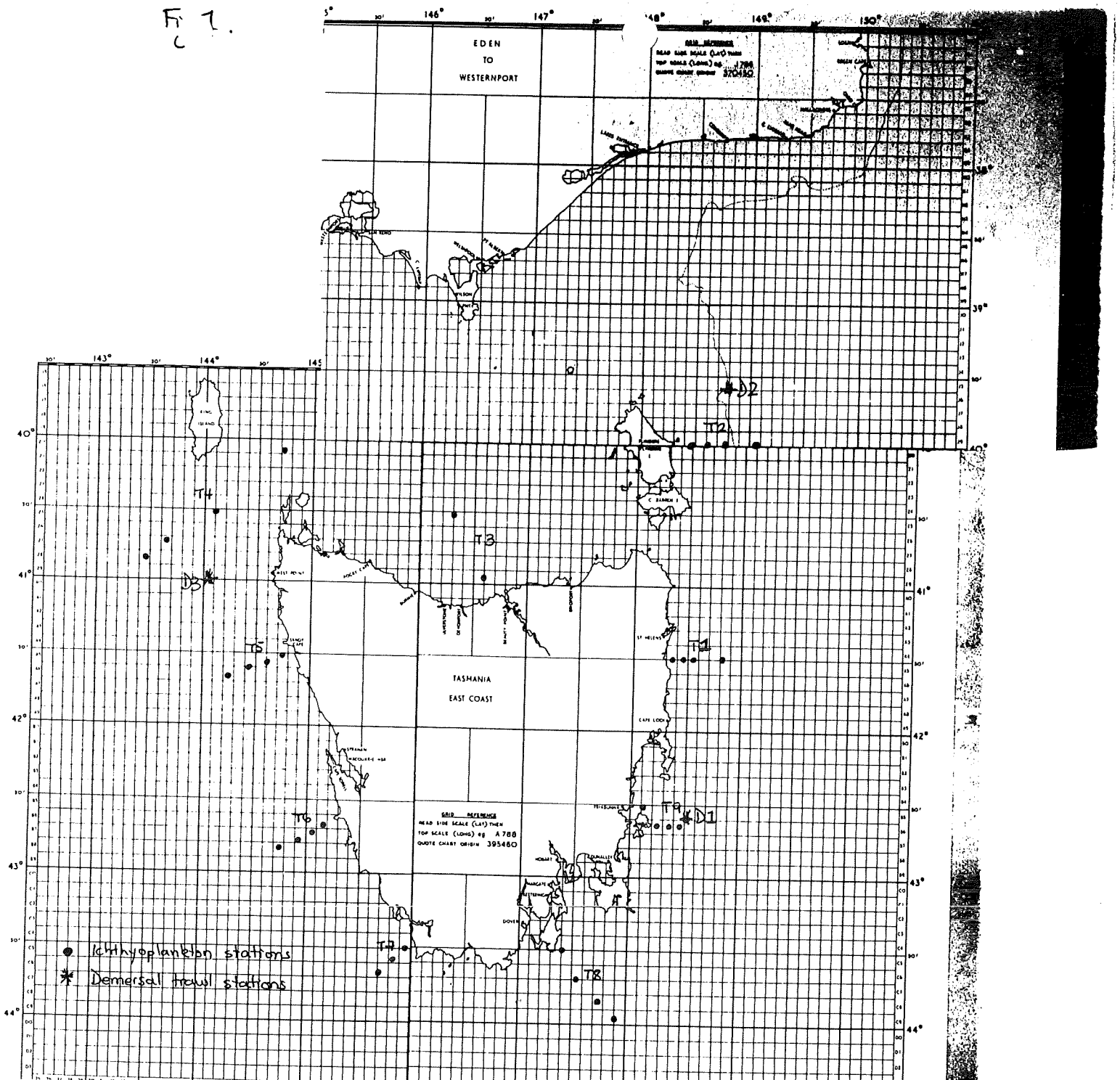
Figure 9. Seasonal changes in female GSI for three demersal trawling stations. Dashed lines indicate ranges.

Figure 10. Size frequency distributions of oocytes in gonads of females in different stages of the reproductive cycle.

Figure 11. Seasonal progression of sub-surface (20 m) water temperatures at the Maria Island hydrographic station in the autumn and winter of 1984 and 1985. Arrows indicate dates of first spawning for the two years.

Figure 12. Retrocast dates of first spawning based on occurence of a temperature of 13.5°C at the Maria Island hydrographic station (solid lines) and the maximum latitudinal penetration of a warm water extension of the East Australian Current during autumn (dashed line) (measured as maximum latitude reached by the 16°C. isotherm during April - June), based on GOSSTCOMP charts. Analysis of warm water penetration based on other isotherms produced a similar pattern of inter-annual variability.

Fig 1.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Demersal trawl stations

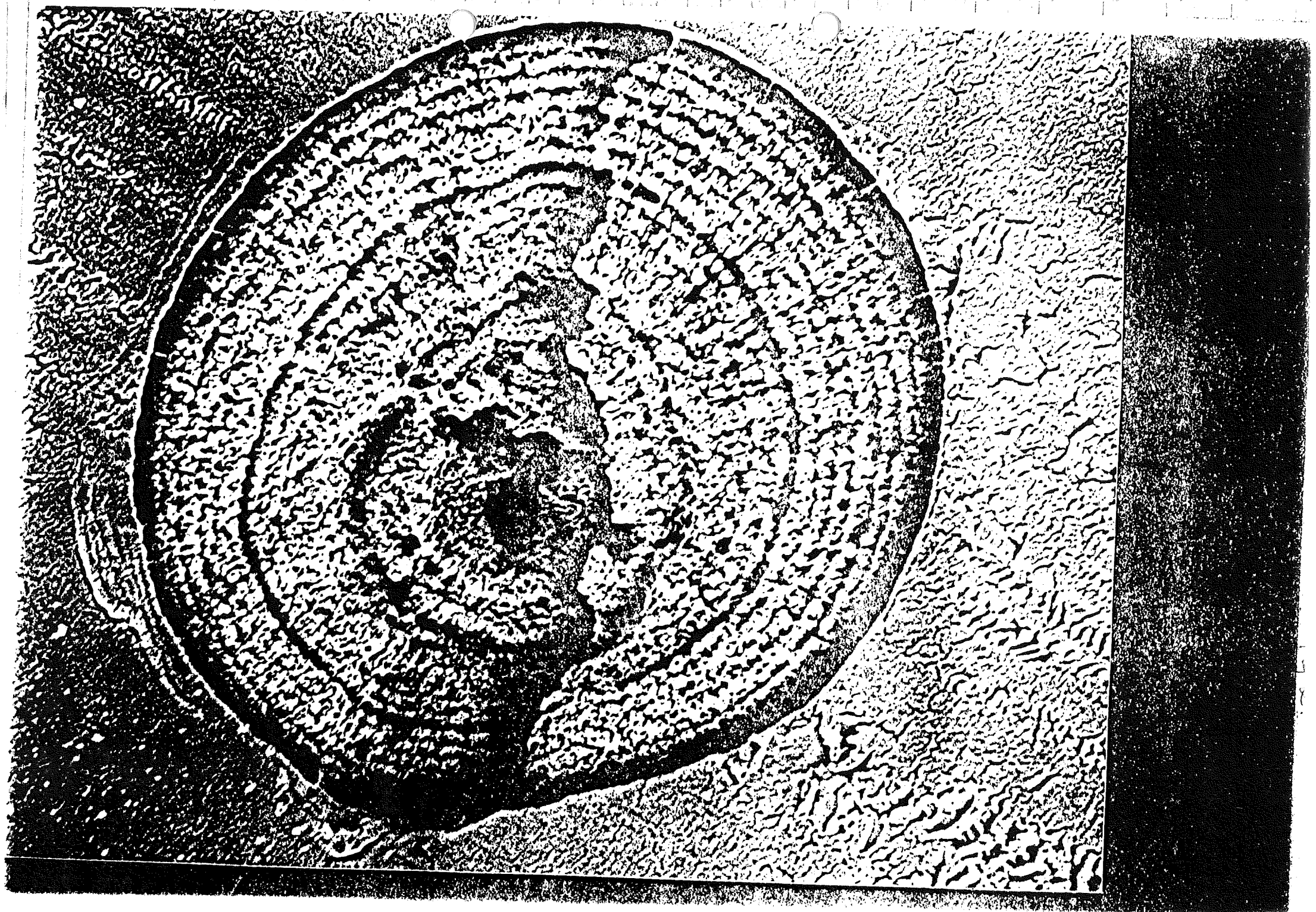


Fig. 3.

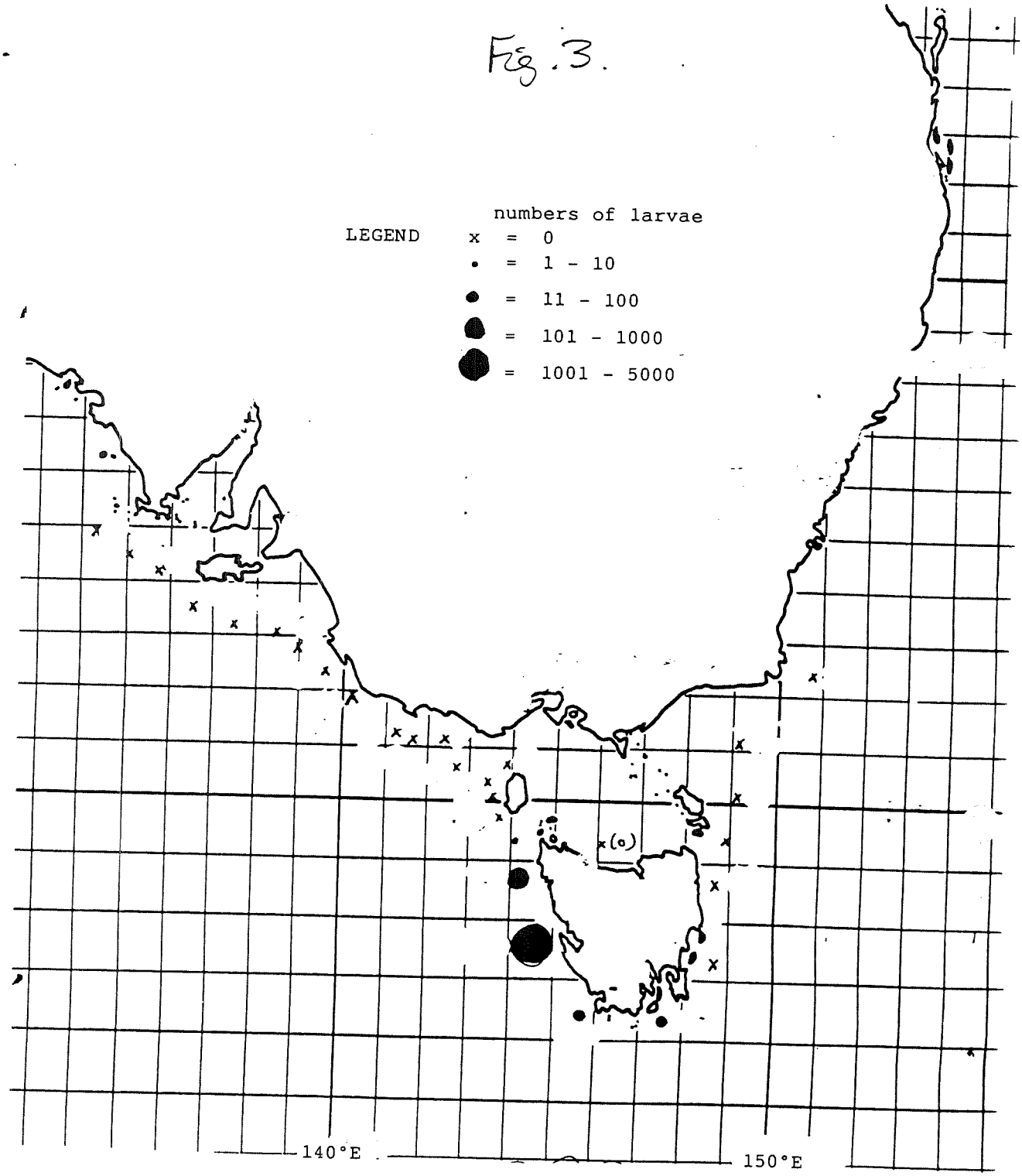
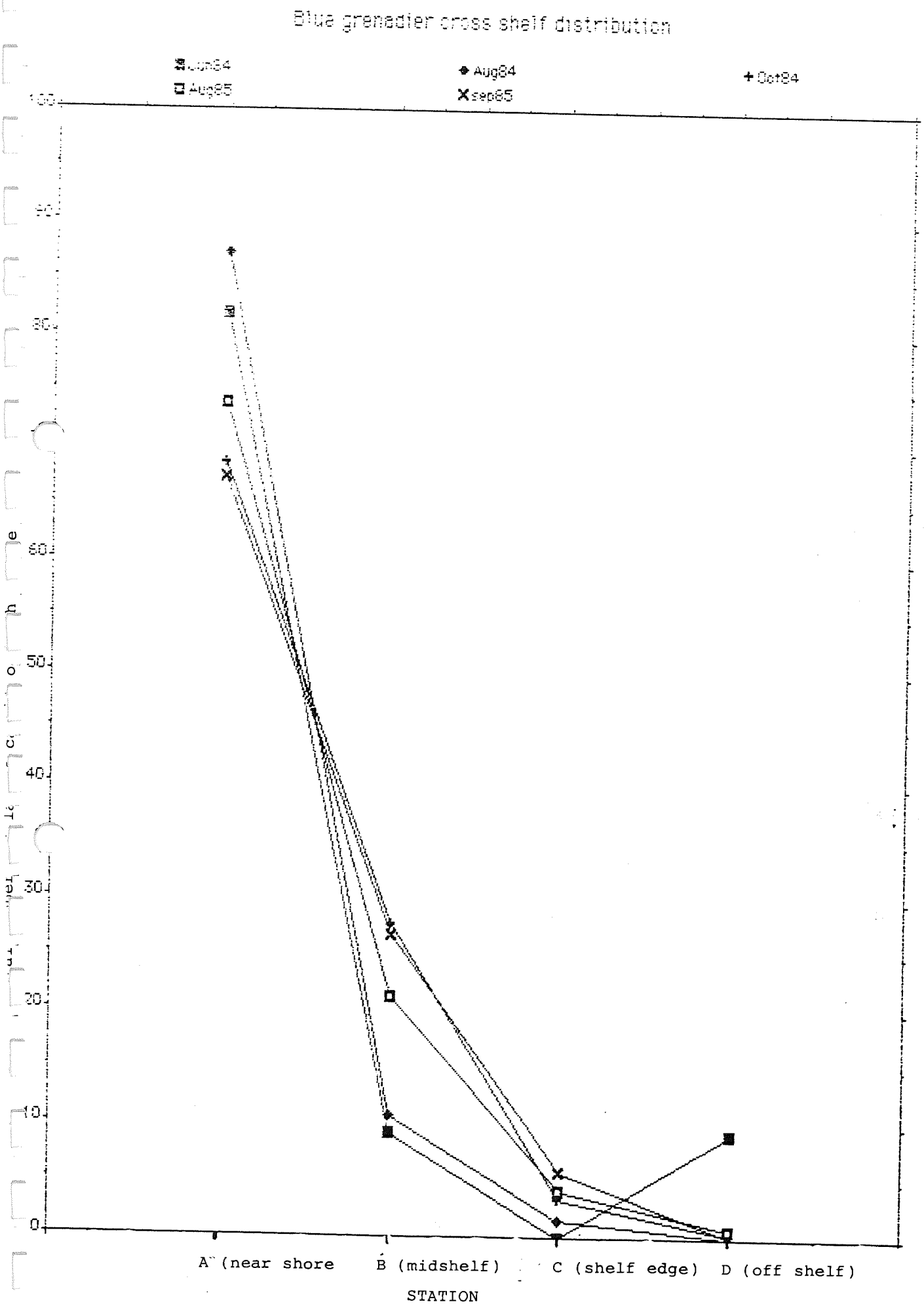
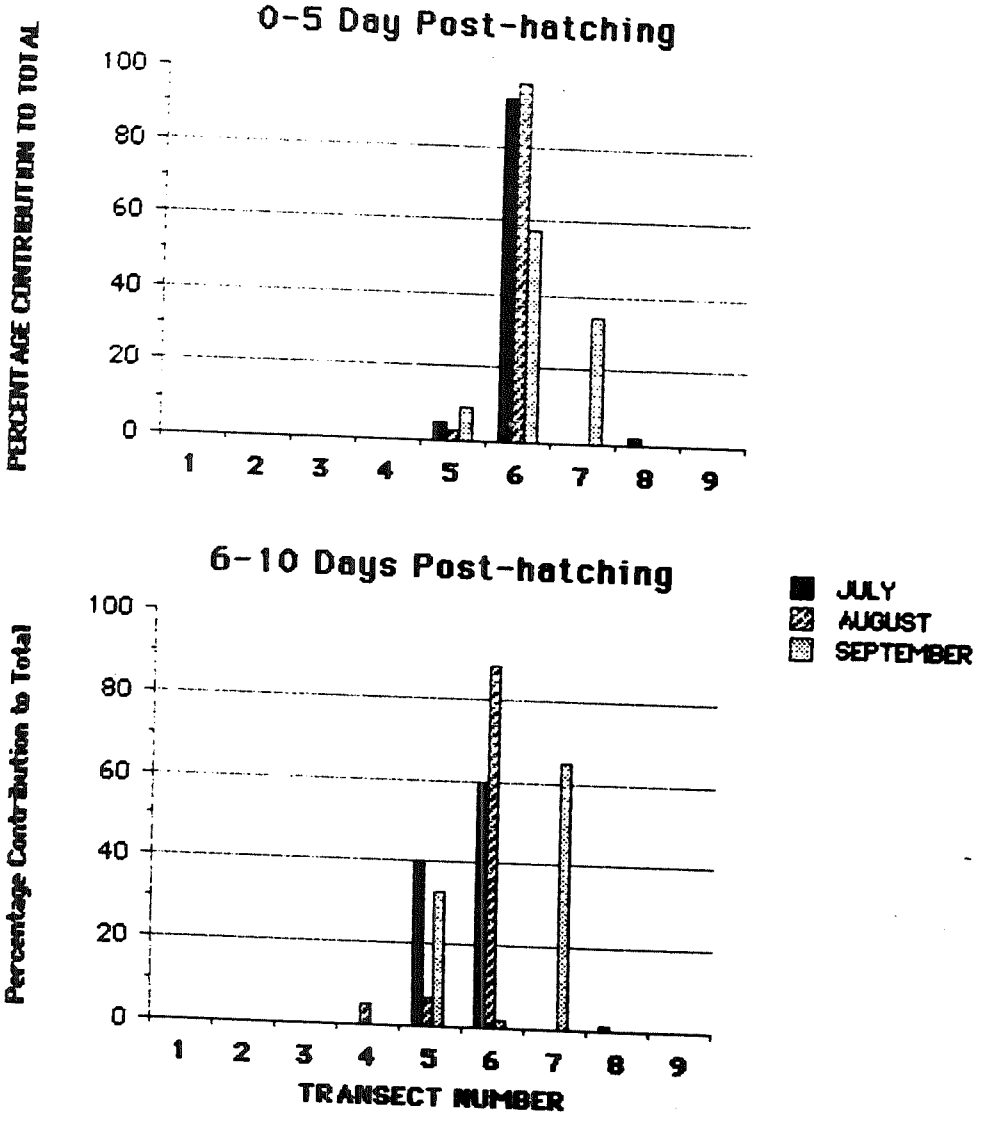

numbers of larvae
LEGEND
x = 0
• = 1 - 10
= 11 - 100
= 101 - 1000
= 1001 - 5000
140°E
150°E

Fig 4


Blue grenadier cross shelf distribution
Jun84
Aug84
Oct84
Aug85
sep85
100
90
80
70
60
50
40
30
20
10
0
A (near shore
B (midshelf)
C (shelf edge)
D (off shelf)
STATION


0-5 Day Post-hatching
PERCENTAGE CONTRIBUTION TO TOTAL
100
80
60
40
20
0
1 2 3 4 5 6 7 8 9
6-10 Days Post-hatching
Percentage Contribution to Total
100
80
60
40
20
0
1 2 3 4 5 6 7 8 9
TRANSECT NUMBER
JULY
AUGUST
SEPTEMBER

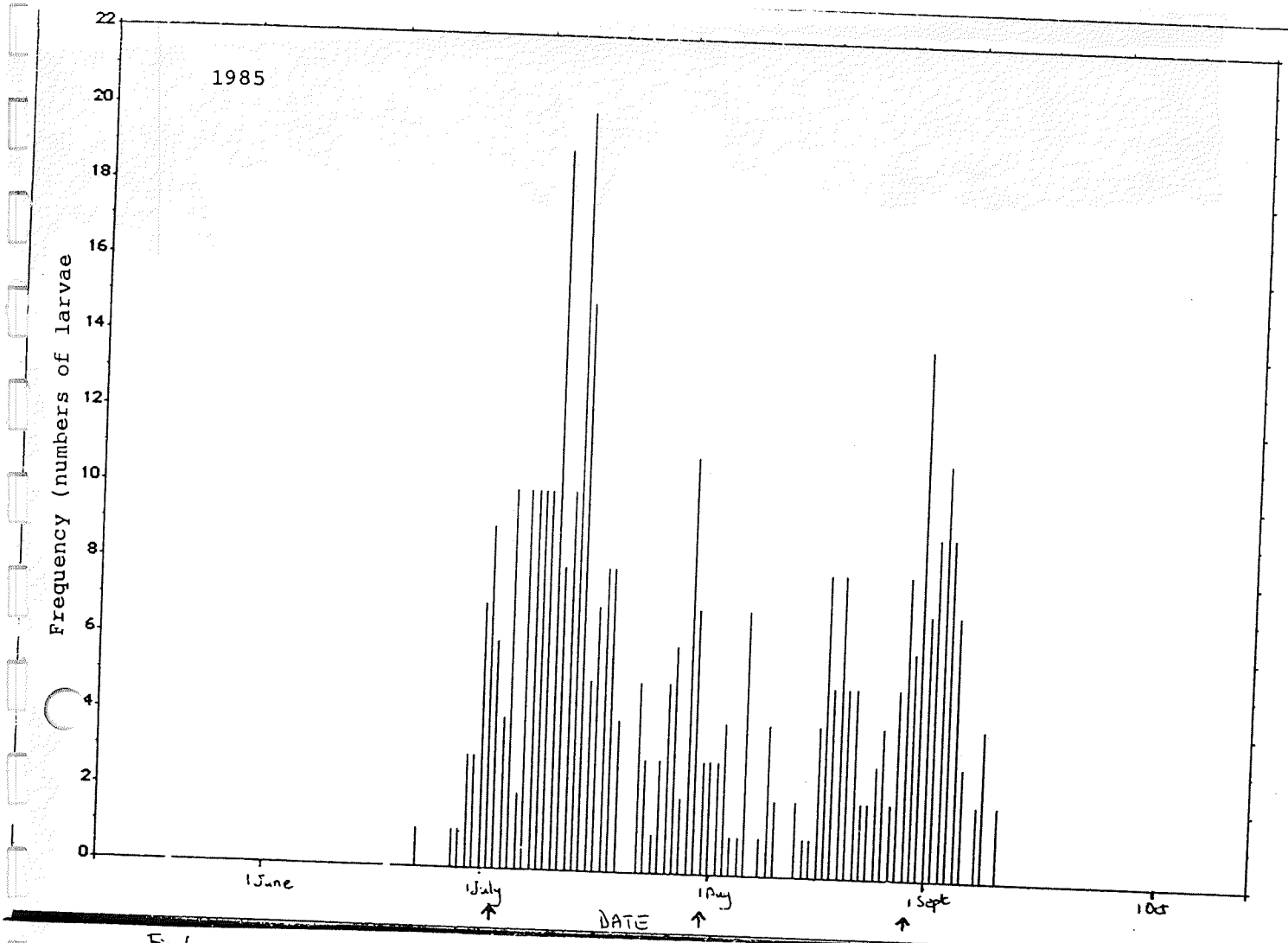

1985
Frequency (numbers of larvae
0
2
4
6
8
10
12
14
16
18
20
22
1 June
1 July
1 Aug
1 Sept
1 Oct
DATE

Fig 6.

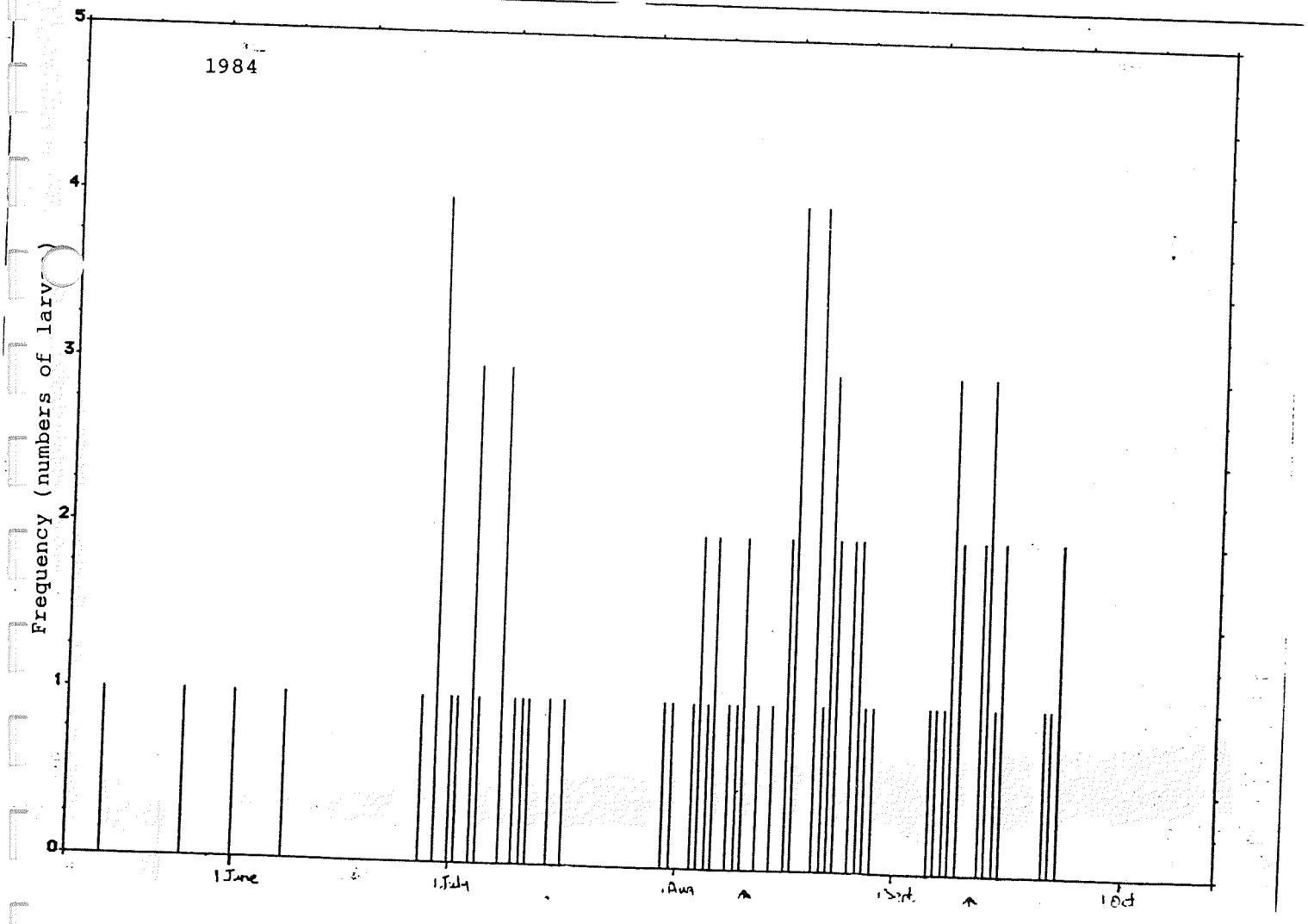
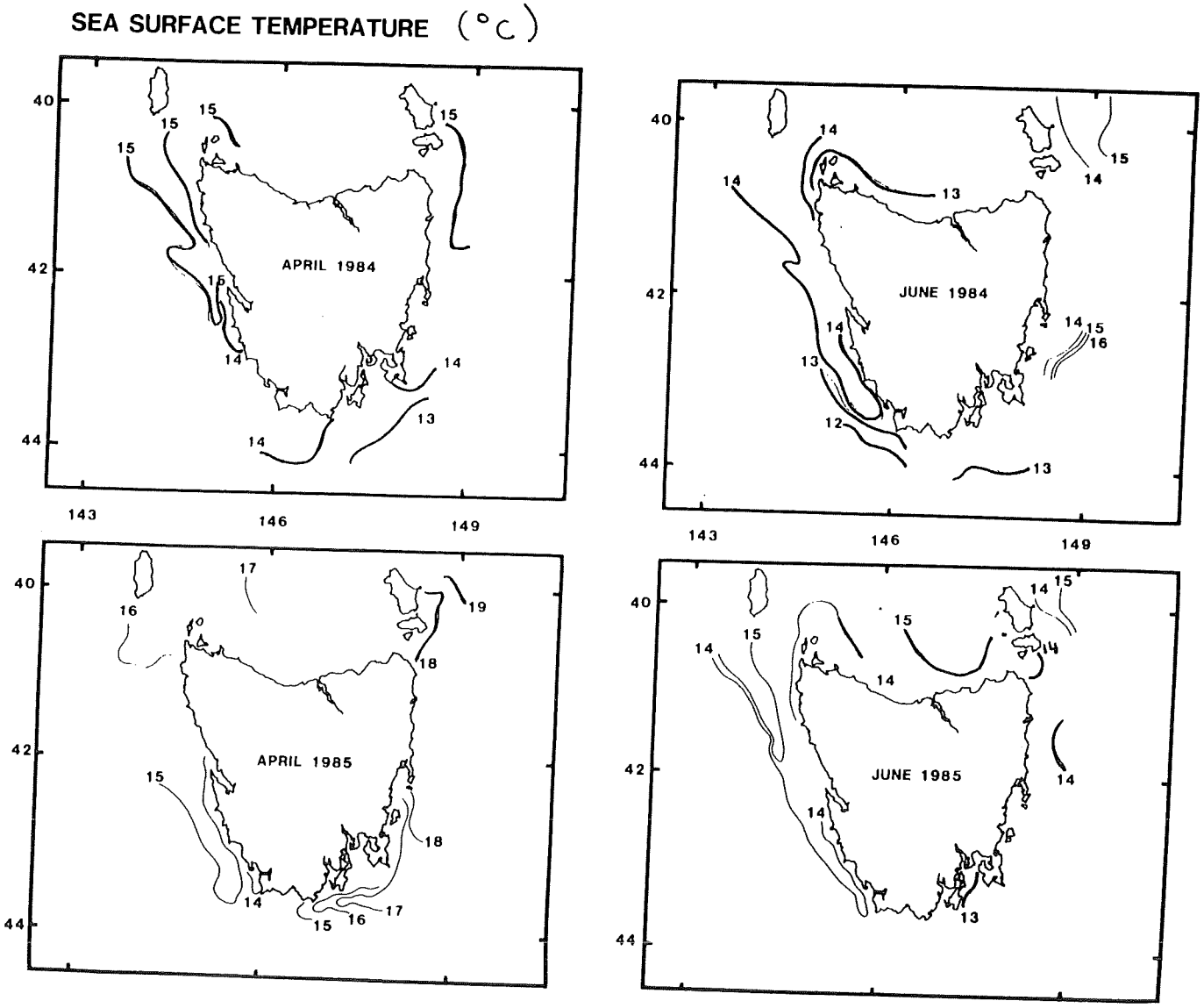
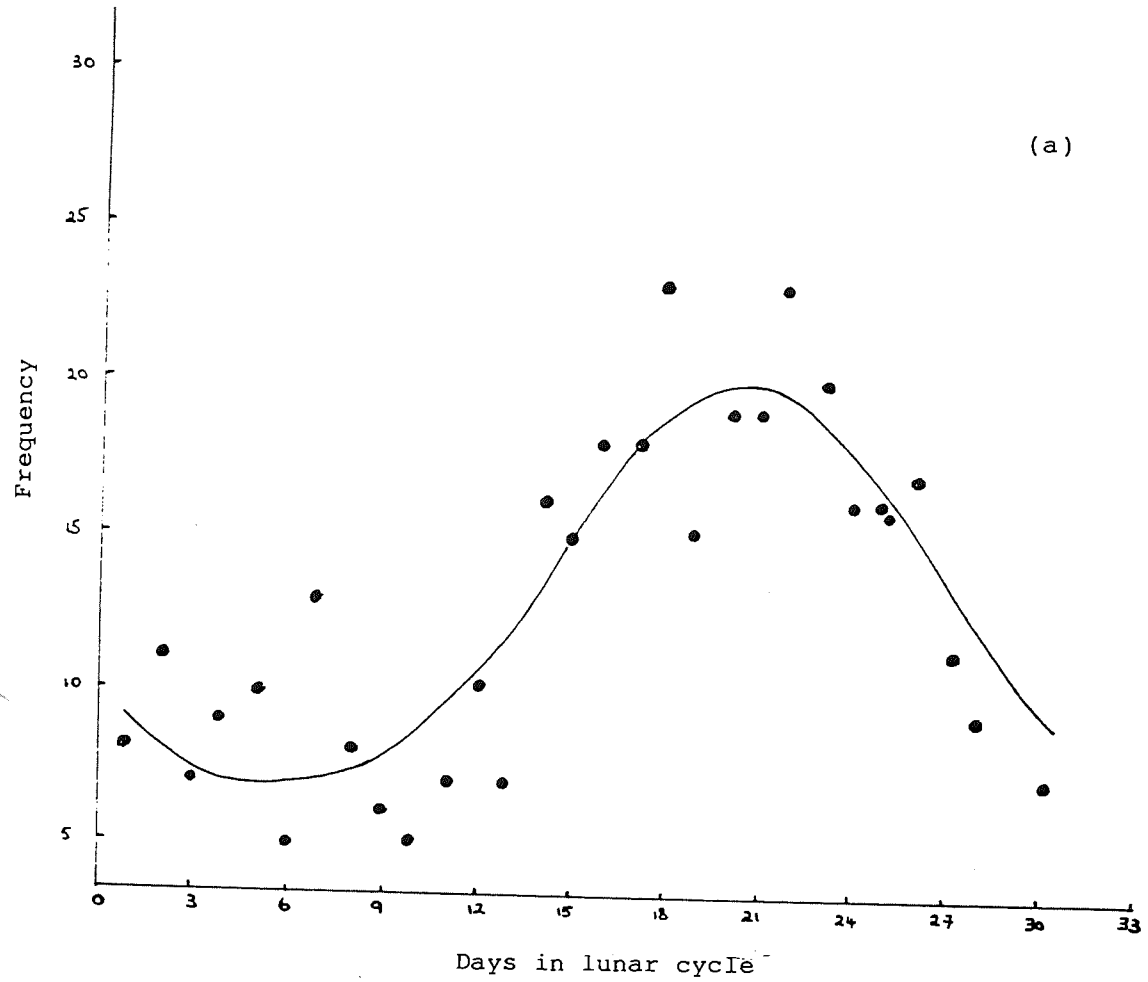

1984
Frequency (numbers of larv
0
1
2
3
4
5
1 June
1 July
Aug
Sept
1 Oct

Fig. 7


SEA SURFACE TEMPERATURE (°C)
APRIL 1984
JUNE 1984
APRIL 1985
JUNE 1985
40
42
44
143
146
149


(a)
Frequency
30
25
20
15
10
5
0
3
6
9
12
15
18
21
24
27
30
33
Days in lunar cycle

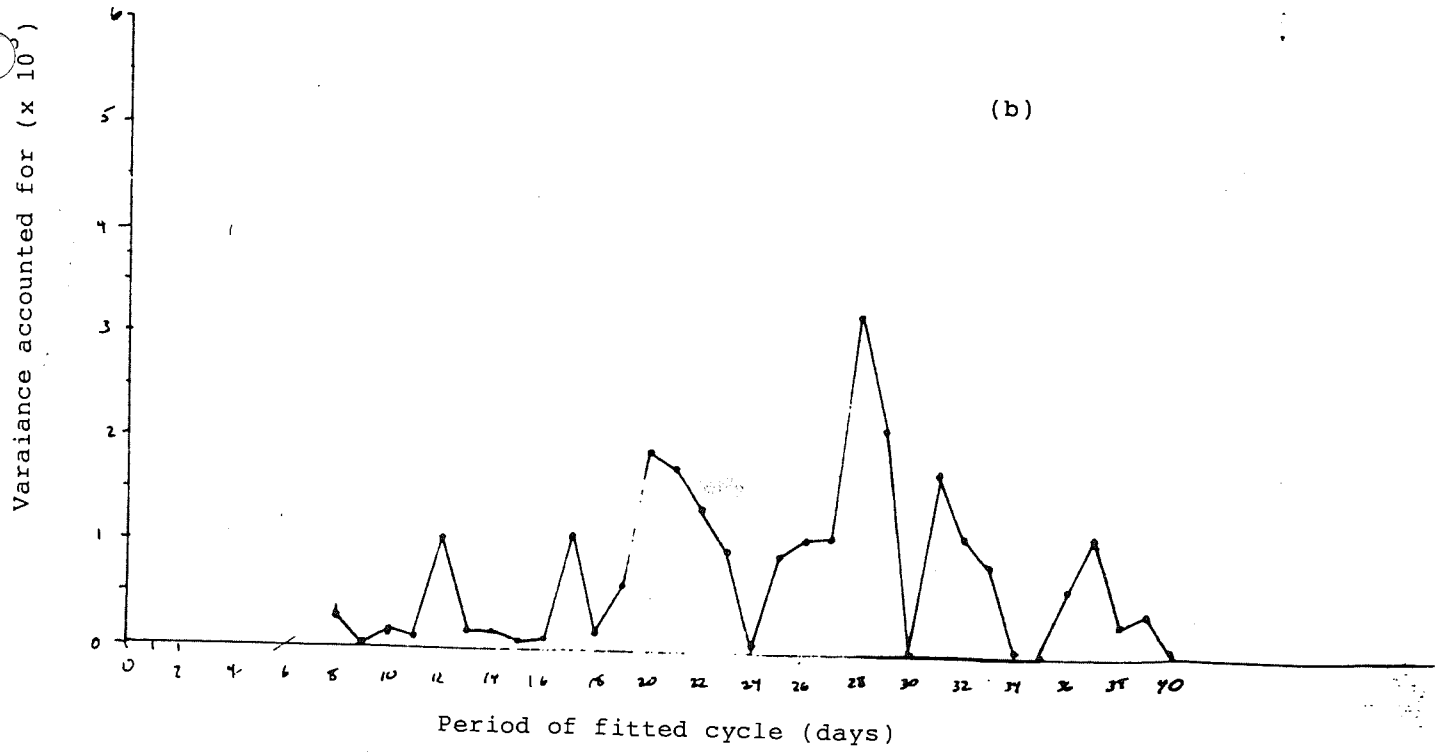
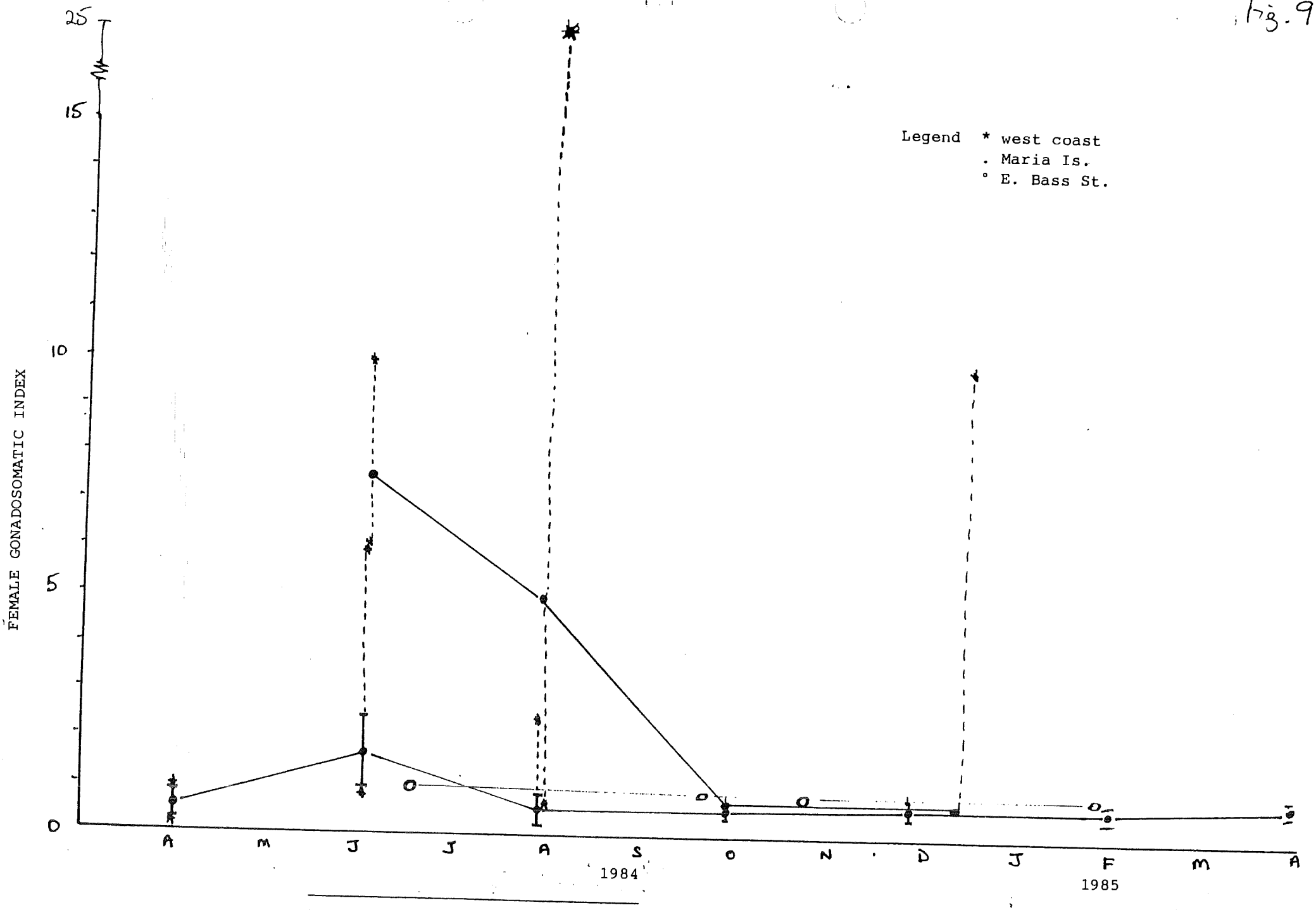

(b)
Varaiance accounted for (x 10⁻³)
6
5
4
3
2
1
0
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
40
Period of fitted cycle (days)

Fig. 9


25
15
10
5
0
FEMALE GONADOSOMATIC INDEX
Legend * west coast
. Maria Is.
° E. Bass St.
A
M
J
J
A
S
O
N
D
J
F
M
A
1984
1985
known spawning season

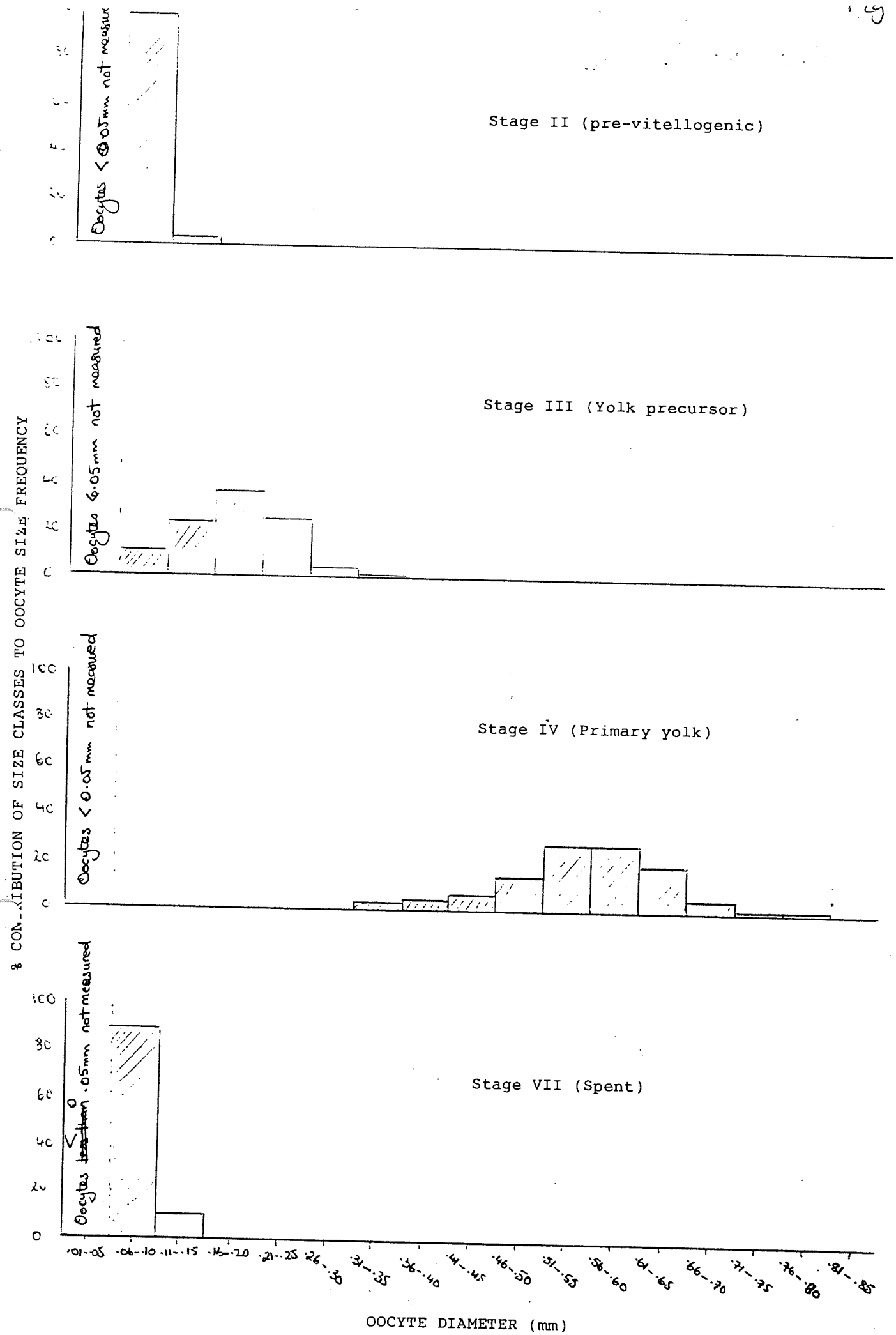
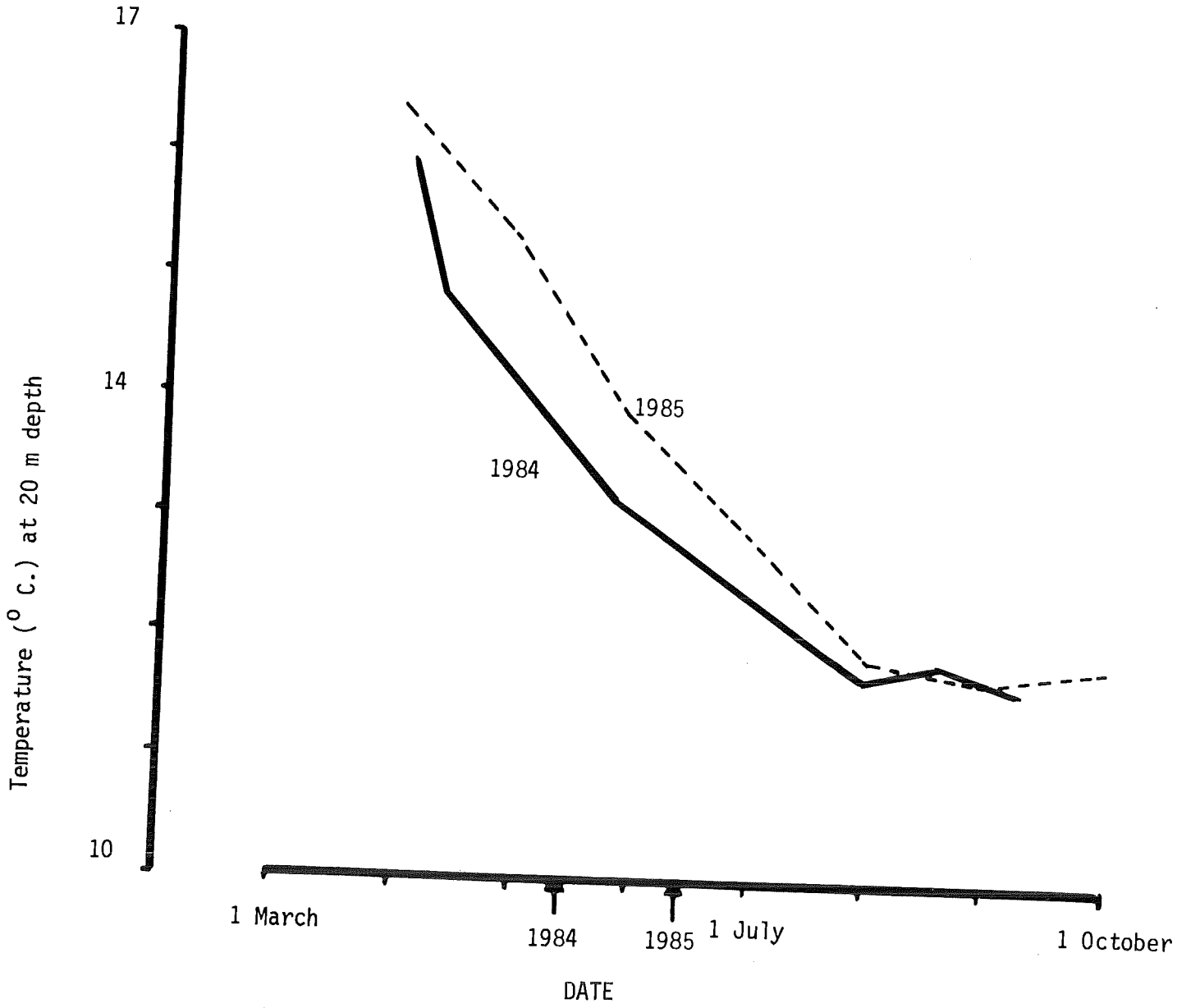

Stage II (pre-vitellogenic)
Oocytes < 0.05mm not measured
Stage III (Yolk precursor)
Oocytes < 0.05mm not measured
Stage IV (Primary yolk)
Oocytes < 0.05mm not measured
Stage VII (Spent)
Oocytes less than .05mm not measured
0
100
80
60
40
20
0
.01-.05
.06-.10
.11-.15
.16-.20
.21-.25
.26-.30
.31-.35
.36-.40
.41-.45
.46-.50
.51-.55
.56-.60
.61-.65
.66-.70
.71-.75
.76-.80
.81-.85
% CONTRIBUTION OF SIZE CLASSES TO OOCYTE SIZE FREQUENCY
OOCYTE DIAMETER (mm)

Fig.


17
14
10
Temperature (° C.) at 20 m depth
1985
1984
1 March
1984
1985
1 July
1 October
DATE

DATE OF FIRST SPAWNING, AS ESTIMATED BY TEMPERATURE OF 13.5^0 at Maria Island

APPENDIX 4

Aust. J. Mar. Freshw. Res., 1986, 37, 621–39

Feeding Ecology of *Macruronus novaezelandiae* (Hector) (Teleostei : Merlucciidae) in South-eastern Australia

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Abstract

The diet and feeding ecology of the demersal merlucciid *M. novaezelandiae* from three areas of the upper continental slope (420–550 m) of south-eastern Australia are described. The food consists almost entirely of mesopelagic fauna. The major prey are myctophid fish *Lampanyctodes hectoris*, other fishes, natant decapods, euphausiids and squid. Energy values of major prey items were determined by bomb calorimetry. Although euphausiids occur frequently in the diet, fish make up 90% of the energy intake. There is little regional variation. *M. novaezelandiae* undertakes diel vertical migrations that are similar to those of its prey, bringing it within 50 m of the surface at night. There is a seasonal trend towards cannibalism by adults on juveniles.

Introduction

Macruronus novaezelandiae (Hector, 1871) (blue grenadier) is an important commercial fish species of the upper continental slope waters of south-eastern Australia. It is also common in New Zealand (Ayling and Cox 1982), and closely related species are found off South Africa and Argentina (Norman 1937; Davies 1950; Torno and Tomo 1980). Its biology and diet in New Zealand have been described (Clark 1980, 1982; Kerstan and Sahrhage 1980; Kuo and Tanaka 1984), but little was known of its ecology in Australian waters. In the present paper, the diet and feeding ecology of *M. novaezelandiae* in Australia are detailed, with particular reference to regional and seasonal variations, diel feeding periodicity, age-related dietary shifts and interrelationships with the mesopelagic prey fauna. The study forms part of a comprehensive investigation by the Division of Fisheries Research, CSIRO, into the biology and ecology of the fishes of the upper continental slope and overlying water column (Blaber 1984).

Study Area

Three areas of the Tasmanian and Victorian continental slope were sampled (Fig. 1). The main study site was 12 nautical miles (22 km) east of Maria Island off the east coast of Tasmania (42°39′S.,148°28′E.), on a small shelf 3 km long and 1 km wide at a depth of 420–550 m (known locally as Darcey's Patch). This site provided the only trawlable slope bottom on the south-eastern coast of Tasmania within 1 day's steaming of Hobart. Bass Strait fish were caught at two sites on the eastern continental slope (Fig. 1), and Tasmanian west coast fish were taken from Sandy Cape northwards (Fig. 1).

Materials and Methods

Sampling

Maria Island (Darcey's Patch)

Fish on or near the bottom were collected by demersal trawling with an Engel High Lift net at 4-hourly intervals over a 28-h period, giving seven tows per cruise, the last tow replicating the first, in each of

0067-1940/86/050621$02.00

April, June, August, October, December 1984 and February and April 1985. In all, 49 routine tows were made plus four additional tows for biomass estimates.

Fish in the water column were captured by pelagic trawling with an Engel 152 trawl, immediately following completion of demersal trawling. Pelagic samples were collected in a depth-stratified random survey (Ulltang 1977), during which trawls were deployed successively over 3 days and nights (except for 2-h periods at sunrise and sunset) following a predetermined random sequence. The following depth strata were fished: 10–60 m; 61–160 m; 161–260 m; 261–360 m. Each stratum was sampled by a stepped oblique tow of approximately 45 min at depth, with from three to five replicates per stratum for both day and night hauls.

At most, 20 adult fish [30–120 cm standard length (SL)] were taken from each catch, weighed and measured and the stomachs removed and preserved in 10% (v/v) neutral formalin. Juvenile fish of less than 30 cm SL caught off Maria Island from December 1984 to April 1985 were treated in the same way.

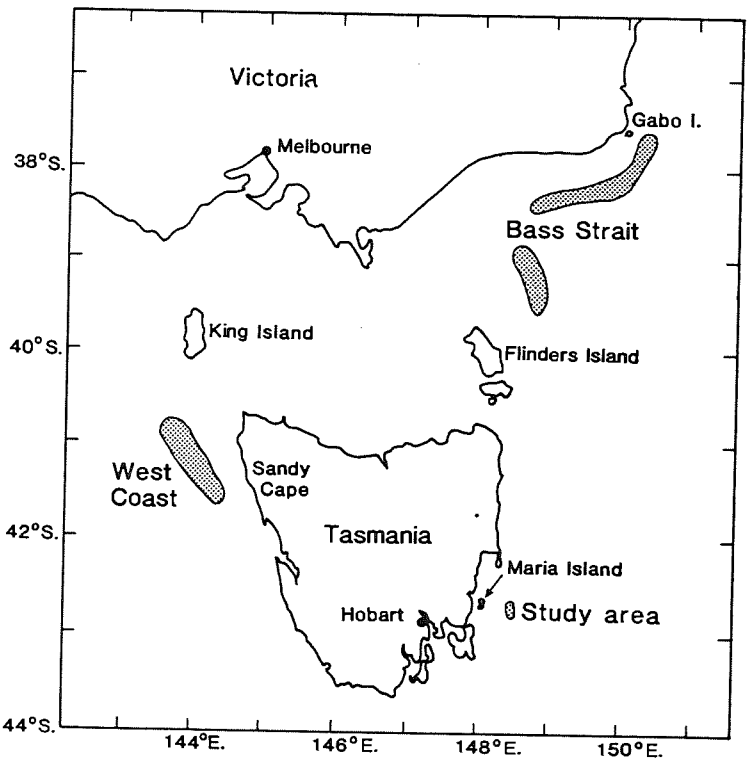

Fig. 1. Map of south-eastern Australia, showing sampling sites (stippled) for *Macruronus novaezelandiae*.

Bass Strait and west coast

Fish from these two areas were only collected from demersal trawls during daylight hours. Sampling began in June 1984 and continued on the same bimonthly basis as at Maria Island. All three areas were sampled within a 2–3-week period. In all, 30 tows were made in Bass Strait and 21 tows on the west coast.

Laboratory Analyses

No fish examined had everted stomachs and thus stomachs not containing food were assumed to be empty when collected. Stomach contents were identified to the lowest possible taxon and counted. In all, 1707 stomachs from adult fish and 244 from juvenile fish were analysed. A photographic index of otoliths from prey fish species was compiled during the initial stages of the study and used to identify

fish digested beyond visual recognition. Prey items were wet weighed after excess moisture had been removed with a paper towel, and then dried to constant weight at 60°C. Energy values (kJ g^{-1}) of prey items (Table 1) were determined with a Parr adiabatic bomb calorimeter. Fresh prey samples collected specifically for calorific determinations were homogenised in a Waring Blender and dried to constant weight at 60°C before being pulverised and made into pellets suitable for bomb calorimetry. Where possible, at least one pellet from each of 10 individuals of a species was made and energy values estimated. When individuals were not large enough to provide a whole pellet, a number of individuals were pooled to provide the pellets. The standard error determined is given to indicate the accuracy of the bomb calorimeter and not the variability of the calorific content of each species.

Diet Analyses

The diet is expressed in terms of the percentage energy contribution and the percentage frequency of occurrence in stomachs containing food of each prey category (Tables 2–4, 6). Using calorific terms to describe the diet obviates the need for using artificial indices commonly in use, such as the Index of Relative Importance (Clark 1982). Energy is a real indication of the importance of various prey items to the diet as it is an accurate description of what prey contribute to the energy budget of the fish. Using percentage frequency alone can be misleading and inaccurate, and even more so when combined with volumetric or numerical methods in an index. Our data were not appropriate to combine and convert into an index of this type. The percentage weight contributed by each prey category to the total dry weight and the mean weight of food consumed (g kg^{-1} fish wet wt) are included in Tables 2–4, 6. For each sampling period, dry weights of each prey category were totalled and converted to energy values using data from Table 1. Seasonal variations in the Maria Island samples and regional variations between sites based on total annual data were assessed using Kendall's co-efficient of concordance (W) and Friedman's rank two-way classification (T) (Tate and Clelland 1957; Conover 1971). Juvenile and adult diets from Maria Island were compared using Spearman's correlation co-efficient (Tate and Clelland 1957).

Stomach fullness of fish from Maria Island was expressed as grams of stomach contents per kilogram of fish weight (wet wt). Pelagic and bottom-caught fish were treated separately. The overall mean stomach fullness for each 4-h time period, from 2400 h, was obtained by grouping means from all trawls in the corresponding time period. Overall feeding periodicity obtained from seven demersal and 21 pelagic diel cycles was tested for by regression analysis.

The vertical distribution of catches of *M. novaezelandiae* was investigated by combining catch data from pelagic and from demersal trawls from the seven cruises, at the Maria Island site, into 4-h intervals from 0000 h. The proportion of the total catch of *M. novaezelandiae* (expressed as kg m^{-2}) in each time interval in each 100-m depth stratum was calculated after correcting for differences between net types and catchabilities (T. Kenchington, personal communication). This does not represent the actual biomass of *M. novaezelandiae* at the Maria Island site.

Sunrise occurred between 0430 and 0740 h during the 14-month period and sunset occurred between 1645 and 1945 h.

Results

Maria Island

Adult fish (30–120 cm SL; 400–5400 g)

The diet consisted predominantly of mesopelagic fish (Table 2); the myctophid *Lampanyctodes hectoris* was the most common prey and the chief contributor to the energy intake, with most of the remainder coming from *Lepidorhynchus denticulatus*, *Maurolicus muelleri*, *Diaphus danae* and juvenile *Macruronus novaezelandiae*. Juvenile *M. novaezelandiae*, which first appeared in adult stomachs in December 1984, made up 20% of energy intake by April 1985.

Crustacea contributed little to the total energy intake. Euphausiids were the most frequently consumed, with *Euphausia similis* var. *armata* the only identifiable species. *Pasiphae* sp. and *Oplophorus* spp., the major carids identified, accounted for one-third of the carid total (Table 2).

Squid occurred frequently in catches in April, contributing one-fifth of that month's energy intake (Table 2). One occurrence in October 1984 accounted for 10% of the energy for that

Table 1. Energy content of prey items of *Macruronus novaezelandiae*
Number of prey items contributing to pooled samples and number of replicate determinations are given

Prey	No. of items	No. of replicates	Energy value ± S.E. (kJ g^{-1} dry weight)		
Annelida					
Polychaeta	20	4	21.3 ± 1.1		
Crustacea					
Haliporoides sp.	13	11	19.4 ± 0.2	$\bar{x}$ = 20.2 ± 0.9	$\bar{x}$ = 19.5 ± 0.9
Pasiphae sp.	8	8	21.9 ± 0.4		
Plesionika martia (A. Milne Edwards, 1883)	26	7	20.4 ± 0.3		
Oplophorus spinosus (Brulle, 1839)	10	10	23.5 ± 0.2		
Campanylotus rathbunae Schmitt, 1926	3	8	18.8 ± 0.2		
Sclerocragnon sp.	3	2	17.4 ± 0.7		
Aristeomorpha foliacea Risso, 1827	10	10	23.9 ± 0.1		
Munida haswelli Henderson, 1888	20	10	16.4 ± 0.1		
Paguridae	10	4	16.3 ± 0.1		
Euphausiidae	200	10	21.7 ± 0.1		
Brachyuran	46	15	14.4 ± 0.2		
Mollusca					
Sepioid	5	10	20.3 ± 0.1	$\bar{x}$ = 22.7 ± 1.5	
Iridioteuthis sp.	8	1	23.8		
Enoploteuthis sp.	2	1	24.1		
Gastropoda (without shell)	10	2	20.6		
Thaliacea					
Pyrosoma atlanticum (Peron, 1804)	3	10	17.9 ± 0.4		

Teleostei				
Lampanyctodes hectoris (Gunther, 1876)	100	9	28.7 ± 0.7	
Diaphus danae Täning, 1932	10	10	26.9 ± 0.3	
Lampichthys procerus (Brauer, 1904)	20	10	25.8 ± 0.1	
Lampanyctus australis Täning, 1932	20	10	27.1 ± 0.1	$\bar{x}$ = 26.6 ± 0.9
Maurolicus muelleri (Gmelin, 1789)	200	11	28.1 ± 0.2	
Photichthys argenteus Hutton, 1872	10	10	23.0 ± 0.1	
Chlorophthalmus nigripinnis Günther, 1878	5	9	24.1 ± 0.3	
Austrophycis marginata (juvenile) (Günther, 1878)	6	10	23.9 ± 0.5	
Macruronus novaezelandiae (juvenile) (Hector, 1871)	4	11	22.5 ± 0.4	
Lepidorhynchus denticulatus (Richardson, 1846)	10	11	23.6 ± 0.4	
Ventrifossa nigromaculata (McCulloch, 1907)	10	18	21.1 ± 0.1	
Coelorinchus sp. 4 [A]	10	11	20.4 ± 0.3	
Genypterus blacodes (Schneider, 1801)	2	10	22.4 ± 0.1	
Hoplostethus intermedius (juvenile) (Hector, 1875)	13	10	25.1 ± 0.2	$\bar{x}$ = 24.7 ± 0.7
Helicolenus percoides Richardson, 1842)	6	2	23.8 ± 0.1	
Apogonops anomalus Ogilby, 1896	1	13	31.0 ± 0.3	
Epigonus denticulatus Dieuzeide, 1950	10	10	28.5 ± 0.1	
Epigonus lenimen (Whitley, 1935)	7	10	26.8 ± 0.1	
Trachurus declivus (Jenyns, 1841)	3	10	25.6 ± 0.2	
Rexea solandri (Cuvier, 1832)	1	10	27.0 ± 0.1	
Azygopus pinnifasciatus (Norman, 1926)	11	8	24.6 ± 0.5	
			$\bar{x}$ of all fish = 25.2 ± 5.6	

[A] CSIRO voucher specimen no. H479

Un-named species: P. McMillan, Fisheries Research Division, Ministry of Agriculture and Fisheries, Wellington N.Z.

Table 2. Diet of adult *Macruronus novae-*

F, percentage frequency of occurrence. *E*, percentage of total energy

Prey Item	April			June		
	F	W	E	F	W	E
Lampanyctodes nectoris	87.5	44.4	47.8	60.3	48.9	53.8
Diaphus danae	3.1	17.6	17.8	–	–	–
Lampanyctus australis	–	–	–	–	–	–
Lampichthys procerus	–	–	–	–	–	–
Maurolicus muelleri	9.4	4.8	5.1	1.7	0.1	0.1
Scopelosaurus meadii	–	–	–	–	–	–
Photichthys argenteus	–	–	–	–	–	–
Lepidorhynchus denticulatus	–	–	–	6.9	45.0	40.7
Austrophycis marginata	–	–	–	–	–	–
Epigonus denticulatus	–	–	–	–	–	–
E. lenimen	–	–	–	–	–	–
Coelorinchus sp.	–	–	–	–	–	–
Rexea solandri	–	–	–	–	–	–
Lepidopus caudatus	–	–	–	–	–	–
Apogonops anomalus	–	–	–	–	–	–
Macruronus novaezelandiae	–	–	–	–	–	–
Unidentified fish	7.8	5.4	5.2	3.4	3.6	3.5
Caridae	7.8	1.7	1.3	–	–	–
Euphausiidae	11.0	0.3	0.2	–	–	–
Penaeidae	–	–	–	–	–	–
Amphipoda	1.6	+	+	–	–	–
Thalassinid	1.6	+	+	–	–	–
Copepoda	–	–	–	–	–	–
Unidentified crustacea	50.0	3.3	2.4	10.3	1.4	2.0
Squid	40.6	22.5	20.2	–	–	–
Other	–	–	–	1.7	0.1	0.3
Total dry wt. of food (g)		61.9			113.9	
No. of stomachs with food		64			58	
Total no. of stomachs		128			91	
Mean wet wt. of food per trawl ± S.E. (g kg^{-1})		2.41 ± 0.52			2.79 ± 1.07	
No. of trawls		13			10	

***zelandiae* from Maria Island, eastern Tasmania**

intake. *W*, percentage of total dry weight of food. + <0·1%. – Absent

1984									1985		
August			October			December			February		
F	W	E	F	W	E	F	W	E	F	W	E
68.6	62.7	66.3	67.6	63.3	67.5	74.6	60.7	63.3	65.6	49.6	53.2
4.4	4.7	4.6	–	–	–	3.4	1.6	1.5	1.0	2.0	2.0
0.7	1.6	1.6	–	–	–	–	–	–	–	–	–
0.7	1.3	1.2	–	–	–	1.7	+	+	–	–	–
–	–	–	7.0	2.8	3.0	10.2	1.9	1.9	4.9	4.2	4.4
–	–	–	–	–	–	1.7	1.6	1.5	–	–	–
–	–	–	–	–	–	1.7	0.8	0.7	2.0	2.7	2.3
2.9	16.5	14.4	1.4	13.5	11.8	5.1	7.4	6.2	2.0	0.1	0.1
0.7	5.1	4.5	–	–	–	–	–	–	–	–	–
0.7	2.5	2.6	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	1.4	4.8	4.7	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	3.4	5.4	5.2	–	–	–
–	–	–	–	–	–	3.4	2.5	2.3	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	6.8	9.6	7.9	2.0	8.2	6.9
16.8	3.6	3.7	16.9	3.9	3.9	16.9	4.5	4.1	28.4	31.3	29.5
0.7	0.3	0.3	2.8	1.6	1.2	3.4	0.1	+	–	–	–
–	–	–	7.0	0.2	0.2	5.1	0.1	0.1	27.5	1.8	1.5
–	–	–	1.4	1.9	1.7	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	3.4	0.1	+	–	–	–
2.2	+	+	2.8	0.7	0.5	3.4	0.1	+	2.9	0.2	0.1
2.2	0.8	0.7	1.4	11.8	10.5	–	–	–	–	–	–
1.4	0.7	0.5	–	–	–	1.7	0.5	0.3	–	–	–
	140.3			88.7			281.6			151.6	
	137			71			59			102	
	175			121			101			127	
	3.71 ± 0.74			4.76 ± 1.94			7.47 ± 2.26			1.99 ± 0.45	
	10			16			14			12	

Table 2 (*contd*)

Prey Item	1985 April			TOTAL		
	F	W	E	F	W	E
Lampanyctodes hectoris	37.6	29.3	32.5	65.4	52.9	57.7
Diaphus danae	1.2	1.5	1.6	2.1	2.8	3.2
Lampanyctus australis	-	-	-	0.2	0.2	0.2
Lampichthys procerus	-	-	-	0.3	0.2	0.2
Maurolicus muelleri	2.3	0.9	1.0	4.3	1.9	2.0
Scopelosaurus meadii	-	-	-	0.2	0.5	0.5
Photichthys argenteus	-	-	-	0.5	0.7	0.6
Lepidorhynchus denticulatus	7.1	18.4	16.9	3.5	13.6	10.4
Austrophycis marginata	-	-	-	0.2	0.7	0.7
Epigonus denticulatus	-	-	-	0.2	0.4	0.4
E. lenimen	-	-	-	0.2	1.4	1.4
Coelorinchus sp.	1.2	0.9	0.7	0.2	0.1	0.1
Rexea solandri	-	-	-	0.3	1.6	1.6
Lepidopus caudatus	-	-	-	0.3	0.7	0.7
Apogonops anomalus	9.4	10.5	12.6	1.4	1.4	1.7
Macruronus novaezelandiae	5.9	23.2	20.1	1.9	7.1	6.1
Unidentified fish	21.2	12.6	12.3	17.2	9.6	8.5
Caridae	4.7	0.3	0.3	2.5	0.4	0.3
Euphausiidae	41.2	1.6	1.4	13.9	0.6	0.5
Penaeidae	-	-	-	0.2	0.2	0.2
Amphipoda	-	-	-	0.2	+	+
Thalassinid	-	-	-	0.2	+	+
Copepoda	-	-	-	0.3	+	+
Unidentified crustacea	4.7	0.1	0.1	9.0	0.6	0.4
Squid	1.2	0.5	0.6	5.4	2.7	2.5
Other	-	-	-	0.7	0.2	0.2
Total dry wt. of food (g)	128.1					
No. of stomachs with food	84					
Total no. of stomachs	98					
Mean wet wt. of food per trawl ± S.E. ($g\ kg^{-1}$)	2.41 ± 0.50					
No. of trawls	11					

month, but, overall, squid occurred in the diet of about 5% of the fish and contributed only a minor part of energy intake.

There was no significant bimonthly variation in diet in terms of energy (energy: $W = 0{\cdot}035$; $T_6 = 3{\cdot}99$; $0{\cdot}75 > P > 0{\cdot}50$), but rankings did vary significantly, based on frequency of occurrence (frequency: $W = 0{\cdot}146$; $T_6 = 16{\cdot}872$; $0{\cdot}01 > P > 0{\cdot}005$).

Juvenile fish (15–29 cm SL; 37–65 g)

Lampanyctodes hectoris occurred in about one-third of stomachs of juveniles caught from December to April, but contributed nearly two-thirds of the energy (Table 3). Euphausiids had a high frequency of occurrence (79·8%) but, as in adult fish, accounted for less of the energy (25%). The incidence of euphausiids in the diet increased over the 3 months (December, February and April) in which juveniles were sampled, while that of *L. hectoris* decreased (Table 3).

The rank orders of prey items of juveniles and adults, sampled from December to April, were not significantly correlated using either energy or frequency of occurrence (energy: Spearman's $r = 0{\cdot}46$, $P > 0{\cdot}9$; frequency: Spearman's $r = 0{\cdot}38$, $P > 0{\cdot}9$).

Bass Strait

The diet of adult *M. novaezelandiae* from Bass Strait varied considerably. It consisted chiefly of fish, with *Lampanyctodes hectoris* the most frequent prey species, although its frequency of occurrence varied bimonthly (Table 4). Other fish species were consumed irregularly: *Lepidorhynchus denticulatus*, *Lepidopus caudatus* and juvenile *M. novaezelandiae* contributed about 65% of energy intake in December 1984, though they occurred at relatively low frequency, whereas *Apogonops anomalus* accounted for over 70% of the energy intake in June 1984 but occurred in only 15% of stomachs. Unidentifiable fish formed a high proportion of the diet.

Crustacea, particularly the carids *Plesionika martia*, *Pasiphae* sp., *Oplophorus spinosus* and *Haliporoides* sp., were consumed frequently but contributed little to energy intake (Table 4). In February 1985, Crustacea occurred in 75% of stomachs, but accounted for less than 10% of energy.

Squid were found in 6% of stomachs (Table 4). Species identified included *Lycoteuthis diadema*, *Iridioteuthis* sp., *Octopoteuthis* sp., *Nototodarus gouldi* and *Todarodes fillipovae*. The total energy contributed by squid was about 7%, although this rose to 20% in February 1985.

West Coast of Tasmania

Diets of west coast adult fish were similar to those of fish from Bass Strait and Maria Island. *Lampanyctodes hectoris* was an important prey item. Some samples from this region were small, which may account for the variation in both frequency and energy totals for some months (Table 6). Although *Lepidorhynchus denticulatus* occurred in only about 4% of stomachs, its energy contribution was similar to that of *Lampanyctodes hectoris*. *Rexea solandri* occurred infrequently, but accounted for 43% of the energy total for February 1985 and biased the annual total.

Crustacea again contributed relatively little to total energy consumed, although euphausiids occurred at an average frequency of 8·5%. The penaeid *Aristeomorpha foliacea* occurred in only 1 month but at a frequency of 6·5%.

Squid were present in 35·7% of fish in June 1984, constituting 53% of the energy for that month. The occurrence of squid declined thereafter; they were absent altogether from December 1984 and April 1985 samples. Overall, their frequency of occurrence was only 6·3% and their energy contribution 7·1%.

Comparison of Diets of M. novaezelandiae *from the Three Sampling Areas*

Although differences occur in actual percentages of frequency of occurrence and energy contributions of various prey items between the three areas, the prey rank orders still agree (energy: $W = 0{\cdot}581$, $T_{18} = 31{\cdot}320$, $0{\cdot}05 < P < 0{\cdot}025$; frequency: $W = 0{\cdot}809$,

Table 3. Diet of juvenile *Macruronus novaezelandiae* off Maria Island, *F*, percentage frequency of occurrence. *E*, percentage of total energy intake. *W*, percentage

Prey Item	December 1984 F	W	E	February 1985 F	W	E
Lampanyctodes hectoris	34.1	76.3	81.6	40.0	63.9	68.3
Maurolicus muelleri	2.3	4.5	4.9	2.9	7.1	7.5
Diaphus danae	2.3	2.2	2.2	-	-	-
Unidentified fish	6.8	0.4	0.5	20.0	5.2	4.9
Euphausiidae	45.5	10.4	8.6	81.4	23.8	19.2
Copepoda	15.9	4.8	1.6	-	-	-
Brachyuran megalops	4.5	1.4	0.5	-	-	-
Unidentified crustacea	-	-	-	-	-	-
Total dry wt. of food (g)	22.7			14.3		
No. of stomachs with food present	44			70		
Total no. of stomachs	60			74		
Mean wet wt. of food per trawl ± S.E. (g kg^{-1})	4.46 ± 5.47			18.78 ± 6.32		
No. of trawls	3			6		

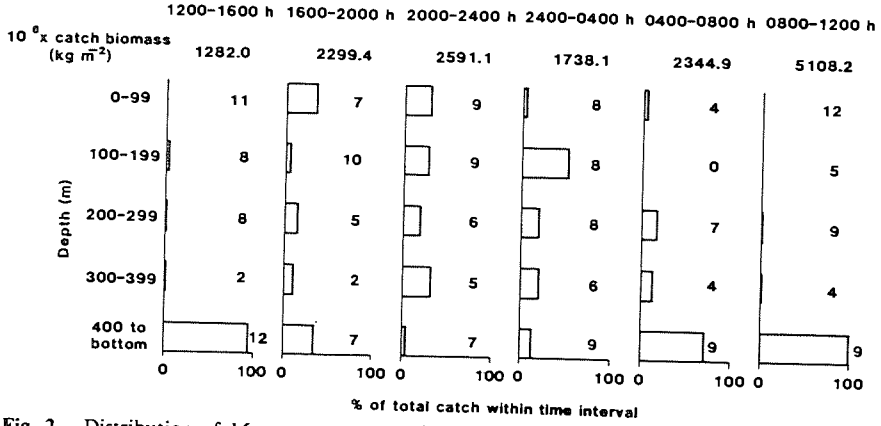

Fig. 2. Distribution of *Macruronus novaezelandiae* through the water column as a percentage of total catch, for each 4-h time interval. Pelagic catches were from 0 to 399 m and demersal catches from 400 m to the bottom. Number of tows in each stratum is indicated.

$T_{18} = 43{\cdot}686$, $P < 0{\cdot}005$). Fish contributed about 90% of the energy consumed in all areas, with *Lampanyctodes hectoris* the single most significant species, although the

eastern Tasmania
of total dry weight of food. + <0·01%. – Absent

April 1985			Total		
F	W	E	F	W	E
30.3	43.0	48.7	34.1	57.0	62.5
4.6	4.9	5.5	3.6	5.8	6.3
–	–	–	0.4	0.3	0.3
8.3	8.7	8.7	11.7	5.9	5.8
92.7	43.2	37.0	79.8	29.9	24.8
–	–	–	3.1	0.7	0.3
–	–	–	0.9	0.2	0.1
3.7	+	+	1.8	+	+
	9.2				
	109				
	109				
	13.64 ± 1.54				
	6				

unidentified fish component was relatively high in Bass Strait samples. *Lepidorhynchus denticulatus* occurred in all regions, contributing 8–17% of total energy consumed for each area. Juvenile *M. novaezelandiae* were not found in any west coast fish but there was a definite seasonal trend in their occurrence at the other sites (Tables 2 and 4).

Crustacea occurred most frequently in Bass Strait samples and least frequently in west coast samples. Their energy contribution was greatest in Bass Strait fish (4·5%) and least in west coast fish (0·6%).

Vertical Distribution

Catch statistics (Fig. 2) indicate that adult *M. novaezelandiae* concentrated on the bottom by midday, remaining there until about 1600 h. Between 1600 and 2000 h, they were caught higher in the water column. By midnight, catches were fairly even in biomass throughout the water column. By early morning this pattern reversed, indicating that the fish were moving back to the bottom. These results are clear evidence for the vertical diel migration that has been postulated in other studies (Clark 1982; Kuo and Tanaka 1984).

Diel Feeding Pattern

The fullness of the stomachs of the fish caught in pelagic and demersal trawls did not vary significantly between day and night (demersal: $F_{(5,40)} = 0{\cdot}524$, $P > 0{\cdot}25$; pelagic:

Table 4. Diet of adult *Macruronus novaezelandiae*
F, percentage frequency of occurrence. *E*, percentage of total energy intake.

	1984					
	June			August		
Prey Item	F	W	E	F	W	E
Lampanyctodes hectoris	27.2	16.5	16.8	94.4	81.4	84.4
Diaphus danae	-	-	-	-	-	-
Lampichthys australis	-	-	-	-	-	-
Photichthys argenteus	-	-	-	-	-	-
Electrona rissoi	-	-	-	-	-	-
Bassinago bulbiceps	-	-	-	-	-	-
Lepidorhynchus denticulatus	-	-	-	-	-	-
Lepidopus caudatus	-	-	-	-	-	-
Apogonops anomalus	15.2	61.5	66.2	-	-	-
Macruronus novaezelandiae	-	-	-	-	-	-
Unidentified fish	42.4	17.0	13.7	5.6	15.6	13.1
Caridae	-	-	-	5.6	0.2	0.2
Penaeidae	-	-	-	5.6	2.3	2.0
Munida haswelli	-	-	-	-	-	-
Euphausiidae	-	-	-	-	-	-
Unidentified crustacea	15.2	3.0	2.0	5.6	0.4	0.2
Polychaeta	-	-	-	-	-	-
Squid	6.1	1.6	1.3	-	-	-
Salp	-	-	-	-	-	-
Total dry wt. of food (g)	36.9			34.2		
No. of stomachs with food present	33			18		
Total no. of stomachs	52			20		
Mean wet weight of food per trawl ± S.E. (g kg^{-1})	2.29 ± 1.85			9.63		
No. of trawls	3			1		

$F_{(4,35)} = 0{\cdot}804$, $P > 0{\cdot}25$). However, mean stomach fullness values for demersal fish caught between 0800 and 1600 h (2·68 g kg^{-1}) were significantly lower than values for pelagic fish caught between 2000 and 0400 h (5·71 g kg^{-1}) ($F_{(1,41)} = 4{\cdot}98$; $P < 0{\cdot}05$) (Table 5). Periods of sunrise (0400–0800 h) and sunset (1600–2000 h) were excluded from this comparison. There was no significant variation in stomach fullness of juvenile fish taken from pelagic trawls in the three summer samplings ($F_{(4,10)} = 0{\cdot}37$; $P > 0{\cdot}25$). These data suggest that most feeding takes place in the water column during the night.

from Bass Strait

W, percentage of total dry weight of food. + <0·1%. – Absent

October			December			1985 February		
F	W	E	F	W	E	F	W	E
24.1	21.0	24.7	36.2	10.5	12.3	7.7	0.5	0.6
5.6	3.2	3.5	5.8	2.5	2.8	–	–	–
8.3	9.1	9.9	2.9	0.8	0.8	–	–	–
1.9	3.4	3.1	–	–	–	1.9	24.9	24.6
0.9	+	+	1.4	0.9	1.0	–	–	–
–	–	–	1.4	0.8	0.8	–	–	–
0.9	2.4	2.3	5.8	21.0	20.4	5.8	4.0	4.0
–	–	–	1.4	19.9	20.0	–	–	–
–	–	–	2.8	3.8	4.8	–	–	–
–	–	–	1.4	26.3	24.2	–	–	–
41.7	42.1	40.1	23.2	12.4	11.8	69.2	45.9	45.8
29.6	12.9	10.8	4.3	0.4	0.6	67.3	4.8	4.4
–	–	–	–	–	–	3.8	0.3	0.3
–	–	–	–	–	–	1.9	0.1	0.1
9.3	0.4	0.4	8.7	0.2	0.2	5.8	+	+
–	–	–	4.3	0.3	0.2	–	–	–
0.9	+	+	–	–	–	–	–	–
8.3	5.6	5.5	1.4	+	+	7.7	19.4	20.0
–	–	–	5.8	+	+	–	–	–
98.4			157.0			151.1		
108			69			52		
156			110			68		
2.54 ± 0.84			2.57 ± 1.02			4.58 ± 2.86		
5			9			5		

Discussion

The main components of the diet of *M. novaezelandiae* were the myctophid fish *Lampanyctodes hectoris*, other fishes, natant decapods, euphausiids and squid. Despite some bimonthly variation, the rankings of principal components did not change. Regional variations between the east and west Tasmanian coasts and Bass Strait may be related to prey availability. Clark (1982) and Kuo and Tanaka (1984) stated that *M. novaezelandiae* in New Zealand waters feed predominantly on euphausiids and myctophids and that regional variations were due

Table 4 (*contd*)

Prey Item	Total F	Total W	Total E
Lampanyctodes hectoris	28.9	15.1	17.1
Diaphus danae	3.6	1.5	1.6
Lampichthys australis	3.9	2.1	2.3
Photichthys argenteus	1.1	8.6	8.1
Electrona rissoi	0.7	0.3	0.3
Bassinago bulbiceps	0.4	0.2	0.3
Lepidorhynchus denticulatus	2.9	8.7	8.4
Lepidopus caudatus	0.4	6.5	6.6
Apogonops anomalus	2.5	6.0	7.6
Macruronus novaezelandiae	0.4	8.6	7.9
Unidentified fish	40.0	29.7	28.2
Caridae	25.4	4.4	3.8
Penaeidae	1.1	0.4	0.3
Munida haswelli	0.4	+	+
Euphausiidae	6.8	0.2	0.1
Unidentified crustacea	3.2	0.4	0.3
Polychaeta	0.4	+	+
Squid	5.7	7.4	7.3
Salp	1.4	+	+
Total dry wt. of food (g)			
No. of stomachs with food present			
Total no. of stomachs			
Mean wet weight of food per trawl ± S.E. (g kg^{-1})			
No. of trawls			

to differences in prey density. However, the diet at the Maria Island site in the present study varied little (Table 2). This indicates a possible preference for the main prey, *L. hectoris*, since this species was consumed in similar quantities throughout the year, despite its fivefold seasonal changes in biomass (Young and Blaber 1986).

Composite catch data from the present study (Fig. 2) show that *M. novaezelandiae* undertakes diel vertical migrations over the continental slope. Kerstan and Sahrhage (1980) recorded vertical migration in *M. novaezelandiae* from New Zealand and suggested that it might be associated

with feeding habits. The stomach fullness value (Table 5) for the period 2000–0400 h for pelagic fish was significantly higher compared with the value for the period 0800–1600 h for demersal fish, indicating that feeding was occurring during the period when fish were migrating upwards. The main prey species, *L. hectoris*, as well as other mesopelagic prey, *Maurolicus muelleri* and *Diaphus danae*, have a similar diel migration pattern (Young and Blaber 1986). Kuo and Tanaka (1984) found a high occurrence of empty stomachs in demersally caught New Zealand fish and postulated that this was due to a scarcity of benthic food resources, however, it could also point to a pelagic feeding habit.

The diet of juvenile *M. novaezelandiae* differs somewhat from that of the adults. The frequency of occurrence of myctophids was between 30 and 40%, but that of euphausiids increased markedly to more than 90% in April 1985 (Table 3). In terms of energy intake, however, myctophids were more significant. Clark (1982) noted a decrease in importance of Crustacea from 80% in smaller *M. novaezelandiae* to 57% in larger fish. Also, he found natant decapods more frequently in larger size classes of fish, particularly those over 70 cm. Results from our study emphasise that fish is the primary source of energy in the diet in Australian waters.

Cannibalism is widespread among fishes and can take a variety of forms (Dominey and Blumer 1984). The form shown by adult *M. novaezelandiae* falls into the category of 'exploitation' or intraspecific predation. Its variation (Tables 2 and 4) may relate to the occurrence and habitat preferences of the juveniles. From the limited data available, it is evident that juveniles from the winter spawning (Kerstan and Sahrhage 1980) occur in summer in the mesopelagic feeding zone of adult *M. novaezelandiae*. They also occur away from the adults in inshore and shelf areas of Tasmania and New Zealand (Kerstan and Sahrhage 1980; Wilson 1981). Differential distribution of adults and juveniles is a mechanism that reduces the incidence of cannibalism in some inshore fishes (Blaber 1979).

Table 5. Mean stomach fullness values of adult *Macruronus novaezelandiae* from Maria Island

4-h period	Mean stomach fullness ± S.E. (g kg^{-1})			
	Demersal trawl		Pelagic trawl	
0400–0800	3·07 ± 1·57		3·81 ± 3·60	
0800–1200	1·83 ± 1·60	2·68 ± 0·75	10·19 ± 6·70	
1200–1600	3·30 ± 1·54		–	
1600–2000	3·49 ± 1·92		1·61 ± 4·00	
2000–2400	4·32 ± 2·33		6·86 ± 2·32	5·71 ± 1·36
2400–0400	2·57 ± 1·34		4·27 ± 1·73	

The mesopelagic fish fauna must be considered the most important food source for adult *M. novaezelandiae*. The energy value of these fish, particularly *L. hectoris*, is higher than for most other fishes (Table 1). The feeding ecology of continental-slope fishes has been little studied, but Sedberry and Musick (1978) place great importance on mesopelagic fauna as a high-energy resource for demersal fishes. Marshall (1979) indicated that several benthic species, mainly macrourids (whiptails), make excursions off the bottom to feed on pelagic prey. Little information is available on the vertical distances moved by demersal predators in search of prey. Sedberry and Musick (1978) postulated that deep-water demersal fish wait for the approach of mesopelagic fauna and feed when the prey is at the deepest point of its vertical migration, not as indicated here for *M. novaezelandiae* (Fig. 2, Table 5). If the cost of seeking prey in the mesopelagic region is high, as suggested by Sedberry and Musick (1978), *M. novaezelandiae* could compensate for this by the capture of food of very high energy content. *M. novaezelandiae*, which lives primarily on the upper continental slope, can thus take advantage of rich mesopelagic food resources, whereas benthic and benthopelagic fishes of the deeper continental slopes are usually restricted in vertical mobility by, at least in part, energy considerations (Sedberry and Musick 1978).

Table 6. Diet of adult *Macruronus novaezelandiae*
F, percentage frequency of occurrence. *E*, percentage of total energy intake.

Prey Item	1984 June F	June W	June E	August F	August W	August E
Lampanyctodes hectoris	7.1	7.7	9.1	13.0	5.3	6.3
Diaphus danae	-	-	-	6.5	8.2	9.1
Lampichthys procerus	-	-	-	-	-	-
Maurolicus muelleri	-	-	-	-	-	-
Diplophos sp.	-	-	-	-	-	-
Photichthys argenteus	-	-	-	-	-	-
Argyropelecus hemigymnus	-	-	-	-	-	-
Coelorinchus sp.	-	-	-	-	-	-
Lepidorhynchus denticulatus	-	-	-	6.5	3.7	4.4
Epigonus denticulatus	-	-	-	-	-	-
Austrophycis marginata	-	-	-	-	-	-
Ventrifossa nigromaculata	7.1	19.0	16.9	-	-	-
Rexea solandri	-	-	-	-	-	-
Unidentified fish	21.4	20.5	20.2	30.4	19.9	19.1
Caridae	-	-	-	8.7	3.4	2.9
Penaeidae	-	-	-	6.5	1.5	1.4
Euphausiidae	7.1	0.5	0.5	2.2	+	+
Squid	35.7	52.3	53.1	6.6	55.2	55.4
Annelida	-	-	-	-	-	-
Pyrosoma atlanticum	-	-	-	2.2	2.7	2.0
Total dry wt. of food (g)		8.8			34.7	
No. of stomachs with food present		14			46	
Total no. of stomachs		35			103	
Mean wet wt. of food per trawl ± S.E. (g kg^{-1})		0.8 ± 0.57			1.67 ± 1.10	
No. of trawls		2			6	

from western Tasmania

W, percentage of total dry weight of food. + <0·1%. – Absent

October			December			1985 February		
F	W	E	F	W	E	F	W	E
8.7	7.5	8.0	100	100	100	50.0	16.8	17.7
26.1	9.8	9.7	–	–	–	–	–	–
4.3	1.8	1.7	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	1.2	2.5	2.4
13.0	18.0	15.3	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	1.2	2.9	2.2
4.3	15.9	16.9	–	–	–	4.9	23.3	24.6
4.3	5.4	11.5	–	–	–	–	–	–
4.3	9.4	8.3	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	1.2	46.0	45.9
34.8	28.6	24.6	–	–	–	22.0	7.4	6.3
13.0	0.9	0.5	–	–	–	4.9	+	0.1
–	–	–	–	–	–	–	–	–
26.1	0.8	0.5	–	–	–	3.7	+	+
4.3	2.0	1.8	–	–	–	2.4	0.9	0.8
–	–	–	–	–		1.2	+	+
–	–	–	–	–	–	–	–	–
	32.5			4.1			201.5	
	23			3			82	
	27			3			117	
	2.95 ± 1.48			1.83 ± 1.1			4.08 ± 0.94	
	2			4			6	

Table 6 (*contd*)

Prey Item	1985 April F	W	E	Total F	W	E
Lampanyctodes hectoris	22.2	18.8	19.4	31.1	15.9	16.9
Diaphus danae	-	-	-	5.1	1.8	1.8
Lampichthys procerus	-	-	-	0.6	0.2	0.2
Maurolicus muelleri	11.1	4.0	3.9	0.6	0.6	0.6
Diplophos sp.	-	-	-	0.6	1.5	1.5
Photichthys argenteus	-	-	-	1.7	1.8	1.5
Argyropelecus hemigymnus	11.1	0.2	0.2	0.6	+	+
Coelorinchus sp.	-	-	-	0.6	1.7	1.3
Lepidorhynchus denticulatus	-	-	-	4.5	16.2	17.3
Epigonus denticulatus	11.1	62.8	64.3	1.1	9.9	11.1
Austrophycis marginata	11.1	11.8	10.2	1.1	2.7	2.4
Ventrifossa nigromaculata	-	-	-	0.6	0.5	0.4
Rexea solandri	-	-	-	0.6	28.1	28.3
Unidentified fish	11.1	1.8	1.5	24.9	10.2	8.8
Caridae	-	-	-	6.8	0.5	0.4
Penaeidae	-	-	-	1.7	0.2	0.1
Euphausiidae	44.4	0.5	0.4	8.5	0.2	0.1
Squid	-	-	-	6.3	7.9	7.1
Annelida	-	-	-	0.6	+	+
Pyrosoma atlanticum	-	-	-	0.6	0.3	0.2
Total dry wt. of food (g)		49.3				
No. of stomachs with food present		9				
Total no. of stomachs		18				
Mean wet wt. of food per trawl ± S.E. (g kg^{-1})		3.8				
No. of trawls		1				

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APPENDIX 5

In press : Marine Biology

Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships

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Suggested running page head : diets of slope fishes

Abstract

Diets of 16 species of demersal and pelagic fishes on the upper continental slope (420-550 m) were determined based on samples taken every two months over 13 months off east Tasmania. The calorific contribution of each prey item to the diets was determined.

The fish could be divided into five trophic categories: pelagic planktivores, pelagic piscivores, epibenthic piscivores, epibenthic invertebrate feeders and benthopelagic omnivores. Dietary overlap between the groups was low. The pelagic piscivores, Trachurus declivis, Lepidopus caudatus, Brama brama, Apogonops anomalus and Macruronus novaezelandiae, primarily consume the shelf-break mesopelagic myctophid, Lampanyctodes hectoris; their diet is narrow, with a large overlap between species. The epibenthic piscivores, Deania calcea and Genypterus blacodes, both take a greater variety of prey, but have little dietary overlap. The fish feeding on epibenthic invertebrates, Centriscops humerosus and Coelorinchus sp. 2, obtain most of their energy from benthic Crustacea and Ophiuroidea, supplemented with L. hectoris; the diet is broad, with little overlap. Among the benthopelagic omnivores: (Coelorinchus sp. 4, Lepidorhynchus denticulatus, Cyttus traversi, Neocyttus rhomboidalis, Helicolenus percoides, Epigonus lenimen and Epigonus denticulatus) most diets are broad and show slight overlap. All but E. denticulatus consume significant quantities of L. hectoris as well as Crustacea, particularly Euphausiacea, Polychaeta and Pyrosoma atlanticum.

Seasonal changes in diet occurred in G. blacodes, Coelorinchus sp. 4, L. denticulatus, H. percoides, E. lenimen, E. denticulatus, T. declivis, and L. caudatus; these were related to changes in abundance of particular prey species, not to alterations in feeding habits. Only three species -- Coelorinchus sp. 2, L. caudatus and H. percoides -- showed significant diel feeding periodicity. Ontogenetic dietary changes were evident in Coelorinchus sp. 2 and 4, L. denticulatus, C. traversi and H. percoides. The last two species progressively changed from crustaceans to fish as their size increased. The diets of size classes within species showed little overlap, except for L. denticulatus, which eats chiefly euphausiids and L. hectoris at all sizes.

In addition to describing the diets and trophic relationships of 90% of the fish biomass the results emphasize the importance to the entire

fish community of mesopelagic food resources, particularly L. hectoris. Many benthopelagic species undertake extensive vertical migrations in search of prey, thus playing a major role in the transport of energy from midwater regions to the benthos of the continental slope.

Introduction

The present paper forms part of a study of the biology and ecology of the pelagic and demersal fishes at an ocean site over the continental slope off east Tasmania. This investigation was the first integrated study of the fishes of the upper slope and overlying water column in the southern hemisphere. The primary aim of the study was to quantitatively describe the structure and functioning of the fish community. As trophic relationships are fundamental to understanding biological interactions, a detailed study of the food and feeding ecology of the fishes was a priority. The present report describes and compares the diets of 15 species which, together with those of the commercially important Macruronus novaezelandiae and the three dominant small mesopelagic species, constitute about 90% of the biomass in the study area (Bulman & Blaber, 1986; Young & Blaber, 1986; May and Blaber., in preparation). Diets were analysed calorifically to provide sufficient precision for meaningful comparisons and to avoid the biases inherent in gravimetric, frequency of occurrence and numerical methods. The trophic relationships between pelagic, mesopelagic and demersal species including vital data on ontogenetic dietary shifts, interspecific dietary overlap, and diet breadths, were investigated in order to assess the relative importance of pelagic and demersal food resources.

Previous research on slope fishes in the southern hemisphere has been less detailed, but includes taxonomic and distribution studies, such as those of Norman (1937), Cowper and Downie (1957) and Last and Harris (1981), as well as trophic studies off Namibia (Macpherson, 1983) and ecological work on species of commercial significance in New Zealand (Clark, 1982; Patchell, 1982; Kuo & Tanaka, 1984; Mitchell, 1984) and South Africa (Rattray, 1947; Davies, 1949).

Materials and methods

Study Area

The site was a 3 km x 1 km area between 420 and 550 m deep on the upper continental slope 20 km east of Maria Island (42°39'S,148°28'E). The area is largely unexploited by commercial fishermen. The bottom is nearly

flat. The substratum consists mainly of sand without ripples and is partially covered by ophiuroid beds (Blaber et al., 1987).

Species on or near the bottom were collected by an Engel High Lift demersal trawl net (cod-end liner mesh size 37 mm) at 4 h intervals over a 24 h period in each of April, June, August, October and December 1984 and February and April 1985. Each trawl covered the depth range of 420 to 550 m. Fish in the water column were captured immediately after the demersal trawling with an Engel 152 pelagic trawl fitted with a 9 mm cod-end liner. Pelagic trawls were deployed continuously over three successive days and nights (except for two hour breaks at sunset and sunrise) in a depth-stratified random sequence which fished the following depth strata: 10-60 m; 61-160 m; 161-260 m; 261-360 m. All four strata were fished during the day and the night and replicates were sometimes taken if they occurred in the random sequence. Twenty fish of each species, if available, were taken from each trawl; their wet weights and standard lengths were recorded and their stomachs preserved in 10% formalin or frozen at -30°C. [Fish with everted stomachs caused by decompression were not included.]

Laboratory analyses

Stomach contents were identified to the lowest possible taxon and counted. Fish digested beyond visual recognition were identified, if possible, from their otoliths. After wet weighing, prey items were dried to constant weight at 60°C. Energy values of prey taxa, (kJ g^{-1}) (Table 1), were determined from whole fresh material by bomb calorimetry using a Parr adiabatic bomb calorimeter.

Diet analyses

The diets were analysed in terms of the contribution of energy and the frequency of occurrence of each prey category in stomachs containing food. Dietary overlaps were determined using a modified percentage similarity (PS) index of Shorygin (Ivlev, 1961) : $PS = \sum \min (a,b)$; where a and b are the percentages of energy contributed by the prey common to the two predators, and the percentage similarity is a summation of the smaller of the values of a and b for each prey. The index ranges from 0 (no overlap) to 100 (complete overlap). Diet breadths (Bs) were calculated for each species, using the formula of Levins (1968) $B = (\Sigma p_i^2)^{-1}$ (where p_i is the proportion each prey category contributes to the diet), standardised to fractions of maximum possible breadth (1) by the method of Hespenheide (1975), $[Bs = (B - 1)/(n - 1)]$.

Diel feeding periodicity was assessed for each species using stomach fullness data (g kg^{-1} wet weight) from the 24 h demersal sampling or the 3 day pelagic sampling. The total weight of each species retained in a trawl was divided into the total weight of food in their stomachs to find the stomach fullness value for each tow. To correct for variations in numbers of each species caught, a weighting was applied so that for every species the grand mean (irrespective of time) equalled the total weight of food divided by the total weight of fish. The dependence of stomach fullness on time of day was determined by linear regression. A curve of period 24 h, consisting of a constant and sine and cosine terms best fitted the data and was fitted to the logarithm of the fullness value. The significance of any deviation by the oscillating component from a straight line was tested using the F statistic.

Results

Overall diets

Deania calcea, Genypterus blacodes, Cyttus traversi, Macruronus novaezelandiae, Trachurus declivis, Lepidopus caudatus, Brama brama and Apogonops anomalus are piscivorous. The last five species mainly consume the myctophid Lampanyctodes hectoris, while the first three take a wider

Table 1. Energy content of prey items of fishes from study site off Maria Island. The number of prey items contributing to pooled samples and the number of replicate determinations are given.

Prey	Prey items (no.)	Replicates (no.)	Energy value ± S.E. (kJ g^{-1} dry wt)		
Cnidaria					
Coral	1	1	15.1		
Annelida					
Polychaeta	20	4	21.3 ± 1.1		
Crustacea					
Haliporoides sp.	13	11	19.4 ± 0.2	$\bar{x}$ = 20.2 ± 0.9 (Caridae)	$\bar{x}$ = 19.5 ± 0.9 (Crustacea)
Pasiphae sp.	8	8	21.9 ± 0.4		
Plesionika martia (A. Milne Edwards, 1883)	26	7	20.4 ± 0.3		
Oplophorus spinosa (Brulle, 1839)	10	10	23.5 ± 0.2		
Campylanotus rathbunae Schmitt, 1926	3	8	18.8 ± 0.2		
Sclerocragnon sp.	3	2	17.4 ± 0.7		
Aristeomorpha foliacea Risso, 1827	10	10	23.9 ± 0.1		
Munida haswelli Henderson, 1888	20	10	16.4 ± 0.1		
Paguridae	10	4	16.3 ± 0.1		
Euphausiidae	200	10	21.7 ± 0.1		
Brachyuran	46	15	14.4 ± 0.2		
Mollusca					
Sepioid	5	10	20.3 ± 0.1	$\bar{x}$ = 22.7 ± 1.5 (Cephalopoda)	
Iridioteuthis sp.	8	1	23.8		
Enoploteuthis sp.	2	1	24.1		
Gastropoda (without shell)	10	2	20.6		
Thaliacea					
Pyrosoma atlanticum (Peron, 1804)	3	10	17.9 ± 0.4		
nodermata					
Ophiacantha fidelis (Koehler, 1930)	12	10	9.6 ± 0.5		
Mediaster australiensis Clark, 1916	3	10	15.3 ± 0.3		
Teleostei					
Lampanyctodes hectoris (Günther, 1876)	100	9	28.7 ± 0.7	$\bar{x}$ = 26.6 ± 0.9 (pelagic)	
Diaphus danae Tåning, 1932	10	10	26.9 ± 0.3		
Lampichthys procerus (Brauer, 1904)	20	10	25.8 ± 0.1		
Lampanyctus australis Tåning, 1932	20	10	27.1 ± 0.1		
Maurolicus muelleri (Gmelin, 1789)	200	11	28.1 ± 0.2		
Photichthys argenteus Hutton, 1872	10	10	23.0 ± 0.1		
Chlorophthalmus nigripinnis Gunther, 1878	5	9	24.1 ± 0.3		
Austrophycis marginata (juvenile) (Gunther, 1878)	6	10	23.9 ± 0.5	$\bar{x}$ = 24.7 ± 0.9 (demersal)	
Macruronus novaezelandiae (juvenile) (Hector, 1871)	4	11	22.5 ± 0.4		
Lepidorhynchus denticulatus (Richardson, 1846)	10	11	23.6 ± 0.4		
Ventrifossa nigromaculata (McCulloch, 1907)	10	18	21.1 ± 0.1		
Coelorinchus sp. 4	10	11	20.4 ± 0.3		
Genypterus blacodes (Scheider, 1801)	2	10	22.4 ± 0.1		
Hoplostethus intermedius (juvenile) (Hector, 1875)	13	10	25.1 ± 0.2		
Helicolenus percoides Richardson, 1842	6	2	23.8 ± 0.1		
Apogonops anomalus Ogilby, 1896	1	13	31.0 ± 0.3		
Nigonus denticulatus Dieuzeide, 1950	10	10	28.5 ± 0.1		
Nigonus lenimen (Whitley, 1935)	7	10	26.8 ± 0.1		
Trachurus declivis (Jenyns, 1841)	3	10	25.6 ± 0.2		
Rexea solandri (Cuvier, 1832)	1	10	27.0 ± 0.1		
Azygopus pinnifasciatus (Norman, 1926)	11	8	24.6 ± 0.5		

$\bar{x}$ of all fish = 25.2 ± 5.6

variety of fish (Table 2). The macrourid Lepidorhynchus denticulatus is the most important prey of G. blacodes and C. traversi and contributes 16% to the energy intake of Helicolenus percoides. The remaining species feed chiefly on invertebrates, but all take appreciable amounts of fish (Table 3). The main prey of Centriscops humerosus and Coelorinchus sp.2 [a] is the ophiuroid Ophiacantha fidelis; that of L. denticulatus, Epigonus lenimen and E. denticulatus are euphausiids, chiefly Euphausia similis var. armata; while that of H. percoides is the pelagic colonial thaliacean Pyrosoma atlanticum. Although more than half the diets of Coelorinchus sp. 4 [b] and Neocyttus rhomboidalis consist of invertebrates, such as polychaetes in the former, and salps in the latter, their single most important source of energy is L. hectoris (Table 3).

Penaeidae, Caridae and Galatheidae are shown as single categories in Tables 2 & 3 but were identified to the following species: Aristeomorpha foliacea, Campylonotus rathbunae, Plesionika martia, Pontophilus gracilis, Lipkias sp., Oplophorus novaezelandiae, Pasiphae sp. and Munida haswelli.

Seasonal diet differences

Insufficient samples of Deania calcea, Neocyttus rhomboidalis, Apogonops anomalus, Centriscops humerosus and Epigonus denticulatus were obtained each month to allow monthly comparisons. Cyttus traversi, Brama brama and Coelorinchus sp. 2 showed few changes from month to month. Significant changes in the diets of the remaining species are described below:

Genypterus blacodes has a catholic diet of fishes and larger crustaceans, but with marked changes from month to month in main prey species. Macruronus novaezelandiae predominated in autumn, the crustacea M. haswelli in winter and the macrourids Coelorinchus spp. and L. denticulatus in summer.

Coelorinchus sp. 4 fed on Lampanyctodes hectoris, Polychaeta, Caridae and Ophiuroidea in different proportions throughout the year.

Lepidorhynchus denticulatus showed a marked change in diet from winter

[a] CSIRO voucher specimen H481

b " " " H479

Table 2 The percentage energy contributions of prey categories to the overall diets of 8 fish species from the upper continental slope off Maria Island, East Tasmania. The percentage frequency of occurrence of each prey category is shown in parentheses. Data for Macruronus novaezelandiae is taken from Bulman and Blaber (1986). (+ = < 0.1%; - = absent; n = number of stomachs analysed.)

	Predator (size range cm S.L.)							
	demersal trawl				pelagic trawl			
Prey	*Dravia oalosa* (42 - 105 cm)	*Macruronus novaezelandiae* (14 - 105 cm)	*Gempylerus blaooides* (45 - 130 cm)	*Cyttus traversi* (9 - 56 cm)	*Apogonops anomalus* (8 - 13 cm)	*Trachurus declivis* (21 - 37 cm)	*Brama brama* (24 - 48 cm)	*Lepidopus caudatus* (97 - 149 cm)
Pisces								
Dravia oalosa	-	-	-	-	-	-	-	-
Muraenichthys sp.	-	-	0.7(0.8)	-	-	-	-	-
Notocanthus sexspinnis	-	-	-	-	-	-	-	-
Bassinago bulbiceps	-	-	-	0.8(1.2)	-	-	-	-
Photichthys argenteus	-	0.6(0.5)	-	-	-	-	-	-
Maurolicus muelleri	-	2.0(4.3)	-	+(0.4)	12.2(2.6)	0.2(1.3)	6.2(23.9)	0.2(1.7)
Chlorophthalmus nigripinnis	-	-	0.5(0.4)	12.0(0.8)	-	-	-	-
Diaphus danae	-	3.2(2.1)	-	0.5(0.4)	-	-	-	-
Diaphus sp.	-	-	-	-	-	-	-	0.5(1.7)
Lampanyctodes hectoris	7.8(22.2)	57.7(65.4)	0.1(1.2)	16.6(16.6)	65.9(7.7)	87.4(75.3)	85.4(85.5)	66.3(55.9)
Lampanyctus australis	-	0.2(0.3)	-	-	-	-	-	-
Lampichthys procerus	3.1(3.7)	0.2(0.2)	-	-	-	-	-	-
Scopelosaurus mundi	-	0.5(0.2)	-	-	-	-	-	-
Austrophycis marginata	-	0.7(0.2)	4.8(5.8)	2.5(5.0)	-	-	-	-
Macruronus novaezelandiae	-	6.1(1.9)	14.1(0.8)	0.2(0.4)	-	-	-	4.3(1.7)
Coelorinchus sp. 4	-	0.1(0.2)	5.9(3.7)	0.3(1.7)	-	-	-	-
Lepidorhynchus denticulatus	-	10.4(3.5)	24.2(5.0)	21.8(8.7)	-	-	-	-
Ventrifossa nigromaculata	-	-	0.2(0.8)	0.2(0.4)	-	-	-	-
Hoplostethus intermedius	-	-	0.4(0.8)	2.0(0.4)	-	-	-	-
Helicolenus percoides	-	-	12.3(2.1)	7.6(5.0)	-	-	-	-
Hoplichthys haswelli	-	-	-	0.2(0.4)	-	-	-	-
Apogonops anomalus	-	1.7(1.4)	0.2(0.4)	1.4(0.4)	-	-	-	-
Epigonus lenimen	-	1.4(0.2)	3.0(0.8)	-	-	-	-	-
Epigonus denticulatus	-	0.4(0.2)	2.2(0.4)	-	-	-	-	-
Trachurus declivis	24.3(3.7)	-	-	-	-	-	-	-
Emmelichthys nitidus	-	-	-	-	-	-	2.1(4.3)	-
Lepidopus caudatus	-	0.7(0.3)	-	-	-	-	-	-
Rexea solandri	-	1.6(0.7)	-	12.1(0.8)	-	-	-	-
Anoplopoma pinnifasciatus	-	-	0.5(0.4)	-	-	-	-	-
Fish larvae	-	-	-	-	-	0.6(2.5)	-	-
Unidentified fish	63.6(63.0)	8.5(17.2)	9.8(17.4)	9.5(24.5)	2.4(5.1)	+(0.6)	1.3(20.5)	1.7(15.2)
Total fish	98.8	96.0	78.9	87.7	80.5	88.2	95.0	73.0
Cnidaria								
Coral	-	+(0.2)	.+(0.8)	+(0.4)	-	+(0.6)	-	-
Annelida								
Polychaeta	-	-	+(1.2)	-	-	-	-	-
Crustacea								
Ostracoda	-	-	0.2(0.4)	-	-	-	-	-
Copepoda	-	+(0.3)	-	-	-	-	-	-
Mysidacea	-	-	-	-	-	+(0.9)	-	-
Amphipoda	-	+(0.2)	-	-	-	0.2(18.8)	-	-
Isopoda	-	-	0.7(7.1)	-	-	+(0.6)	-	-
Euphausiacea	-	0.5(13.9)	+(2.1)	0.1(0.8)	17.1(51.2)	9.0(50.6)	3.3(65.8)	26.9(35.6)
Caridea	1.0(11.1)	0.3(2.5)	0.9(2.8)	9.1(24.6)	-	+(0.6)	+(1.7)	0.1(3.4)
Penaeidae	-	0.2(0.2)	0.1(0.4)	0.4(1.2)	-	-	-	-
Galatheidae	-	-	7.1(37.3)	0.4(4.6)	-	-	-	-
Brachyura	-	-	1.3(7.1)	-	-	+(3.2)	+(3.4)	-
Thalassinidae	-	+(0.2)	-	-	-	+(1.9)	1.3(35.9)	-
Unidentified crustacea	-	0.4(9.0)	0.1(6.2)	2.4(18.3)	2.4(33.3)	0.5(17.7)	+(9.4)	-
Total crustacea	1.0	1.4	10.4	12.4	19.5	9.5	4.8	27.0
Mollusca								
Gastropoda	-	-	0.1(2.1)	-	-	2.0(15.2)	+(2.6)	-
Squid	+(7.4)	2.5(5.4)	10.4(1.2)	-	-	0.1(1.3)	+(0.9)	-
Thaliacea								
Pyrosoma atlanticum	-	+(0.3)	-	-	-	-	-	-
Echinodermata								
Ophiuroidea	-	-	+(1.2)	-	-	+(0.6)	-	-
Other	-	0.2(0.4)	+(1.2)	+(2.9)	-	-	-	-
n	64	832	449	433	107	169	129	78
% n empty	57	29	46	43	62	7	7	24
total dry wt of food (g)	58.0	961.8	575.7	325.5	1.5	599.3	355.6	158.3

Table 3 The percentage contribution of prey categories to the overall diets of 8 species of invertebrate feeders from the upper continental slope of Maria Island, East Tasmania. The percentage frequency of occurrence of each prey category is shown in parentheses. (+ = <0.1%; - = absent, n = number of stomachs analysed). All were captured in the demersal trawl

	Predator (size range cm S.L.)							
Prey	*Coelorinchus* sp. 4 (10 - 33 cm)	*Coelorinchus* sp. 2 (23 - 46 cm)	*Lepidorhynchus denticulatus* (8 - 51 cm)	*Neocyttus rhomboidalis* (24 - 37 cm)	*Centriscops humerosus* (14 - 25 cm)	*Helicolenus percoides* (8 - 38 cm)	*Epigonus denticulatus* (18 - 15 cm)	*Epigonus lenimen* (10 - 19 cm)
Pisces								
Deania calcea	-	-	-	-	-	5.2(0.1)	-	-
Muraenichthys sp.	-	0.3(0.7)	-	-	-	0.2(0.6)	-	-
Notocanthus oxeopinnis	-	-	-	-	-	0.2(0.1)	-	-
Bassinago bulbiceps	-	-	-	-	-	0.6(0.4)	-	-
Nemurolicus mollari	-	-	-	-	-	0.1(0.1)	-	-
Chlorophthalmus nigripinnis	-	-	-	-	-	0.9(0.3)	-	-
Diaphus danae	-	-	-	-	-	0.9(0.6)	-	-
Diaphus sp.	-	-	-	-	-	0.1(0.6)	-	-
Lampanyctodes hectoris	31.8(5.7)	5.2((1.5)	20.4(5.2)	18.5(4.6)	18.9(4.6)	4.7(5.9)	-	11.8(3.0)
Lampanyctus australis	-	-	0.8(0.2)	-	-		-	-
Austrophycis marginata	-	-	-	-	-	2.3(1.3)	-	-
Macruronus novaezelandiae	-			-	-	0.3(0.1)	-	-
Coelorinchus sp. 4	-	-		-	-	0.2(0.1)	-	-
Lepidorhynchus denticulatus	-	-	0.8(0.2)	-	-	15.7(1.4)	-	-
Ventrifossa nigromaculata	-	-	-	-	-	0.2(0.3)	-	-
Helicolenus percoides	-	-	2.0(0.2)	-	-	0.5(0.1)	-	-
Apogonops anomalus	-	-	-	-	-	0.1(0.1)	-	-
Trachurus declivis	-	-	-	-	-	4.0(0.1)	-	-
Rexea solandri	-	-	-	-	-	3.9(0.1)	-	-
Unidentified fish	13.5(16.6)	8.2(20.1)	13.2(20.0)	9.7(40.0)	8.2(5.6)	9.5(6.9)	35.1(7.4)	15.4(5.5)
Total fish	45.3	13.7	37.2	38.2	27.1	49.4	35.1	29.2
Cnidaria								
Coral	-	+(0.7)	-	+(1.5)	0.9(3.6)	0.2(1.9)	-	-
Annelida								
Polychaeta	22.0(29.8)	12.8(31.4)	1.2(0.2)	-	0.9(1.0)	0.8(4.0)	-	2.7(0.3)
Crustacea								
Ostracoda	+(0.9)	-	-	-	1.6(13.3)	+(0.1)	-	-
Copepoda	0.3(1.2)	0.9(2.2)	+(0.4)	-	4.9(2.6)	0.1(0.1)	8.1(17.9)	3.0(10.8)
Hyalidacea	-	-	-	3.1(3.1)	-	-	0.4(0.3)	-
Amphipoda	+(2.4)	+(0.7)	+(0.2)	+(3.6)	+(0.3)	-	-	-
Isopoda	2.8(3.3)	-	0.7(0.7)	6.4(7.7)	11.5(2.1)	4.3(5.7)	+(0.4)	-
Euphausiacea	4.1(12.3)	0.3(2.2)	49.1(54.0)	+(4.6)	+(0.5)	0.2(0.7)	37.8(24.5)	59.0(49.2)
Caridae	3.4(7.2)	21.3(8.9)	2.2(1.6)	2.4(4.6)	-	0.4(2.0)	+(0.4)	1.0(1.9)
Penaeidae	-	-	0.5(0.4)	-	-	-	-	-
Galatheidae	1.3(2.1)	8.5(16.4)	-	-	+(0.5)	7.4(19.0)	-	-
Brachyura	1.3(2.4)	10.2(12.7)	-	-	+(1.5)	8.9(15.5)	-	-
Thalassinidae	+(0.3)	-	-	-	0.9(1.5)	-	-	-
Unidentified crustacea	14.1(38.6)	8.2(26.9)	7.7(22.0)	16.5(20.0)	18.9(58.5)	0.3(4.9)	18.9(55.6)	4.6(14.1)
Total crustacea	27.3	49.4	60.2	28.4	36.2	21.6	64.8	68.0
Mollusca								
Gastropoda	1.9(3.6)	1.2(3.0)	+(0.4)	-	1.6(15.9)	0.7(2.0)	-	-
Squid	-	+(0.7)	1.4(1.1)	-	-	0.1(0.3)	-	-
Thaliacea								
salp	-	-	-	21.3(15.4)	-	+(0.1)	-	-
Pyrosoma atlanticum	-	-	-	14.5(10.8)	-	19.4(31.8)	-	0.2(0.3)
Echinodermata								
Asteroidea	-	0.3(0.7)	-	-	-	-	-	-
Ophiuroidea	3.5(11.4)	19.5(36.6)	+(0.2)	-	30.3(36.4)	7.7(19.5)	-	-
Other	+(2.7)	0.6(1.4)	+(3.3)	0.8(3.1)	1.8(5.1)	+(0.1)	+(7.8)	+(1.2)
n	685	208	655	165	272	948	363	597
% empty	52	38	15	61	28	28	29	40
total dry wt of food (g)	14.6	21.2	54.4	12.0	7.8	659.6	1.3	17.0

(April-October) to summer (December-April). During winter L. hectoris formed about 50% of energy intake. After October this declined to less than 9%, when euphausiids became the most important source of energy.

Helicolenus percoides consumed a variety of prey but Pyrosoma atlanticum was the major food item and contributed most to energy intake in June and October, while Brachyura were important in August.

Epigonus lenimen relied mainly on euphausiids, although fish were more important in April 1984 and August.

Trachurus declivis fed mainly on L. hectoris, except in October when pelagic Gastropoda and fish larvae formed the bulk of the prey.

Lepidopus caudatus likewise consumed L. hectoris, but they were largely replaced by euphausiids in October and juvenile M. novaezelandiae in February.

Diel feeding periodicity

Comparison between day and night samples showed that only 3 of the 15 species had a well-defined and statistically significant diel cycle (Fig. 1). Coelorinchus sp. 2 fed mainly at night (maximum fullness 0200 h, minimum fullness 1400 h; $F_{(2,23)} = 6.2$, $P < 0.01$); Lepidopus caudatus during the night and early morning (maximum fullness 0600 h, minimum fullness 1600 h; $F_{(2,17)} = 8.12$, $P < 0.01$); and Helicolenus percoides during the day (maximum fullness 1600 h, minimum fullness 0400 h; $F_{(2,45)} = 3.4$, $P < 0.05$). Macruronus novaezelandiae has a diel cycle in which maximum fullness occurs at night (Bulman & Blaber, 1986).

Ontogenetic changes in diet

Only the adult fish of most species were caught in the study area (Tables 2 & 3). However, both juveniles and adults of Coelorinchus sp. 2 and sp. 4, Lepidorhynchus denticulatus, Cyttus traversi and Helicolenus percoides were sampled. Diet analyses of these species by size classes irrespective of sampling times and months, together with calculations of percentage similarities between the diets of size classes within species (Fig. 2) showed the following:

Coelorinchus sp. 2: with increasing length, the proportion of the diet consisting of polychaetes (53% to 6%) and ophiuroids (36% to 15%),

decreased, while the proportion of Isopods increased (7% to 63%) (Table 4). However, the diet of adjacent size classes had considerable overlap (Fig. 2).

Coelorinchus sp. 4: all size classes ate similar proportions of polychaetes, euphausiids and brachyurans. There was a reduction in the proportion of carid shrimps (20% to 3%) and an increase in fish and ophiuroids with increased length of fish up to 24 cm (Table 4). Although the diet of adjacent size classes had some overlap, those of the small and large fish were dissimilar (Fig. 2).

Lepidorhynchus denticulatus: euphausiids were the most important food of all size classes except the smallest and largest, where fish predominated (Table 4). The overlap of diets ranged from partial to extensive, with the exception of the small and large fish (Fig. 2). Likewise the diet of all size classes except those less than 20 cm and more than 45 cm overlapped partially or extensively with the diet of Epigonus lenimen (Fig. 2), due to the high proportion of euphausiids.

Cyttus traversi: the proportion of Crustacea, chiefly Caridae and Munida haswelli, decreased with length while the proportion of fish increased (Fig. 3). There was little similarity between size classes (Fig. 2).

Helicolenus percoides: as in C. traversi, the proportions of Crustacea and fish were inversely related as length increased (Fig. 3). Brachyura were the single most important prey in fish of less than 20 cm but were replaced by Pyrosoma atlanticum and teleosts in larger size classes. There was medium to high dietary overlap between all size classes above 20 cm and low overlap only between those of less than 20 cm and more than 30 cm (Fig. 2).

Dietary overlap

The pelagic piscivores, Trachurus declivis, Lepidopus caudatus, Brama brama and the vertically migrating Apogonops anomalus and Macruronus novaezelandiae, all feed primarily on Lampanyctodes hectoris. Similarly, L. denticulatus and Epigonus lenimen have a chiefly euphausiid diet (Table 3). Lampanyctodes hectoris forms a significant component of the diets of the pelagic piscivores and Coelorinchus sp. 4, otherwise there was little similarity in diets.

Table 4. Diets of size classes of three species of Macrouridae from off Maria Island expressed in terms of the percentage contribution of each prey category to total energy intake. Items contributing less than 0.2% are excluded.

Species	*Coelorinchus* sp. 2					*Coelorinchus* sp. 4				*Lepidorhynchus denticulatus*						
size classes cm (S.L.)	< 25	25-29	30-34	35-39	> 40	< 15	15-19	20-24	25-30	< 20	20-24	25-29	30-34	35-39	40-44	> 45
prey	% energy intake					% energy intake				% energy intake						
L hectoris	-	-	10.9	-	8.6	-	29.1	18.5	-	-	-	21.6	6.0	15.0	3.7	
L. denticulatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14.3
Unidentifiable fish	-	7.2	1.3	-	-	19.4	6.8	11.6	29.4	92.7	21.4	16.3	22.2	34.4	14.3	63.3
Euphausiacea	-	0 5	0.3	-	-	4.3	2.8	3.8	-	5.2	64.2	46.9	60.7	37.5	72.7	10.2
Caridea	-	7.4	2.2	-	-	20.9	7.1	2.6	10.8	-	-	1.2	0.5	-	-	12.2
Munida haswelli	-	8.1	8.5	22.0	-	-	0.3	-	13.7	-	-	-	-	-	2.4	
Brachyura	-	16.2	14.8	13.0	-	2.9	1.2	2.3	-	-	-	-	-	-	-	
Isopoda	-	7.0	25.1	29.9	63.0	-	2.8	3.9	9.3	-	-	0.8	0.8	1.2	-	
Unidentified Crustacea	9.4	11.1	3.5	18.8	0.9	22.3	18.4	17.7	15.2	2.1	5.3	10.2	9.8	7.1	2.4	-
Polychaeta	52.9	6.3	10.3	-	6.3	23.7	26.4	28.1	14.7	-	7.5	-	-	-	-	-
Squid	-	-	-	-	-	-	-	-	-	-	-	-	-	4.0	4.3	
Ophiuroidea	36.4	28.6	22.2	14.7	18.8	1.4	2.2	9.3	-	-	1.6	-	-	-	-	-
Gastropoda	-	4.5	-	-	2.5	1.4	1.5	2.1	6.9	-	-	-	-	-	-	-
Percentage of total energy intake	98.7	96.9	99.4	98.4	97.6	96.3	97.1	97.8	100.0	100.0	100.0	97.0	100.0	99.2	99.8	100.0
Total dry weight of food (g)	0.6	5.9	7.4	2.4	2.8	0.8	3.9	5.7	1.0	0.4	0.9	13.2	16.6	10.9	7.2	2.0
Number of fish	6	63	39	16	6	34	132	93	19	15	18	195	202	81	46	8

From the diet (Tables 2 & 3) and dietary overlap data (Fig. 4) the fish can be divided into four groups (Table 5):
i) pelagic piscivores that feed mainly on Lampanyctodes hectoris; (ii) benthic piscivores that take a variety of prey fish; (iii) epibenthic invertebrate feeders that take mainly polychaetes, brachyurans and ophiuroids; and (iv) benthopelagic omnivores that feed extensively on mesopelagic fish such as L. hectoris, as well as a range of benthic and pelagic invertebrates. There is little overlap between the diets of these groups (Figs 2 & 4) and, except for the pelagic piscivores, there is little overlap within groups.

Diet breadth

Three of the pelagic piscivores that take Lampanyctodes hectoris have very narrow diets, whereas the other two, Apogonops anomalus and Lepidopus caudatus, which take significant quantities of euphausiids, occupy a wider trophic niche (Table 6). The epibenthic piscivores have a somewhat broader diet. The two epibenthic invertebrate feeders have relatively broad diets that include a small proportion of fish. Similarly, with the exception of Lepidorhynchus denticulatus and Epigonus lenimen, over half of whose diet is euphausiids, the benthopelagic omnivores occupy wide feeding niches.

Discussion

The fish community of the upper continental slope of east Tasmania can be grouped into five trophic categories: the zooplankton-feeding Myctophidae and Sternoptychidae described separately by Young and Blaber (1986), and the four reported in this paper (Table 5). Although they could be fitted into the groups listed by Mauchline and Gordon (1985), their depth-related ecological separation would be masked. Moreover, the determination of diets from energy values of prey, as used here, allows more precise quantitative comparisons.

In the present study area, myctophids dominated the diet of pelagic piscivores. Maxwell (1979) found that Trachurus declivis caught over deep water fed mainly on fish, as in this study, whereas Webb (1976) stated

Table 5. Trophic categories and diet breadths of 16 species of fishes from the continental slope of east Tasmania.

Trophic category	Species	Diet breadth
Pelagic piscivores		
	Trachurus declivis	0.023
	Lepidopus caudatus	0.158
	Brama brama	0.026
	Apogonops anomalus	0.217
	Macruronus novaezelandiae	0.072 [a]
Epibenthic piscivores		
	Deania calcea	0.225
	Genypterus blacodes	0.246
Epibenthic invertebrate feeders	*Centriscops humerosus*	0.312
	Coelorinchus sp.2	0.404
Benthopelagic omnivores	*Coelorinchus* sp.4	0.321
	Lepidorhynchus denticulatus	0.141
	Cyttus traversi	0.307
	Neocyttus rhomboidalis	0.480
	Helicolenus percoides	0.268
	Epigonus lenimen	0.130
	Epigonus denticulatus	0.280

[a] Calculated from data in Bulman and Blaber (1986)

that their diet over the shelf consisted of 99.9% euphausiids. Trachurus declivis switched from myctophids to alternative foods in October, demonstrating some flexibility in diet, although the small diet breadth (Table 5) indicates a specialist feeding ecology (Hurlbert, 1978). Lepidopus caudatus, which also primarily takes Lampanyctodes hectoris, has a slightly wider diet (Table 5) and likewise switches prey occasionally. Although its diet is similar to that reported for the same species in the Mediterranean (Macpherson, 1979a), fish prey were more important in Tasmanian waters. During the day, when Macruronus novaezelandiae is not feeding, it forms part of the benthic fish community; at night however, it is pelagic and undertakes extensive vertical migrations similar to those of L. hectoris, its principal prey (Bulman & Blaber, 1986). Competition between the pelagic piscivores is probably minimized by the superabundance of L. hectoris (May and Blaber, in preparation) and, possibly, by differences in feeding periodicity, such as that between M. novaezelandiae, which feeds at night, and L. caudatus, which feeds early in the morning (Fig. 1).

The extent to which benthopelagic omnivores ascend the water column to feed is not clear, but Lepidorhynchus denticulatus, Cyttus traversi and Helicolenus percoides have been captured in midwater regions (May & Blaber, in preparation) They, like the pelagic piscivores, eat significant quantities of L. hectoris (Tables 2 & 3). The phenomenon of demersal slope fishes feeding on mesopelagic fauna is documented for northern hemisphere waters (Sedberry & Musick, 1978; Marshall, 1979), particularly for some macrourids and for a scorpaenid similar to Helicolenus (Pereyra et al., 1969) and for a number of berycomorphid and percomorphid species (Mauchline & Gordon, 1984b).

In a review of feeding strategies among macrourids, McLellan (1977) showed that diet is related to the anatomical structure of the head as well as to depth distribution: specialist bottom-feeders occur mainly on the continental slope, while less specialized feeders live at greater depths. In a study of 12 species of macrourids from the Rockall Trough (400 - 2900 m), Mauchline and Gordon (1984a) showed that all were generalist feeders, but that ecological separation was maintained by a

combination of differential depth distribution and feeding habits. They ranged from entirely benthopelagic feeders to predominantly epibenthic feeders. Similarly, Macpherson (1979b) showed that rates of competitive exclusion was low between four species in the Mediterranean, but states that macrourids, in general, have narrow diets, exhibiting some specialisation. Since this family comprises some 260 species (Nelson, 1984), considerable diversity in feeding ecology would be expected, especially as many species are geographically widespread and occupy broad depth ranges. Three macrourids were examined in the present study. Two species of Coelorinchus had broad diets (generalist) while Lepidorhynchus denticulatus occupied a relatively narrow trophic (specialist) niche (Table 5). Coelorinchus sp. 2 is an epibenthic feeder while Coelorinchus sp. 4 and L. denticulatus are benthopelagic. Their diets had little overlap, although Lampanyctodes hectoris was an important prey item. Diet changes with increasing body size in all three species (Fig. 2), but there was no indication, as there was in a species off Norway (Eliassen and Jobling, 1985), that the feeding habits changed from epibenthic to benthopelagic. Coelorinchus sp. 4 merely ate more fish and fewer carids, and L. denticulatus altered the proportions of euphausiids and mesopelagic fish in its diet. Competition between macrourids in the study area is probably negligible because their diets and feeding habits are different. This was not the case with L. denticulatus and Epigonus lenimen, where dietary overlap occurred with all size classes and diet breadths were similar (Figs 2 & 4, Table 5).

The most piscivorous of the benthopelagic omnivores were Cyttus traversi and Helicolenus percoides (Table 2). Their diets partially overlapped (Fig. 4), but both exhibited marked ontogenetic dietary changes (Fig. 3): juveniles ate pelagic Crustacea and adults mainly ate pelagic fish. As with macrourids, these changes may reflect a combination of changes in prey availability and prey size in relation to the predator, rather than any alterations in the benthopelagic feeding habit. Davies (1949) found that Helicolenus in South Africa also had a very varied diet. Neocyttus rhomboidalis is unusual among the benthopelagic group in that its diet overlaps very little with any of the other species (Fig. 4) yet is the broadest diet (Table 5). It feeds on Lampanyctodes hectoris

and a variety of Crustacea as well as Pyrosoma atlanticum and salps, all in significant quantities (Table 3), which suggests that it is a generalist and opportunistic feeder.

Among the epibenthic species, two are piscivorous and two are primarily invertebrate feeders. Although their diets are similarly broad (Table 5), the diets of the piscivores, Deania calcea and Genypterus blacodes, apparently overlap very little (Fig. 4). This result may, however, be affected by the high proportion of unidentifiable fish in D. calcea, a result similar to that reported by Mauchline and Gordon (1983a) for the same species in the Rockall Trough. Mitchell (1984) showed that G. blacodes in New Zealand eat mainly Macruronus novaezelandiae and the galatheid Munida sp. The former was important energetically in the diet of Australian fish in the present study, whereas the latter was insignificant overall (Table 2) although it was an important prey in August. The fact that D. calcea and G. blacodes consumed myctophids (Table 2) and carid shrimps suggests that some feeding takes place above the substratum, as reported for D. calcea by Mauchline and Gordon (1983a) and Macpherson (1983), but not for G. blacodes by Mitchell (1984).

The epibenthic, largely invertebrate-feeding Coelorinchus sp. 2 and Centriscops humerosus obtain most of their energy from benthic Crustacea and ophiuroids, but supplement their diet with varying quantities of the myctophid Lampanyctodes hectoris.

No species showed any marked changes in feeding habit from month to month. The changes noted in the diets of some species may be related to changes in the abundance or availability of different prey. Lampanyctodes hectoris occurred in the diets of all species, other than Epigonus denticulatus, throughout the year, with the exception of August when it was consumed by only five predators. May and Blaber (in preparation) indicate that L. hectoris is least abundant at this time. Euphausiids are taken at various times of year by all species except the shark Deania calcea, but were eaten by more species in summer (October-April) when they are most abundant (see Young & Blaber, 1986) in the study area.

The absence of any detectable diel feeding periodicity in most species may be related to depth distribution. A significant diel pattern has been reported for Macruronus novaezelandiae (Bulman & Blaber, 1986); it is linked with diel vertical migrations. A similar pattern could perhaps be expected for other benthopelagic and pelagic species that make vertical migrations, and was detected for Helicolenus percoides, but not for Lepidorhynchus denticulatus. Possibly epibenthic feeders, or those benthopelagic feeders that remain close to the bottom, do not exhibit a diel pattern related to daylength because they are below the depth of light penetration. Macpherson (1981) showed that slope species in the Mediterranean likewise exhibit few diel variations in feeding. There is little other information on this aspect of the feeding ecology of deeper-water fishes, despite its relevance to ecological overlap and considerations of niche partitioning.

Rates of competitive exclusion may, Grassle and Sanders (1973) have suggested, be low in deep-sea fishes. Both the work of Macpherson (1979b, 1981) and, in general, the present study support this suggestion. However, when the entire water column is examined, as in this study, two additional important points emerge. Firstly, the great significance of mesopelagic food resources, particularly myctophids, to the whole fish community; and secondly, the extent to which the diets of pelagic predators overlap.

The importance of mesopelagic fauna as a food source for demersal slope fishes has been emphasized by Sedberry and Musick (1978) and Marshall (1979), who postulate that much of it is captured near the bottom. Present data point to extensive vertical migrations of at least some predators in search of prey. Movement of demersal fish from the slope into mesopelagic regions can also be lateral, as Mauchline and Gordon (1983b) noted. However, the main prey in the region studied, Lampanyctodes hectoris, only occurs in large concentrations close to the shelf break, over the upper continental slope, and not over adjacent deeper water (Ahlstrom et al., 1976). Therefore horizontal movement of benthopelagic feeders from the upper slope would not bring them into contact with L. hectoris.

Vertical migrations are reported for macrourids by Haedrich (1974), Sedberry and Musick (1978) and Pearcy and Ambler (1974), and McLellan (1977) suggests that the benthopelagic fish that feed on mesopelagic prey play a major role in transporting energy from midwater regions to the benthos. This study on the Tasmanian upper slope supports this hypothesis and further indicates that much of this energy is derived from the myctophid Lampanyctodes hectoris, which has a high energy content (Table 1) and is very abundant.

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Young, J. W. and S. J. M. Blaber: The feeding ecology of three species of midwater fishes associated with the continental slope of eastern Tasmania. Mar. Biol. 93,147-156 (1986)

LEGEND FOR FIGURES

Fig. 1. Diel feeding periodicities of Helicolenus percoides, Lepidopus caudatus and Coelorinchus sp. 2 off Maria Island, showing stomach fullness values for each net tow and regression curves.

Fig. 2. Percentage similarities of the diets of 5 cm size classes of (a) Lepidorhynchus denticulatus (also compared with combined size classes of Epigonus lenimen) (b) Helicolenus percoides (c) Cyttus traversi (d) Coelorinchus sp. 4 and (e) Coelorinchus sp. 2.

Fig. 3 Ontogenetic changes in the diets of (a) Cyttus traversi and (b) Helicolenus percoides expressed in terms of the percentage contributions of major prey categories to the overall energy intake of each 5 cm size class. (n = number of fish sampled)

Fig. 4. Percentage similarities of the diets of sixteen species from off Maria Island based on overall diets in terms of the relative energy contributions of prey items.

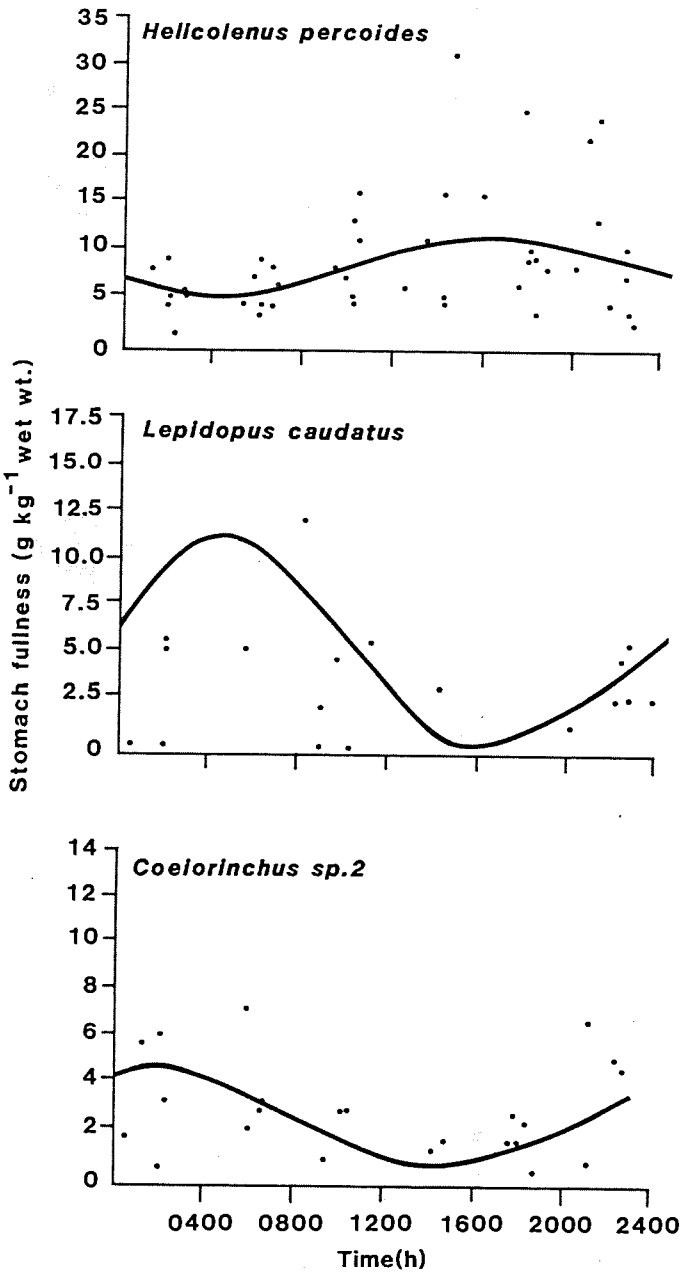
Hellcolenus percoides
Lepidopus caudatus
Coelorinchus sp.2
Stomach fullness (g kg^{-1} wet wt.)
Time(h)
0400
0800
1200
1600
2000
2400

Fig. 1.

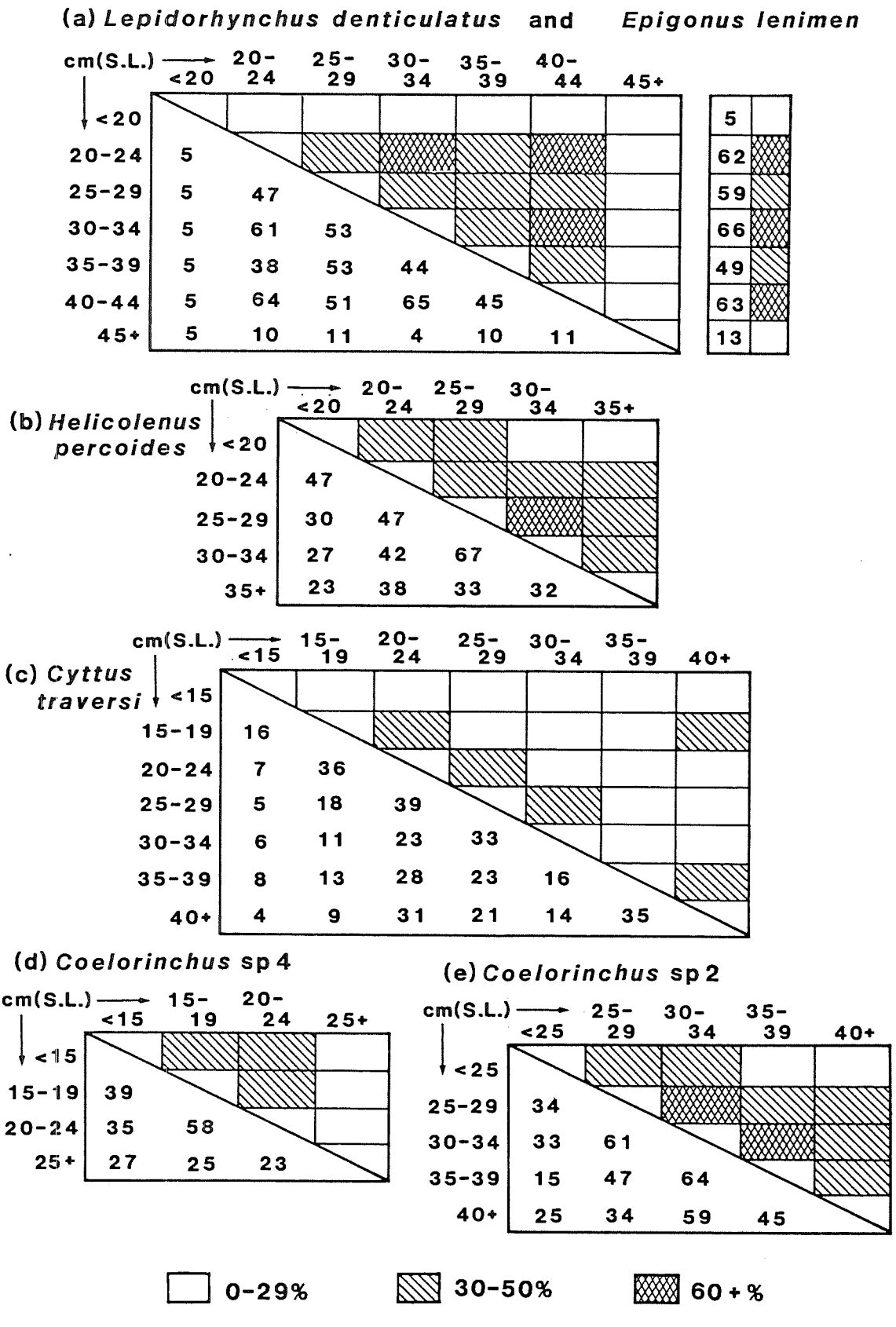
(a) Lepidorhynchus denticulatus and Epigonus lenimen
cm(S.L.) → 20- 25- 30- 35- 40-
<20 24 29 34 39 44 45+
<20
20-24 5
25-29 5 47
30-34 5 61 53
35-39 5 38 53 44
40-44 5 64 51 65 45
45+ 5 10 11 4 10 11
5
62
59
66
49
63
13
(b) Helicolenus percoides
cm(S.L.) → 20- 25- 30-
<20 24 29 34 35+
<20
20-24 47
25-29 30 47
30-34 27 42 67
35+ 23 38 33 32
(c) Cyttus traversi
cm(S.L.) → 15- 20- 25- 30- 35-
<15 19 24 29 34 39 40+
<15
15-19 16
20-24 7 36
25-29 5 18 39
30-34 6 11 23 33
35-39 8 13 28 23 16
40+ 4 9 31 21 14 35
(d) Coelorinchus sp 4
cm(S.L.) → 15- 20-
<15 19 24 25+
<15
15-19 39
20-24 35 58
25+ 27 25 23
(e) Coelorinchus sp 2
cm(S.L.) → 25- 30- 35-
<25 29 34 39 40+
<25
25-29 34
30-34 33 61
35-39 15 47 64
40+ 25 34 59 45
0-29%
30-50%
60+%

Fig 2.

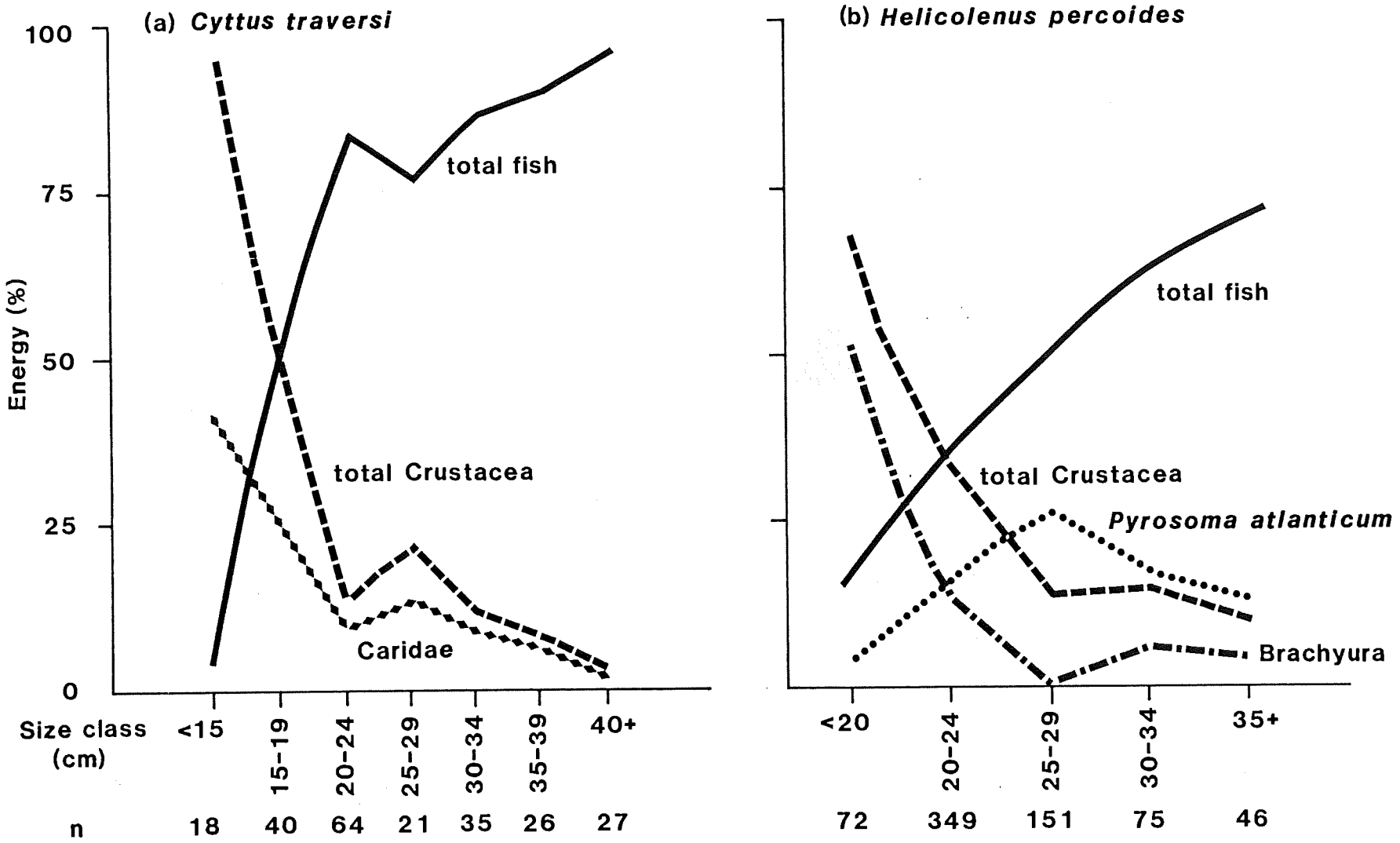
(a) Cyttus traversi
100
75
50
25
0
Energy (%)
total fish
total Crustacea
Caridae
Size class (cm)
<15
15–19
20–24
25–29
30–34
35–39
40+
n
18
40
64
21
35
26
27
(b) Helicolenus percoides
total fish
total Crustacea
Pyrosoma atlanticum
Brachyura
<20
20–24
25–29
30–34
35+
72
349
151
75
46

Fig. 3.

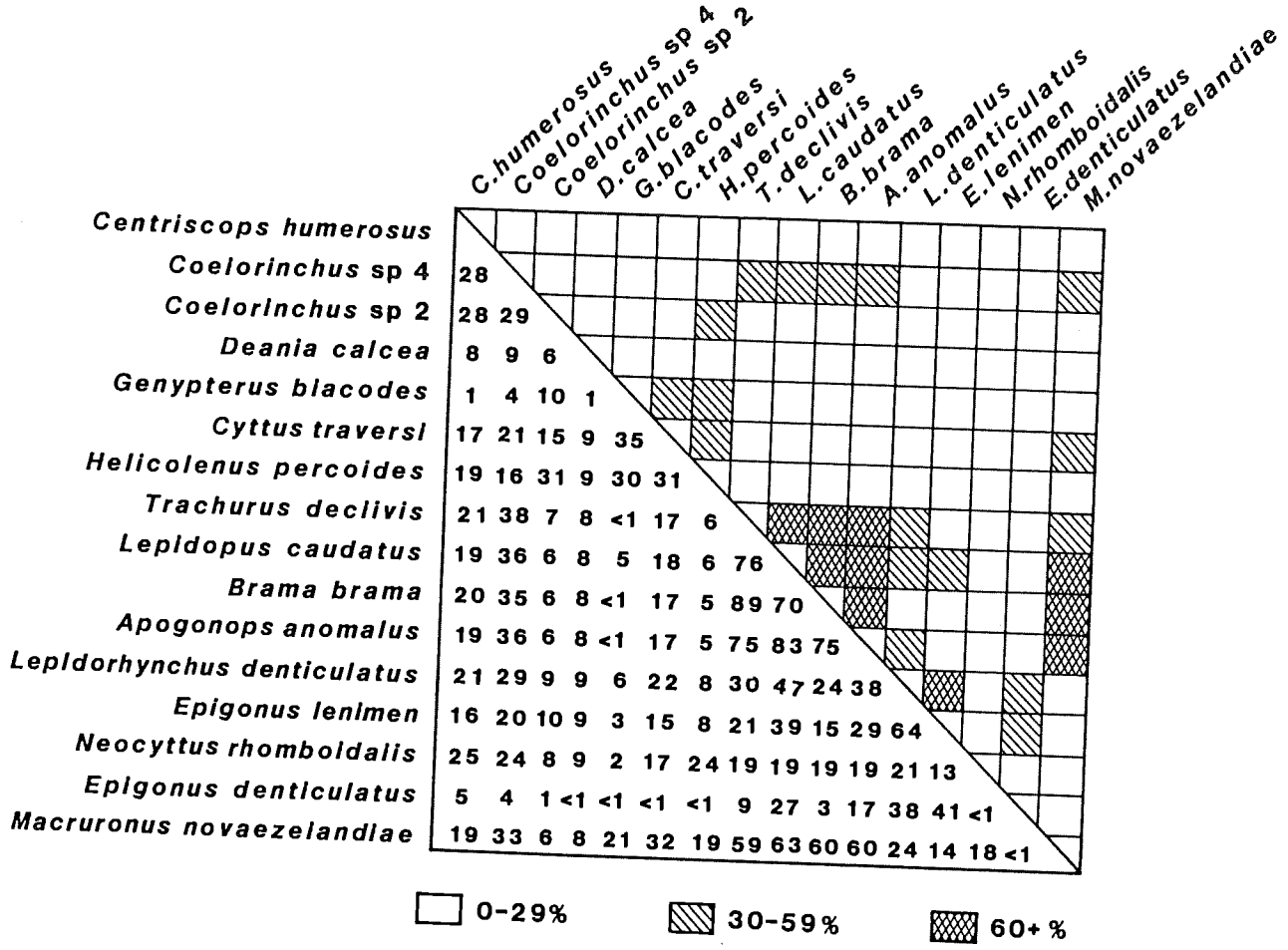
C.humerosus
Coelorinchus sp 4
Coelorinchus sp 2
D.calcea
G.blacodes
C.traversi
H.percoides
T.declivis
L.caudatus
B.brama
A.anomalus
L.denticulatus
E.lenimen
N.rhomboidalis
E.denticulatus
M.novaezelandiae
Centriscops humerosus
Coelorinchus sp 4 28
Coelorinchus sp 2 28 29
Deania calcea 8 9 6
Genypterus blacodes 1 4 10 1
Cyttus traversi 17 21 15 9 35
Helicolenus percoides 19 16 31 9 30 31
Trachurus declivis 21 38 7 8 <1 17 6
Lepidopus caudatus 19 36 6 8 5 18 6 76
Brama brama 20 35 6 8 <1 17 5 89 70
Apogonops anomalus 19 36 6 8 <1 17 5 75 83 75
Lepidorhynchus denticulatus 21 29 9 9 6 22 8 30 47 24 38
Epigonus lenimen 16 20 10 9 3 15 8 21 39 15 29 64
Neocyttus rhomboidalis 25 24 8 9 2 17 24 19 19 19 19 21 13
Epigonus denticulatus 5 4 1 <1 <1 <1 <1 9 27 3 17 38 41 <1
Macruronus novaezelandiae 19 33 6 8 21 32 19 59 63 60 60 24 14 18 <1
0-29%
30-59%
60+%

Fig. 4.

Marine Biology 93, 147–156 (1986)

APPENDIX 6

Marine Biology

Feeding ecology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia

J.W. Young and S.J.M. Blaber

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Abstract

The feeding ecology of *Maurolicus muelleri, Lampanyctodes hectoris* and *Diaphus danae* was examined from samples collected from continental slope waters of eastern Tasmania between April 1984 and April 1985. A total of 2 232 stomachs was analysed. *M. muelleri, L. hectoris* and *D. danae* fed primarily on euphausiids and secondarily on copepods, although larger *D. danae* (> 60 mm standard length) fed on other lanternfish (chiefly *L. hectoris*). The diets of *M. muelleri* and *L. hectoris* overlapped substantially. Diet overlaps between *D. danae* and the former species was low, however, due to the large biomass of fish present in *D. danae*. The prey taxa consumed changed with time of year and predator size. Stomach fullness (feeding intensity) varied seasonally in all three species, but only *M. muelleri* showed significant diel differences in fullness. The synchronization of the size structure of the predator populations and their feeding intensity, with seasonal variations in preferred prey, is proposed as a mechanism whereby each species maximizes its share of the available food resources.

Introduction

Mesopelagic fishes, dominated by the lanternfish *Lampanyctodes hectoris,* form dense aggregations over the upper continental slope off South Africa, New Zealand and southeastern Australia (Anonymous, 1977; Robertson, 1977; Crawford, 1980). Despite the fact that they are the major component of the pelagic fish biomass in these waters and are the main prey of many continental slope fishes (Clarke, 1982; Bulman and Blaber, in press), little is known of their basic biology.

Oceanic midwater fish are generally considered to be opportunistic feeders, migrating to surface waters at night to feed, mainly on crustacean zooplankton (Hopkins and Baird, 1977; Clarke, 1978; Kinzer and Schulz, 1985). However, in regions of high productivity (usually close to land masses or in upwelling areas), less distinct feeding cycles have been reported (Kinzer, 1977, 1982). Diets are modified both by seasonal variations in zooplankton (Hopkins and Baird, 1977; Gjosaeter, 1981 a, b) and individual predator size (Paxton, 1967; Tyler and Pearcy, 1975; Hopkins and Baird, 1977; Scotto di Carlo *et al.,* 1982). Gjosaeter (1981 a) found that the diet of *Maurolicus muelleri* differed with season and size of individual, but found no evidence for diel feeding.

As part of a larger study of the community ecology and trophic structure of the continental slope fish-community of eastern Tasmania (Blaber, 1984), samples of the three dominant midwater-fish species – *Maurolicus muelleri* (family Sternoptychidae), *Lampanyctodes hectoris* and *Diaphus danae* (both family Myctophidae) – were collected for dietary analysis. This paper examines their feeding ecology in relation to seasonal and diel cycles and to the size of individuals.

Materials and methods

Maurolicus muelleri, Lampanyctodes hectoris and *Diaphus danae* were collected from 88 trawls over the upper continental slope (420 to 550 m depth) approximately twelve nautical miles east of Maria Island, Tasmania (42°39′S; 148°28′E) on seven cruises of F.R.V. "Soela" between April 1984 and April 1985. An "Engel 152" pelagic trawl was used after initial comparisons with two other trawls, the rectangular midwater trawl (RMT 8) and the International Young Gadoid Pelagic Trawl (IYGPT) had shown that the Engel net sampled a wider range of size classes of the target species (Fig. 1). Trawl depth was monitored with a Simrad FB Trawl eye mounted on the trawl headrope. During the first three cruises (April, June and August 1984) trawls were aimed at sound-scattering marks over the diel period and lasted approximately 40 min at depth. The next four

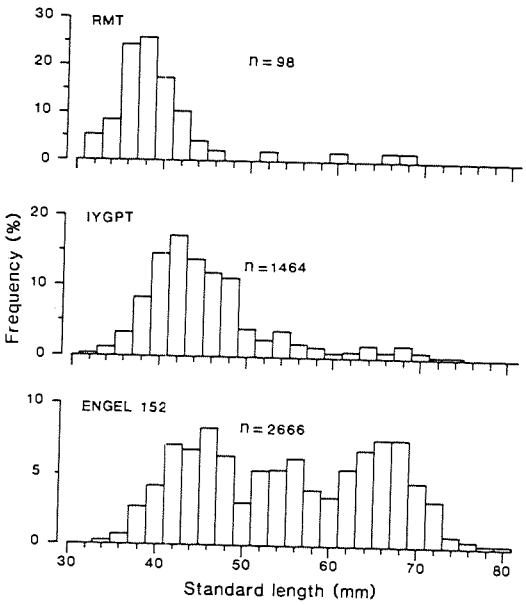

Fig. 1. *Lampanyctodes hectoris.* Length-frequency distributions from RMT-8, IYGPT, and "Engel 152" midwater trawls taken during April 1984. *n:* number of individuals

cruises (October and December 1984, and February and April 1985) employed a stratified random sampling strategy in order to determine abundance (J. May *et al.,* in preparation). This consisted of at least three replicate, 40 min tows within each of the depth strata of 10 to 60 m, 60 to 160 m, 160 to 260 m and 260 to 360 m made during daylight and repeated at night. No samples were taken at dusk or dawn because the depth distributions of the target species change at these times (Backus *et al.,* 1969). As net type, trawl duration, depths and area fished were the same for each trawling method, we assumed that the samples obtained throughout the year were directly comparable.

A sample of up to 20 fish of each species was taken from each trawl and immediately fixed in buffered seawater-formalin. Fish for stomach analysis were chosen from trawls made at 4 h intervals from midnight, and from the widest range of depth intervals. To minimize contamination from net-feeding (Clarke, 1978), fish with fresh prey in the mouth were discarded.

Fish for dissection were weighed (±0.01 g) and measured (standard length, SL, ±0.5 mm) and their stomachs removed. The wet weight of the stomach contents (±0.01 mg) divided by the wet weight of the whole fish, gave a quantitative measure of stomach fullness expressed in g kg^{-1} of fish wet weight. The contents were then identified to the lowest possible taxon using the keys of Nyan Taw (1975) and Tafe (1979) for copepods, Kirkwood (1982) for euphausiids and Bowman and Gruner (1973) for amphipods. The total length (TL) of whole prey was measured with an ocular micrometer and converted to millimeters (±0.1). The number (where possible) and wet weight of each prey taxon was recorded. The prey were then dried to constant weight at 60 °C and the dry weight recorded for each taxon.

Diet was determined from the percentage dry weight (biomass) and percentage frequency of each prey taxon and was calculated only from fish containing prey. Dietary overlaps were measured from the biomass data using the percentage similarity index of Shorygin (Ivlev, 1961). This index ranges from 0 (no overlap) to 100% (complete overlap). Biomass data were used as this was the closest measure of caloric content available (Wallace, 1981).

Regression analysis was used to test for seasonal changes in the dry weight proportions of the major prey taxa. This analysis was used to construct analysis-of-variance tables, because the number of individuals and number of trawls taken varied within and between seasons. A parameter was fitted for each month and the hypothesis that all parameters were equal was tested with the *F* test. This test should not be greatly affected by non-normality (Clarke, 1978), as it tests for differences between means, which are asymptotically normal. Stomach fullness (feeding intensity) was also compared using regression analysis, with respect to month, time of day and depth. For each of these effects, the corresponding parameters were tested for equality with the *F* test. Time of day was divided into four 6 h intervals starting at midnight and depths into four 100 m intervals from the sea surface.

The relationship between fish length and prey type was examined using a contingency table with one nominal classification (main prey taxon by weight in a stomach) and one ordinal (predator length). The data were analysed with a loglinear model for an ordinal-nominal classification (Agresti, 1983). The initial hypothesis tested was that all size classes have the same proportions of major prey items (the "homogeneity" hypothesis). If this hypothesis was rejected, we tested the hypothesis that the proportions of each prey type changed linearly with predator size (the "column-effects" hypothesis).

Results

Overall diet and dietary overlap

A total of 719 stomachs of *Maurolicus muelleri* (78% contained prey), 975 stomachs of *Lampanyctodes hectoris* (81% contained prey) and 538 stomachs of *Diaphus danae* (91% contained prey) was analysed. The size range of individuals examined is given in Table 1. Euphausiids and calanoid copepods, respectively, were the main dietary components in *M. muelleri* and *L. hectoris* (Table 2), consequently dietary overlap between these species was high (Shorygin's index = 70.5). The major difference between *M. muelleri* and *L. hectoris* was that the latter consumed a relatively higher dry weight proportion of euphausiids and a wider range of prey taxa. The diet of *D. danae* consisted mainly of *L. hectoris,* copepods and euphausiids. Calanoid copepods were eaten in large numbers by *D. danae,* but accounted for less than 1% of the total prey biomass. Even though *D. danae* fed on many of the prey types of either *M. muelleri* or *L. hectoris,* or both, dietary overlap between *D. danae* and the former species was low (15.9 and 17.4, respective-

Table 1. *Maurolicus muelleri, Lampanyctodes hectoris* and *Diaphus danae.* Size range of individuals examined for stomach contents. SL: standard length in mm; (*n*): number of fish examined

Month	*M. muelleri*		*L. hectoris*		*D. danae*	
	SL	(*n*)	SL	(*n*)	SL	(*n*)
1984						
April	29–52	(113)	31–73	(257)	29–116	(88)
June	29–51	(107)	35–65	(104)	34– 76	(103)
August	31–42	(60)	37–73	(138)	34– 71	(123)
October	32–55	(120)	27–69	(143)	55–119	(35)
December	32–54	(78)	27–72	(120)	66–122	(95)
1985						
February	28–54	(121)	34–71	(71)	64–121	(32)
April	29–53	(120)	34–73	(142)	66–122	(62)

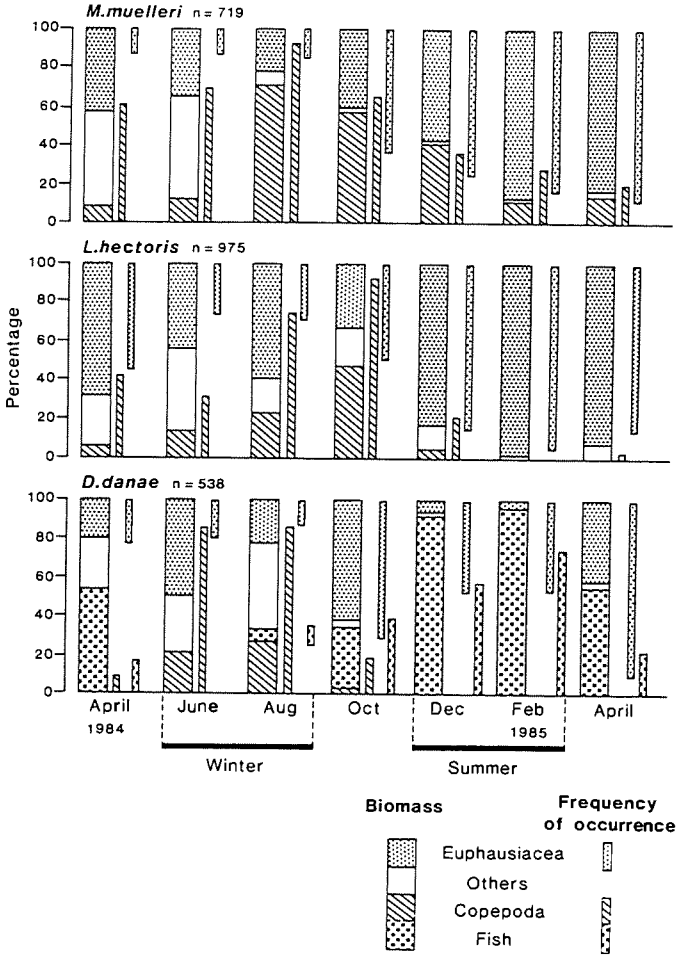

Fig. 2. *Maurolicus muelleri, Lampanyctodes hectoris* and *Diaphus danae.* Seasonal changes in percentage (dry weight) biomass and frequency of occurrence of major prey taxa in stomachs. *n:* number of fish examined

ly). This was due to the predominantly piscivorous diet of *D. danae* in summer and autumn (Fig. 2). Other prey items that occurred less frequently, but which were important in the diet of all three species in certain months, were ostracods, hyperiid amphipods, crab larvae (only in *D. danae*), pelagic gastropods, salps and fish scales.

Seasonal changes in diet

Maurolicus muelleri

Copepods were the main prey consumed during winter and spring, whereas euphausiids dominated in summer and early autumn (Fig. 2). Significant seasonal differences were found in the prey biomass of calanoid and cyclopoid copepods, euphausiids and crustacean remains (Table 3). The calanoids *Candacia bipinnata* and *Pleuromamma abdominalis* were the main prey during June and August. The main calanoid species identified in October and December were *Neocalanus tonus* and *Euchirella rostrata*, respectively: the former was still occurring in stomachs in April 1985. The cyclopoids *Oncaea media* and *O. venusta* were eaten between April and October, and especially in August, but scarcely affected the overall prey biomass. *Euphausia similis* var. *armata* was the main euphausiid eaten during summer, although *Nematoscelis megalops* was also an important prey item. *Nyctiphanes australis*, an abundant shelf species (Nyan Taw, 1975), was rarely found in the fish examined. Fish scales and eggs were consumed intermittently.

Lampanyctodes hectoris

Euphausiids were the main prey of *Lampanyctodes hectoris* throughout the year except in August and October, when calanoid copepods were the main prey eaten (Fig. 2). Significant seasonal differences were found in the prey biomass of calanoids, hyperiid amphipods, euphausiids, crustacean remains and gastropods (Table 3). Between December 1984 and April 1985, *Euphausia similis* var. *armata* and, less frequently, *E. lucens, Nematoscelis megalops* and *Thysanopoda egregia* were the main euphausiids consumed, accounting for over 85% of both dry weight and frequency of occurrence values. During August, calanoid copepods, primarily *Lucicutia flavicornis* and *Pleuromamma* spp., contributed 21% dry weight; by October, they contributed 46% dry weight. *Calanoides carinatus, Metridia lucens,* and *Neocalanus tonsus* occurred less frequently. The dry weight contribution by cyclopoids (*Oncaea media* and *O. venusta*) was very little (< 1%) between April and October, although frequency of occurrence values were 20 to 35%. No cyclopoids were consumed after October.

Other prey were important during certain months. Salps were present during August and October, while gastropods were found in October and December. Hyperiid amphipods, mainly *Parathemisto gracillipes*, were consumed during August when they were common in the plankton (Young, unpublished data). Small amounts of fish (occasionally *Maurolicus muelleri*), fish scales and eggs were consumed between June and December.

Diaphus danae

Midwater fishes, mostly *Lampanyctodes hectoris* and occasionally *Maurolicus muelleri*, were the main prey con-

Table 2. *Maurolicus muelleri*, *Lampanyctodes hectoris* and *Diaphus danae*. Composition of diets of fish from continental slope waters off eastern Tasmania. % Biomass: % of total dry weight of prey; % F: % frequency of occurrence; *n*: number of stomachs examined; percentage totals for each main prey taxa are given in parentheses; –: prey absent

Prey	*M. muelleri* 28–55 mm SL 0.12–0.76 g DW[a] [0.30±0.02 g DW][b] (*n*=719)		*L. hectoris* 27–73 mm SL 0.10–1.28 g DW[a] [0.65±0.08 g DW][b] (*n*=975)		*D. danae* 29–122 mm SL 0.15–9.00 g DW[a] [2.07±0.33 g DW][b] (*n*=538)	
	% Biomass	% F	% Biomass	% F	% Biomass	% F
Chaetognatha	(–)	(–)	(–)	(–)	(< 0.1)	(0.2)
Siphonophora	(–)	(–)	(0.6)	(0.1)	(–)	(–)
Crustacea	(98.7)	(99.0)	(93.3)	(98.2)	(17.2)	(81.4)
Ostracoda	(< 0.1)	(0.7)	(< 0.1)	(1.0)	(< 0.1)	(3.7)
Copepoda	(37.1)	(44.0)	(10.9)	(42.9)	(0.2)	(39.8)
Calanoida	36.5	42.5	10.7	38.0	< 0.1	38.6
Acartia clausii	–	–	–	–	< 0.1	0.2
Calanoides carinatus	0.1	2.5	< 0.1	0.5	–	–
Calanus australis	0.2	2.3	< 0.1	0.9	–	–
Calanus finmarchicus	–	–	< 0.1	0.1	–	–
Candacia bipinnata	0.9	5.0	0.5	3.7	< 0.1	4.7
Candacia pectinata	–	–	< 0.1	0.3	–	–
Euchaeta marina	–	–	0.2	0.8	–	–
Euchirella rostrata	2.2	2.9	< 0.1	0.4	–	–
Euchirella spp.	1.3	2.5	–	–	–	–
Heterorhabdus papilliger	–	–	< 0.1	0.1	–	–
Lucicutia flavicornis	–	–	5.7	7.1	< 0.1	0.2
Metridia lucens	< 0.1	0.2	0.1	1.9	–	–
Neocalanus tonsus	10.0	9.1	0.2	1.8	< 0.1	0.2
Pleuromamma abdominalis	3.4	9.8	0.3	5.2	< 0.1	5.3
Pleuromamma gracilis	< 0.1	0.2	0.7	11.2	< 0.1	6.3
Pleuromamma remains	1.7	3.2	0.8	8.3	0.1	23.5
Unidentified calanoids	16.5	30.3	2.0	25.8	< 0.1	11.4
Cyclopoida	0.7	20.3	0.2	15.5	< 0.1	4.7
Corycaeus spp.	–	–	–	–	< 0.1	0.2
Oithona spp.	–	–	< 0.1	0.3	–	–
Oncaea conifera	–	–	< 0.1	0.3	–	–
Oncaea media	0.1	7.5	< 0.1	3.4	< 0.1	0.8
Oncaea venusta	0.6	19.4	0.1	13.4	< 0.1	3.5
Oncaea spp.	< 0.1	0.4	< 0.1	1.3	< 0.1	0.6
Leptostraca	(< 0.1)	(0.2)	(–)	(–)	(–)	(–)
Mysidacea	(–)	(–)	(0.1)	(0.3)	(–)	(–)
Amphipoda	(0.2)	(1.2)	(0.4)	(1.5)	(< 0.1)	(3.1)
Hyperiidae	–	–	0.2	0.6	< 0.1	1.2
Parathemisto gracillipes	–	–	0.2	1.3	< 0.1	0.4
Pronoidae	–	–	–	–	< 0.1	0.2
Amphipod remains	–	–	–	–	< 0.1	1.2
Euphausiacea	(54.8)	(51.1)	(78.5)	(59.1)	(14.9)	(36.5)
Euphausia longirostris	–	–	–	–	< 0.1	0.2
Euphausia lucens	–	–	3.1	3.8	1.3	2.2
Euphausia similis var. *armata*	18.9	12.3	34.7	21.6	9.0	26.3
Euphausia spp.	0.8	2.9	6.6	13.9	–	–
Nematoscelis megalops	1.4	1.1	0.5	1.6	0.7	0.6
Nematoscelis microps	–	–	< 0.1	0.1	–	–
Nematoscelis spp.	–	–	0.1	0.1	–	–
Nyctiphanes australis	0.1	0.2	< 0.1	0.1	–	–
Thysanopoda egregia	–	–	0.6	0.5	–	–
Unidentified euphausiids	30.9	32.9	33.1	19.1	3.8	8.0
Caridea (juveniles)	(–)	(–)	(< 0.1)	(0.1)	(0.1)	(0.6)
Brachyura (larvae)	(–)	(–)	(–)	(–)	(1.1)	(2.5)
Unidentified crustacean remains	(6.5)	(23.8)	(3.3)	(11.2)	(0.8)	(20.4)
Gastropoda	(< 0.1)	(0.2)	(1.5)	(5.8)	(< 0.1)	(0.8)
Bivalvia	(< 0.1)	(0.5)	(–)	(–)	(< 0.1)	(0.2)
Thaliacea (Salpidae)	(< 0.1)	(0.2)	(0.4)	(1.8)	(0.1)	(5.9)

Table 2 (continued)

Prey	*M. muelleri* 28–55 mm SL 0.12–0.76 g DW[a] [0.30 ± 0.02 g DW][b] (n = 719)		*L. hectoris* 27–73 mm SL 0.10–1.28 g DW[a] [0.65 ± 0.08 g DW][b] (n = 975)		*D. danae* 29–122 mm SL 0.15–9.00 g DW[a] [2.07 ± 0.33 g DW][b] (n = 538)	
	% Biomass	% F	% Biomass	% F	% Biomass	% F
Pisces	(< 0.1)	(0.7)	(1.4)	(3.0)	(82.9)	(22.5)
Lampanyctodes hectoris	–	–	–	–	72.5	14.5
Maurolicus muelleri	–	–	–	–	10.0	0.8
Unidentified fish	< 0.1	0.5	–	–	< 0.1	1.4
Fish eggs	< 0.1	0.4	–	–	< 0.1	4.1
Fish scales	< 0.1	0.4	0.2	2.7	0.2	4.1
Unidentified remains	(1.3)	(6.2)	(3.3)	(23.5)	(–)	(–)
Dry weight range of stomach contents (mg)	0.1 – 22.1		0.5 – 25.0		10.2 – 555.2	
Mean dry weight of stomach contents (mg) ± SE (mg)	2.3 ± 0.24		1.8 ± 0.17		23.1 ± 3.66	

[a] Dry weight range [b] Mean dry weight (± SD)

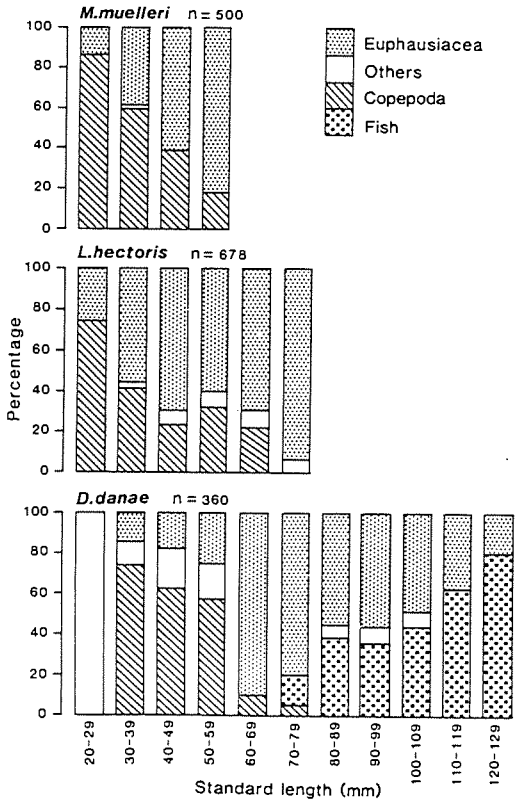

Fig. 3. *Maurolicus muelleri*, *Lampanyctodes hectoris* and *Diaphus danae*. Frequency of occurrence of major prey taxa across size classes. *n*: number of fish examined

sumed by *Diaphus danae* in summer and autumn, whereas copepods and euphausiids were consumed at other times of the year (Fig. 2). There were significant seasonal differences in the prey biomass of calanoids, amphipods, euphausiids, salps and fish (Table 3). Calanoids, typically *Candacia bipinnata*, *Pleuromamma abdominalis* and *P. gracilis*, were eaten between June and August, as were the cyclopoids *Oncaea media* and *O. venusta*. Euphausiids were consumed between April and December. In summer, *Euphausia lucens* and *E. similis* var. *armata* were the main euphausiids identified. Ostracods, hyperiid amphipods (families Hyperiidae and Pronoidae), salps, fish scales and eggs were consumed in small quantities between April and August. Crab larvae were consumed only in December and the following April.

Relationships between fish length and prey type

The hypothesis that the proportions of major prey taxa were homogeneous across size classes in *Maurolicus muelleri* was rejected. The hypothesis that the proportions of each prey taxon change linearly with predator size was retained (Table 4). The proportion of euphausiids in the stomach contents increased with increasing predator size, whereas the proportion of copepods decreased (Fig. 3, Table 4). It is noteworthy that the frequency of occurrence of cyclopoid copepods (< 3 mm TL) was 92% (107 out of a total of 113) in *M. muelleri* less than 40 mm SL, whereas the frequency of occurrence of calanoid copepods (3 to 8 mm TL) in the same fish was only 67% (146 occurrences out of 240).

Homogeneity of the proportions of prey taxa across size classes was similarly rejected for *Lampanyctodes hectoris*, although these proportions did not change linearly with predator size (Table 4). Nevertheless, euphausiids became predominant in the diet of larger individuals (Fig. 3). In addition, small gastropods (shell diam = 1.5 to 3.0 mm) were recorded mainly from individuals of 40 to 60 mm SL, while hyperiid amphipods (5 to 7 mm TL) were found chiefly in individuals of 50 to 60 mm.

Table 3. *Maurolicus muelleri*, *Lampanyctodes hectoris* and *Diaphus danae*. Seasonal changes in prey biomass (mg dry weight) in stomachs between April 1984 and April 1985. Significance values for acceptance (NS) or rejection ($P < 0.05$) of the hypothesis that prey proportions do not vary with season are listed beside each major prey taxon. –: prey absent

Prey	*M. muelleri*								*L. hectoris*							
	Apr.	June	Aug.	Oct.	Dec.	Feb.	Apr.	*P*	Apr.	June	Aug.	Oct.	Dec.	Feb.	Apr.	*P*
Calanoida	4.5	7.7	57.7	291.7	135.7	32.0	29.2	< 0.001	14.1	5.2	31.7	175.9	9.4	–	1.0	< 0.001
Cyclopoida	6.2	6.1	0.1	–	–	–	–	< 0.005	2.6	0.2	1.3	1.5	–	–	–	NS
Amphipoda	–	–	–	–	–	–	–	–	–	–	8.0	< 0.1	–	–	–	< 0.001
Euphausiacea	53.6	38.5	17.4	209.0	184.2	232.3	157.4	< 0.01	243.9	20.5	93.6	136.9	142.6	353.5	268.9	< 0.001
Crustacean remains	53.3	57.9	4.9	–	–	–	–	< 0.001	–	17.2	7.7	37.1	–	–	–	< 0.001
Gastropoda	–	–	–	–	–	–	–		–	–	–	17.9	–	–	–	
Others	7.7	0.3	1.0	4.7	< 0.1	–	3.7	NS	89.1	0.8	7.8	9.0	–	–	0.4	< 0.001
Total dry wt of stomach contents (mg)	125.3	110.6	81.2	506.4	319.9	264.3	190.2		349.8	45.1	154.8	384.3	166.5	356.1	285.3	
Total dry wt of fish examined (g)	22.51	16.32	9.04	37.90	23.12	23.76	20.29		138.63	50.98	68.55	80.17	36.33	43.99	35.72	
g kg^{-1} fish dry wt (±SE)	5.57 (1.56)	6.78 (1.61)	8.98 (2.29)	13.36 (2.09)	13.84 (1.71)	11.12 (2.85)	9.37 (2.42)		2.52 (0.44)	0.89 (0.24)	2.26 (0.50)	4.79 (0.75)	4.58 (1.29)	8.09 (1.59)	7.98 (1.37)	
No. of stomachs with food	96	87	46	100	55	85	95		214	81	108	140	90	62	96	

Prey	*D. danae*							
	Apr.	June	Aug.	Oct.	Dec.	Feb.	Apr.	*P*
Calanoida	2.5	28.6	21.4	0.8	–	–	–	< 0.001
Cyclopoida	< 0.1	0.6	1.6	–	–	–	–	NS
Amphipoda	–	0.3	5.7	< 0.1	–	–	–	< 0.05
Euphausiacea	173.5	77.1	21.1	28.3	329.5	190.0	1 411.9	< 0.001
Crustacean remains	–	185.7	15.5	2.4	< 0.1	–	–	NS
Gastropoda	–	–	–	–	–	–	–	
Others	17.8	22.2	16.9	1.2	100.8	–	82.0	< 0.001
Total dry wt of stomach contents (mg)	835.5	148.7	86.0	44.3	4 278.5	3 836.6	3 183.3	
Total dry wt of fish examined (g)	281.25	50.05	42.87	85.40	287.13	141.51	272.94	
g kg^{-1} fish dry wt (±SE)	2.97 (1.24)	2.97 (0.91)	2.01 (0.41)	0.52 (0.14)	14.90 (4.80)	27.11 (10.19)	11.66 (2.43)	
No. of stomachs with food	88	100	116	34	70	26	56	

Prey type also varied with the size of *Diaphus danae* (Table 4). Copepods were progressively replaced by euphausiids in fish up to 60 mm SL. In larger individuals there was a shift from euphausiids to fish as the dominant prey (Fig. 3, Table 4). The low linearity measure for euphausiids reflects their predominance as prey of middle-sized *D. danae*.

As the main prey taxa of both *Maurolicus muelleri* and *Lampanyctodes hectoris* were copepods and euphausiids, we compared the proportions of the prey of these two species. *L. hectoris*, the larger predator, consumed a significantly higher relative biomass (84%; $P < 0.001$) of the larger prey type, euphausiids, than did *M. muelleri* (64%). Conversely, *M. muelleri* fed on a relatively higher biomass of copepods.

Diet in relation to depth

Similar proportions of the major taxa were found above and below 160 m in all three species (Table 5). The proportions varied slightly in *Maurolicus muelleri* as the large number of small individuals from shallow depths contained chiefly copepods.

Table 4. *Maurolicus muelleri, Lampanyctodes hectoris* and *Diaphus danae.* Relationship between fish length and prey taxa in stomachs. Values are number of occurrences of a taxon as the main prey by dry weight in a stomach, by size class. C: copepods; E: euphausiids; F: fish; O: other taxa; (*n*): number of stomachs examined

	M. muelleri			*L. hectoris*					*D. danae*				
	C	E	(*n*)	C	E	F	O	(*n*)	C	E	F	O	(*n*)
Size class (mm SL)													
20– 29	6	1	(7)	3	1	0	0	(4)	0	0	0	0	(0)
30– 39	171	116	(287)	45	62	1	0	(108)	30	6	0	5	(41)
40– 49	58	94	(152)	43	123	8	8	(182)	58	18	3	16	(95)
50– 59	9	42	(51)	71	126	3	11	(211)	6	3	2	0	(11)
60– 69				34	107	8	6	(155)	0	33	21	0	(54)
70– 79				0	17	0	1	(18)	1	16	1	2	(20)
80– 89									0	29	21	5	(55)
90– 99									0	33	21	6	(60)
100–109									0	12	11	2	(25)
110–119									0	14	24	0	(38)
120–129									0	1	4	0	(5)
Total no. of occurrences	244	253	(497)	196	436	20	26	(678)	95	165	108	36	(404)
Likelihood – ratio test statistics (G^2), degrees of freedom (DF) and significance levels for homogeneity and column-effects hypotheses													
	G^2	DF	*P*	G^2	DF		*P*		G^2	DF		*P*	
Homogeneity hypothesis	46.18	3	< 0.001	35.86	9		< 0.001		293.4	21		< 0.001	
Column effects hypothesis	0.33	2	> 0.5	24.29	6		< 0.001		28.41	18		> 0.05	
Linearity parameters (values further from zero imply increasing linearity and are analogous to slope coefficients)													
Copepods		– 0.94			–					– 1.08			
Euphausiids		0.94								0.35			
Fish										0.80			
Others										– 0.07			

Table 5. *Maurolicus muelleri, Lampanyctodes hectoris* and *Diaphus danae.* Percentage occurrence of major prey items in stomachs above and below 160 m depth. C: copepods; E: euphausiids; F: fish; (*n*): number of fish examined

Depth (m)	*M. muelleri*			*L. hectoris*			*D. danae*		
	C	E	(*n*)	C	E	(*n*)	E	F	(*n*)
≧ 160	58	42	(87)	37	60	(214)	55	43	(83)
≦ 160	46	54	(431)	29	66	(444)	53	40	(121)

Stomach fullness

A significant relationship ($P < 0.05$) between time of year and stomach fullness was found in *Maurolicus muelleri*, with the highest values recorded between June and October (Table 6), when copepods were the main prey. Lowest values occurred in February and April, 1985. Significant diel and depth differences indicated that *M. muelleri* fed mainly in the evening (18.00–24.00 hrs) ($P < 0.05$) above 200 m depth ($P < 0.05$). Stomach fullness values were significantly higher in *M. muelleri* than in either *Lampanyctodes hectoris* or *Diaphus danae* ($P < 0.05$) (Fig. 4).

In *Lampanyctodes hectoris*, a significant relationship ($P < 0.005$) existed between time of year and stomach fullness. Highest stomach fullness values were found in December and February (Table 6), when euphausiids were eaten almost exclusively (Fig. 2). Lowest values occurred during winter (particularly June). No significant diel or depth differences were detected, although Fig. 4 shows that feeding was more intensive between 18.00 and 24.00 hrs than at other times.

A significant seasonal relationship ($P < 0.005$) with stomach fullness was found in *Diaphus danae*. Stomach fullness values were highest in February 1985 (Table 6), when fish were the main prey. Lowest values were found in spring, when euphausiids were consumed. No significant diel or depth differences were detected, although stomach fullness values were generally higher in the evening (Fig. 4).

Discussion

The major prey taxa of *Maurolicus muelleri* and *Lampanyctodes hectoris* were euphausiids and copepods, respectively, while *Diaphus danae* fed mainly on other lanternfish (chiefly *L. hectoris*), copepods and euphausiids. The relative importance of the types of prey eaten, however, was dependent on the time of year and on the size of the individual predator. The importance of copepods

Table 6. *Maurolicus muelleri, Lampanyctodes hectoris* and *Diaphus danae*. Bimonthly mean stomach fullness values (g stomach contents wet wt kg^{-1} fish wet wt) between April 1984 and April 1985. Results of regression analyses are shown at bottom of table. (*n*): number of fish examined. *t* = Student's *t* test

	M. muelleri			*L. hectoris*			*D. danae*		
	$\bar{x}$	±SE	(*n*)	$\bar{x}$	±SE	(*n*)	$\bar{x}$	±SE	(*n*)
1984									
April	16.6	4.9	(113)	9.5	1.5	(257)	11.7	2.7	(88)
June	22.3	5.0	(107)	3.0	2.3	(104)	14.6	2.2	(103)
August	19.9	6.8	(60)	6.0	2.0	(138)	8.7	2.0	(123)
October	21.9	4.7	(120)	8.6	2.1	(143)	3.6	3.8	(35)
December	15.2	5.6	(78)	15.7	2.0	(120)	12.6	2.3	(95)
1985									
February	12.5	4.7	(121)	13.2	2.8	(71)	24.1	4.0	(32)
April	9.2	4.7	(120)	8.8	2.0	(142)	14.0	2.8	(62)
	(t=2.37; DF=40; $P<0.05$)			(t=3.25; DF=52; $P<0.005$)			(t=2.98; DF=32; $P<0.005$)		

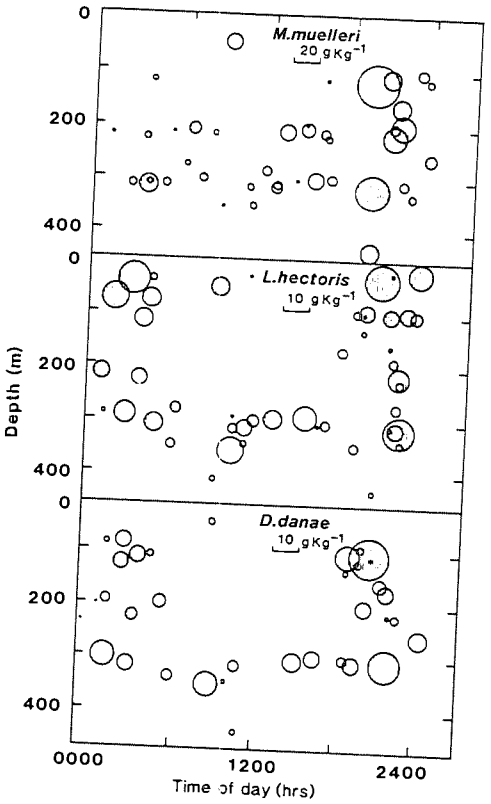

Fig. 4. *Maurolicus muelleri, Lampanyctodes hectoris* and *Diaphus danae*. Stomach fullness in relation to depth and time of day. Each circle represents mean stomach fullness value per trawl; scale refers to diameter of circle; shaded circles represent hours of darkness

(Hopkins and Baird, 1977; Clarke, 1980; Kinzer and Schulz, 1985) and euphausiids (Paxton, 1967; Samyshev and Schetinkin, 1971; Tyler and Pearcy, 1975) as prey of midwater fish is well documented. Generally, euphausiids are more prevalent in midwater fish found in productive upwelling regions or waters close to land (as in this study) and copepods are the main prey of oceanic species. However, the predation of one myctophid species on another to the extent shown by *D. danae* on *L. hectoris* has not previously been reported.

Dietary overlap was high between *Maurolicus muelleri* and *Lampanyctodes hectoris*. The copepods *Candacia bipinnata, Neocalanus tonsus, Pleuromamma* spp., species of *Oncaea*, and the euphausiids *Euphausia similis* var. *armata*, and *Nematoscelis megalops* were common to each predator, implying little dietary specialization. This phenomenon has been reported for other high-latitude midwater fish (Tyler and Pearcy, 1975). However, the overlap between *Diaphus danae* and the former species was low, even though all three species had many prey species in common (Table 2). This can be explained by the seasonal importance of *L. hectoris* in the diet of *D. danae*.

Marked seasonal differences in diet were found. Copepods were the dominant prey item in *Maurolicus muelleri* during late winter and early spring, being gradually replaced by euphausiids with the approach of summer. A similar pattern was observed in *Lampanyctodes hectoris*, although euphausiids were more prevalent throughout the year and dominated the diet of this species between December and April. Copepods and euphausiids were restricted mainly to winter and early spring in *Diaphus danae*, after which time fish became increasingly important and were the main prey consumed in summer. Seasonal differences in diet have also been reported by Gjosaeter (1981 a), who found that *M. muelleri* off Norway consumed mainly copepods in spring, and euphausiids in winter. Similarly, the myctophids *Benthosema glaciale* and *Notoscopelus elongatus* ate euphausiids in winter and copepods during summer (Gjoesaeter, 1973, 1981 b).

A seasonal change in diet is typical of temperate fishes. Hopkins and Baird (1977) suggested that it was related to seasonal changes in prey distribution and abundance. This is supported by data from eastern Tasmania. Nyan Taw (1975) reported that copepods were most abundant during winter and spring, which is when they most frequently occurred as prey of all three species. *Neocalanus tonsus*, one

of the few abundant summer copepods reported by Nyan Taw, was a frequent prey item of *Maurolicus muelleri* in the present study between October and April. Euphausiids are most abundant during summer (Nyan Taw, 1975; CSIRO, unpublished data). *Lampanyctodes hectoris*, the major prey of *Diaphus danae* between December and April, was also most abundant over the summer months.

Our results indicate that size-selective predation (O'Brien, 1979) may determine not only the types of prey eaten by all three species but may also be related to the size of the individual predator. Smaller individuals of *Maurolicus muelleri* fed on copepods, while larger fish ate euphausiids. Copepods were progressively replaced by euphausiids in *Diaphus danae* less than 60 mm SL; above this size, fish became increasingly important. In *Lampanyctodes hectoris*, although euphausiids were the main prey in all but the smallest size class, their importance increased with size. Similar results have been reported from other midwater feeding studies. Gjosaeter (1981a) found that *M. muelleri* smaller than 20 mm fed primarily on copepods, while larger fish fed equally on copepods and euphausiids. Samyshev and Schetinkin (1971) also found a correlation between predator size and diet in *M. muelleri* and in species of *Diaphus*. Small individuals of another myctophid species, *Hygophum benoiti*, feed almost exclusively on copepods, while larger individuals take primarily euphausiids (Scotto di Carlo *et al.*, 1982).

No correlation was found between prey type and depth. This contrasts with the findings of Pearcy *et al.* (1979), who reported little similarity in either the diets or rank order of common prey of individuals of the myctophid *Stenobrachius leucopsarus* separated by depth in deep water off Oregon (USA). The slope-species studied here are distributed between the surface and approximately 500 m depth (CSIRO, unpublished data) and hence have a much narrower range in which to feed. As all three species migrate vertically, they are likely to encounter most prey types present in the water column.

Significant diel feeding-periodicity was found only in *Maurolicus muelleri*, which fed mainly at night above 200 m. This contrasts with the findings of Gjosaeter (1981a), who found no evidence for diel feeding in *M. muelleri*. In oceanic waters near Hawaii, Clarke (1978) found that nine of ten species of myctophid examined fed "solely or principally at night in the upper layers". This is perhaps true of most vertically migrating oceanic midwater-fish (Hopkins and Baird, 1977; Kinzer and Schulz, 1985). Nevertheless, in more productive areas such as upwelling zones (Kinzer, 1977, 1982) or water close to land (Paxton, 1967; Tyler and Pearcy, 1975; Gjosaeter, 1981a, b), myctophids tend to feed continuously. This view is supported by the present study, although our results suggest that feeding was more intensive in both *Lampanyctodes hectoris* and *Diaphus danae* during the night (Fig. 4).

Synchronization of growth with availability of prey

Present results indicate that time of year and predator size were the major determinants of the type and amount of prey eaten. Feeding intensity (as indicated by stomach fullness) and the size structure of the population may be synchronized with seasonal variations in prey abundance in order to maximize each species' share of the available food resource.

During August, when the mode of *Maurolicus muelleri* was less than 40 mm SL, feeding intensity was highest, and copepods, abundant during winter, were the main prey consumed. In October, the population mode had increased to 45 mm SL and euphausiids were becoming more important as prey. By December, when euphausiid abundance peaks, euphausiids dominated the diet and the maximum length had been reached. In *Lampanyctodes hectoris* feeding intensity was highest and juvenile recruitment occurred in summer, when euphausiids were abundant. Small *Diaphus danae* occurred during winter when copepods were abundant, but by summer had reached their maximum length and shifted to fish as their main prey; stomach fullness values were highest at this time.

In a similar feeding study of the three most abundant myctophids off Oregon, Tyler and Pearcy (1975) suggested that competition for the available food resource was reduced by spatial separation in the water column. We suggest competition may also be reduced by the synchronization of the seasonal growth cycles of each species with the abundance of its prey.

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APPENDIX 7

Submitted for publication

Reproductive biology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia

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Abstract

The reproductive biology of *Lampanyctodes hectoris* and *Maurolicus muelleri* and *Diaphus danae*, from continental-slope waters of eastern Tasmania, was examined between April 1984 and June 1985. *Lampanyctodes hectoris* spawned in winter, whereas *M. mulleri* spawned from late winter to early summer. Apart from one ripe male, no reproductive activity was detected in *D. danae*; this species may be an expatriate in these waters. Fecundity was positively correlated with standard length in *L. hectoris*, but not in *M. muelleri*. The ratio of females to males increased with length in all three species. The spermatozoa of *L. hectoris* is atypical of vertebrates and has no tail.

Introduction

Information on the reproductive biology of myctophid and stomiatoid fishes is limited and few comparative data are available. Reproductive studies have concentrated on either macroscopic staging of gonads (Paxton, 1967; Clarke, 1973, Badcock and Merrett, 1976; Karnella and Gibbs, 1977; Robertson, 1977; Gjosaeter, 1981a) or sizing of eggs (Halliday, 1970; Smoker and Pearcy, 1970; Pertseva-Ostromouva, 1973; Clarke, 1982). Few histological studies have been attempted (O'Day and Nafpaktitis, 1967; Zurbrigg and Scott, 1972) and none, to our knowledge, have examined seasonal changes in gonad maturity.

Lampanyctodes hectoris (Gunther, 1876) (Myctophidae), Maurolicus muelleri (Gmelin, 1789) (Sternoptychidae), and Diaphus danae Taning, 1932 (Myctophidae) are the most abundant midwater fishes on the upper continental slope of eastern Tasmania (Young and Blaber, 1986). Midwater fishes, particularly L. hectoris, are the main diet of many slope fishes in these waters (Blaber and Bulman, in preparation); however, a seasonal cycle in the abundance of these fishes has been reported (J. May, pers. comm.). To understand the basis for this seasonality the reproductive biology of these species was examined. Aspects of the reproductive biology of M. muelleri in eastern Australian waters were studied by Clarke (1982), but little has been reported on L. hectoris (Robertson, 1977; Crawford, 1980, Cruickshank, 1983) and nothing on D. danae.

Ripe Lampanyctodes hectoris, together with planktonic eggs, have been found off New Zealand during August (late winter) (Robertson, 1977). Larvae of L. hectoris have been taken off South Africa between August and

November (Ahlstrom *et al*, 1976) The principal spawning season of *Maurolicus muelleri* is between late winter and spring off eastern Australia (Clarke, 1982), coinciding with increased plankton production in the area. In New Zealand waters the main spawning period occurs later, in spring and summer (Robertson, 1976). No reproductive data are available for *Diaphus danae*.

This paper examines seasonal changes in the reproductive biology of each species, using gonad histology and gonadosomatic indices. It presents data on fecundity and sex ratios and provides a description of the mature spermatozoa of *Lampanyctodes hectoris*.

Materials and Methods

Midwater fishes were collected at two-monthly intervals between April 1984 and June 1985 over the upper continental slope 12 nautical miles east of Maria Island, Tasmania (42°39'S, 148°28'E). Sampling details are given in Young and Blaber (1986). The three most abundant midwater species, Maurolicus muelleri, Lampanyctodes hectoris and Diaphus danae, were selected for reproductive examination. A size range of each species collected on each cruise was preserved in Bouins fluid (Hale, 1958) and later transferred to 70% alcohol in the laboratory. Additional samples, preserved in 10% formalin, were taken for determination of fecundity. Profiles of water temperature and salinity were taken over the study area on each cruise from standard hydrocasts to 400 m.

In the laboratory, fish were measured (Standard length, SL, ± 0.5 mm) and weighed (±0.001 g) and the gonads removed and weighed (±0.001 g). Gonads were embedded in paraffin wax, sectioned at 8 μm and stained with haemotoxylin and eosin (McManus and Mowry, 1964). Gonad maturation was classified according to Dipper and Pullin (1979) for females, and Cyrus and Blaber (1984) and Davis (1977) for males. Each gonad was staged, based on the relative amounts of developmental cells, as follows:

Females:

Stage	Histology
1. immature	oogonia present
2. resting/developing	mainly (>50% of all egg types) pre-vitellogenic oocytes; some oogonia
3. maturing	mainly non-staining yolk; some yolk precursors

4. ripe	mainly red-staining yolk, some non-staining yolk
5. ripe-running	homogeneous yolk; development complete
6. spent-resting	atresion of ripe oocytes plus pre-vitellogenic oocytes

Males:

Stage	Histology
1. immature	spermatogonia and some primary spermatocytes
2. resting/developing	few spermatids; primary and secondary spermatocytes
3. maturing	mainly spermatids and secondary spermatocytes
4. ripe	mainly spermatozoa; some spermatids
5. ripe-running	gonad all spermatozoa

No macroscopic staging was attempted because of the lack of obvious gonad differentiation in all but ripe fish. The fecundity of Lampanyctodes hectoris was established from oocytes larger than 0.30 mm. These were translucent to opaque and distinguishable from smaller, transparent oocytes. In Maurolicus muelleri fecundity was estimated from the number of enlarged, yolked oocytes (>0.35 mm; Clarke, 1982). Because of an apparent bimodality in mature egg size in L. hectoris and M. muelleri, random samples of approximately 100 eggs were measured from ripe fish to determine whether there was evidence for multiple spawning. Scanning electron micrographs were taken of mature spermatozoa of L. hectoris after etching with HCl and gold plating.

Data analysis

Seasonal variations in gonad maturation stage of females and males were compared, using analysis of variance. If a significant difference between months was found, pair-wise t-tests were used to test which months were significantly different. Gonadosomatic indices (GSI) were calculated as the ratio of gonad wet weight to total fish wet weight, expressed as a percentage. The GSI data were transformed to logarithms, as the samples from the populations had unequal variances. Seasonal variations in GSI values of females and males were examined, using either analysis of covariance (ancova) or analysis of variance. An ancova was used if a regression of log (GSI) on log (SL), fitted separately to the fishes from each cruise, accounted for a significantly greater amount of variation than fitting only mean GSI values. Otherwise an analysis of variance was used. Pair-wise t-tests were again used to identify months that were significantly different. As gonad maturation stage was not a continuous variable in Lampanyctodes hectoris and Maurolicus muelleri, the correlation between gonadosomatic index and gonad maturation stage was examined using the non-parametric Spearman rank correlation (r_s) test (Zar, 1984). Individuals were sexed from histological examinations as there was no readily identifiable sexual dimorphism in the three species examined. Differences in sex ratios between cruises and with size were statistically tested using chi-squared (χ^2) goodness of fit.

Results

Physical environment

Mean sea-surface temperature ranged from 12.2°C in October to 18.5°C in the following April (Fig. 1), following the annual influx of surface tropical East Australian Current water to the prevailing modified subantarctic water (G. Harris, in preparation). Temperatures at a depth of 200 m remained between 11.6°C and 13.5°C throughout the year. Surface salinity values mirrored the temperature changes, with lowest salinities in October and December 1984 and highest in February and March 1985.

Reproduction

A total of 454 fish were examined. Table 1 gives the number, sex and size range of individuals examined from each sampling period.

Lampanyctodes hectoris

Seasonal changes in gonad development and gonadosomatic index

Ripe females of *Lampanyctodes hectoris* were usually greater than 55 mm SL, although one individual was ripe at 32 mm SL (Fig. 2). Ripe males ranged from 32 mm to 62 mm. A seasonal difference was found in mean gonad stage in female *L. hectoris* ($F = 50.7$; $df = 7,137$; $P<0.01$) which, from pair-wise t-tests, was significantly higher in April, June and August ($P<0.01$) than in other months (Fig. 3). Ripe females were present mainly in August 1984, when mean water temperature was below 13°C (Fig. 1). Maturing females were found in April and June, 1984 and one maturing female was found in June 1985 (Fig. 2). A seasonal difference was also found in male gonad activity ($F = 16.1$; $df = 4,58$; $P<0.01$). Ripe and

Figure 1

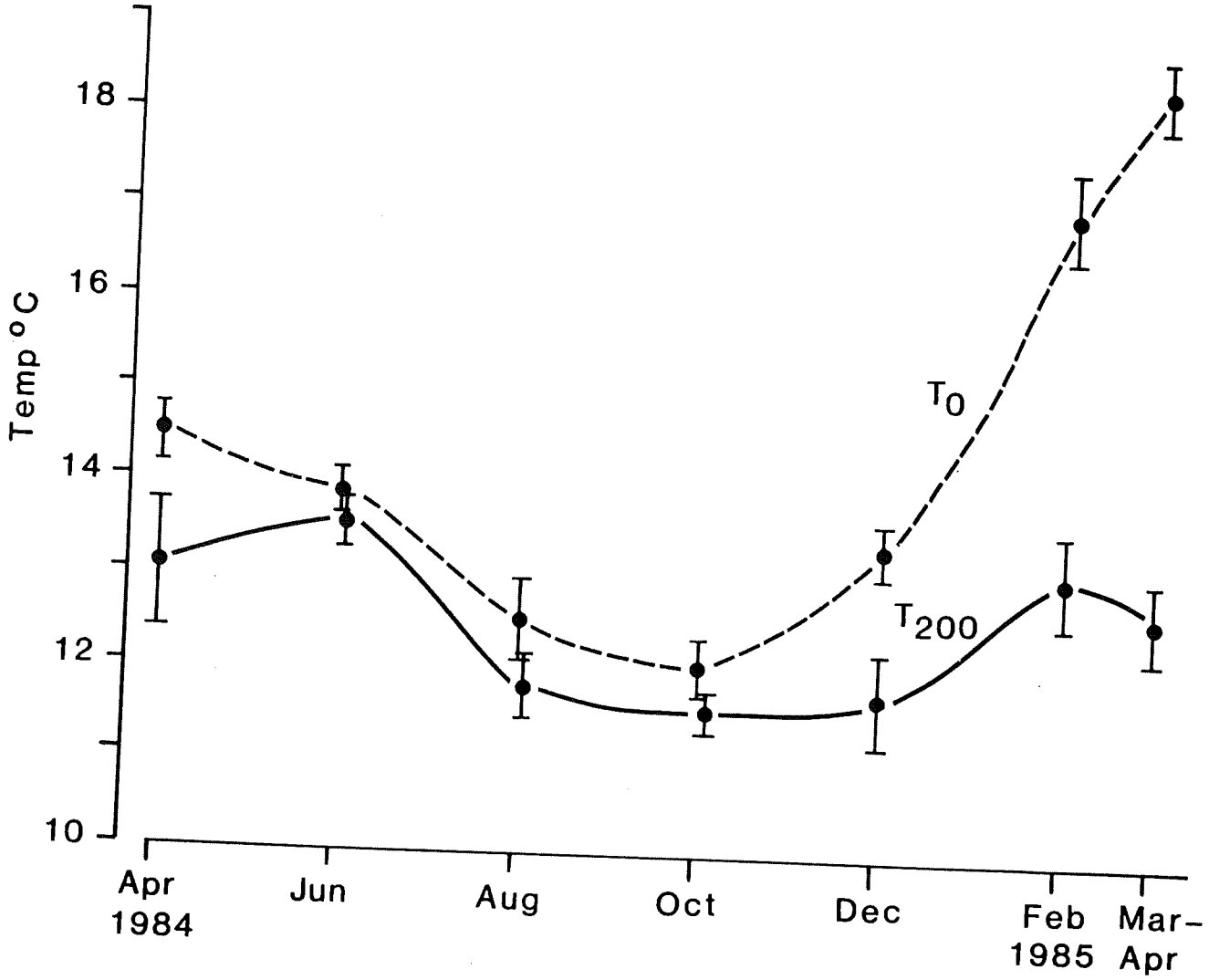

Temp °C
18
16
14
12
10
T_0
T_{200}
Apr 1984
Jun
Aug
Oct
Dec
Feb 1985
Mar–Apr

Table 1: *Lampanyctodes hectoris*, *Maurolicus muelleri* and *Diaphus danae*. Size range, sex and number of individuals whose gonads were examined from off Maria Island between April 1984 and June 1985 (Size range is S.L. in mm; F = females, M = males).

	L. hectoris			*M. muelleri*			*D. danae*		
		numbers			numbers			numbers	
Month	Size range (mm)	F	M	Size range (mm)	F	M	Size range (mm)	F	
April 1984	42-65	20	-	34-49	6	-	-	-	-
June	38-64	22	24	34-52	13	5	38-51	4	
August	32-66	25	17	34-41	7	2	39-50	11	-
October	50-66	13	6	39-51	11	12	62-96	3	1
December	31-72	16	3	43-54	17	13	66-115	20	12
February 1985	55-71	12	1	35-53	22	1	70-109	4	
March	33-72	17	6	34-53	19	3	80-111	-	
June	36-60	20	-	-	-	10	66-107	23	6
Total numbers		145	67		95	36		69	42
F/M Sex ratio		2.16:1			2.64:1			1.64:1	

ripe-running males of L. hectoris were found between June and October, with ripe-running males contributing 71% of males sampled in August (Fig. 2). Gonad stages were significantly higher ($P<0.01$) (Fig. 3) at this time than in the following autumn.

As the regression slopes of log (GSI) vs log (S.L.) for each two monthly period were parallel and significantly different from zero ($F = 21.7$; $df = 1,136$; $P<0.01$), seasonal differences in GSI values were tested using ancova (see Methods). A seasonal difference in GSI of females was found ($F = 120.2$; $df = 7,136$; $P<0.01$), with significantly higher values in June and August 1984 and June 1985 ($P<0.01$) (Fig. 3). A seasonal difference was found in male GSI values ($F = 8.0$; $df = 4,58$; $P<0.01$), with significantly higher values occurring in June and August ($P<0.05$). There was no relationship between size and GSI in males.

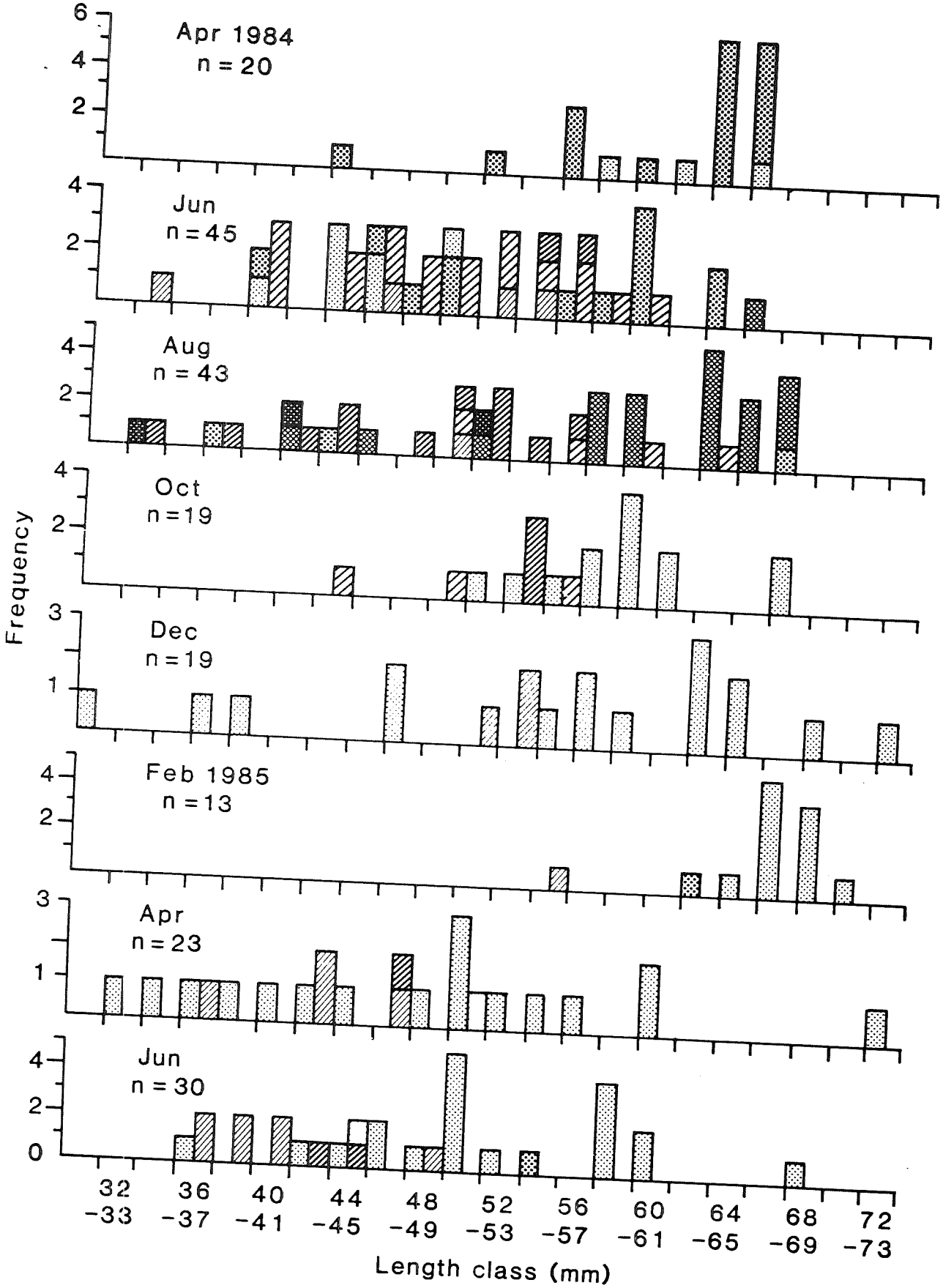
Gonadosomatic index was correlated with gonad stage as determined by histological examination in both females ($r_s = 0.68$, $df=141$, $P<0.01$) and males ($r_s = 0.36$, $df=65$, $P<0.005$) of Lampanyctodes hectoris.

Fecundity

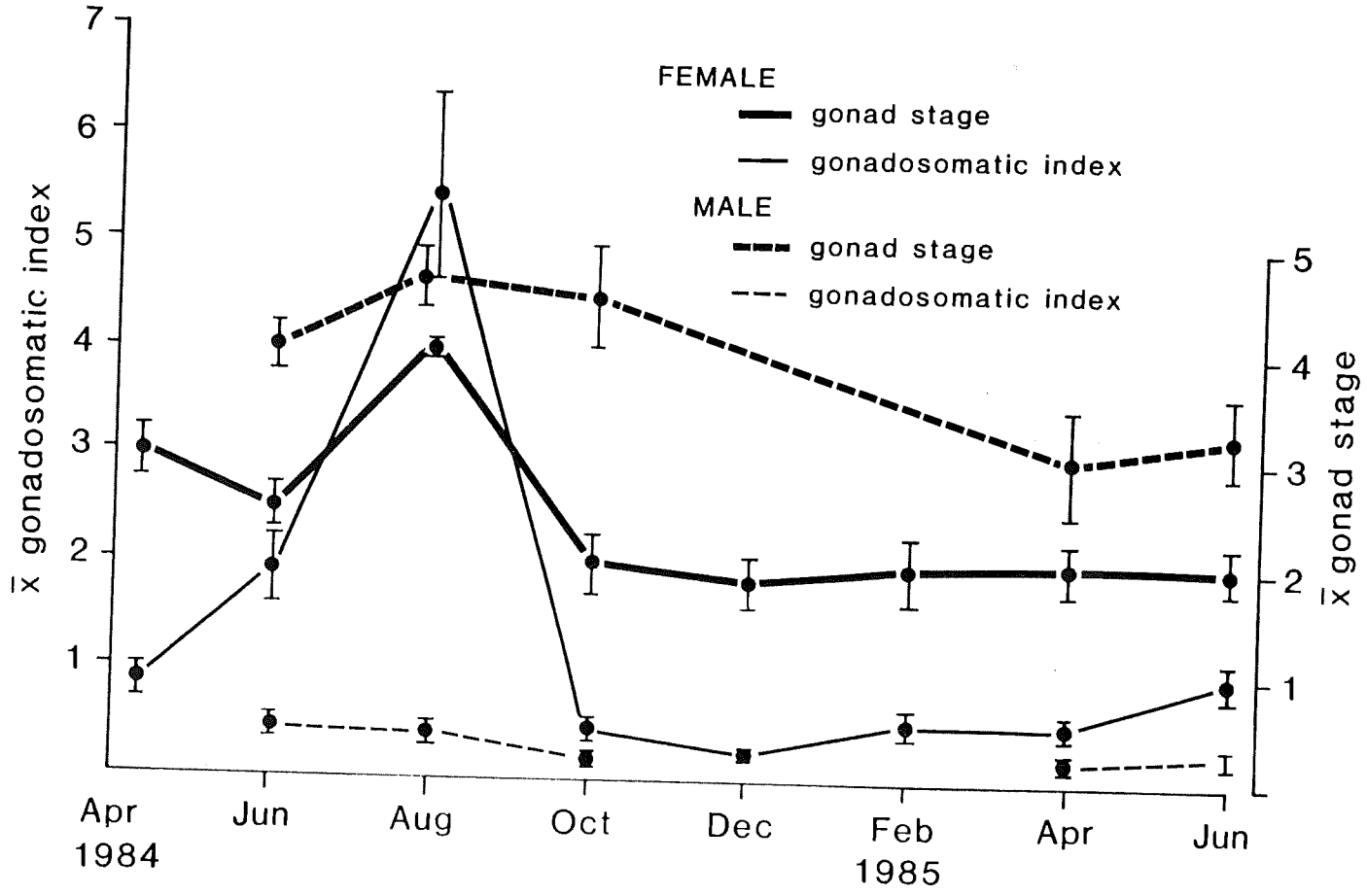
The fecundity of Lampanyctodes hectoris was determined from fish taken in June ($n = 16$) and August 1984 ($n = 19$). Egg counts ranged from 1 309 to 2 798 ($\bar{x} = 1\ 956 \pm$ S.E. = 101.9) in fish from 51 mm to 70 mm ($\bar{x} = 62.55$ mm $\pm$ S.E. = 1.18). A significant correlation existed ($r = 0.57$, $df = 18$, $P<0.01$) between the number of eggs and standard length. The relationship between fecundity (Y) and length (X) was $LnY = 1.585\ LnX + 1.0027$. There was no correlation between egg size and standard length. Egg size per fish ranged from 0.317 mm to 0.499 mm.

In all fish examined, a single mode of mature or maturing eggs was

Figure 2


Apr 1984
n = 20
Jun
n = 45
Aug
n = 43
Oct
n = 19
Dec
n = 19
Feb 1985
n = 13
Apr
n = 23
Jun
n = 30
Frequency
32 -33
36 -37
40 -41
44 -45
48 -49
52 -53
56 -57
60 -61
64 -65
68 -69
72 -73
Length class (mm)
KEY
FEMALE
stage 1 & 2
stage 3
stage 4
stage 5
MALE
stage 1 & 2
stage 3
stage 4
stage 5

Figure


FEMALE
gonad stage
gonadosomatic index
MALE
gonad stage
gonadosomatic index
x̄ gonadosomatic index
x̄ gonad stage
1
2
3
4
5
6
7
Apr
1984
Jun
Aug
Oct
Dec
Feb
1985
Apr
Jun

present in a matrix of smaller (<0.3 mm) translucent eggs. However, in one fish taken in June 1984, a bimodal distribution of egg size was found: the smaller mode was at the lower egg-size limit (0.3 mm) (Fig. 4), while the larger mode was comparable in size to the planktonic eggs of Lampanyctodes hectoris (Robertson, 1977). This bimodal distribution points to multiple spawning.

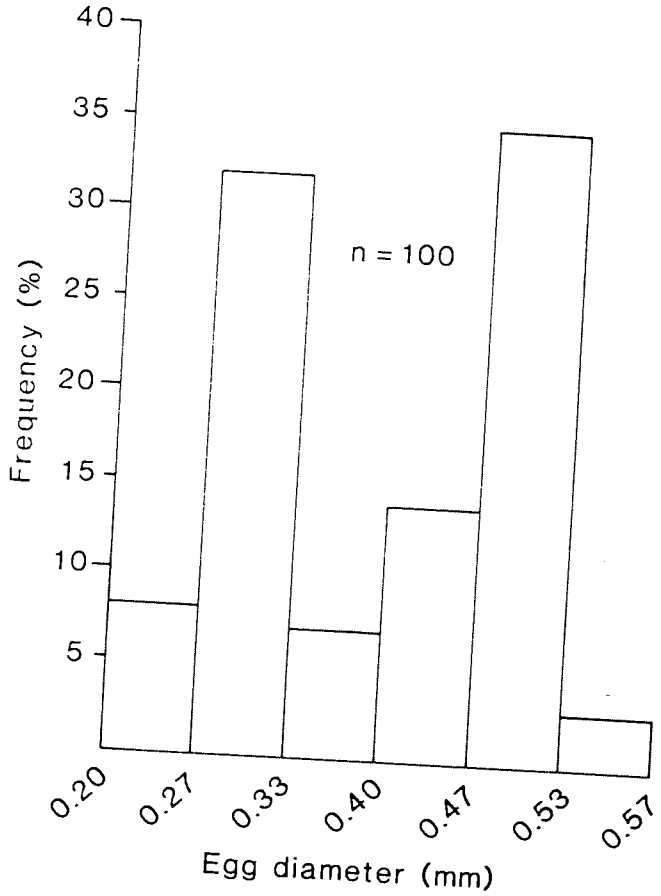
Description of male gonad

The testes appear to be of the 'unrestricted spermatogonial testis-type' (Grier, 1981, p.348) typical of most teleosts: the spermatogonia are not confined to small peripheral cysts within the tubule but are spread along its length. The spermatogonia are, however, more prominent in some localities. Nearer to the sperm duct, sperm are a major component of the ripe testis. Interstitial cells are present as a triangular mass of tissue between the tubules.

The spermatozoa are unusual in being aflagellate. No sperm tails or midpieces were visible at the light microscope level in any histological section in which spermatozoa were found. In these sections, the spermatozoa are crescent or sickle-shaped, some of which appear to be twisted, which may be an artefact of preparation.

The spermatozoa are clearly visible, after ion etching, under the scanning electron microscope (Fig. 5). They are approximately 3-4 μm in length. The pointed distal tip appears blunted at this magnification but the wide base appears slightly rounded or flat. In Lampanyctodes hectoris

Figure 4


40
35
30
25
20
15
10
5
Frequency (%)
n = 100
0.20
0.27
0.33
0.40
0.47
0.53
0.57
Egg diameter (mm)

the sperm head stains uniformly blue with haematoxylin and little cytoplasm is apparent around the nucleus.

Sex ratio

As sexual dimorphism is not obvious in Lampanyctodes hectoris, only gonads checked by histology were used in determining sex ratio. The overall female to male ratio was 2.16:1 (n = 212). Sex ratios differed between months and the number of females relative to males was observed to increase over summer (Table 1). Sex ratios differed significantly with size (χ^2 = 41.83, df = 4, $P<0.001$), with the ratio of females to males increasing steadily from an initial 1:1 ratio in fish less than 40 mm. No males greater than 70 mm SL were recorded (Table 2).

Maurolicus muelleri

Seasonal changes in gonad development and the gonadosomatic index

Ripe females of Maurolicus muelleri ranged in size from 38 mm to 53 mm S.L., although no ripe females between 40 mm and 44 mm S.L. were found. Mature males were generally smaller, ranging in size from 39 mm to 46 mm S.L. Reproductive activity began in August 1984 and continued until December 1985 (Fig. 6). Gonads of both sexes were immature in February and April 1985. Female gonad stage differed significantly between months (F = 75.0; df = 6,88; $P<0.01$). The high August, October and December values were significantly different ($P<0.01$) from other months (Fig. 7).

Male gonad stage also differed seasonally (F = 26.8; df = 2,27; $P<0.01$),

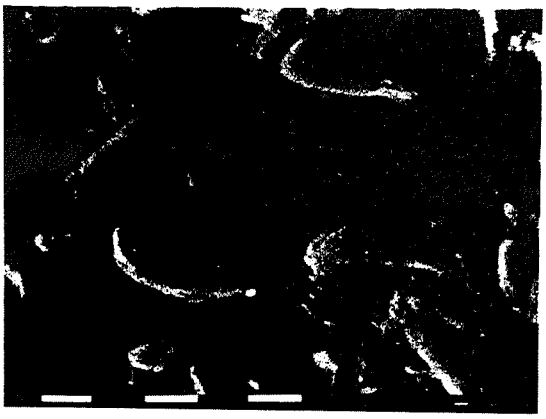
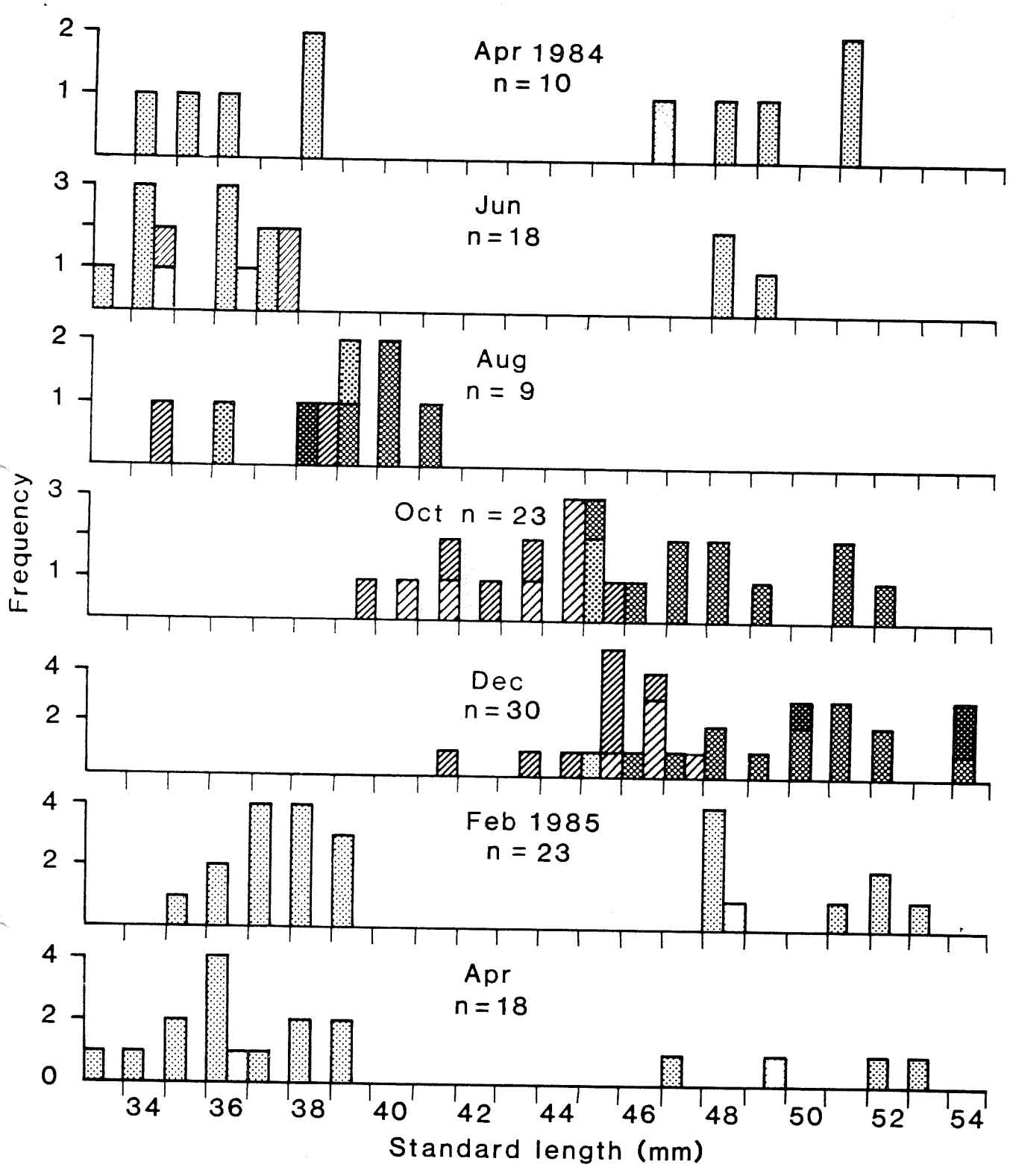
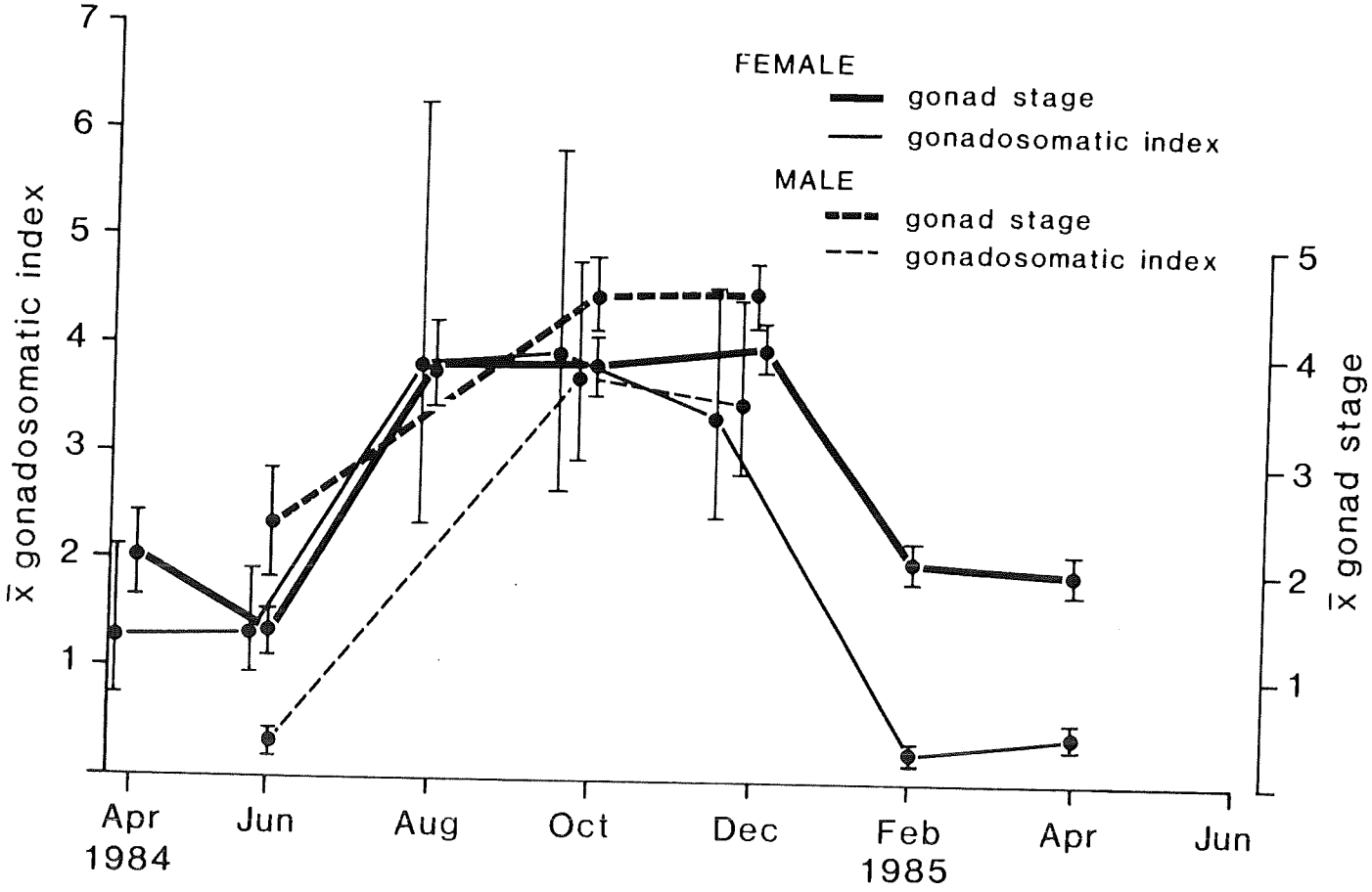


Table 2: Lampanyctodes hectoris. Ratio of females (F) to males (M) in relation to size (n, number of fish in each size class).

Size class (SL mm)	F	M	n	F/M
<40	13	13	26	1.0:1
41-50	32	29	61	1.1:1
51-60	48	23	71	2.0:1
61-70	48	1	49	48.0:1
≥71	3	0	3	∞


Apr 1984
n = 10
Jun
n = 18
Aug
n = 9
Oct n = 23
Dec
n = 30
Feb 1985
n = 23
Apr
n = 18
Frequency
Standard length (mm)
34
36
38
40
42
44
46
48
50
52
54
KEY
FEMALE
stage 1 & 2
stage 3
stage 4
stage 5
MALE
stage 1 & 2
stage 3
stage 4
stage 5


FEMALE
gonad stage
gonadosomatic index
MALE
gonad stage
gonadosomatic index
x̄ gonadosomatic index
x̄ gonad stage
7
6
5
4
3
2
1
5
4
3
2
1
Apr
1984
Jun
Aug
Oct
Dec
Feb
1985
Apr
Jun

with the highest stage in October and December ($P<0.01$).

The regression slopes of Log (GSI) vs Log (SL) in females were significantly different from zero ($F = 76.5$; $df = 1,87$; $P<0.01$) so an ancova, with length as the independent variable, was used to test for seasonal differences in GSI. A significant difference between months ($F = 43.2$; $df = 6,87$; $P<0.01$) in female GSI was found. Gonadosomatic indices in August, October and December were significantly higher ($P<0.01$) than in other months (Fig. 7). No difference was found in GSI between August and October, but these values were significantly higher ($P<0.01$) than in December, which suggests that August-October was the time of peak spawning.

Because of the low numbers of males in some months, only samples from June, October and December were tested. There was significant difference in GSI between months ($F = 8.0$; $df = 4,58$; $P<0.01$): October and December 1984 values were significantly higher ($P<0.01$) than those of June 1984 (Fig. 7).

In Maurolicus muelleri the gonadosomatic index was correlated with gonad stage determined by histological examination in females ($r_s = 0.75$, $df = P<0.01$) and males ($r_s = 0.57$, $df = 34$, $P<0.01$).

Fecundity

The fecundity of Maurolicus muelleri was examined in maturing and ripe fish sampled in October and December 1984. Egg counts ranged from 104 to 942 ($\bar{x} = 376 \pm$ S.E. $= 45.23$) in fish ranging in size from 43 mm to 54 mm ($\bar{x} = 49.09 \pm$ S.E. $= 0.64$) ($n = 22$). Egg size ranged from 0.53 mm to 0.84 mm. There was no correlation between fish size and number or

size of eggs over the length range examined.

Bimodal distributions in egg size occurred in all fish examined from a trawl made at 2040 h on December 14 (Fig. 8a). The larger mode (approx. 1.10 mm) corresponded with egg sizes reported from the plankton (Robertson, 1976). Fish examined from trawls immediately afterwards (0008 h, December 15) (Fig. 8b) and subsequently on December 16 contained only eggs of the smaller mode (> 0.50 mm), indicating that spawning had occurred between December 14 and December 15. As the smaller mode was significantly larger than the size of maturing ova reported by Clarke (1982), a further spawning was considered likely.

Sex ratio

The overall ratio of females to males was 2.64:1 (n = 131). Sex ratios differed between months (Table 1), but there was no consistent pattern. A significant difference in sex ratios between length classes occurred (χ^2, 39.69, df = 4, $P<0.001$): females outnumbered males in each size class, except the 41-45 mm class, where males were more numerous (Table 3). No males greater than 50 mm were recorded.

Diaphus danae

Seasonal changes in gonad development and the gonadosomatic index

No actively maturing or ripe females of *Diaphus danae* were found

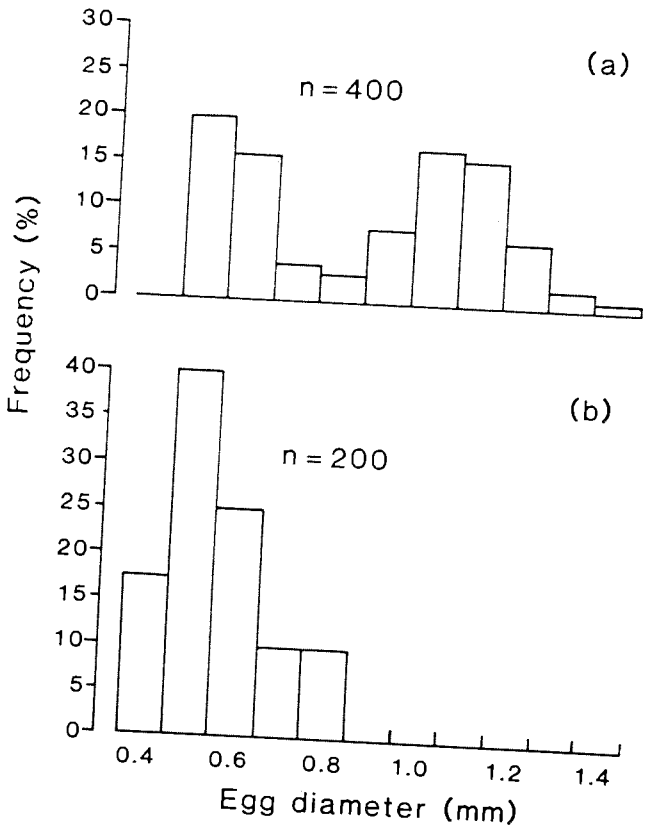

30
25
20
15
10
5
0
(a)
n = 400
Frequency (%)
40
35
30
25
20
15
10
5
0
(b)
n = 200
0.4
0.6
0.8
1.0
1.2
1.4
Egg diameter (mm)

Table 3: Maurolicus muelleri. Ratio of females (F) to males (M) in relation to size (n, number of fish in each size class).

Size class (SL mm)	F	M	n	F/M
≤35	11	3	14	3.7:1
36-40	36	7	43	5.1:1
41-45	5	17	22	0.3:1
46-50	23	9	32	2.5:1
≥51	20	0	20	∞

(Fig. 9). Macroscopic examination of many more ripe females showed that this was not a sampling artefact. Maturing males were found between October 1984 and June 1985. One ripe male was found in October, but no ripe females were found. Sperm were of the aflagellate type described for L. hectoris.

No significant seasonal differences in female GSI occurred and values were low (below 1.00) throughout the study period. A linear correlation existed between gonosomatic index (Y) and fish SL (X). ($Ln\ Y = 0.0206\ LnX - 3.085$; $r = 0.83$, $df = 65$, $P<0.001$).

Sex ratio

The ratio of females to males in Diaphus danae for all months combined was 1.64:1 ($n = 111$). No consistent seasonal pattern in sex ratios was found. Sex ratios differed significantly with size ($\chi^2 = 47.42$, $df = 4$, $P<0.001$) (Table 4), and males were absent from the two largest size classes.

Discussion

Spawning periods

Spawning in Lampanyctodes hectoris started in June (winter) and continued until October, with peak spawning in August. Maurolicus muelleri spawned mainly from August (late winter) to October, although ripe and spent females collected in December indicated that the spawning season of this species continues until early summer.

Myctophids in temperate and subtropical waters generally spawn from late winter to summer (Fast, 1960; Odate and Ogawa, 1961; Halliday, 1970; Smoker

Figure 9

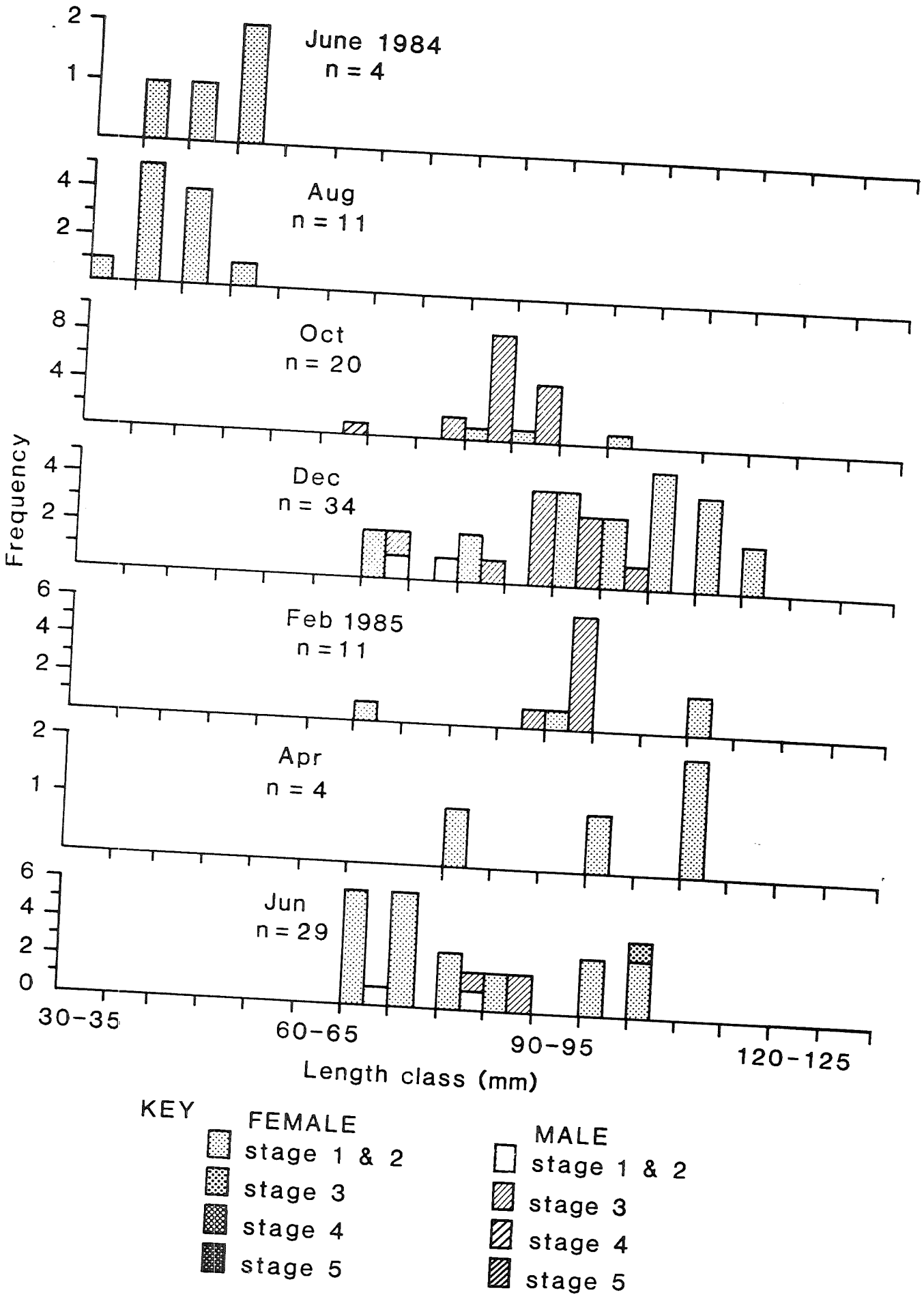

June 1984
n = 4
Aug
n = 11
Oct
n = 20
Dec
n = 34
Feb 1985
n = 11
Apr
n = 4
Jun
n = 29
Frequency
30-35
60-65
90-95
120-125
Length class (mm)
KEY
FEMALE
stage 1 & 2
stage 3
stage 4
stage 5
MALE
stage 1 & 2
stage 3
stage 4
stage 5

Table 4: Diaphus danae. Ratio of females (F) to males (M) in relation to size (n, number of fish in each size class).

Size class (SL mm)	F	M	n	F/M
≤50	13	0	13	∞
51-60	2	0	2	∞
61-70	7	5	12	1.4:1
71-80	9	11	20	0.8:1
81-90	9	18	27	0.5:1
91-100	9	8	17	1.1:1
101-110	17	0	17	∞
≥111	5	0	3	∞

and Pearcy, 1970; Goodyear et al., 1972; Clarke, 1973; Go et al., 1977; Karnella and Gibbs, 1977;). This is also true for the sternoptychid Maurolicus muelleri (Okiyama, 1971; Robertson, 1976; Gjosaeter, 1981a; Clarke, 1982). Clarke (1973) postulated that reproductive cycles in midwater fishes, particularly myctophids, were timed to coincide with the spring bloom (and the consequent increase in zooplankton abundance). In subarctic and subantarctic waters, however, spawning in some species of myctophids is confined to winter (Smoker and Pearcy, 1970; Robertson, 1977), as with L. hectoris in this study. According to Gjosaeter and Kawaguchi (1980), winter spawning in high latitude may be 'an adaptation to low water temperature, since hatching takes much longer than in low latitudes.' (p.22) As juveniles of L. hectoris were present in the water column off Maria Island during late spring, when zooplankton abundance was increasing, early spawning may ensure that enough of the young of the year have reached maturity to take full advantage of the increased zooplankton production. Maurolicus muelleri spawned later, however, and juveniles were not present in the water column until February (Young unpubl.). This may be explained by the relatively larger egg size of M. muelleri (approximately twice that of L. hectoris eggs). Egg volume has been positively correlated with larval size at hatching in pelagic spawners (Blaxter and Hempel, 1963). Therefore, the initial development of M. muelleri may be synchronized to the occurrence of larger plankters occurring later in the spring plankton succession (thus reducing competition for the available food). This possibility is supported by Okiyama (1971), who found that early postlarvae of M. muelleri 'can directly take the larger and much advanced organisms' (p.22) of the plankton.

No spawning period was identified for Diaphus danae. Large individuals of D. danae (>70 mm) were not collected in June or August 1984 when

reproductive maturity was most likely. However, as large D. danae were equally likely to be captured then as at other times of the year, it is possible that the population of D. danae off Maria Island was an expatriate one (Ekman, 1953). This is similar to that reported for myctophid species in other waters (O'Day and Nafpaktitis, 1967; Zurbrigg and Scott, 1972; Gjosaeter, 1981b) where populations exist vegetatively outside their spawning area.

Fecundity

Although data are limited, fecundity in myctophids is approximately proportional to body length (Gjosaeter and Kawaguchi, 1980). Kawaguchi and Mauchline (1982) reported that larger myctophid species have higher fecundities (e.g. Benthosema glaciale 33 mm SL, < 300 eggs; Lampanyctus macdonaldi 123 mm SL, 7072 eggs). In the present study, fecundity and length were positively correlated in Lampanyctodes hectoris, similar to that reported by Gjosaeter and Kawaguchi (1980) for B. glaciale.

Different relationships between fecundity and length in Maurolicus muelleri have been reported. Clarke (1982) found that fecundity was proportional to length in individuals examined off south-eastern Australia; Okiyama (1971), Badcock and Merrett (1980), Gjosaeter (1980) and the present study found no relationship. However, Macgregor (1968) pointed out that the relationship between fecundity and length is unclear unless the largest fish in the sample is more than twice as long as the smallest fish. The ratio in the present study was only 1.3:1, whereas in Clarke's (1982) study it was 1.5:1, which may explain the different results. The fecundity of M. muelleri reported here compares very closely with that reported elsewhere (e.g.

Okiyama, 1971), which suggests that the fecundity of this species shows little latitudinal variation.

Multiple spawning

The presence of different-sized modes of yolked oocytes suggests multiple spawning, usually over several months of the year (Le Clus, 1979). This assumes that all yolked cells are capable of developing to maturity, although total or partial resorption is possible (Macer, 1974). Smoker and Pearcy (1970) argued that the presence of a smaller mode of gametes in the myctophid Stenobrachius leucopsarus did not necessarily imply multiple spawning, as the immature gametes could either be expelled into the plankton or resorbed. Similarly, Taning (1918) could not confirm multiple spawning in myctophids from the Mediterranean Sea.

Neverthless, there is supporting evidence for multiple spawing in Lampanyctodes hectoris. In some marine fish (e.g. Trachurus symmetricus) the presence of an intermediate size mode of yolked oocytes indicates multiple spawning (Macgregor, 1976). In these fish further evidence for more than c spawning can be found (e.g. an extended spawning season). In the present study such a mode was present in one mature female of L. hectoris. Also, the individual examined came from the start of the reproductive season (June), which suggests that a further spawning was likely.

The evidence for multiple spawning in Maurolicus muelleri is stronger. Not only were bimodal distributions of egg-size present in many individuals but also reproductive activity continued over an extended period (Fig. 7), which is consistent with multiple spawning (Milton and Arthington, 1983;

Williams and Clarke, 1983). Previous examinations of egg sizes of M. muelleri (Okiyama, 1971; Gjosaeter, 1981a; Clarke, 1982), and growth studies (Yuuki, 1984) also support this conclusion.

Sex Ratios

Midwater fishes off Hawaii were found to generally exhibit a 1:1 ratio of females to males, with some exceptions, particularly among larger myctophid species where 'females were either more abundant or larger than males' (Clarke, 1983, p. 203). In the present study all three species showed, overall, a positive bias in the ratio of females to males and a decline in the proportion of males with increasing size. Seasonal trends were apparent only in Lampanyctodes hectoris, which may have been due to small sample sizes. However, in some trawls, sexed subsamples, particularly of the myctophids, contained either all females or all males, which suggests that spatial segregation of sexes (Klingbeil, 1978) may occur. Other factors such as species size (Clarke, 1983), depth distribution (Badcock and Merrett, 1976) and differential avoidance of nets (Klingbeil, 1978) may have accounted for the bias towards females in this study. However, similarly biased catches of L. hectoris were reported off South Africa (Crawford, 1980). Possibly this bias is as an adaptation to 'maximize egg-producing biomass' (Clarke, 1983, p.203) in waters where food reserves are low. This may be the case in the present study, as maturing females (excluding D. danae) are present before the onset of the spring bloom, when food may still be limited.

Sperm structure

The testes conform to the usual teleost pattern. However, the structur of the sperm is unusual. Although aflagellate sperm are found in several teleost families (Mattei et al., 1970), the sperm of Lampanyctodes hectoris resembles normal flagellate sperm, but without midpiece or tail. O'Day and Nafpaktitis (1967) reported that the sperm of the myctophid Lobianchia dofleini, which is very similar in shape to that of L. hectoris, does have a flagellum. However, they gave no evidence for this conclusion.

Other aflagellate sperm have simple cell-like bodies. The sperm of Gymnarchus niloticus, for example, are rounded cells with a central nucleus (Mattei et al 1967). The sperm of L. hectoris go through the complex stages of sperm-head formation typical of most vertebrate species, but neither a midpiece nor tail is visible. The functional implication of an aflagellate sperm, which suggests limited mobility, is unclear. Perhaps the fact that L. hectoris occurs in dense aggregations (May & Blaber, in preparation), and that males are reproductively active for longer than females (Figure 2), reduces the need for a mobile sperm.

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Legends

Figure 1: Mean sea-surface temperatures (To) and mean temperatures at 200 m (T200) depth over the continental slope, east of Maria Island betwe n April 1984 and March-April 1985 (Bars define 95% confidence intervals).

Figure 2: Lampanyctodes hectoris. Gonad stages determined by histology from fish sampled between April 1984 and June 1985.

Figure 3: Lampanyctodes hectoris. Mean gonadosomatic indices and mean gonac stages for males and females between April 1984 and June 1985 (Bars define 95% confidence intervals).

Figure 4: Lampanyctodes hectoris. Size distribution of eggs of a mature female (70 mm SL) taken in June 1984.

Figure 5: Lampanyctodes hectoris. Scanning electron micrograph of mature spermatozoa (10000 x magnification) (scale interval = 1 μm).

Figure 6: Maurolicus muelleri. Gonad stages determined by nistology from fish sampled between April 1984 and April 1985.

Figure 7: Maurolicus muelleri. Mean gonadosomatic indices and mean gonad stages for males and females between April 1984 and April 1985 (Bars define 95% confidence intervals).

Figure 8: Maurolicus muelleri. Egg-size distributions of mature females on (a) December 14, 1984 and (b) December 15-16, 1984 (b) (n = number of eggs measured).

Figure 9: Diaphus danae. Gonad stages determined by histology from fish sampled between June 1984 and June 1985.

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Appendix 8

Larval Development and Caudal Osteology of Blue Grenadier, *Macruronus novaezelandiae* (Hector), from Tasmanian Waters

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ABSTRACT

The development of Macruronus novaezelandiae is described from both reared specimens and larvae from plankton samples. Larvae hatch at 2.2 - 2.3 mm. Pigmentation combined with a myomere count of 76 - 80 and caudal development separate M. novaezelandiae from other known gadiform larvae. Development is direct with no marked changes in body morphology. Fin development proceeds in the sequence: second dorsal, anal, first dorsal, pelvic caudal, pectoral. However adult fin complements are reached in the sequence: first dorsal, pelvic, anal, second dorsal, caudal, pectoral.

Caudal development is late in Macruronus. Flexion commences at 20 mm and is not complete until 28 mm. A full caudal complement was not present in a 34.2 mm specimen. The caudal fin is similar to other (tailed) Merluccids in being based on two ural centra, four hypurals and two epurals, however considerable variation exists in the appearance, number and insertion of accessory caudal elements.

INTRODUCTION.

The family merlucciidae contains some of the world's most important temperate commercial fish species. These include the hakes in the subfamilies merlucciinae and macruroninae. The macruroninae comprises three known genera, Macruronus, Lyconus and Lyconodes. The genus Steindachneria is probably also affiliated with the macruroninae (Marshall, 1966).

Macruronus itself consists of five nominal species, Macruronus novaezelandiae (Hector), M. magellanicus (Lonnberg), M. capensis (Davies), M. maderensis (Maul) and M. caninus (Maul). M. maderensis and M. caninus are known only from type specimens collected at Maderia in the eastern Atlantic (Svetovidor, 1978). The remaining three species occur in different parts of the southern hemisphere, M. magellanicus off South America (Norman, 1937), M. capensis off southern Africa (Smith, 1961) and M. novaezelandiae off New Zealand and southern Australia (Ayling and Cox, 1984; Last et al, 1983). All are primarily inhabitants of continental slope and shelf waters with the three southern species supporting commercial fisheries. Annual catches of M. novaezelandiae in New Zealand, for example, range up to 97,750 tonnes (Patchell, 1982). Off Tasmania, a smaller fishery of approximately 1,100 tonnes exists targeted primarily on spawning fish. Despite their economic importance and widespread distribution the only published information on early life history stages of Macruronus is a study of egg and larval distribution of M. novaezelandiae in New Zealand waters by Patchell (1982).

In 1984, CSIRO Division of Fisheries Research established a multidisciplinary programme to investigate the biology and ecology of blue grenadier in Tasmanian waters. An integral part of this programme was a study of larval ecology. As such, it was necessary to establish the identity of blue grenadier larvae. The present paper describes larval development of M. novaezelandiae from Tasmanian waters and examines osteological development of the caudal complex. Caudal development of gadiform fish has received considerable recent attention both as a tool for identification and as an indicator of phylogenetic relationships (Matarese et al, 1981; Markle, 1982; Dunn and Vinter, 1984).

MATERIALS AND METHODS.

Specimens were obtained from samples collected aboard FRV Soela between April 1984 and September 1985 as part of a biological study on blue grenadier in Tasmanian waters by CSIRO Division of Fisheries Research, Hobart.

Larvae were obtained from three sampling systems - an RMT 1+8 (Baker et. al. 1973), a 1 metre diameter ring net (500 um mesh) and free fall, vertical drop nets of 64 um and 200 um mesh (Heron, 1983). Drop nets provided material in the best condition and where possible specimens for description have been taken from these samples.

Juvenile specimens were obtained from midwater trawls using an Engels 352 pelagic trawl fitted with a 10 mm. liner.

Newly hatched larvae were reared from eggs fertilized at sea. Eggs

and milt were stripped from ripe adults trawled from 500m and mixed in 1 litre plastic jars filled with seawater. Despite the jars being located in a seawater bath, incubation temperatures varied considerably (12 C to 18 C).On return to the laboratories at Hobart, eggs were transferred to 2 litre glass jars and placed in a constant temperature incubation chamber set at 14.0 C (+/- 0.2 C). Incubation jars were not aerated and no attempt was made to feed larvae.

All specimens used for description were fixed in a 10% formaldehyde/seawater solution buffered with sodium B-glycerophosphate and later transferred to a 5% solution.

This description is based on a series of 74 larvae 2.2mm to 34.2mm in length, although comments on pigment and meristic variability stem from routine examination of several hundred specimens.A representative series of larvae is deposited with the Ian S. Munro Ichthyological Collection, C.S.I.R.O., Hobart, Tasmania.

Developmental terminology follows Ahlstrom et. al. (1976).Body measurements follow Matarese et. al. (1981).Length measurements are reported as notochord length - NL (i.e. from the snout tip to the end of the notochord) in preflexion and flexion larvae and standard length - SL (i.e. from the snout tip to the posterior margin of the superior hypural elements) in postflexion larvae and juveniles.Measurements were made with the aid of an ocular micrometer and a camera lucida for larvae and vernier calipers for juveniles.Lengths are expressed to the nearest 0.1mm for larvae and to the nearest 1.0 mm for juveniles.

Meristic counts and examination of ossification sequences were made on specimens cleared and stained using Alizarin Red S - KOH - glycerine (Hollister, 1934).Alizarin uptake by bones is variable (Dunn, 1983) and structures were considered ossified even if only slightly stained.Cranial terminology follows Mujib (1967) and that for caudal osteology follows Inada (1981), Marshall and Cohen (1973) and Monod (1968).

Vertebral counts include the first vertebrae, the neural spine of which is fused to the supraoccipital crest (Marshall, 1966) and both ural centra.Vertebral centra were counted as ossified only when a complete band of stain was present connecting both neural and haemal spines.

RESULTS

Identification of M. novaezelandiae larvae was based on their typical gadiform features (large head, compact gut, tapering body form), myomere count, the development of confluent dorsal-caudal-anal fins and was confirmed by comparison to reared specimens.

Distinguishing features.

Small larvae of M. novaezelandiae superficially resemble morid and macrourid larvae.A myomere count of 78-79 is useful in separating M. novaezelandiae from the generally lower counts of morids (42-72) and the generally higher counts of macrourids (10-16 + 70->100; Marshall and Iwamoto, 1973 - reported as precaudal and caudal vertebrae).Such large numbers of myomeres are, however, often difficult to count, particularly towards the caudal area where myomeres are closely packed.In the case of macrourid larvae, the posteriad myomeres are often damaged or missing thus making total counts impossible.

Both M. novaezelandiae and most morid larvae show moderately pedunculate pectorals - a feature common in gadiform larvae with delayed caudal development (Fahay and Markle, 1984).Macrourid larvae have very prominently stalked pectorals and are further separated by precocious pelvic development.

M. novaezelandiae larvae have 1-3 prominent melanophores along the ventral midline behind the anus (although variable in appearance - see section on trunk pigmentation) and a double series of dorsal melanophores ;they lack pigment on the notochord tip.Macrourid larvae may also have a similar ventral sequence but do not develop the dorsal rows of melanophores, have less lateral body pigment and usually show 1-2 small melanophores around the tip of the notochord.Morid larvae found in the same area show diffuse ventral pigment from the anus to approximately 75%-80% SL.Lateral pigment may be present as a band extending to the dorsal surface in small (4mm.- 6mm.) larvae. However, they too lack the double dorsal rows found in M. novaezelandiae and show notochord pigment similar to macrourids.

At larger sizes, M. novaezelandiae are readily distinguished by their long based second dorsal and anal fins confluent with the caudal.Ophidiid larvae have similarly confluent dorsal-caudal-anal fins but lack a separate first dorsal, show very little body pigment and form a chin barbel.Larvae of Lyconus species are currently unknown.It is possible that they are similar to Macruronus larvae.

Pigmentation (figures 1 and 2).

Although pigmentation in M. novaezelandiae is variable, certain features persist that, when combined with meristic and morphormetric information, enable identification. Variation in the appearance of pigmentation is a result of differences in the number of melanophores and their degree of expansion.Melanophore appearance can change on a diurnal rhythm (????).However, in samples examined, there appeared to be no relationship between time caught and melanophore expansion with a broad range present in all samples.

Head Pigmentation.

Newly hatched larvae (2.2mm.-2.3mm.) show scattered melanophores around the orbit, extending over the sides of the head and snout (figure 1A).This gradually contracts to a series of small melanophores located on the snout and by 3.6mm. some have migrated dorsally to the top of the head (figure 1B).Eyes become pigmented at this size in reared larvae.By 4.5mm., dorsal head pigment consists of a series of 3-11

melanophores scattered over the hindbrain and extending posteriorly to above the cleithrum.Pigment gradually extends over the midbrain with 1-2 melanophores usually present between the eyes by 5.3mm. Melanophores develop externally over these initial mid and hindbrain spots extending posteriorly as a double row to the dorsal fin anlage by 7.2mm.Dorsal pigment gradually intensifies with melanophores increasing in number and forming a complete cap over mid and hindbrains by 16.0mm. Snout pigment gradually increases with melanophores extending down between the eyes to the tip of the maxilla by 12.0mm.Internal pigment expands over the forebrain in larvae from 9.0mm.-15.0mm. forming a complete cap by 17.0mm.

Ventral head pigment first develops as a series of 3-5 melanophores between the dentaries along the median cartilage to the urohyal in larvae of 4.2mm.This increases to 10-12 melanophores by 12.0mm., forming a continuous line by 14.0mm.

The onset of dentary pigment is variable with none present on some larvae as large as 7.0mm. Most develop 1-2 melanophores over the posterior section of the dentary by 5.3mm. and add melanophores anteriorly along its length with 5-6 usually present by 7.1mm.Dentary pigment becomes particularly prominent in larvae over 11.0mm. in length expanding around the anterior tip and forming a complete line by 25.0mm.

Melanophores surrounding the orbit may be present in larvae as small as 4.5mm. with all larvae above 7.0mm. showing obvious circumorbital pigment. Melanophores are added anteriorly, gradually forming a continuous line from the level of the top of the operculum around underneath the orbit then extending diagonally above the maxilla to the snout tip leaving an unpigmented area around the nostrils (figure 1H).

Two melanophores may be present around the otic capsule by 7.0mm. but become obscured by overlying tissue by 10.0mm.Scattered melanophores develop over the pterotic region by 25.0mm. with the operculum and preoperculum remaining largely unpigmented even in the largest specimen of the series (34.2mm.).

Gut Pigmentation

Newly hatched larvae show a heavily pigmented region around the developing gut, extending over the yolksac and the lateral body surfaces.The oil droplet (0.37mm. diameter at hatching) may also show some pigment (figure 1A).With the development of the gut, pigment concentrates over the dorsal gut surface leaving the lateral surfaces free of pigment.In small larvae (3.6mm.-4.0mm.), gut pigment exists internally along the dorsal surface from the cleithrum to just anterior of the anus. This pigment expands anteriorly to form a prominent cap over the gas bladder by 4.2mm. Melanophores are gradually added to the lateral gut surfaces throughout the larval period until the entire gut (including the ventral surface) becomes pigmented by 30.0mm.

Two to ten melanophores develop between the cleithral symphis and the pelvic fin buds (when formed) in larvae of 3.6mm. to 7.2mm.One, two or three melanophores may also be present just anterior to the cleithral symphis.These are still visible in larvae up to 15.0mm. but are not visible in larvae greater than 16.0mm. These regions then remain largely unpigmented in larvae up to 34.2mm. (the largest specimen examined in this series).

Trunk Pigmentation.

Dorsal pigment first appears on larvae of 3.8mm. to 4.5mm. as a group of scattered melanophores at approximately 60% NL.This rapidly intensifies to form a double row in larvae of 5.0mm. covering an area from 51% to 67% NL.Some lateral melanophores may also develop above the body midline in this region. Concurrently, a similar double row of melanophores appears and extends posteriorly from the head (figure 1F).These rows join by 10.5mm. and extend posteriorly to the caudal region by 29.0mm.Pigment also appears internally on the dorsal surface of the vertebrae in larvae of 9.5mm. extending anteriorly to approximately 50% SL and posteriorly to the last vertebrae by 34.0mm.

Single melanophores (one per base) develop around the 40th fin ray base of the second dorsal fin by 14.0mm.These increase in number both anteriorly and posteriorly covering all bases by 29.0mm.

Pigment along the ventral midline appears in newly hatched larvae as a diffuse region extending from the yolksac to 75% to 82% NL.This contracts to 1-3 melanophores (most commonly 2) located 52% to 65% NL in larvae of 3.8mm. to 4.0mm. Additional melanophores (up to 6) may be added during development but the initial 1-3 melanophores persist throughout the larval period.In larvae greater than 7.0mm. they appear internally above the anal fin ray bases and are gradually obscured by overlying musculature and external melanophores. These ventral melanophores are a useful diagnostic character although their appearance is quite variable depending on their degree of expansion.This is particularly evident in small larvae where expanded ventral melanophores may extend over the lateral body surfaces almost to the dorsal area (figure 2).

Lateral pigment gradually intensifies throughout the larval period. Areas developing pigment shadow the expansion of dorsal pigment.The area immediately above the gut remains largely void of pigment even in the largest specimen (34.2mm.).

Morphology (table 1).

Variability.

M. novaezelandiae larvae showed considerable variation in development at length. In general, specimens captured in ring net and RMT samples appeared to develop features at slightly earlier sizes than those taken from drop net samples. This is likely a result of differential shrinkage of specimens between the different capture systems. Hay, (1981) reported that considerably more shrinkage occurred in Pacific Herring when larvae were killed prior to fixation and that shrinkage increased with tow length. Ring net and RMT tows varied in length from 15 to 110 minutes with most larvae dead by the time the net was retrieved and the catch fixed. Drop net samples were at maximum 3 minutes in length. Many larvae were still alive on fixation and thus may not have suffered as severe shrinkage effects as those from ring net and RMT samples. This shrinkage effect may also account for the relatively more advanced development at length of the smallest larvae caught by net verses larvae reared in the laboratory, although differences in temperature, salinity and general water quality cannot be discounted. Some variability in development at length can also be

expected in field collected larvae as a reflection of past history (e.g. feeding success) but would be unlikely to account for the observed differences between capture techniques.

General Morphology.

Larvae hatched at 2.2mm.-2.3mm. after 55-60 hours. Yolk absorption was not quite complete in specimens reared to 3.7mm. (6 days post-hatch) although field collected specimens generally showed complete absorption by 3.6mm. Jaw development was first visible at 3.5 days post-hatch with a functional mouth present in larvae of 5.5 days (3.7 mm.). Pectoral buds and pigmented eyes were first observed in larvae 4.5 days post-hatch (3.2mm.). The anus opened laterally to the right in all reared larvae and most field collected larvae (approximately 5% of field collected larvae show a left lateral opening). This changes to vertical through the ventral midline by 5.1mm. A lateral anal opening in M. novaezelandiae larvae is consistent with that reported for other gadiform species (Marak, 1967; Matarese et al, 1981; Fahay and Markle, 1984; Dunn and Vinter, 1984).

Larvae are moderately elongate with a large head and compact gut. Body proportions (expressed as percentage NL or SL) generally show a gradual decrease during development (table 1).

Meristics and Osteology (table 2).

Head and axial skeleton.

The first structures to ossify are the maxilla, premaxilla, dentary and the cleithrum. All four structures show alizarin uptake in the smallest specimen stained (3.7mm.). Initial ossification of the jaw probably occurs concurrently with the development of a functional mouth.

Ossification of branchiostegals commences in larvae of 4.6mm., with a full complement of 7 ossified by 11.5mm. Ossification sequence is from upper to lower. Gill rakers are first discernable in larvae of 9.4mm.-9.9mm. with a full complement of 7 + 22-23 present by 28.9mm.

Ossification of neural and haemal spines generally precedes vertebral centra. Ossification of centra, neural spines and haemal spines occurs anterior to posterior proceeding slowly in larvae less than 9.0mm. in length and thence rapidly with a full complement present by 23.2mm. Elements associated with the caudal complex are the last to ossify.

Fins.

Completion of fin development in M. novaezelandiae occurs in the sequence: first dorsal and pelvic (almost simultaneously); anal; second dorsal; caudal; pectoral.

Pelvic fins first appear as slight swellings either side of the gut in larvae of 5.7mm-5.8mm. although they do not form distinct buds until 6.9mm. Ossification may commence as early as 9.4mm. with a full complement (8 rays) present by 16.3mm. Ossification proceeds from the outer to the inner most rays.

The second dorsal fin anlage is visible in larvae of 5.7mm.

covering an area from 65% NL to 79% NL. Distinct bases are first visible by 6.9mm. with ray ossification commencing by 7.3mm. Although the anal fin anlage is not present until 6.9mm. complete ossification is reached prior to that of the second dorsal. Distinct anal fin bases are first visible in 7.2mm. larvae and ossification has consistently commenced by 9.9mm. Ossification of both anal and second dorsal elements commences within the region from 64% NL to 78% NL. Ossification proceeds more rapidly anteriorly than posteriorly with rays developed to the first bases by 12.0mm. A full complement of anal rays is present by 21.0mm. and second dorsal rays by 23.2mm.

The first dorsal commences development slightly later than the second dorsal although it is the first fin to complete ossification. A full complement of 12-13 elements is present by 16.3mm.

Despite initial development of the pectoral fin bud (the larval pectoral of Matarese et al, 1981) in reared larvae by 3.2mm., the pectoral fin is the last to complete development. Ossification of pectoral rays commences by 16.3mm. with a 34.2mm. specimen showing only 15 ossified rays, still short of the 20 rays of juveniles. Sequence of ossification is from upper to lower.

Caudal fin development.

The caudal fin first appears as a slight swelling on the ventral surface of the notochord just anterior to the tip in larvae of 10.4mm. Flexion does not commence until 20mm. and is usually complete by 28mm. Ossification of all caudal elements was not complete in a 34.2mm. specimen. Insufficient material of the appropriate size was available to define the completion of caudal ossification.

The caudal complex in M. novaezelandiae is based on two ural vertebrae, two epurals and four hypurals (hypurals 3 and 4 fused to the second ural centrum) - figure 3. Eight to nine rays articulate with the epurals and hypurals - one or two rays on EP2, two rays each on HP2 and HP4 with single rays on the remainder. Single rays also articulate with the elongate neural and haemal spines of the first preural centrum which brings the total caudal ray count to 10-11 elements.

Two variations of the caudal complex were observed.In the first type, X-Y bones (the accessory bones of some authors) are absent. However, the first preural centra shows a twin haemal spine the most posterior of which supports a single ray (figure 3). Additionally, preural centra 3-8 show greatly elongated haemal spines (1.3-1.4x the length of corresponding neural spines). In the second type, PU1 shows a single haemal spine and although no X-bone is present, a radial is inserted between the haemal spines of PU1 and PU2. This radial supports a single ray and is identical in appearance to reported Y-bones. Haemal spines of preural vertebrae in specimens with this caudal configuration are similar in length to their corresponding neural spines.

DISCUSSION.

Development of M. novaezelandiae is similar to other merlucciid species. General morphology and pigmentation show broad similarities to Merluccius and to gadine gadids. Characteristic differences between M. novaezelandiae and Merluccius species occur in fin structure and sequence of fin development. In Merluccius, the caudal fin is the first

to form followed by the pelvic. In Macruronus, the caudal is the second last to form. Macruronus larvae show a more predominantly stalked pectoral than Merluccius similar to morids which also show a late-forming caudal. Fahay and Markle (1984) have suggested that this pectoral modification in larvae with delayed caudal development may reflect a compensatory response associated with swimming - a feature that reaches an extreme in macrourids. Fin structure and position may also be useful in separating Macruronus from larvae of Lyconus and Lyconodes. No information exists on larvae from these genera however, based on this study and Marshall (1966), pelvic insertion should distinguish Macruronus (pelvics inserted behind pectorals) from Lyconus (opposite) and Lyconodes (abdominal).

The caudal fin of M. novaezelandiae, although having the same basic structure as merlucciid species, shows some variation in the appearance, number and insertion of elements. Marshall (1966) reported considerable variability in structures associated with caudal vertebrae of M. magellanicus. Double neural arches and "supernumerary elements" occurred in three of his specimens. Caudal variability amongst gadiform species is not confined to Macruronus. Markle (1982) reported that extra ossifications and fusions are frequently encountered. Unfortunately, insufficient specimens over the appropriate 35mm. to 150mm. size range were available to assess developmental characteristics of these variations.

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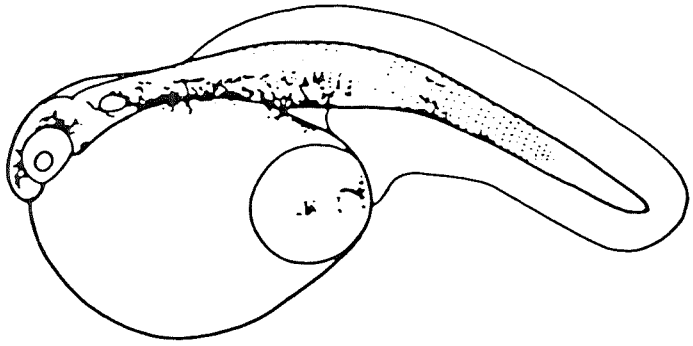
Figure Captions.

Figure 1. Larvae of M. novaezelandiae: (A) 2.2mm. reared specimen; (B) 3.5mm. reared specimen; (C) 3.6mm. ; (D) 5.3mm. ; (E) 7.2mm. ; (F) dorsal view of above; (G) 12.0mm. ; (H) 24.2mm.

Figure 2. Variability in trunk pigmentation. (4·9 mm. larvae)

Figure 3. Caudal osteology of a juvenile M. novaezelandiae (181mm. SL.).

A



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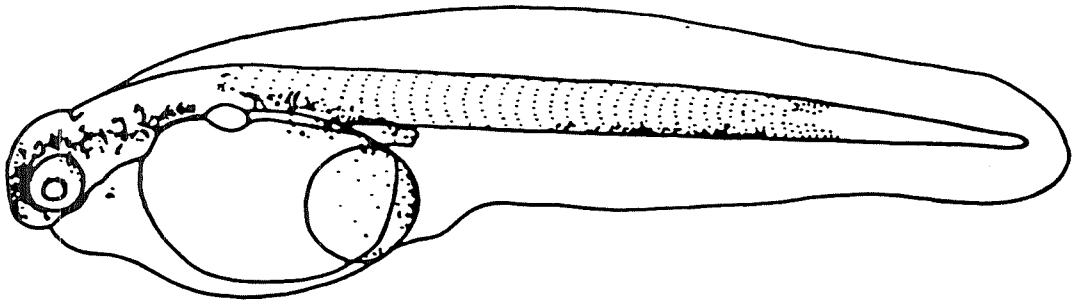

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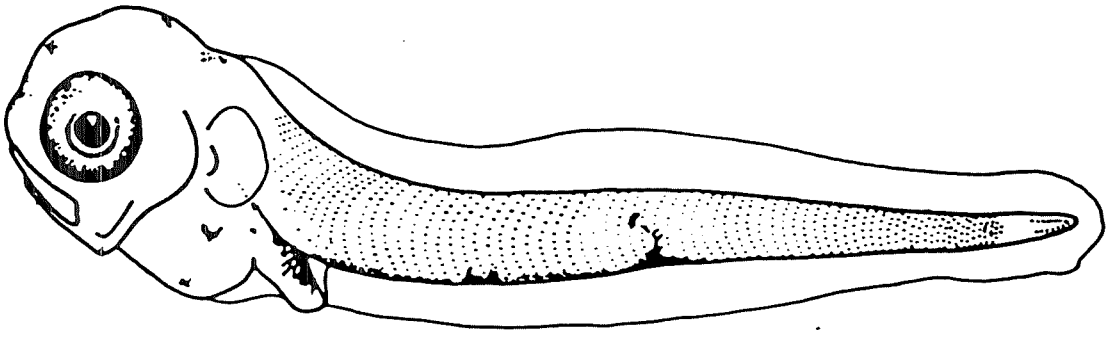

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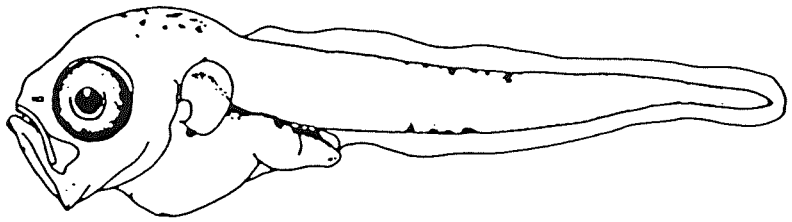

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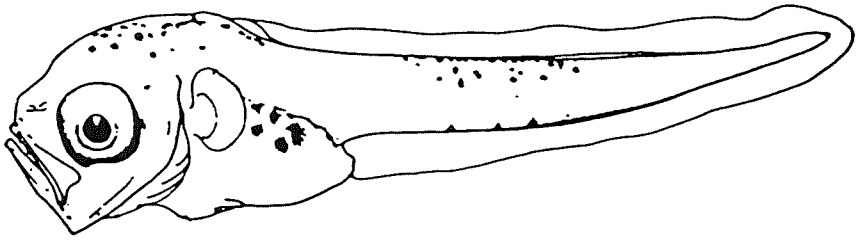

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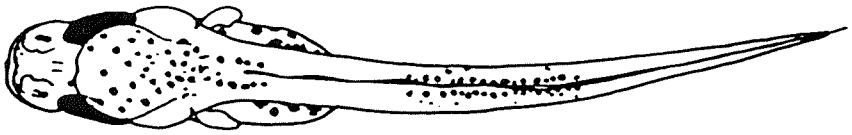

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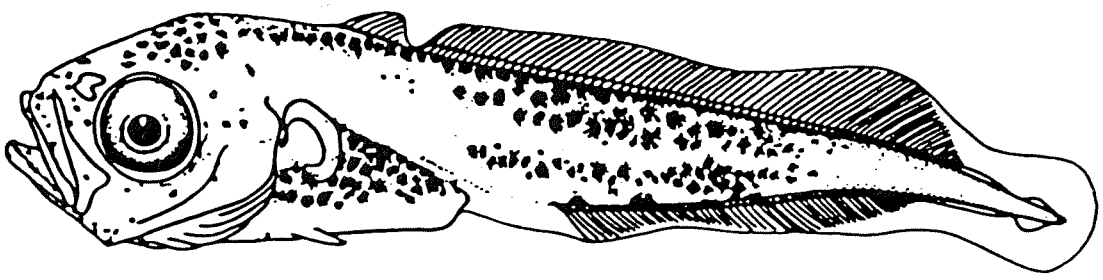

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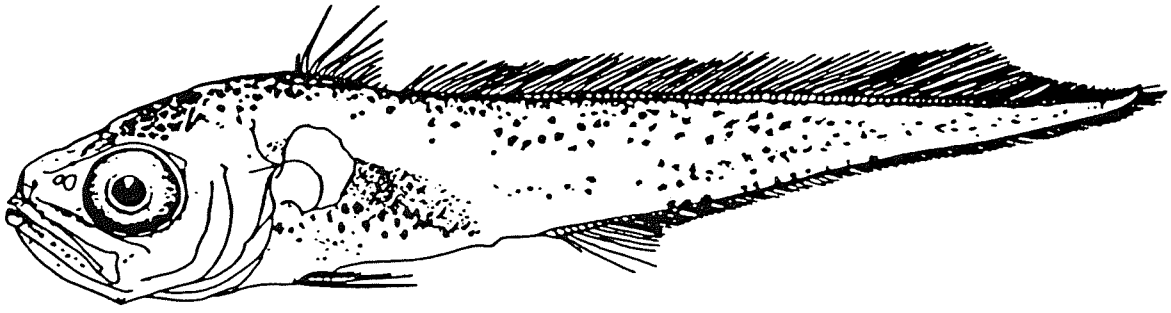


Fig. 2

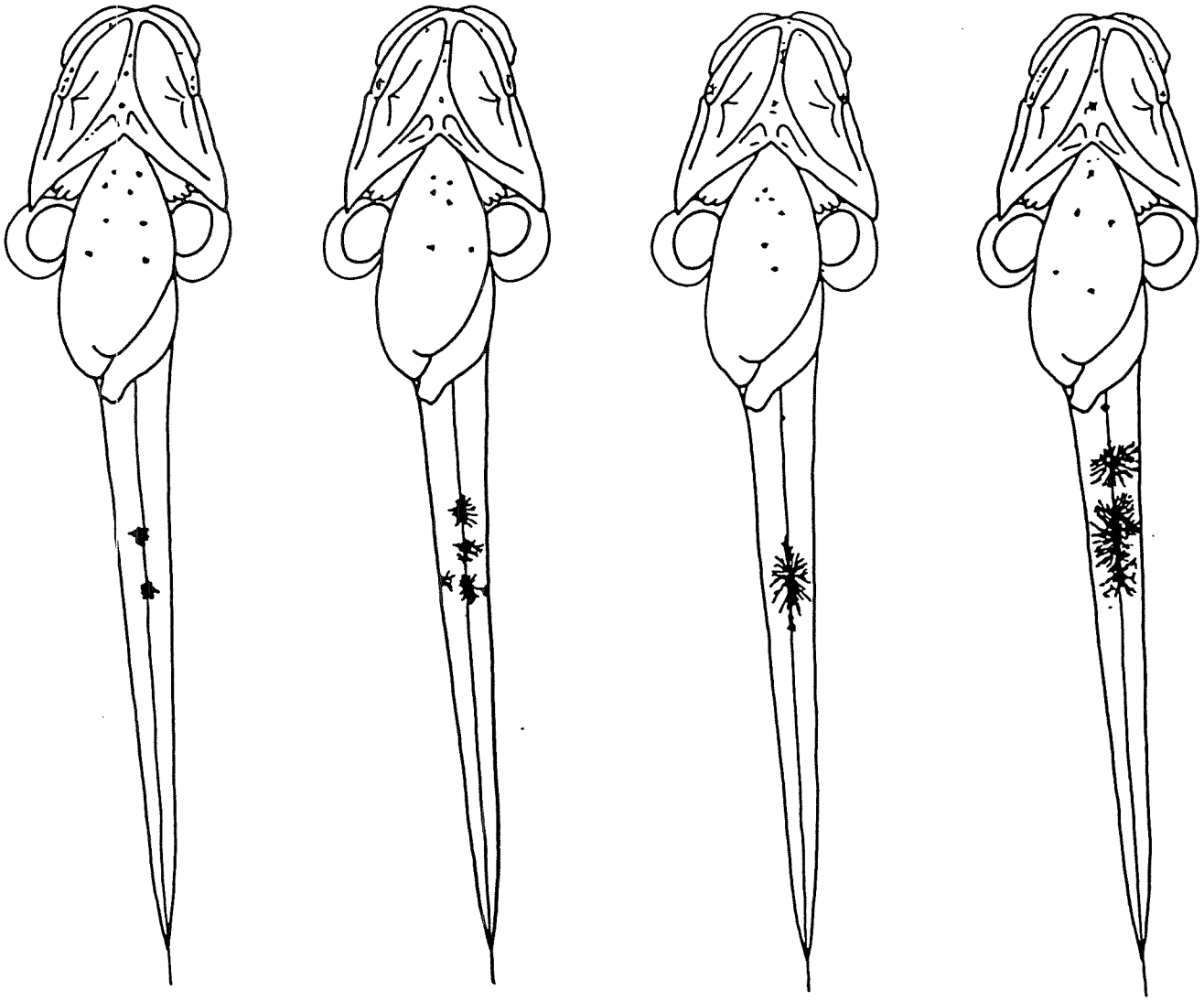
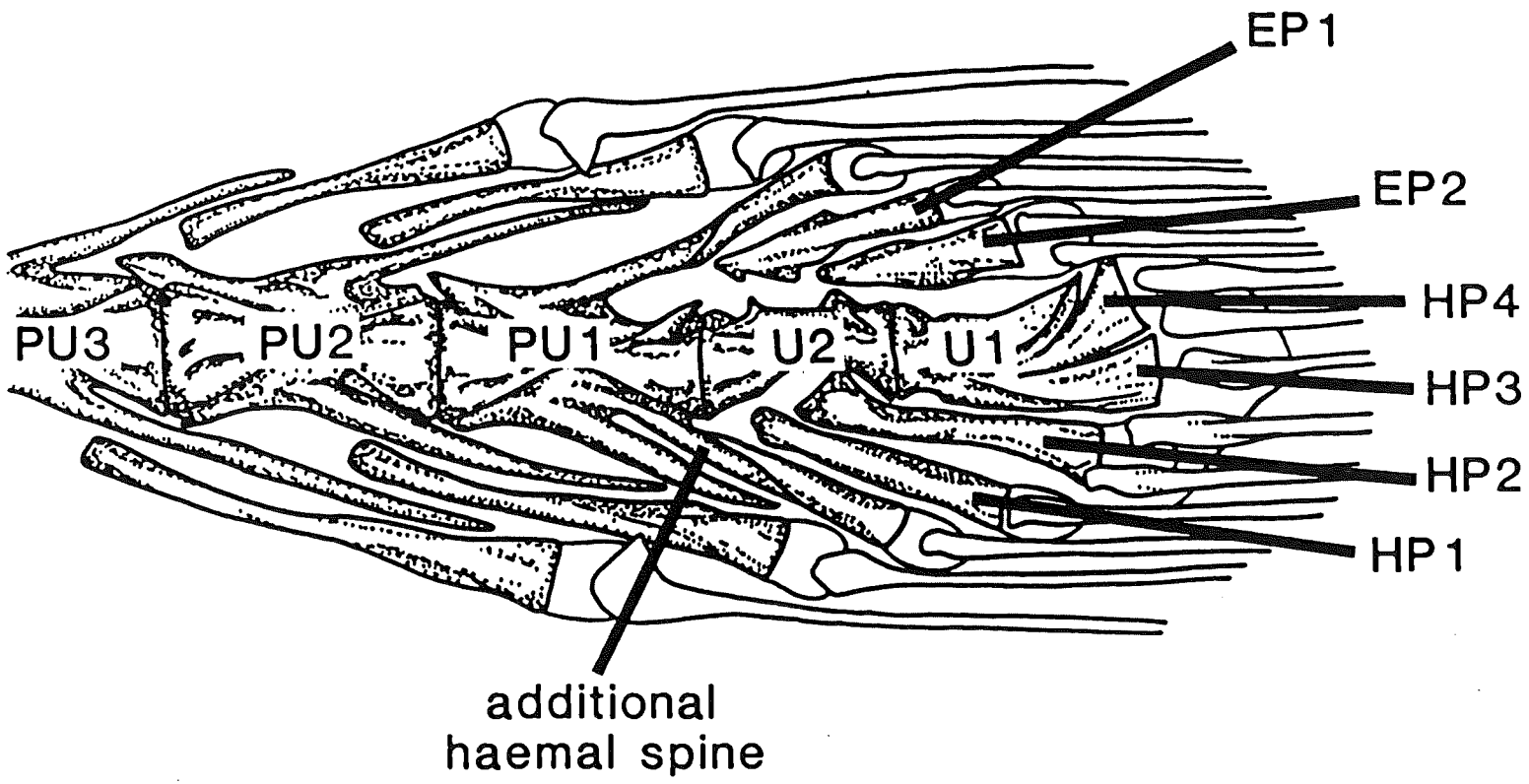


Fig. 3.



EP epural

HP hypural

U ural centra

PU preural centra

Table 1. Body proportions of larvae and juveniles of Macruronus novaezelandiae (expressed as percentage NL or SL): mean, standard deviation, range.

body proportion	preflexion			flexion			postflexion			juvenile		
sample size		42			4			4			2	
length (mm.)	8.9	4.5	(3.6-19.0)	23.5	2.3	(20.6-26.1)	30.0	2.9	(27.6-34.2)	189.0	1.4	(188.0-190.0)
head length	22.7	1.7	(18.3-24.7)	23.7	1.0	(22.3-24.7)	22.3	1.4	(20.5-23.6)	17.6	0.4	(17.3-17.9)
eye diameter	9.2	0.7	(8.1-10.3)	7.9	0.4	(7.3-8.3)	7.3	0.7	(6.5-8.0)	4.2	0.4	(4.4-5.2)
snout length	6.1	0.9	(4.6-7.7)	6.2	0.6	(5.7-7.0)	5.9	0.5	(5.4-6.5)	4.9	0.1	(4.8-5.0)
depth at pectoral	22.3	1.7	(21.0-24.4)	17.9	0.6	(17.2-18.5)	16.6	2.0	(13.7-18.5)	13.1	0.1	(13.0-13.2)
depth at anus	12.0	2.4	(8.2-15.2)	13.1	0.3	(12.6-13.4)	13.0	0.8	(12.3-13.8)	12.7	0.6	(12.3-13.1)
snout to first dorsal fin	27.5	1.3	(25.2-29.3)	26.6	0.8	(26.0-27.7)	25.3	0.8	(24.2-26.0)	20.7	0.2	(20.6-20.9)
snout to anal fin	51.4	0.9	(49.6-50.6)	50.4	0.5	(49.6-50.6)	46.6	1.5	(45.0-48.4)	46.5	1.2	(45.7-47.4)

Table 2. Meristic counts from larval and juvenile M. novaezelandiae. Specimens between dashed lines are undergoing notochord flexion.

length (mm.)	fin rays dorsal	fin rays anal	fin rays pectoral	fin rays ventral	branchio-stegal rays	gill rakers upper	gill rakers lower	gill rakers total	total centra	neural spines	haemal spines	caudal elements
3.7	-	-	-	-	-	-	-	-	-	-	-	-
3.9	-	-	-	-	-	-	-	-	-	1	-	-
4.2	-	-	-	-	-	-	-	-	-	1	-	-
4.6	-	-	-	-	1	-	-	-	-	2	-	-
4.8	-	-	-	-	1	-	-	-	-	2	-	-
5.2	-	-	-	-	3	-	-	-	-	2	-	-
6.0	-	-	-	-	3	-	-	-	-	3	-	-
7.4	-	-	-	-	5	-	-	-	5	6	-	-
9.4	4+28	18	-	3	6	-	8	8	42	55	37	-
9.9	0+19	4	-	-	6	-	6	6	38	54	34	-
11.5	9+74	60	-	4	7	-	12	12	55	58	42	-
16.3	12+84	73	4	8	7	1	15	16	70	70	55	3
17.4	12+86	76	4	8	7	3	15	18	71	70	55	3
19.8	13+87	86	3	8	7	5	15	20	73	74	57	4
23.2	12+100	90	9	8	7	5	17	22	76	74	57	5
26.1	13+99	90	13	8	7	5	21	26	76	74	57	5
28.9	13+99	91	9	8	7	7	22	29	78	76	57	a
188	13+94	90	20	8	7	7	22	29	b	b	b	b
190	13+96	90	20	8	7	7	23	30	b	b	b	b

a specimen damaged
b juveniles not stained