Spawning and Reproductive Characteristics of Blue Warehou in South-East Australian Waters

Ian A. Knuckey & K. P. Sivakumaran

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Principal Investigator: **Dr. Ian A. Knuckey**

Address: **Marine and Freshwater Resources Institute**
PO Box 114 Queenscliff VIC 3225
Telephone: 03 5258 0111 Fax: 03 5258 0270

Objectives

1. Determine the location and timing of spawning of blue warehou in the SEF area, and describe the relationship between spawning and the catching patterns of the trawl and gill net sectors of the fishery.
2. Estimate size/age at first sexual maturity and the sex ratios of spawning fish.
3. Describe gonad maturation cycles and the relationship between size/age and egg production (fecundity) in females.
4. Conduct per-recruit analyses to identify harvest strategies which allow optimum blue warehou egg production (and therefore recruitment).

NON-TECHNICAL SUMMARY

Blue warehou (*Seriolella brama*) is an important commercial species in the South East Fishery (SEF), sold predominantly as fresh fish in the Sydney and Melbourne Fish Markets. Trawled blue warehou catches come mainly from outer shelf and upper slope waters off southern NSW, eastern Bass Strait and western Victoria, and significant gill net catches come from shelf waters in eastern Bass Strait and around Tasmania (Smith 1994). There is also a significant recreational catch in some coastal waters.

Catches of blue warehou increased during the 1980's and by the early 1990's total landings were around 3000 tonnes per annum. Subsequently, catches decreased during the mid-1990s and in 1997, the total catch (trawl and non-trawl) of blue warehou had fallen to around 1000t with a value of $1.5 million. In conjunction with declining catches, blue warehou catch rates in both the trawl and non-trawl sectors also declined and were accompanied by significant

reduction in the mean catch-at-age in some sectors of the fishery. This lead to concerns over the status of blue warehou stocks and the South East Fishery Assessment Group (SEFAG) recommended that a formal stock assessment should be undertaken. To assist in the assessment of the status of blue warehou stocks, a research project was initiated to gain better information on their reproductive biology. This report details the results of that research.

Monthly samples of blue warehou were collected between May 1996 and December 1997 from commercial catches taken in three regions of the SEF: off the east coast of Victoria; eastern Tasmania; and western Bass Strait. Biological information was collected from these fish and the gonads were removed for detailed examination. Important reproductive parameters such as sex ratio, gonadosomatic index, macroscopic and histological development, size at maturity, fecundity and eggs–per–recruit were estimated. The reproductive cycle was described and the location and timing of spawning was determined. The main spawning period was during winter – spring and there was evidence of spawning in each of the three regions. Blue warehou reach maturity at between 30 – 40 cm fork length at an age of about 3 years. They have a determinate annual fecundity and spawn around three batches of eggs during a season. Eggs–per–recruit analyses revealed maximum egg production around 40 cm (4-5 years) in an unfished population. Mesh net fishing, which targets fish larger than 45 cm, was less likely to impact the relative eggs–per–recruit in a population than trawl fishing, which catches a wider range of smaller fish. The implications of these results are discussed in light of the current management arrangements in the SEF. The findings of the present study do not only provide a better understanding of the reproductive biology of blue warehou, they will form an essential component of models developed to assess the impact of fishing on the long-term sustainability of the blue warehou resource in the SEF.

Keywords: *Seriollela brama*; blue warehou; reproduction; spawning; development.

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BACKGROUND

Blue warehou (*Seriolella brama*) is an important component of the South East Fishery (SEF), sold predominantly as fresh fish in the Sydney and Melbourne Fish Markets. Trawled blue warehou catches come mainly from outer shelf and upper slope waters off southern NSW, eastern Bass Strait and western Victoria, and significant gill net catches come from shelf waters in eastern Bass Strait and around Tasmania (Smith 1994). Blue warehou is also becoming an increasingly important recreational target species in coastal waters of Victoria, Tasmania and southern NSW.

Historical catch records often failed to distinguish blue warehou from the closely related silver warehou (*S. punctata*), grouping them together as warehou or "Tassie trevally". Catches of warehou increased dramatically during the 1980's and total landings of the two species in the early 1990's were in excess of 4000 tonnes per annum, with an annual landed value of about $10 million. The combined catch of these species has since stabilised around this tonnage, but the proportion (by weight) of the more valuable blue warehou dropped from about 70% to 40% during the mid-1990s. In 1997, the total catch (trawl and non-trawl) of blue warehou had fallen to around 1000t with a value of $1.5 million.

In conjunction with declining catches, blue warehou catch rates in both the trawl and non-trawl sectors declined during the mid-1990s and was accompanied by significant reduction in the mean catch-at-age in some sectors of the fishery. This lead to concerns over the status of blue warehou stocks in the 1994 and 1995 stock assessments (Smith 1995; MacDonald and Smith 1996). Such concerns were compounded by a poor understanding of blue warehou population dynamics and the complex spatial and temporal fluctuations in their distribution which prevented assessment of the relative importance of fishing pressure versus other factors in producing these trends. As a result, the South East Fishery Assessment Group (SEFAG) recommended that a range of research projects be undertaken with the ultimate goal of providing the information needed to develop an age-structured model of the different sectors of the fishery (Staples and Tilzey 1995). One of the main research projects was to address a lack of knowledge of the spawning and reproductive characteristics of blue warehou. It was proposed that a fishery-dependent study of the timing and location(s) of gonad maturation would assist in the interpretation of fluctuations in blue warehou abundance and population structure and provide updated maturity estimates and fecundity data for per-recruit analyses (Chesson 1996). The present report details the results of this research.

NEED

Tagging studies have been undertaken in an attempt to obtain information on movement patterns and stock structure of blue warehou in south-east Australia (Knuckey *et al.* 1999). Unfortunately, the results were inconclusive, but the lack of tag recaptures indicated that tagging may not be an appropriate stock assessment tool for blue warehou at this stage. However, blue warehou, like spotted warehou, are known to undertake major migrations (Gavrilov and Markina 1979) and they are generally perceived to be highly mobile species with a broad distribution of breeding locations. As such, although there have been no studies on the stock structure of blue warehou in Australian waters, the species is assumed to comprise a single stock for fisheries assessment and management purposes. Nevertheless, considerable spatial and temporal structuring is evident within the fishery (Smith *et al.* 1998). Fish caught in the East by the gill net sector are generally larger and older than those caught by the trawl sector in other areas of the fishery (Smith 1998). Uncertainty about the stock structure and the effects of fishing on the spawning populations has caused conflict between the various sectors of the Industry. Definition and reduction of these uncertainties can only be achieved through the development of appropriate models which incorporate accurate biological and fishery information.

A comprehensive study on the spawning and reproductive characteristics of blue warehou will provide a range of population parameters necessary for the development or tuning of any age-structured model of blue warehou population dynamics. Knowledge of mean age/size of females at the onset of sexual maturity provides an estimate of the lag period before any cohort begins to contribute to egg production. Once fish reach maturity, examination of the ovaries provides information on gamete development patterns, proportions of ova mature at any given time, and the relationship between size/age and the production of mature ova. These maturation and fecundity data, together with age and growth data provided from the Central Ageing Facility, are required to conduct eggs-per-recruit analyses of the impact of different types and levels of fishing on egg production capacity (and therefore future recruitment). These types of data, together with an analysis of the spatial and temporal distribution of trawl and gill net catches, will provide insight into the direct impact on spawning stocks of using particular fishing methods at particular locations and/or times. Such information will be a valuable input to the development and evaluation of any harvest strategy designed to optimise reproductive capacity of blue warehou populations in south-east Australia.

OBJECTIVES

The project was designed with the following objectives:

1. Determine the location and timing of spawning of blue warehou in the SEF area, and describe the relationship between spawning and the catching patterns of the trawl and gill net sectors of the fishery.
2. Estimate size/age at first sexual maturity and the sex ratios of spawning fish.
3. Describe gonad maturation cycles and the relationship between size/age and egg production (fecundity) in females.
4. Conduct per-recruit analyses to identify harvest strategies which allow optimum blue warehou egg production (and therefore recruitment).

MATERIALS AND METHODS

Sampling regime

The study was undertaken in the shelf and mid-slope waters of three main fishing regions within the boundaries of the South East Fishery (SEF), defined in the present study as: East - from Eden to Lakes Entrance; Eastern Tasmania; and West - near Portland off the western Victorian coast (Fig. 1). Preliminary sampling began in May 1996 to determine the most suitable sampling methods, preservation techniques and establish appropriate gonad staging classifications. Intensive monthly sampling of the three regions began in January 1997 and continued for a full year. Random samples of at least 100 blue warehou were collected each month from each region. Both trawl and mesh net catches were sampled from the East, but lack of mesh net catches of blue warehou by SEF vessels in the West and Eastern Tasmania regions restricted the sampling in these regions to only trawl catches. The date, region, port of landing and gear type were recorded for each sample.

Fishery data

Logbook data from the commercial trawl (SEF1) and non-trawl (GN01) sectors of the South East Fishery were used to determine the timing of the main fisheries in the different regions. Data from 1986 to 1997 were used in the analyses. The mean monthly catch ± standard error were calculated and plotted for each region and gear type.

Biological data

After capture, all fish samples were retained on ice and returned to the laboratory for dissection. The sex (male, female or immature), caudal fork length measured down to the nearest centimetre (LCF), total weight (± 50 g), macroscopic gonad stage, left and right gonad weight (± 0.5 g), and gonadosomatic index $\left(\mathrm{GSI},\ \frac{\text{Gonad weight}}{\text{Total weight}} \times 100\right)$ were determined for each fish.

Length frequency distributions were plotted for male and female blue warehou caught in the different regions and by the different gears. The gonads from a sub-sample of these fish were used for histological examination. In addition, the sagittal otoliths were removed from between 10 and 30 randomly selected fish in each monthly sample from each region. These were embedded in resin and sectioned for age determination using standard techniques at the Central Ageing Facility (Morison *et al.* 1998).

Macroscopic staging

A means of staging both the male and female gonads by eye was developed. Such "macroscopic" staging was based on similar reproductive studies (eg. Hunter and Macewicz 1985a, 1985b; Schaefer 1987; West 1990; Davis and West 1993; Marshall *et al.* 1993), especially those of another Centrolophidae, blue eye trevalla (*Hyperoglyphe antarctica*), (Baelde 1996). Slight modifications to these classifications were made following examination of blue warehou gonads from preliminary samples. Having established these classifications, the reproductive stage of all fish collected during the project was determined.

Gonad preservation

Initially, the gonads were only fixed and preserved in 10% vapour suppressed formalin (a solution containing 100 ml formaldehyde, 680 ml propylene glycol and 36 g hexamine added to 220 ml seawater to make one litre). Whilst this technique was sufficient for most samples, it proved inadequate for histological examination of female gonads that were running ripe (Stage VI), because the samples were not firm enough to allow sectioning. As a consequence, estimation of fecundity from samples collected during 1996 was prevented and a modified technique was established. This involved initial preservation of the entire gonad in 10% formalin in seawater for a week before a transverse medial portion of about 30g of gonad was removed and preserved in Davidson's solution. In the case of ripe female gonads (Stage V and VI), the whole left or right ovary was preserved in Davidson's solution. Davidson's solution has proven to be an excellent fixative for marine fish gonads for histological examination (Bell *et al.* 1992; Baelde 1996). Sectioning, mounting and histological studies were only undertaken after the gonads had been fixed for at least one month. Transverse medial portions of material were blocked in paraffin wax and 6 μm sections were cut, mounted and stained in Harris' heamatoxylin and eosin (Luna, 1968). An understanding of the processes occurring at a cellular level during the different stages of the female reproductive cycle was enabled by histological examination of the ova.

Microscopic staging

To avoid possible variation in the developmental stage of oocytes due to their position in the ovary, only the transverse medial portion of the gonad was removed from each sample for histological examination (Forberg 1982; Chubb and Potter 1984; Mayer *et al.* 1984; Bell *et al.* 1992; Hyndes *et al.* 1992; Gooley *et al.* 1995). In many studies, no significant differences in oocyte frequency distribution and maturation have been found between right and left ovaries (Laroche and Richardson 1980; DeMartini and Fountain 1981; West 1990). In the present study, we usually removed the portion from the left-hand ovary unless it was damaged.

Oocytes undergo the same basic pattern of growth and development in all teleost species (Coward and Bromage 1998). Thus, based on other histological studies of reproductive development in fish (Mayer *et al.* 1984; West 1990; Baelde 1996) we describe the oocyte development of blue warehou. Oocyte size was measured by taking the mean of the maximum and minimum diameter of the largest oocytes which had been sectioned through the nucleus. This procedure has been shown to be representative of the true oocyte diameter by Foucher and Beamish (1980). Relationships between oocyte development, ova size and gonad development for blue warehou were developed.

Ovaries were staged based on the most advanced type of oocytes present, regardless of their abundance (Wallace *et al.* 1987; West 1990; Baelde 1996). Once staging techniques were developed and perfected, all gonad samples were re-staged. Relationships were established between the macroscopic and microscopic stages.

Size/age at maturity

Size and age at maturity was established by plotting maturity ogives against both length and age. In each case, the number of mature fish within each length/age class was expressed as a percentage of the total number of fish of that length/age-class. Length – classes of 1-cm and age-classes of 0.1 year were used. Data were pooled across areas. A logistic curve was fitted using a non–linear least squares procedure and the length and age at which 50% of females were mature was determined ($L_{50\%\ mature}$, $t_{50\%\ mature}$ respectively). The form of the logistic equation used was:

$$\%\ \text{mature} = 100 / (1 + e^{a \times (b - c)})$$

Where a is a parameter indicating the rate of increase in maturity;

b is a parameter representing 50% maturity;

c is the 1–cm length–class or 0.1–year age–class.

Spawning season

The presence of postovulatory follicles in ovaries was used to identify females that had begun to spawn (Hunter and Macewicz 1985b; Schaefer 1987). Post-ovulatory follicles are the ruptured, empty follicles marking positions of mature oocytes which have ovulated. They quickly degenerate, however, which is apparent by their reduced size and fewer loops. Individuals with postovulatory follicles , or with hydrated oocytes were considered either to have spawned or to be capable of spawning (Bell *et al.* 1992).

After spawning, residual oocytes and unwanted material are reabsorbed in a process known as atresia (Macer 1974; Hunter and Macewicz 1985a; Marshall *et al.* 1993). Atretic oocytes are recognised by their irregular shape, breakdown in fine structure (disintegration of the nucleus and liquefaction of yolk granules) and hypertrophy of the granulosa cells (Davis 1977). As degeneration progresses it becomes more difficult to distinguish atretic oocytes from advanced degeneration of postovulatory follicles (described as beta atresia by Hunter and Macewicz 1985b). Nevertheless, high levels of any atretic material, combined with the lack of hydrated oocytes and postovulatory follicles, were used to confirm when spawning had ceased.

Subsamples of ovaries preserved in Davidson's solution were mixed in small jars with water and shaken manually to dissociate the oocytes. All ovaries used had been previously staged histologically, and histological sections were used to stage corresponding whole oocytes under microscope (Table 4) adapted from West (1990) and Baelde (1996). One hundred oocytes were measured along the maximum diameter for 55 females at various stages of maturity.

Fecundity

In cases where the stock of oocytes destined to be spawned in a season is identifiable at the beginning of the spawning season, annual fecundity may be considered to be determinate, (Yamamoto 1956; Hunter and Macewicz 1985a,b) even though the fishes may spawn repeatedly during the season. The annual fecundity of blue warehou was estimated from the standing stock of yolked oocytes (Stage IV and V) from samples collected during 1997 spawning season. The average relative fecundity was measured as the number of oocytes per gram (gutted weight).

Fish may spawn more than one batch of eggs within a spawning season. The number of eggs spawned in a single batch is termed "batch fecundity". Ovaries with hydrated oocytes visible to the naked eye (Stage VI) were potentially suitable for the estimation of batch fecundity. Further visual screening of these samples once they had been fixed, was carried out in the laboratory. The presence of loose and hydrated oocytes in the lumen of the ovary suggested that some eggs had already been shed and these samples were rejected (Watson *et al.* 1992). All ovaries used in the estimation were also screened histologically for recent spawning activity, indicated by the presence of fresh postovulatory follicles and atresia. Only ovaries that showed no sign of previous spawning in that season, no sign of postovulatory follicles and no sign of major atresia were used to estimate batch fecundity. Also, due to their volume and weight, handling of Stage VI ovaries is extremely difficult and the ovaries may be easily damaged and therefore unsuitable for batch fecundity estimation. Initially, five fish were selected which met all of the criteria needed for batch fecundity estimation.

To ensure correct weighting factors were used for determination of batch fecundity, the gonads of these five fish were carefully dissected. We used ANOVA to compare the number of oocytes per gram between fish, and between subsamples within the ovary (near the periphery and near the centre) and along the ovaries (within the anterior, median, and posterior regions). ANOVA showed no significant differences between fish ($F_{1,5}$ = 3.215, P=0.116), or between subsamples within the ovaries ($F_{1,8}$= 1.24, P=0.29), or between subsamples along the ovaries ($F_{2,12}$= 0.05, P=0.95). Given these results, one-gram portions were randomly removed from the anterior, median and posterior regions of the left gonad of another 43 fish with Stage VI ovaries. Histological screening of these samples revealed that only a further four were suitable for batch fecundity estimation. Overall, then, of the total of 48 fish collected with Stage VI ovaries, only nine were suitable for estimation of batch fecundity. The gonad portions from these nine fish were weighed accurately (±0.001) and batch fecundity was determined using the gravimetric method (Hunter *et al.* 1985) to estimate the number of hydrated oocytes (Stage VI) within the gonads.

Eggs–per–recruit

Eggs–per–recruit analyses were undertaken to determine the size/age at which optimum egg production of blue warehou is achieved in an unfished population. This was compared with the relative eggs–per–recruit of a population fished by mesh nets in the East and trawlers in the West. These analyses are a modification of the typical age–based yield–per–recruit models (Thompson and Bell 1934; Ricker 1945; and Beverton and Holt 1957) which include a fecundity parameter to determine eggs-per- recruit (remaining in the population) instead of the yield (removed from the population).

A Microsoft Excel ™ spreadsheet was used to undertake the eggs–per–recruit modelling in a manner similar to Sanders (1995). The eggs–per–recruit was modelled against both age and length. Time intervals of 0.25 years and length–classes of 1–cm were used to model the recruit over a period of ten years.

To model growth, the von Bertalanffy (1938) growth function was used, in the form:

$$L_t = L_\infty\left(1 - e^{-K\,(t - t_0)}\right)$$

where L_t is the length (cm) at time t (years);
L_∞ is the asymptotic maximum length (cm);
K is the Brody growth coefficient defining growth rate; and,
t_0 is the theoretical age at zero length.

The values for these parameters for female blue warehou were calculated based on ageing of sectioned otoliths by the Central Ageing Facility at MAFRI and were: L_∞ = 55.14 cm; K = 0.28 year^{-1} and t_0 = -0.07 years.

Natural mortality (M) was applied from age zero and was assumed to be constant over time (although this was a simplistic approach, no information on age-specific natural mortality rates was available). Four methods, based on life history parameters, were used to estimate natural mortality: Beverton and Holt (1957); Hoenig (1983); Rikhter and Efanov (1976); and Pauly (1980). The equations used in these estimation techniques are given below.

Beverton and Holt (1957):

$$L_{50\%\ mature} = 3 \times L_\infty / (3+M/K)$$

where $L_{50\%mature}$ is the length at which 50% of the population is mature; and, L_∞, and K are the von Bertalanffy growth parameters.

Hoenig (1983):

$$M = -ln(0.05/ t_{50\%\ mature})$$

where $t_{50\%mature}$ is the age (years) at which 50% is mature. This value was calculated from $L_{50\%\ mature}$ from the von Bertalanffy equation.

Rikhter and Efanov (1976):

$$M = 1.521 / (t_{50\%\ mature})\ 0.720 - 0.155$$

where $t_{50\%\ mature}$ is the age (years) at which 50% is mature.

Pauly (1980):

$$log_{10} M = -0.0066 - 0.279\ log_{10} L_\infty + 0.6543\ log_{10} K + 0.4634\ log_{10} T$$

where T is the water temperature in °C Based on information from SEF fishers, blue warehou are generally caught in waters with temperatures ranging from 10 to 14 °C. A temperature of 12°C was used for this estimation.

To compare the eggs-per-recruit of populations fished by different gears, estimates of the range of fishing mortality (*F*) and the size-selectivity of the different gears were derived from Punt (1999). The only modification of Punt (1999) was that the left-hand side of the trawl selectivity ogive was estimated from back-calculation of total mortality from length-converted catch curve analysis (eg. Jensen 1982; Pauly 1984) on length frequency distributions obtained from on-board observer measurements. Comparisons were made between the mesh net fishery in the East and the trawl fishery. Fishing mortality *(F)* was assumed to be constant across all age/lengths and was applied in proportion to the selectivity of the gear.

DETAILED RESULTS

Sampling regime

The collection of fish for this study was based solely on commercial catches and therefore reflected seasonal changes in the availability of fish to the fishing gear. The effects of this were apparent in the lack of samples from Eastern Tasmania during winter and spring (Table 1). We also endeavoured to collect monthly samples of fish from both the trawl and mesh net sectors in the East region. This was achieved between January to July 1997, but in the subsequent months there was no mesh net catches of blue warehou and samples were based only on trawl catches. Similarly, a lack of trawl-caught blue warehou from the West region during December 1997 prevented the collection of samples. Despite these sampling shortfalls, information on the reproductive condition of over 3300 blue warehou was collected from the three regions during the study.

Fishery data

In the East, mean monthly catches in the trawl fishery were generally below 20t, but increased to a peak of 60 to 80t in August to October before rapidly dropping off to less than 20t in November (Fig. 2a). Over the longer term, there was no obvious seasonal pattern apparent in the gill-net fishery catches, although in 1997, when the sampling was undertaken, there was a peak in monthly catches around June – with minimal catches (<5t) from August to December (Fig. 2b). Off eastern Tasmania, the blue warehou fishery was essentially restricted to Summer (November to March), with minimal catches during the rest of the year (Fig. 2c). In contrast, the catch by trawl fishery in the West was negligible during Summer, with the mean monthly catch increasing to 40 to 60t during the winter and spring months (Fig. 2d). These results are consistent with Smith *et al.* 1998.

Biological data

There were noticeable differences in the size range of fish caught by the different gears and in the different regions, although little apparent difference existed between the size range of the different sexes (Fig. 3). The size of blue warehou caught by trawlers in the East ranged between 25 and 55 cm, but most were evenly distributed between 35 and 50 cm. The mesh net catches in the East, however, generally consisted of larger fish between 45 and 55 cm, with a mode around 48-49 cm. A greater proportion of the fish above 50 cm were female. In contrast to the East, trawl-caught fish in the West region generally ranged between 30 and 45 cm with a mode around 37 cm. Throughout the study only sixty specimens of indeterminate sex were collected. These fish ranged between 21 and 25 cm.

Gonad and oocyte development during the reproductive cycle

Macroscopic descriptions of the various developmental stages of gonads from male and female blue warehou are shown in

Table 2 and **Table 3** respectively. Histological descriptions of the various stages of blue warehou oocytes are presented (**Table 3**) together with images of the various stages (Plates A-F). A summary of the ova development is provided below.

In immature females (Stage I), the ovaries are thread-like, pink and translucent and GSI is negligible. Oocytes are not visible to the naked eye. Microscopic examination reveals small oocytes with a nucleus surrounded by a thin layer of cytoplasm. These constitute the reservoir of oocytes that are present throughout the life of the fish. In Stage II, the ovary walls become transparent. Histological examination shows nucleoli at the periphery of the nucleus and oocytes are larger (<90 μm) as the cytoplasm thickens, but they are still not individually visible to the naked eye. During Stage III, the oocytes become visible (100 –300 μm), the ovaries change colour from pink to yellow-orange and occupy 20 – 70% of the length of the body cavity. Mean GSI is around 2%. Under the microscope, lampbrush chromosomes may be visible in the nucleus and cortical alveoli and oil vesicles appear in the cytoplasm. The zona radiata is apparent. As they develop into Stage IV, the opaque oocytes are clearly visible in the ovaries, which are yellow and may run the entire length of the body cavity, giving a mean GSI of around 5%. There is a marked increase in oocyte size as the cytoplasm fills with yolk granules and the number and size of oil vesicles and cortical alveoli increases. The ovaries then become ripe (Stage V), occupying between 70 and 100% of the length of the body cavity. The oocytes become larger (1.0 – 1.3 mm), and increasingly transparent as hydration occurs. The nucleus moves to the periphery of the oocyte and in the cytoplasm, the yolk granules fuse to form yolk plates and the oil vesicles fuse to form an oil droplet. When the ovaries are running-ripe (Stage VI), oocytes are may be expressed with slight pressure on the abdominal cavity. The hydration process continues until ovulation (spawning), when the follicular epithelium surrounding the oocyte breaks and the egg is released. The eggs are large (1.1 – 1.5 mm), very translucent, and an oil droplet is visible to the naked eye. Within the ovary, the follicular cells then form strings, which are folded in the space left by the egg. These post-ovulatory follicles undergo rapid degeneration. Some mature oocytes fail to release during spawning and are resorbed. After spawning, the ovaries are flaccid and the walls appear grey and wrinkled. A few atretic oocytes may be apparent. After spawning, the gonads enter a resting phase prior to redeveloping for the next reproductive cycle.

As would be expected, mean GSI values increased as the gonads developed prior to spawning but there was a large amount of variation between individual GSI values at any given developmental stage **(Fig. 4.)**

Size at maturity

The relationship between GSI and gonad stage enabled GSI to be used as a broad indicator of blue warehou maturity. Generally, mature individuals had GSI values greater than 3%, and these fish were usually greater than 30 cm LCF for both males **(Fig. 5)** and females (Fig. 6). There were a number of exceptions to this general rule, however, specifically resulting from fish whose gonads were redeveloping after spawning. These fish often had GSI values less than 3% although they were mature. It was extremely difficult, either macroscopically or histologically, to distinguish between immature developing males and mature males with gonads that were redeveloping subsequent to spawning. Because of this, a maturity ogive was not developed for males. Female maturity was more easily determined through macroscopic and microscopic examination of the gonads. Fish with ovaries in the immature (Stage I) or early developing stage for the first time (Stage IIa) were identified by their ribbon-like ovaries and classed as immature. Females with ova that had returned to the redeveloping stage after spawning (Stage IIb) were more likely to have a thick flaccid gonad wall and could be recognised histologically by post-ovulatory follicles and/or atretic material around the oocytes. These were classed as mature fish. Importantly, if no post-ovulatory follicles or atretic material were evident, it was almost impossible to distinguish Stage II from Stage IIb females through histological examinations. In these cases, only macroscopic examination of the gonad could be used to determine maturity. All fish with gonads at Stage III and beyond were easily recognised as mature.

Although the GSI of immature females was less than 3% (Fig. 6a), there were also many mature females over a range of sizes with GSI values less than 3% (Fig. 6b). These individuals usually had Stage IIb or Stage III ovaries. Mature female blue warehou in spawning condition usually had a GSI higher than 5%, most females greater than 45 cm had a GSI of more than 10% and some had a GSI of around 20% (Fig. 6c). GSI values in spawning fish were variable because some individuals had already shed an unknown number of oocytes, resulting in loss of ovary mass (partially spent). Generally GSI values for spawning females were considerably higher than those for spawning males, which rarely exceeded 10% (see **Fig. 5**).

The logistic equation for the maturity ogive of female blue warehou plotted against length was % mature $=100 / (1 + e^{0.309 \times (33.40 - L)})$. This indicates that the length at 50% maturity was 33.4 cm (Fig. 7). When plotted against age, the equation for the maturity ogive was % mature $=100 / (1 + e^{1.748 \times (3.28 - t)})$, which places the age at 50% maturity at 3.28 years (Fig. 8).

Spawning season

In the East, females with developing ova were apparent throughout the year, but the main occurrence of spawning and spent females was between the months of May and August (Fig. 9a). A similar trend was apparent in the West, although there was no evidence of spawning until June (Fig. 9c). In both of these regions, some spawning and spent females were evident up until November, although there was one month in which no spawning fish were apparent (September in the East and August in the West). Data from Eastern Tasmania were sparse and not conclusive, but supported evidence of spawning in May (Fig. 9b). The gonad condition of males in the different regions parallelled those of the females and supported a winter spawning period (Fig. 10).

In the East, peaks in GSI during June for both males and females (Fig. 11) supported a winter spawning period in line with the results of the gonad condition. In the west, however, determination of spawning season based on observations of GSI alone was more uncertain than using gonad stages. A defined peak in GSI was not nearly as apparent as in the East, but values were at a minimum in May for both males and females (Fig. 12) and increased towards the end of the year.

The percentage of females (30 - 50 cm LCF) in the monthly samples of blue warehou collected throughout the study (including the spawning season) ranged between 50 to 75% but was usually around 60% (Fig. 13). The proportion of females increased slightly for fish >50 cm, but the total number of samples was small (<100 fish). Overall, there were significantly more females caught than males ($P<0.0001$). The males and females collected during the present study ranged from 2 to 7 years and 2 to 9 years of age respectively. Although not all of these fish were mature, mature gonads appeared in male and female fish ≥2 years of age.

Fecundity

As the unyolked oocytes developed to stage III (Fig. 14a), they became larger (90 – 320 μm) than the standing stock of oocytes (< 90 μm – not shown) and were easily distinguishable as a group of larger oocytes (400 – 1000 μm) once they had reached the yolked stage (Stage IV, Fig. 14b). These were the oocytes that were to be spawned during the oncoming season and provided the evidence of determinate annual fecundity. As they developed further (Stage V onwards), a bimodal distribution in the oocyte's diameter became apparent. The larger oocytes (>1000 μm) were those in the "batch" that had begun to hydrate prior to spawning (Fig. 14c). When hydration was complete and spawning was imminent (Stage VI), these oocytes ranged from 1.29 mm (1290 μm) to 1.52 mm (1520 μm, Fig. 14d). After these are spawned, a subsequent batch of the yolked oocytes will hydrate in preparation for spawning.

The oocyte diameters mentioned above were those measured from fresh gonad samples. They were slightly larger than those in the histological samples, especially in the later stages of development (Fig. 15), because histological processing causes shrinkage of oocytes (West 1990, Rickey 1995). Oocytes from sectioned Stage II to Stage VI gonads ranged from 34-176 μm, 94-329 μm, 279-912 μm, 488-960 μm and 645 -1157 μm respectively.

The annual fecundity and batch fecundity were studied for 35 and 9 fish respectively. The annual fecundity (*AF*) was estimated from the standing stock of yolked oocytes in stage IV and stage V ovaries. It ranged from 0.43 to 1.35 million oocytes per fish, and although varying considerably at given length (**Fig. 16**), it showed significant exponential increase with the length of females, following the equation:

$$AF = 10.397 \times LCF^{2.9216}$$

The linear regression between log-transformed data was statistically significant ($F_{1,34}$= 50.3308, P<0.0001, R^2 =0.60). The average relative fecundity was 417 oocytes (± 99 SD) per gram (gutted weight) and ranged between 200 and 780 oocytes/gram. Relative fecundity was not significantly related to fish length ($F_{1,34}$= 0.08648, P>0.77, R^2 =0.002).

The batch fecundity estimated for ripe females (n=9) ranged from 0.21 to 0.36 million oocytes per fish (**Fig. 17**). The linear regression against the length of the fish was statistically significant ($F_{1,8}$=7.3852, P<0.05, R^2 =0.48). Comparison of the regressions of log-transformed batch fecundity with log-transformed annual fecundity against length revealed that around three batches of eggs are spawned each year.

Eggs–per–recruit

A range of natural mortality estimates resulted from application of the various life-history methods. These were: 0.37 year $^{-1}$ (based on Hoenig 1983); 0.44 year $^{-1}$ (Pauly 1980); 0.49 year $^{-1}$ (Rikhter and Efanov 1976); and 0.55 year $^{-1}$ (Beverton and Holt 1957). Obviously, the results of the eggs–per–recruit analyses were considerably influenced by this range of natural mortality estimates. Nevertheless, in a scenario with no fishing mortality, the peak in eggs–per–recruit occurred for fish around 40 cm (Fig. 18) or between four and five years old (Fig. 19) for all natural mortality estimates.

For further analyses of eggs–per–recruit, a natural mortality estimate of 0.44 year $^{-1}$ was chosen (similar to the base case of 0.45 year $^{-1}$ used by Smith 1999) and the effect of fishing by trawl and mesh net methods was compared. Actual selectivity ogives for blue warehou caught by trawl and mesh net methods have not been established experimentally. Based on data derived from a stock assessment of blue warehou using integrated analysis (Punt 1999), the mesh net selectivity can be represented by the logistic equation as: % retained =100 / (1 + $e^{0.422 \times (49.64 - L)}$). This selectivity was based on the larger blue warehou targeted by mesh net methods in eastern Bass Strait during the 1990's and therefore also incorporates the availability of fish to that method. The decreased selectivity of trawl gear to larger blue warehou (the right-hand side of the trawl selectivity ogive) was derived from Punt (1999) and also reflected the availability of fish to that method. This was represented by the logistic equation: % retained $=100 - 100 / (1 + e^{0.745 \times (55.65 - L)})$ which was applied to fish greater than 45 cm. The left-hand side of the trawl selectivity ogive was estimated from length-converted catch curve analysis and can be represented as: % retained $=100 / (1 + e^{1.570 \times (34.56 - L)})$. The resultant selectivity ogives used for the two methods are shown in Fig. 20. Overall, the selectivity of the mesh nets was towards a smaller range of larger fish than trawl gear.

Eggs–per–recruit estimates for a range of fishing mortalities are shown for populations fished by trawls and mesh nets (Fig. 21). As a result of the different selectivities of the two fishing methods, the eggs–per–recruit remaining in the population at any particular level of fishing mortality was reduced more by trawling than by mesh nets, even though fishing pressures were generally higher in the Eastern mesh net fishery than for the trawl component (Smith 1999).

DISCUSSION

Distribution of spawning

Considerable spatial and temporal structuring is evident within the blue warehou fishery off south east Australia (Smith *et al.* 1998). Although there have been no studies on the stock structure of blue warehou in Australian waters, the species is assumed to comprise a single stock for fisheries assessment and management purposes. This is because blue warehou, like spotted warehou (*S. punctata*), are known to undertake major migrations (Gavrilov and Markina 1979) and they are generally perceived to be highly mobile species with a broad distribution of breeding locations. Tagging studies have been undertaken in an attempt to obtain information on movement patterns of blue warehou in south-east Australia, but lack of tag recaptures prevented conclusive results (Knuckey *et al.* 1999). Nevertheless, the present study revealed that blue warehou do spawn over a wide range of areas within the South East Fishery. These results are supported by a recent investigation of the larval distribution of blue warehou (Bruce *et al.* submitted to MFR special SEF edition) in which concentrations of young blue warehou larvae were found from Kangaroo Island in South Australia to southern

Tasmania, with a major concentration off the north-western coast of Tasmania and another off the eastern Victoria / New South Wales border. Interestingly, the region off north-western Tasmania which had the highest concentrations of larvae does not form a major part of the commercial fishery for blue warehou and was not sampled in the present study. Furthermore, only low concentrations of blue warehou larvae were found off the east coast of Tasmania and in eastern Bass Strait (Bruce *et al.* submitted to MFR special SEF edition) and there is no major fishing in these areas during the spawning season. Although the present study found spent fish off eastern Tasmania in May, the lack of samples from winter and spring limited firm conclusions being drawn about spawning in this area.

Timing of Spawning

In the present study there was no spatial or temporal difference in the spawning characteristics of males and females. There was, however, persistently more females than males caught during the study. The cause of this can not be explained based on the present results, although we established that it was not due to a catch bias towards larger females. The preponderance of females remained throughout the entire year and across the different areas and methods in the fishery. Assuming the sex ratio of the entire population is not skewed in preference to females, further research would be needed to determine whether any characteristic of the distribution, behaviour or some other aspect of the species' life history makes males less vulnerable to capture in the South East Fishery.

A previous study of gonadosomatic indices of blue warehou established that they spawned during winter in western Bass Strait (Smith *et al.* 1995). Smith (1994) noted that this was slightly earlier than the spring-summer spawning period observed in New Zealand, Gavrilov (1976). Through an extensive range of macroscopic and histological analysis of blue warehou gonads, the present study confirmed that the main spawning period of blue warehou in Australia was during winter and into spring.

A range of other studies has revealed that the ovaries of spawning females display histological evidence of past spawning (postovulatory follicles) or imminent spawning (hydrated oocytes or migratory-nucleus-stage oocytes; West 1990; Karlou-Riga and Economidis 1996, 1997). Postovulatory follicles are rapidly reabsorbed in number of temperate species (Mashall *et al.* 1993) and are often difficult to identify one to two days after spawning (eg. Hunter and Goldberg 1980; Alheit *et al.* 1984; Melo 1994; Schaefer 1996) after which time they may not be distinguished from intermediate stages of atretic oocytes (Hunter and Macewicz 1985a).

The occurrence of atretic ova marks the end of spawning (Hunter and Macewicz 1985b) and is associated with spent ovaries. Thus, Hunter and Macewicz (1980) suggested that the best indicator of the time of spawning was the occurrence of both hydrated eggs and postovulatory follicles.

Based on these criteria, the present study established that the main spawning period in the East occurred between May – August, and this was about a month earlier than in the West (June – October). Very few spawning fish were found outside these months. These results are consistent with those of Bruce *et al.* (submitted to MFR special SEF edition) who used back-calculation of larval ages to establish a winter or winter-spring spawning period, and also noted that spawning occurred earlier in the East than in the West. Interestingly, while the main fishing season in the West approximately corresponds to the spawning season, most of the catches in the East are taken after the main spawning period. The large spatial separation between the main spawning areas in the East and West (Bruce *et al.* submitted to MFR special edition) and their different spawning times lead Bruce *et al.* (submitted to MFR special edition) to conclude that these could be considered as separate spawning stocks.

Size at maturity

The size at which 50% of female blue warehou were mature was about 33 cm LCF and 90% were mature at 40 cm. This corresponds to fish between 3 and 4 years old. All fish under 30 cm were immature. Due to the difficulty in distinguishing between the gonads of males that were maturing for the first time and the redeveloping gonads of mature fish, a maturity ogive could not be established for males. Nevertheless, the GSI data indicated that males develop to maturity at a similar size as females. The size frequency of fish caught during this study and those from more extensive sampling programs (Knuckey and Sporcic 1999) show that very few fish less than 30 cm are caught by commercial vessels in the SEF and the majority are greater than 35 cm. As a consequence, most of the commercial blue warehou catch in the SEF will consist of mature fish. Outside the SEF, smaller fish (20 – 30 cm LCF) are caught by anglers in inshore waters or by commercial gill net operators using 90 – 125 mm gill nets in Tasmanian state waters (Knuckey *et al.* 1999). This fish are likely to be immature.

The size at maturity determined in the present study is somewhat lower than has been found in previous research. A size at maturity of 40 – 45 cm LCF has been recorded for blue warehou in New Zealand waters (Gavrilov and Markina 1979). Based on a survey in western Bass Strait during the late 1980s, Smith *et al.* (1995) also reported that female blue warehou mature at between 40 and 45 cm. This conclusion was based largely on GSI information from a low number of fish (~250) caught between June and September. Without detailed macroscopic examination and/or histological information, however, it is difficult to distinguish fish with redeveloping gonads from those maturing for the first time. In both cases these fish will have low GSI's, and, size at maturity based on analysis of GSI data alone could be overestimated if fish with redeveloping gonads were mistakenly classified as immature.

Fecundity

The high relative fecundity of blue warehou (417 ± 99) is similar to blue-eye trevalla (*Hyperoglyphe antarctica,* 480 ± 125 oocytes/gram), another centrolophid found in these waters (Baelde 1996). Similarly, both of these fish are group-synchronous batch spawners with a determinate annual fecundity. The annual fecundity of blue warehou increases exponentially with the length of females (0.43 to 1.35 million oocytes per fish between 38 and 55 cm LCF). These oocytes are released in about three large batches of between 0.21 to 0.36 million oocytes per fish increasing with length of females. Because postovulatory follicles usually persist in fish ovaries for only a short period (Macewicz and Hunter 1993; Hunter and Goldberg 1980; Alheit *et al.* 1984; Melo 1994), the co-occurrence of postovulatory follicles and ripe oocytes in blue warehou ovaries suggests successive batches of oocytes may be released within a few days. More intensive sampling over short time periods within the spawning season would be required to prove this.

Implications for the fishery

Recruitment, via reproduction, is important to a fishery because it is the means by which the resource is renewed. If indiscriminate harvesting of a population occurs, the number of animals that reach maturity can be reduced to an extent where the reproductive capacity of the population is diminished. One way of reducing this possibility is to ensure that minimal fishing pressure is applied to the population prior to the fish reaching maturity. Often this is achieved by setting restrictions on mesh size which can be used to catch the fish. Within the South East Fishery, blue warehou have been caught predominantly by trawl and gill net (non-trawl) fishing. A Total Allowable Catch (TAC), managed through a system of individual transferable quotas was introduced into the trawl sector in 1993. During 1998 a global TAC was introduced (across the trawl and non-trawl sectors) and leasing of quota between sectors was enabled. This, combined with the different selectivity of the two types of gears has important implications for the fishery in terms of the potential impact on the reproductive capacity of the stock.

Although most blue warehou caught in the commercial fishery are mature (present study), those caught in the East by the gill net sector are generally larger and older than those caught by the trawl sector in other areas of the fishery (Smith 1999). This primarily reflects differing selectivities of the trawl codend mesh (90 mm minimum) compared to the gill nets (150 mm minimum), but may also be influenced by the fact that larger fish tend to be caught in the East compared to the West. In Australian waters, blue warehou live to a maximum age of around eight years, and based on the results of the present study, at the size/age that the fish are caught by mesh nets, they have less reproductive potential than the newly matured younger fish captured in the trawl fishery. In recent years, catches from the gill net fishery have been poor (Smith and Wayte 1999) and under the global TAC, most quota has been leased from the non-trawl sector to the trawl sector (AFMA, unpublished data). On a purely per-recruit basis, if this non-trawl quota was caught by trawl operators, it would potentially reduce the reproductive capacity of the blue warehou stock to a greater degree, than if the quota was caught by gill nets. Although this point should be considered by fishery managers, it is a simplistic scenario. Per–recruit analyses do not incorporate information about the actual levels of recruitment in a fishery (Sainsbury 1992), which is one of the main sources of variability in the total yield from a fishery (MacLennan 1993). More sophisticated models of the fishery are being developed that will integrate the information on maturity, fecundity and seasonal reproductive patterns gained from the present study with other factors such as variable recruitment, the spatial structuring of the fishery and inter-sectorial leasing of quota (Punt 1999). The results of these models will help support management decisions that ensure the long term viability of blue warehou stocks as an important component of the South East Fishery.

BENEFITS

In managing the South East Fishery, the Australian Fisheries Management Authority endeavours to ensure that the blue warehou resource is utilised in a manner consistent with the principles of ecologically sustainable development. To help achieve this, the Blue Warehou Assessment Group was formed to undertake a formal assessment of the status of the resource. Development of a fleet-disaggregated virtual population analysis model applied to catch-at-age and standardised fishing effort data forms the cornerstone of this assessment (Smith 1999, Punt 1999). The primary benefit of undertaking the current research on blue warehou reproduction, is that improved population parameters can be incorporated into this model. Such improvements help to reduce levels of uncertainty in the model, thereby increasing confidence in model outputs and the management recommendations they underpin. Ultimately, this should lead to the long-term viability of the blue warehou fishery and benefit the recreational and commercial (trawl and non-trawl) sectors that utilise the resource.

FURTHER DEVELOPMENT

Punt's (1999) fleet-disaggregated virtual population analysis incorporates a range information on blue warehou biology with extensive time-series data inputs from the fishery. Research undertaken in the present study has gone a long way towards supplying the reproductive population parameters required in the model. This information will be incorporated in the model and reanalysed as part of the 2000 stock assessment. One major change to the model which will be initiated as a result of the present study is that the fishing year will be altered to begin in May so as to better reflect the timing of the spawning season. In addition, the sex ratio data, together with size at maturity, fecundity and eggs–per–recruit information will be incorporate in the model and reanalysed. Having incorporated this information, it is unlikely that more detailed data on blue warehou reproduction will be required in the short term. Instead, research examining factors such as the details of commercial catch and effort data, inclusion of recreational catches, historical discard rates, variable cohort growth and evaluation of alternative performance indicators will take a high priority (Smith 1999). In terms of cost/benefit, these are the areas that are likely to lead to greatest improvement in the model's applicability.

If further work was to be undertaken on blue warehou reproduction, one of the more important areas would be determining the extent of blue warehou spawning in the different regions of the fishery. Based on the findings of Bruce *et al.* (submitted to MFR special SEF edition), it would be interesting to determine the level of spawning off Tasmania's west coast, a region not included in the present study. The likelihood that there are two separate spawning stocks, in the East and West also warrants further research. As an offshoot of the present study, one of the more interesting findings was the higher proportion of females in commercial catches. More extensive spatial and temporal sampling of the blue warehou population by monitoring of commercial catches as well as fishery independent methods would be valuable to help understand the reasons behind the lower occurrence of males in commercial catches and the implications this may have for the fishery.

CONCLUSION

Macroscopic and histological examination of the gonads of blue warehou revealed that they were batch spawners with a determinate annual fecundity. The gonad maturation cycle for females is described. The annual fecundity of blue warehou can reach around 1.3 million oocytes per fish and increases exponentially with fish length. During spawning, these oocytes are released in about three large batches. Blue warehou spawn across a wide area, from waters off western Victoria, around Tasmania and off the south east coast of New South Wales. The main spawning season is during winter/spring, although some low-level spawning may occur throughout the year. The sex ratio of fish in commercial catches during the spawning season and at other times of the year was around 60:40 in favour of females. In conjunction with the results of Bruce *et al.* (submitted to MFR special SEF edition), there may be evidence that fish aggregate in certain areas during spawning. In the West, the fishery tends to target these spawning aggregations off Portland, but there is limited fishing for blue warehou off the west coast of Tasmania. Targeting of spawning fish is less defined in the East. Blue warehou reach maturity at between 30 and 40 cm LCF, at an age of about three years. Based on the selectivity of current trawl and gill net configurations in the South East Fishery, commercial catches will consist of predominantly mature fish. Eggs–per–recruit analyses revealed maximum egg production around 40 cm (4-5 years) in an unfished population. Mesh net fishing, which targets fish larger than 45 cm, was less likely to impact the relative eggs–per–recruit in a population than trawl fishing, which catches a wider range of smaller fish. The current management regime allows leasing of quota between the trawl and non-trawl sectors, but due to poor catches in the gill net sector over recent years, most quota has been leased from the non-trawl sector to the trawl sector (AFMA, unpublished data). To better understand the full implications of these results, more sophisticated models of the fishery need to be developed which integrate the information on maturity, fecundity and seasonal reproductive patterns gained from the present study with other factors such as variable recruitment, the spatial structuring of the fishery and inter-sectorial leasing of quota. This work is currently being undertaken by the Blue Warehou Assessment Group and it is expected that the outcomes of this assessment will help support management decisions that ensure the long term viability of blue warehou stocks as an important component of the South East Fishery.

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TABLES

Table 1. Monthly sample numbers from the east coast, east Tasmania and Western Zone of male (M), female (F) and immature (I) blue warehou collected for examination of gonad condition

Month	East Coast				East Tasmania				Western Zone				Total
	Male	Female	Immature	Total	Male	Female	Immature	Total	Male	Female	Immature	Total	
May-96	0	0	0	0	0	0	0	0	0	21	0	21	21
Jun-96	3	28	0	31	0	0	0	0	0	30	0	30	61
Jul-96	6	10	0	16	8	19	0	27	21	19	0	40	83
Aug-96	19	21	0	40	0	0	0	0	0	0	0	0	40
Sep-96	11	21	0	32	0	0	0	0	11	20	0	31	63
Oct-96	29	16	0	45	0	0	0	0	0	0	0	0	45
Nov-96	9	20	0	29	0	0	0	0	0	0	0	0	29
Dec-96	10	18	0	28	0	0	0	0	0	0	0	0	28
Jan-97	43	39	0	82	78	80	2	160	9	12	0	21	263
Feb-97	43	77	0	120	0	0	0	0	18	28	1	47	167
Mar-97	51	95	1	147	17	52	0	69	3	6	0	9	225
Apr-97	40	70	0	110	24	54	0	78	28	55	6	89	277
May-97	49	71	50	170	44	47	0	91	65	57	0	122	383
Jun-97	70	106	0	176	0	0	0	0	56	67	0	123	299
Jul-97	56	85	0	141	0	0	0	0	94	87	0	181	322
Aug-97	74	90	0	164	0	0	0	0	19	61	0	80	244
Sep-97	21	31	0	52	0	0	0	0	73	120	0	193	245
Oct-97	45	57	0	102	0	0	0	0	51	95	0	146	248
Nov-97	21	45	0	66	0	0	0	0	53	72	0	125	191
Dec-97	12	24	0	36	10	20	0	30	0	0	0	0	66
Total	612	924	51	1587	181	272	2	455	501	750	7	1258	3300

Table 2. Macroscopic description of the developmental stages and of the gonads of male blue warehou.

Stage		Macroscopic description
I	**Immature**	Testes very small, flat, and thread-like
II	**Early developing**	Testes flat/rounder in shape Testes occupy 20 to 70% of the length of body cavity
III	**Developing**	Testes lobed in formation Marked groove in the middle of each testis visible Testes occupy 40 to 70% of the length of body cavity Creamy or white milt sometimes present
IV	**Late Developing / Running-ripe**	Testes very large and lobed/multilobed Testes occupy 40 to 70% of the length of body cavity Free-flowing milt Testes white or pinkish, sometimes bloodshot
V	**Spent & Resting**	Testes very bloodshot Testes occupy 20 to 50% of the length of body cavity Milt sometimes present Testes brownish and rubbery as they regress to resting stage

Table 3. Macroscopic and histological descriptions of the developmental stages of the gonads of female blue warehou.

Stage		Macroscopic description	Histological description
I	**Immature**	Small thread-like ovaries Ovaries pink and translucent	Chromatin nucleolar stage: very small oocytes, nucleus surrounded by a thin layer of dark-blue-stained cytoplasm
II	**Early developing**	Oocytes not visible Ovaries pink and translucent	Perinucleolar stage: oocyte size increases slightly as dark-blue-stained cytoplasm thickens, nucleoli appear at the periphery of nucleus
IIa IIb	**Developing** **Redeveloping**	Ovary wall thin and transparent Ovaries flaccid, ovary wall thick Ovary colour pink/greyish to yellow-orange, and opaque	
III	**Developing**	Small oocytes becoming visible, still translucent Ovaries sometimes change from pink to yellow-orange Ovaries occupy 20 to 70% of the length of body cavity	Cortical alveoli stage: appearance of cortical alveoli in pale-blue-stained cytoplasm, pink-stained zona radiata distinguishable, oil vesicles appearing, lampbrush chromosomes often visible in the nucleus
IV	**Late Developing (yolked)**	Small opaque oocytes clearly visible Ovary wall thin and transparent Ovaries occupy 20 to100% of the length of body cavity	Yolk stage: marked increase in oocyte size, cytoplasm filled with pink-stained yolk granules, cortical alveoli and oil vesicles increase in size and number; degenerating postovulatory follicles visible if spawning has started
V	**Ripe**	Large transparent (hydrating) oocytes visible among Ovaries occupy 70 to100% of the length of body cavity	Nuclear migration stage: migration of nucleus to periphery of oocyte, fusion of yolk granules into yolk plates; fusion of oil vesicles into the oil droplet; degenerating postovulatory follicles visible if spawning has started
VI	**Running-ripe**	Hydrated oocytes are very large, almost totally translucent with oil droplet visible. They are easily expressed from ovaries Ovaries occupy 70 to100% of the length of body cavity	Hydration stage: further increase in size of oocytes, all yolk granules fused into a few plates
VII	**Spent & Resting**	Some residual oocytes visible within translucent material Ovaries flaccid, greyish ovary wall thickened and wrinkled Ovaries occupy 20 to 70% of the length of body cavity	Postovulatory follicles clearly visible, no yolked oocytes left except for a few undergoing atresia; structure of ovaries generally loose, hydrated oocytes may be present in lumen

FIGURES

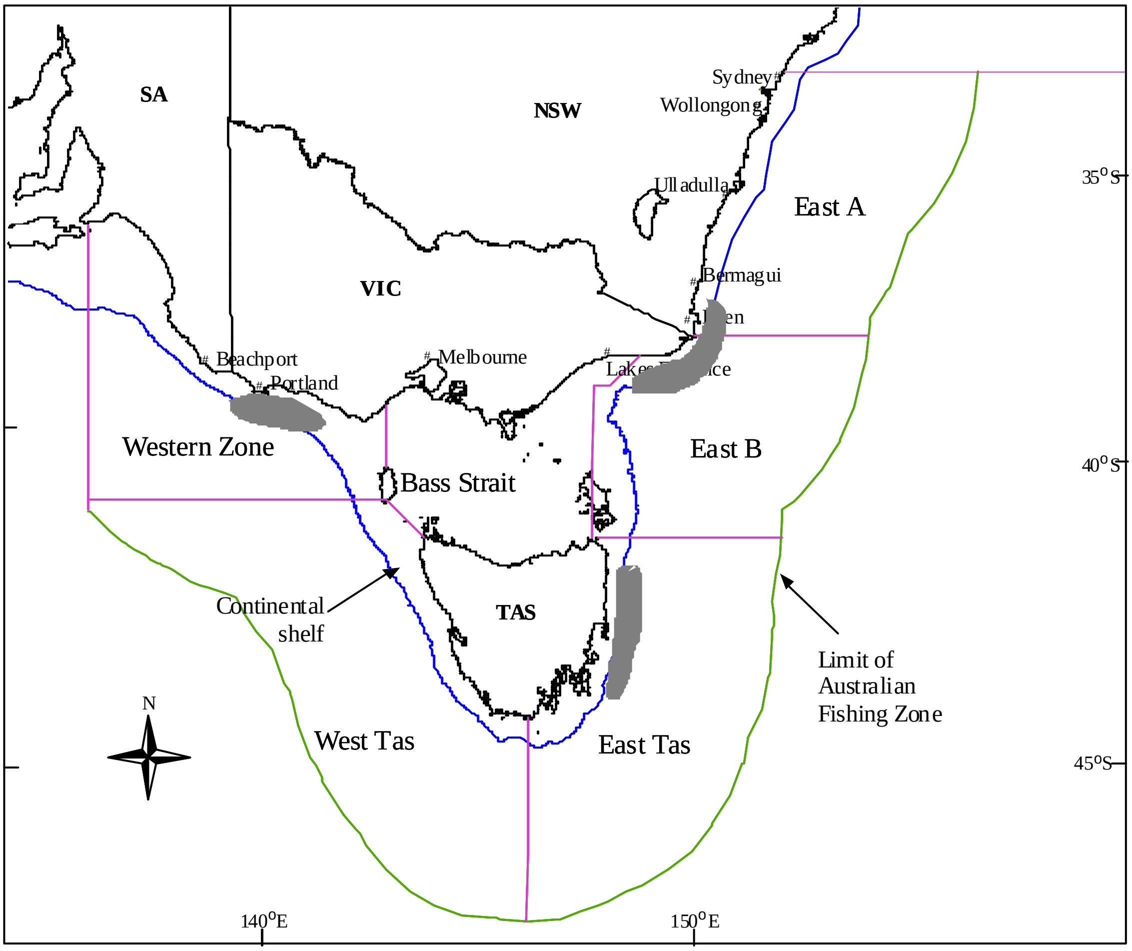


Fig. 1. Blue warehou were sampled from shelf and mid-slope waters within three regions (shaded) of the South East Fishery: East Coast, off Eden and Lakes Entrance; West Coast off Portland and Eastern Tasmania.

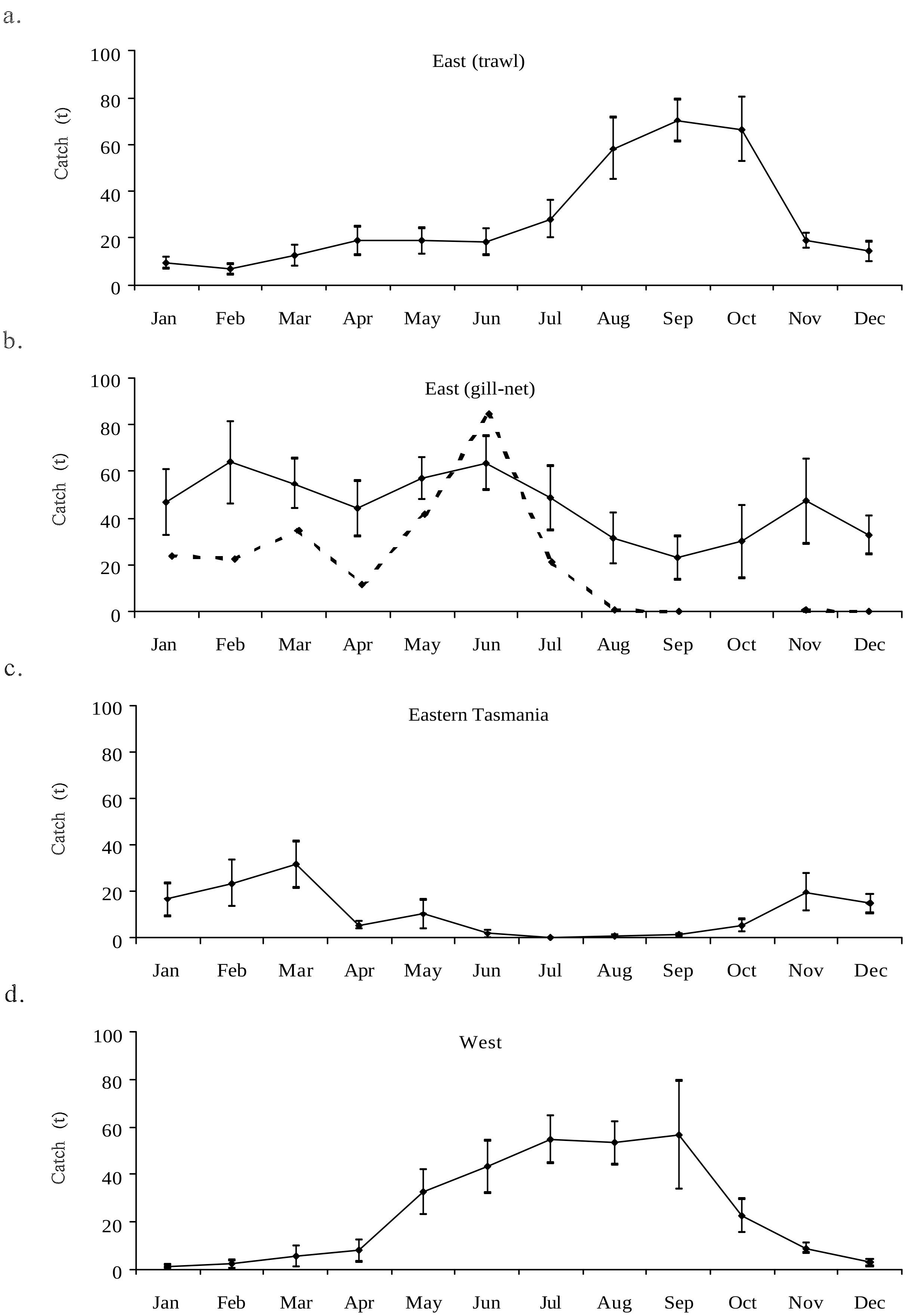


Fig. 2. Mean monthly catch of blue warehou (tonnes ± S.E.) landed by SEF trawl and gill-net vessels in the three regions. Trawl data based on SEF1 logbook data from 1986 to 1997 and mesh net data based on Victorian catch and effort logbooks for 1986 to 1996 and Commonwealth GN01 logbooks for 1997 and 1998. The monthly mesh net catch during the 1997 sampling period is indicated by a dashed line.

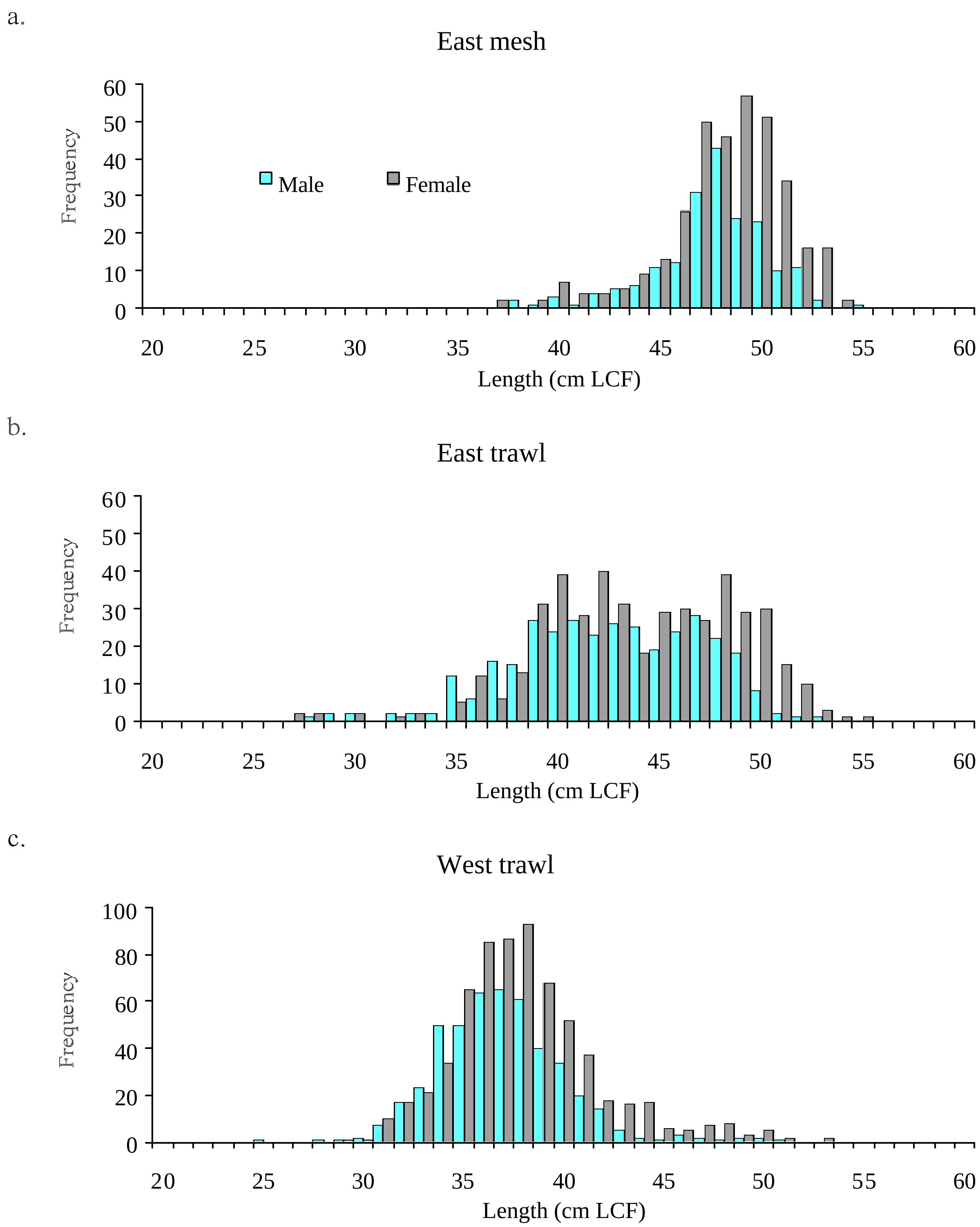


Fig. 3. Length frequency distribution of male and female blue warehou collected between January 1997 and December 1997 for analysis of reproductive development.

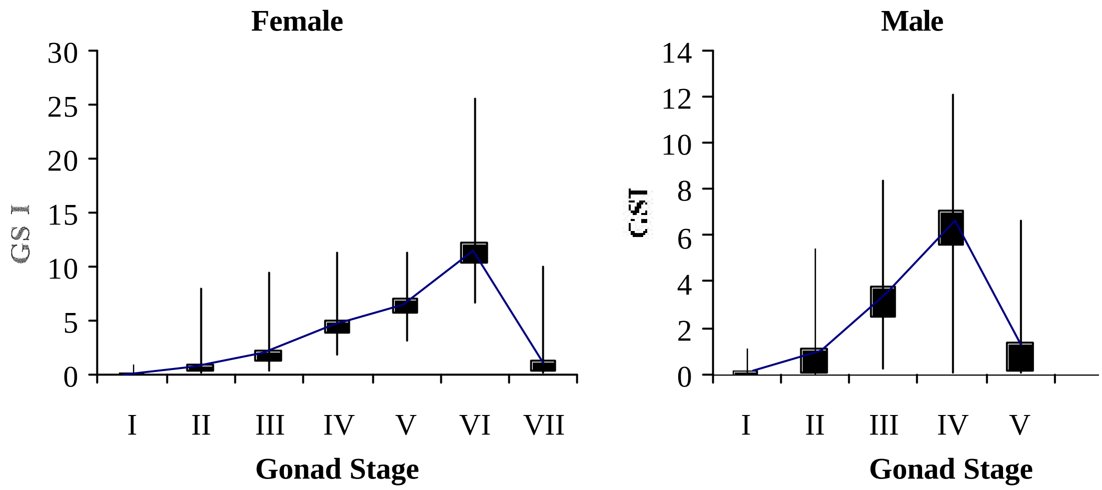


Fig. 4. Mean, ±1 S.E (█) and range (|) of GSI for female and male blue warehou plotted against macroscopic stage of the gonad. Analyses performed on data collected between May 1996 and December 1997 and pooled over area.

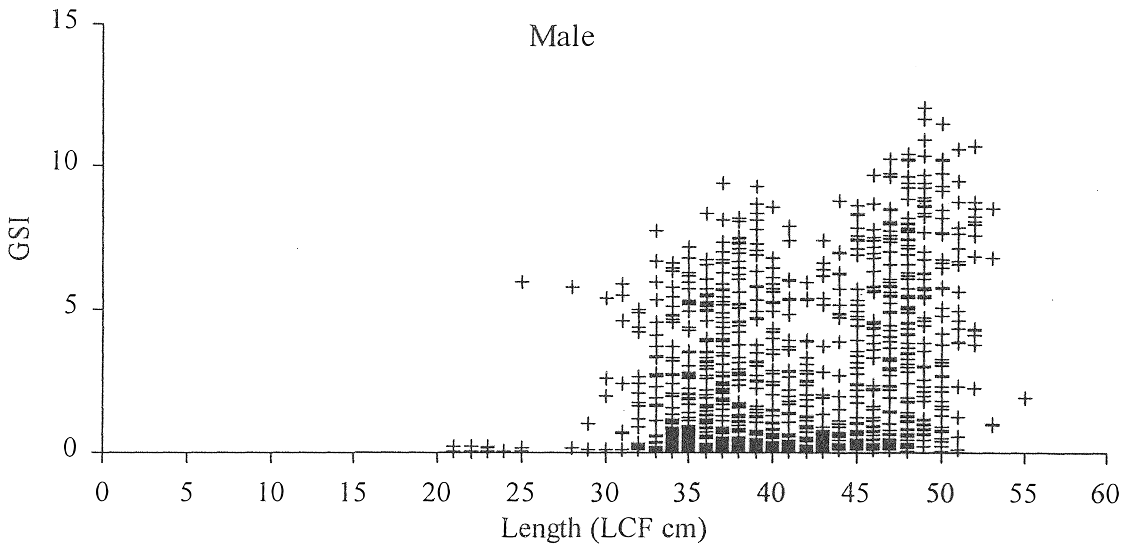


Fig. 5. GSI of male blue warehou plotted against length (LCF cm). Data pooled over region.

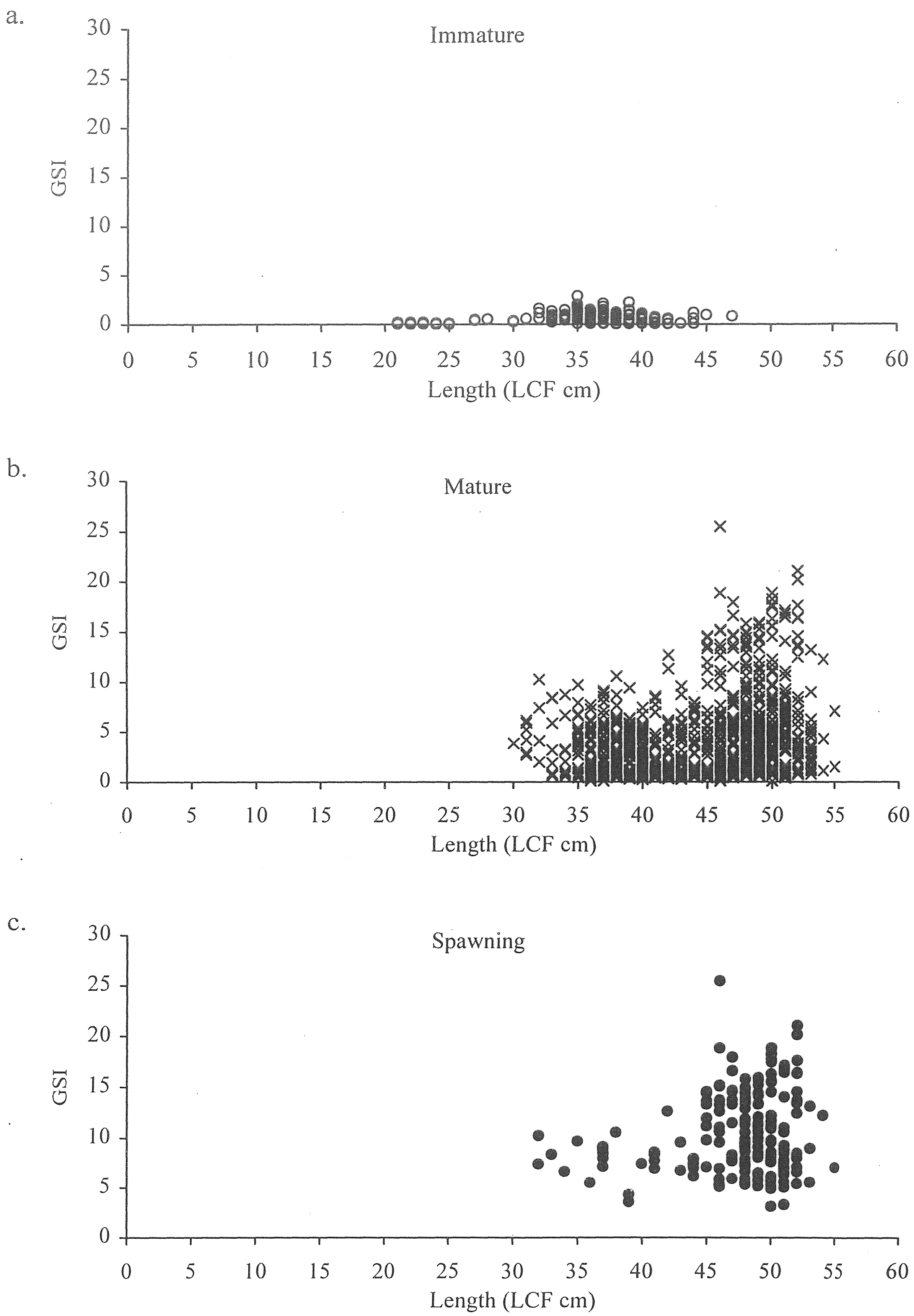


Fig. 6. GSI of female blue warehou plotted against length (LCF cm) for: a) immature (Stages I and II); b) mature (Stage IIa, III - IV); and c) mature fish in spawning condition (Stage V and VI only). Data pooled over region.

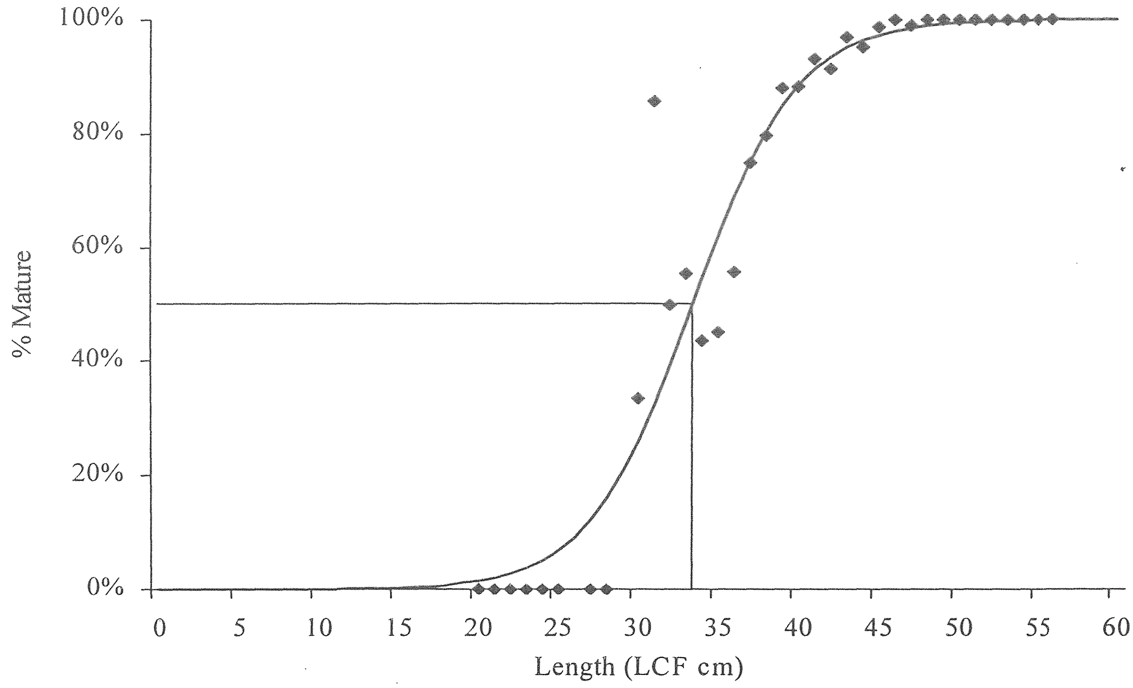


Fig. 7. Maturity ogive for female blue warehou plotted against length (LCF cm). Data points (◆) represent the % mature in 1- cm length classes and the equation of the logistic regression line is % mature =100 / (1 + $e^{0.309 \times (33.40 - L)}$) indicating a length at 50% maturity of 33.4 cm. . Analyses performed on data collected between May 1996 and December 1997 and pooled over area.

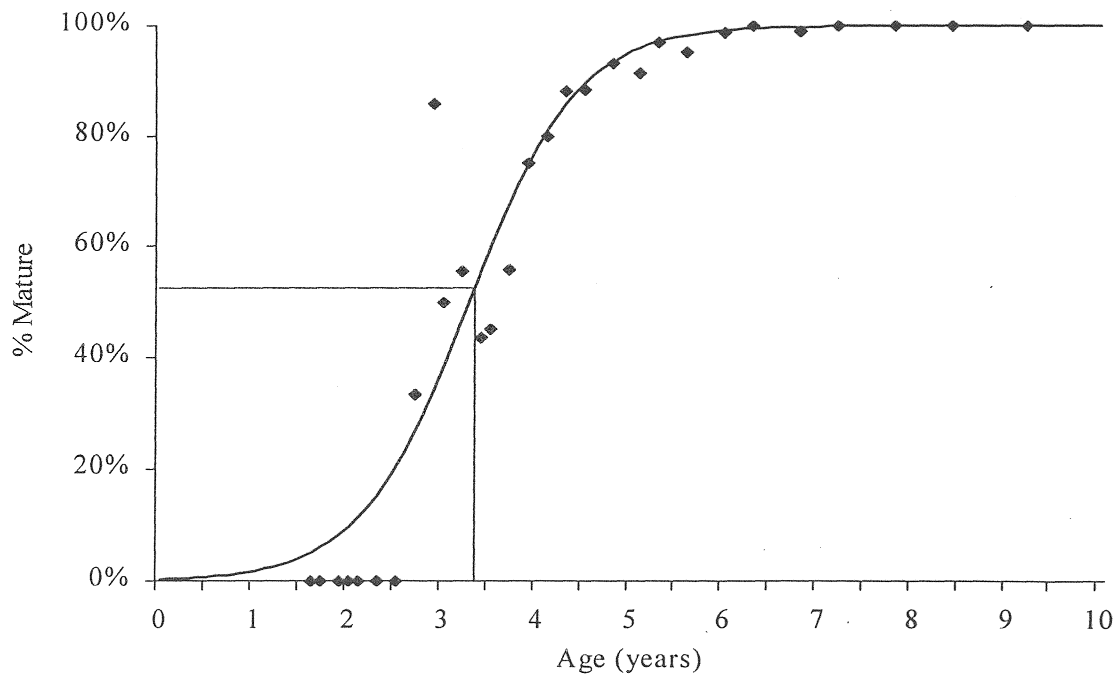
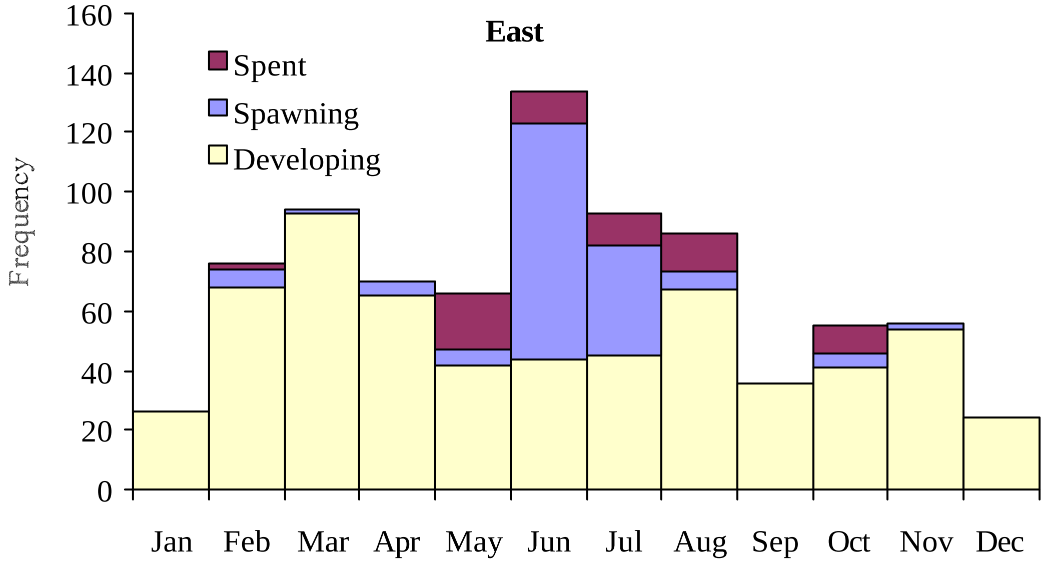
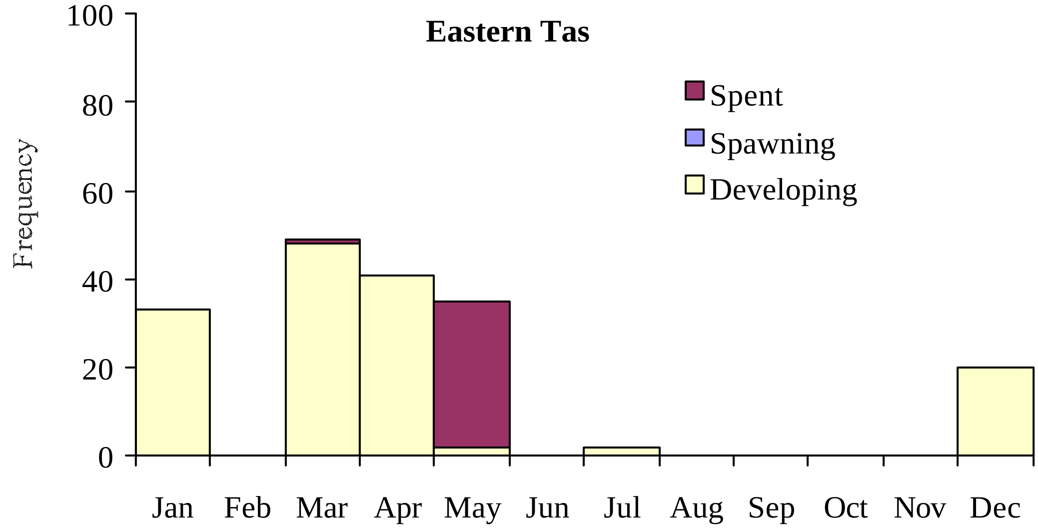


Fig. 8. Maturity ogive for female blue warehou plotted against age (years). Data points (◆) represent the % mature in 0.1 year age-classes and the equation of the logistic regression line is % mature =100 / (1 + $e^{1.748 \times (3.28 - t)}$) indicating an age at 50% maturity of 3.28 years. . Analyses performed on data collected between May 1996 and December 1997 and pooled over area.

a.



b.



c.

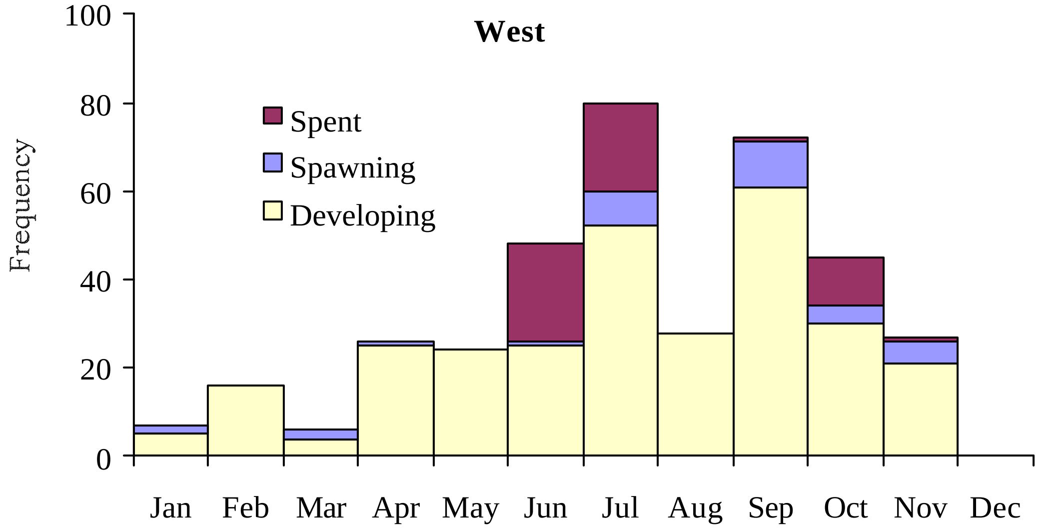
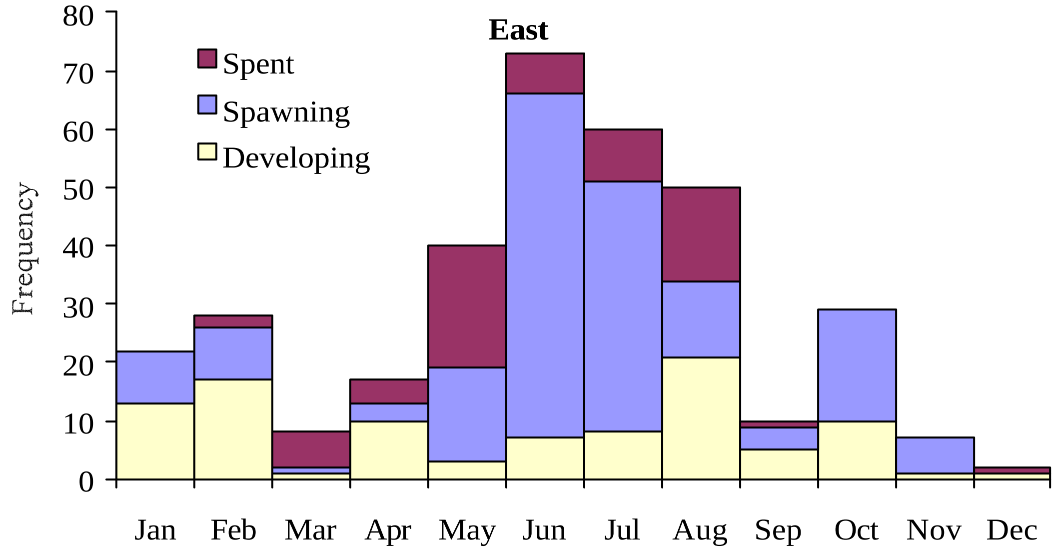
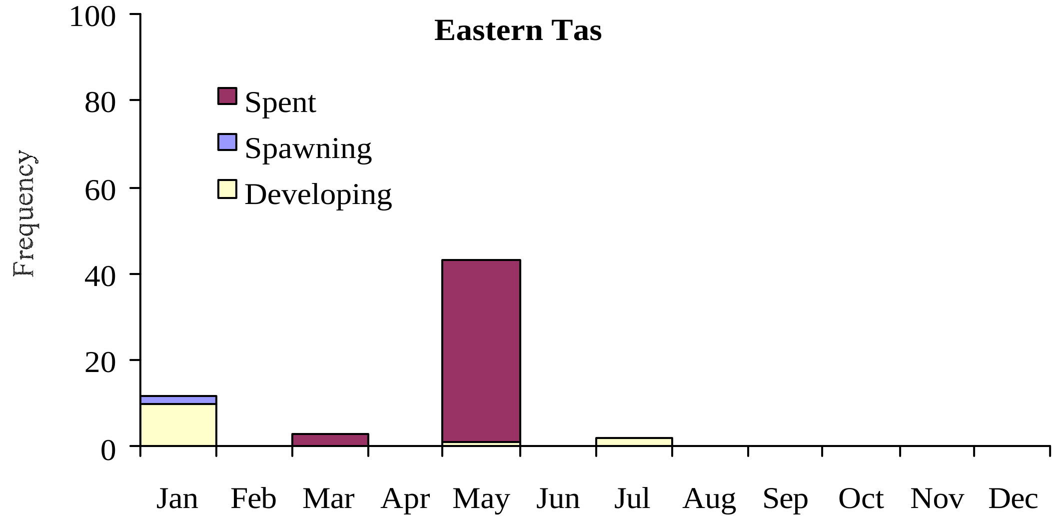


Fig. 9. Frequency of mature female blue warehou with gonads in various developing stages (Stage IIb, III and IV), in spawning condition (Stage V and VI) and spent (Stage VII) in: a) East; b) Eastern Tasmania; and c) West regions.

a.



b.



c.

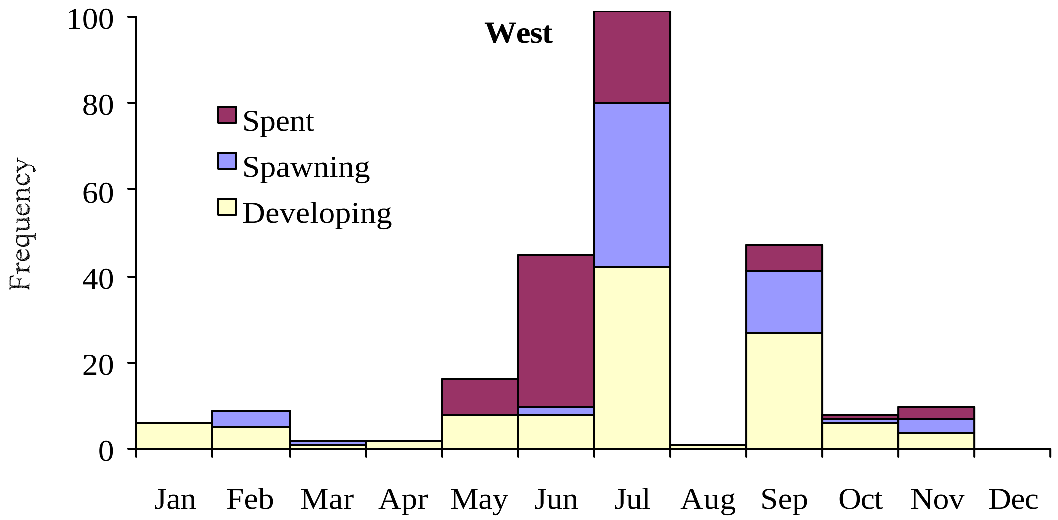


Fig. 10. Frequency of mature male blue warehou with gonads in a developing stage (Stage III), in spawning condition (Stage IV) and spent/resting (Stage V) in: a) East; b) Eastern Tasmania; and c) West regions. Males with Stage II developing gonads were not included, as it was difficult to determine their maturity.

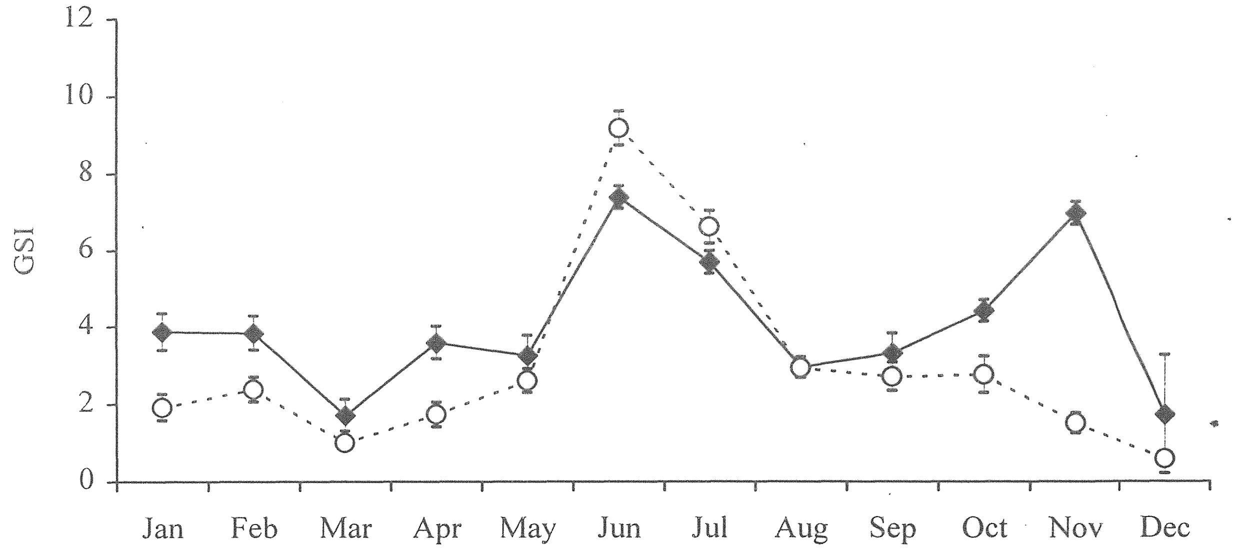


Fig. 11. Mean monthly GSI $\underline{+}1$ S.E. of male (—o—)and female (- - -♦- - -) blue warehou collected from the East region between January 1997 and November 1997.

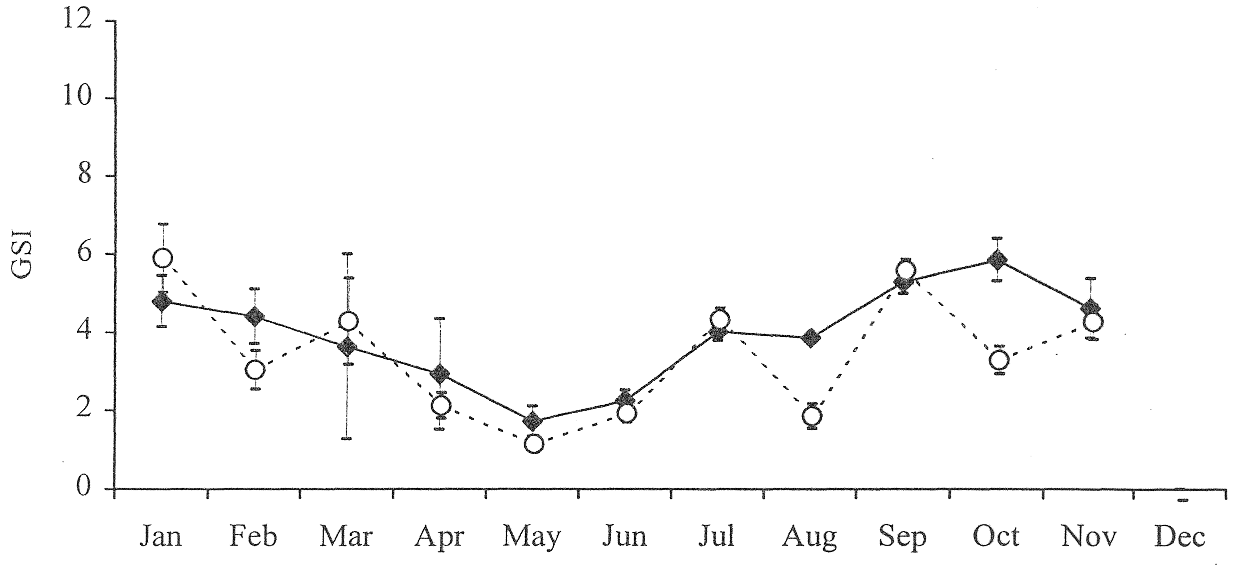


Fig. 12. Mean monthly GSI $\underline{+}1$ S.E. of male (—o—)and female (- - -♦- - -) blue warehou collected from the West region between January 1997 and November 1997.

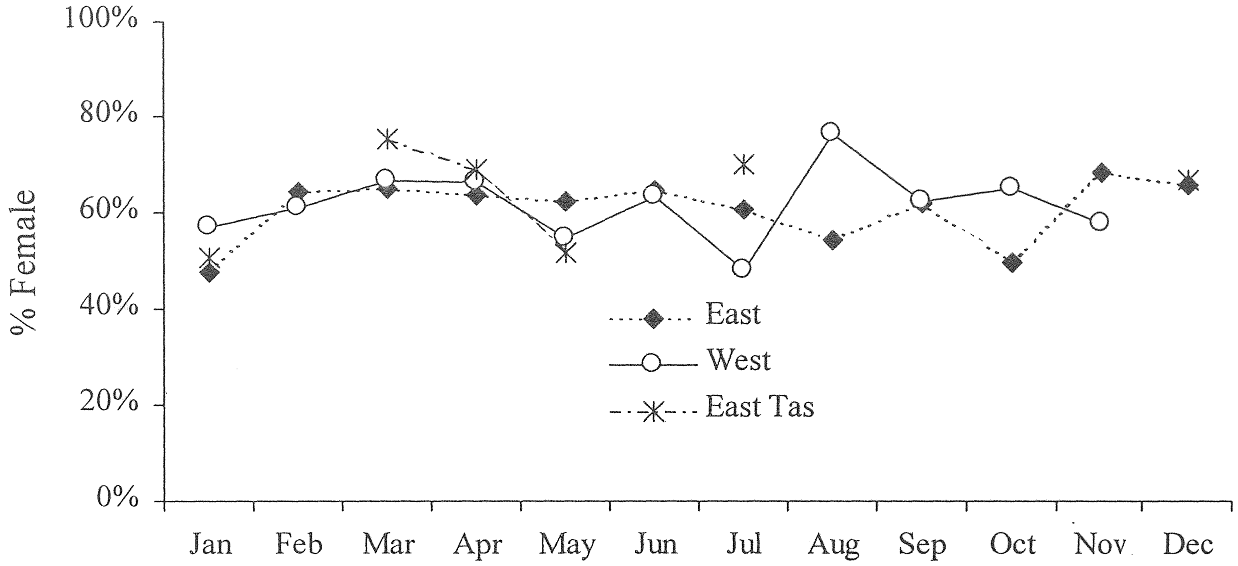


Fig. 13. Percentage of female blue warehou in samples collected from the East, West and East Tasmanian regions between January 1997 and November 1997.

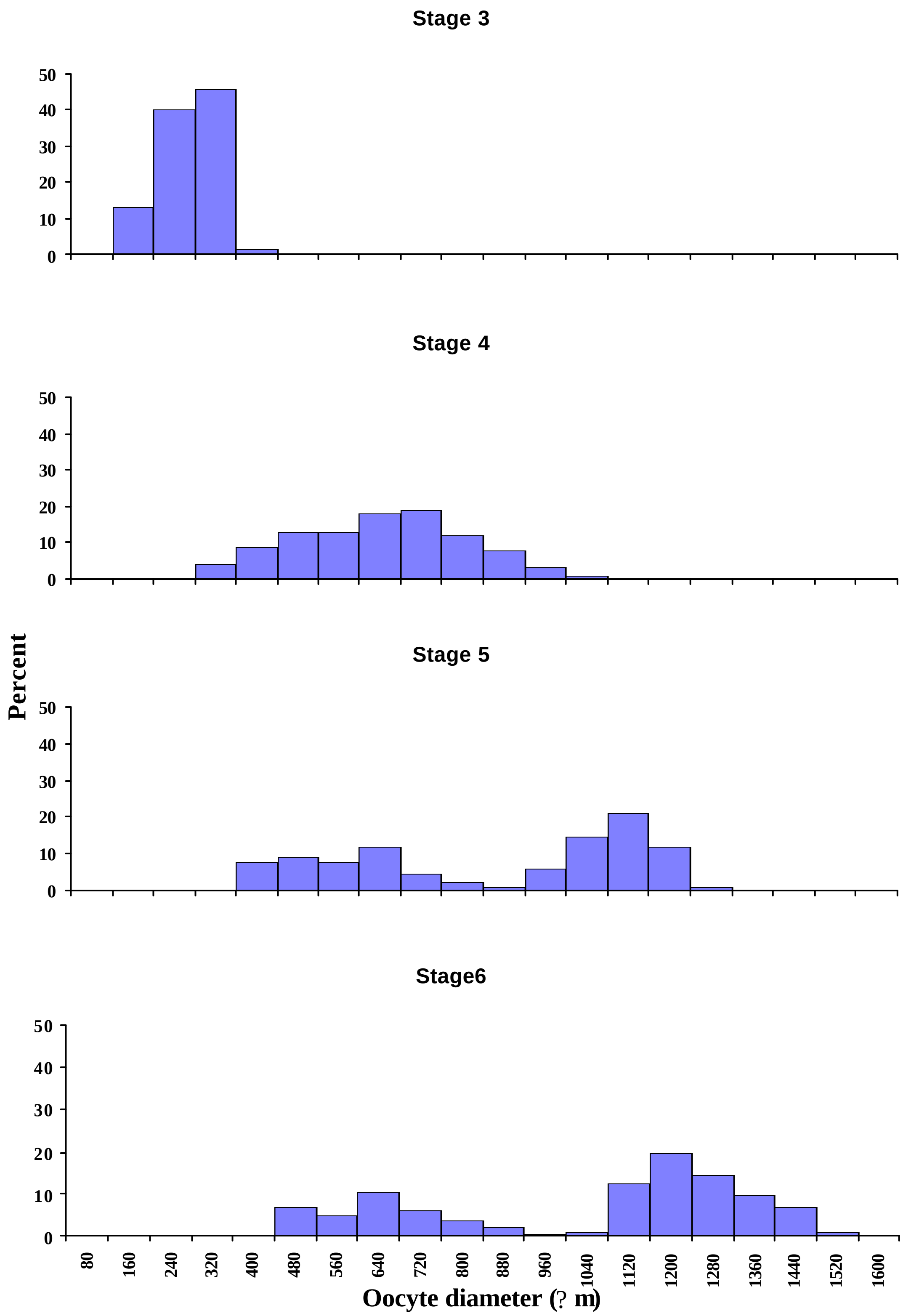


Fig. 14. Frequency distribution of blue warehou oocyte diameter (μm) by stage of maturity. Data pooled from fish collected in different regions.

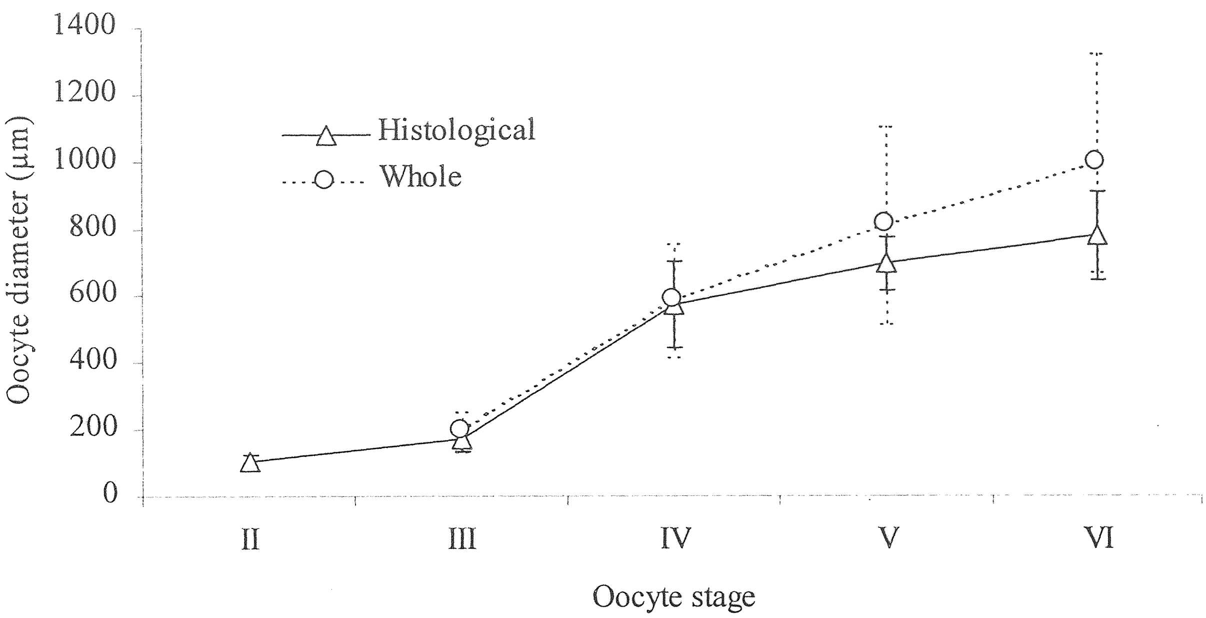


Fig. 15. Mean diameter (μm ± standard deviation) of Stage II to Stage VI oocytes measured from whole and histological preparations. Data pooled from fish collected in different regions.

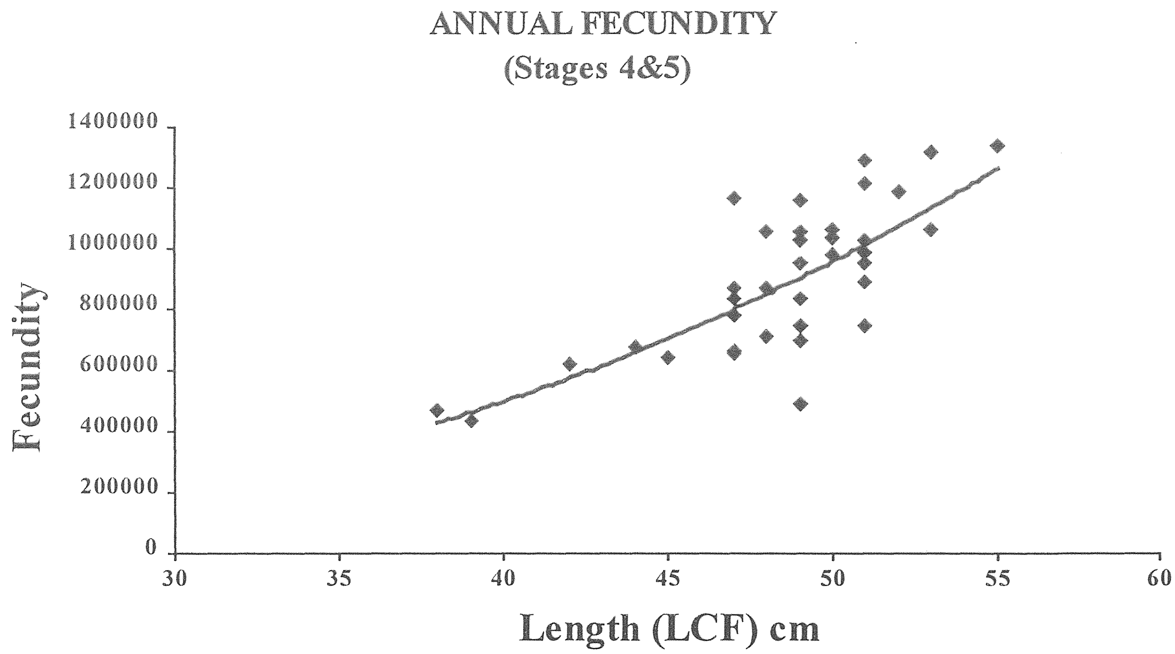


Fig. 16. Annual fecundity estimates and power relationship between annual fecundity and size of females (line drawn from equation $F = 10.397 \times LCF^{2.9216}$) for blue warehou.

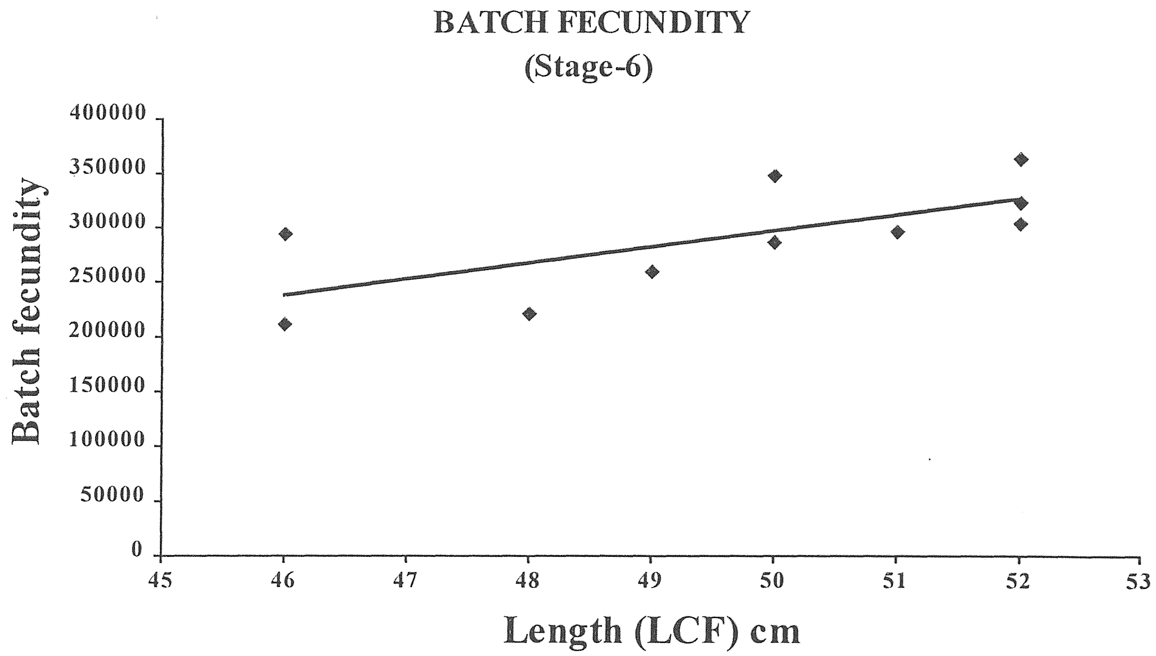


Fig. 17. Linear relationship between batch fecundity and size of females for blue warehou. Line drawn from the equation *Batch fec.* $= 14758 \times LCF - 441294$.

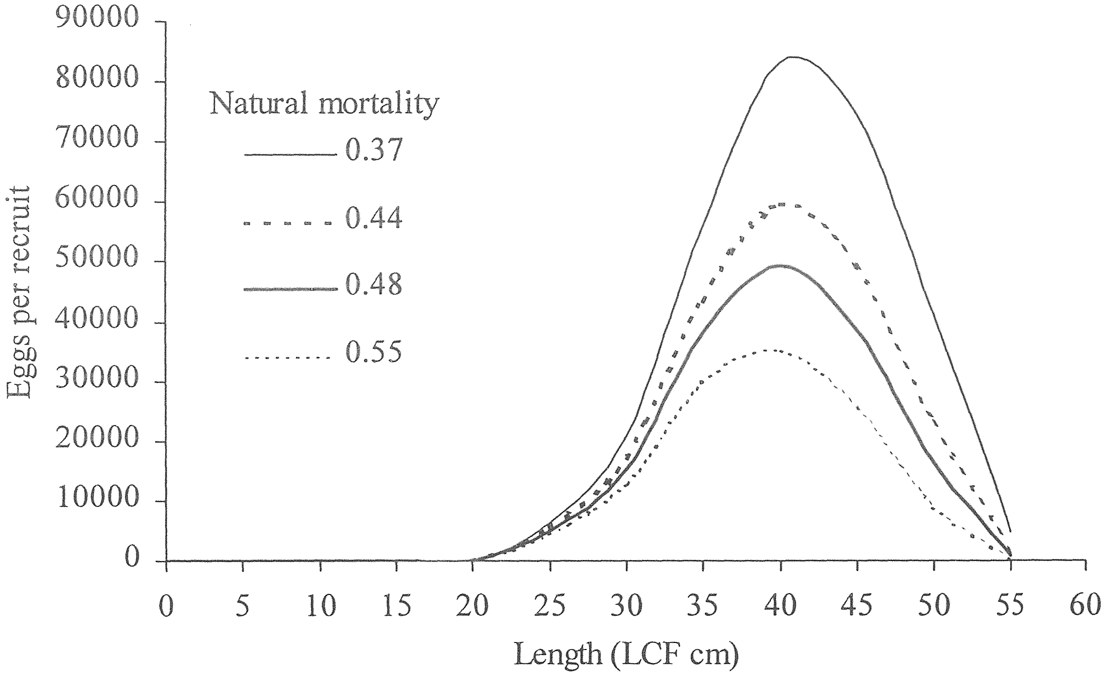


Fig. 18. Eggs–per–recruit for female blue warehou plotted against length (LCF cm) for a range of natural mortality estimates. No fishing mortality has been incorporated into these analyses.

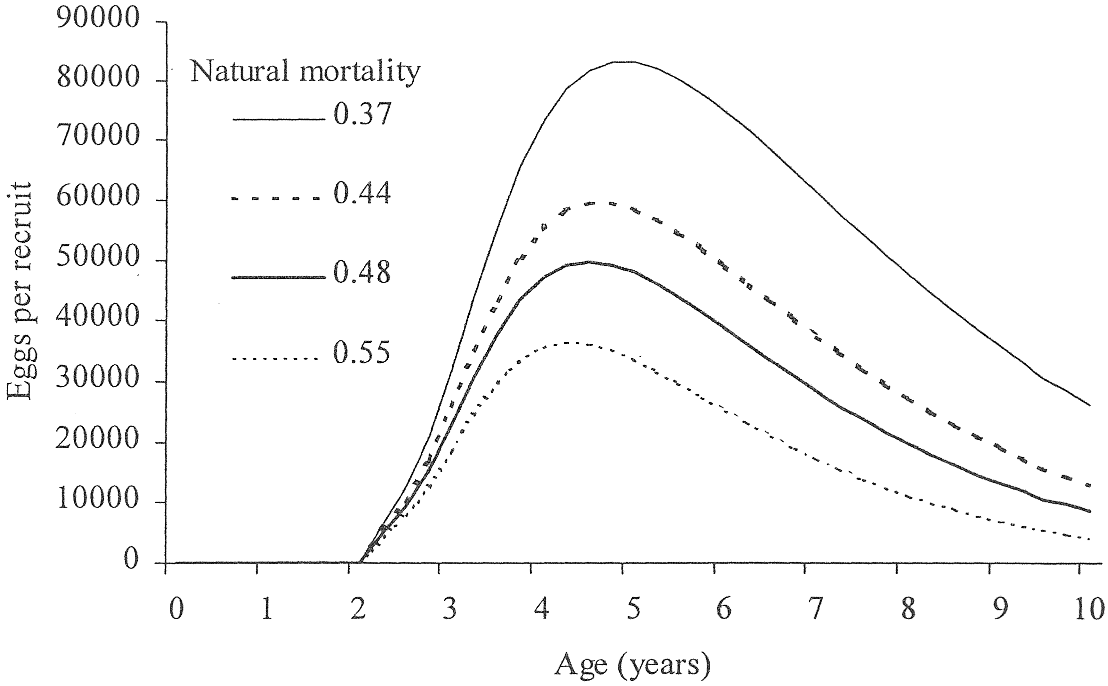


Fig. 19. Eggs–per–recruit for female blue warehou plotted against age (years) for a range of natural mortality estimates. No fishing mortality has been incorporated into these analyses.

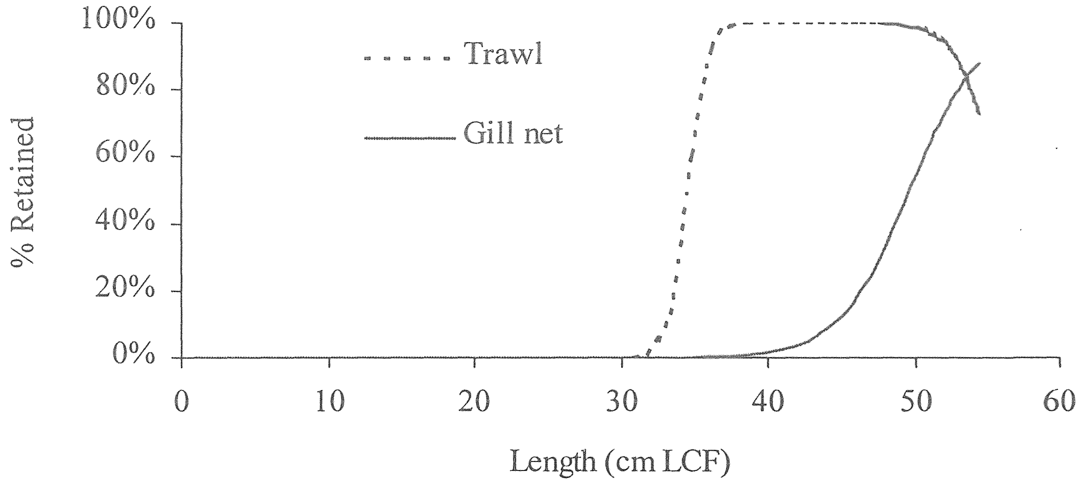


Fig. 20. Selectivity ogives used in the eggs–per–recruit analyses for trawl and mesh net fishing methods. The ogives incorporate the selectivity of the gear as well as the availability of fish to capture by that gear.

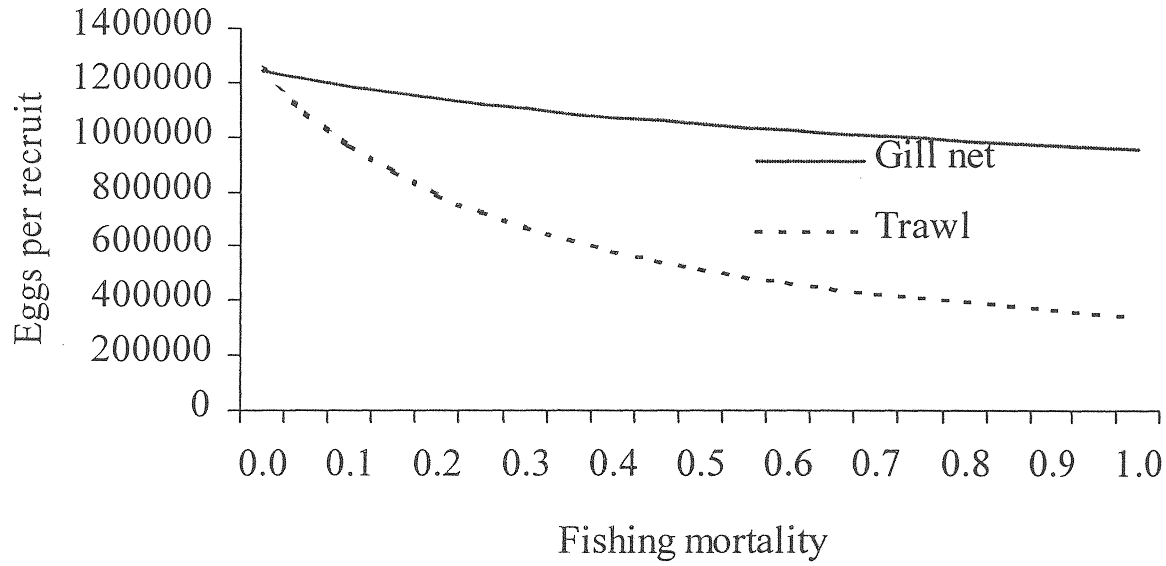
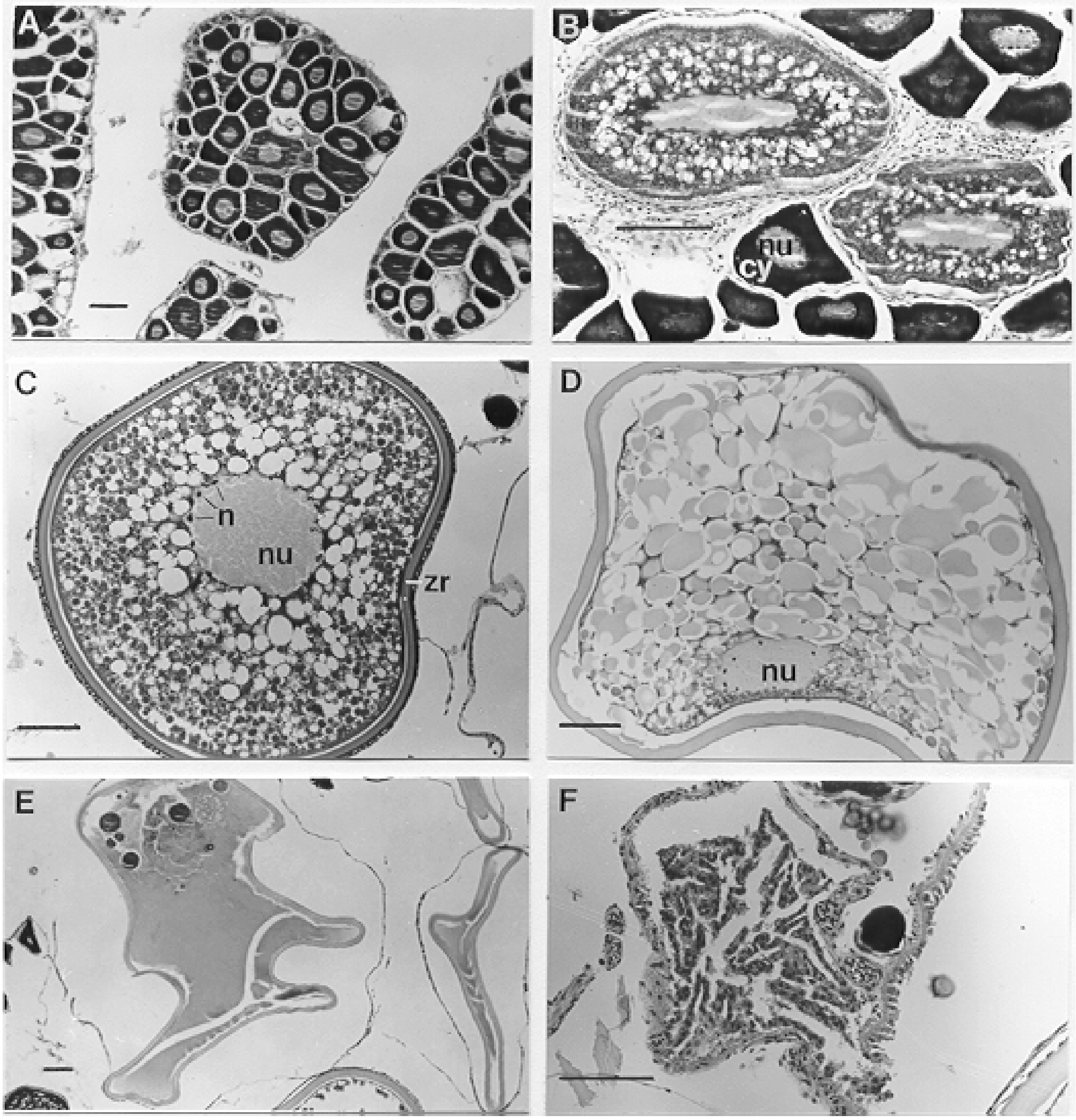


Fig. 21. Eggs–per–recruit for female blue warehou plotted against age (years) for a range of natural mortality estimates. No fishing mortality has been incorporated into these analyses.



Plates A – F. Histological sections showing the maturation of blue warehou oocytes from Stage II to Stage VII respectively (Scale bar = 50 μm). In the early stages, nucleoli (n) appear at the periphery of nucleus (nu) and cortical alveloli are apparent in the cytoplasm (cy) which is bounded by the zona radiata (zr). By stage IV (Plate C), there is a marked increase in oocyte size and the cytoplasm is filled with yolk vesicles (yv), cortical alveoli and oil vesicles. The nucleus migrates to the periphery of oocyte in Stage V (Plate D) and the yolk granules begin to fuse into yolk plates (yp). Stage VI (Plate E) is marked by the onset of hydration (causing cells to collapse during histological processing) and yolk granules fused into a few plates. After spawning the postovulatory follicles (pov) are clearly visible.

APPENDIX 1 INTELLECTUAL PROPERTY

No intellectual property has been gained as part of this study.

APPENDIX 2 STAFF

Dr Ian Knuckey	Senior Scientist (MAFRI)
Dr K. P. Sivakumaran	Project Scientist (MAFRI)

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