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Australian Society for Fish Biology Workshop

LARVAL BIOLOGY

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D.A. Hancock

Department of Primary Industries and Energy
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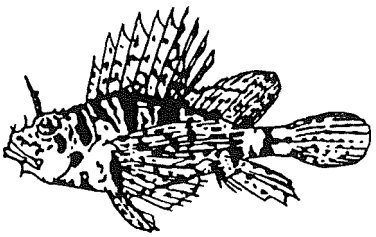

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The Bureau of Rural Resources within the Department of Primary Industries and Energy was established in October 1986. It provides scientifically objective advice to the Commonwealth Government on rural issues. The Bureau's mission statement is 'applying science and technology to improve the use of rural resources for the benefit of all Australians'.

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PRESIDENT'S INTRODUCTION

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Ladies and Gentlemen, welcome to the 1991 National Workshop Series of the Australian Society for Fish Biology. First I want to commend the Fishing Industry Research and Development Council for their generous support in the funding of this workshop. In our application for support, we said we wanted:

(i) To promote the opportunity during the Australian Society for Fish Biology annual conference for the national fisheries research expertise to focus on a technical area or subject of current or perceived national or regional fisheries significance. Such area or subject to be identified by the membership of the Society *or by the Council* as appropriate.

(ii) To support *where appropriate* visiting fisheries scientists of acknowledged expertise in the workshop subject to offer a national or international perspective.

(iii) To assist in the publication of workshop proceedings as a benchmark document of current knowledge in the workshop subject area, and

(iv) As a result, to identify and define research questions of national fisheries significance.

This workshop on "Larval Biology", and the associated workshop on "Recruitment Processes", bring together the national expertise to discuss issues of significance to the Australian fishing industry. I am sure I speak for our membership in saying Australia's fish biologists appreciate the FIRDC support.

As in previous years, the Society acknowledges the assistance given by Dr Don Hancock and Dr Kay Radway Allen with the planning of the workshops, and by Dr Hancock, Dr Gregg Berry and the Bureau of Rural Resources with the editing and publishing of the forthcoming proceedings. Dr John Gunn is to be congratulated on his role in overseeing the domestic arrangements, and the provision of these excellent facilities by CSIRO is greatly appreciated.

The Society is also pleased to have with us the Hon. David Llewellyn, Tasmanian Minister for Primary Industry, who has come to officially launch this workshop.

The Larval Biology topic is one that was suggested by a small, enthusiastic (fanatical ?) group within our membership. In particular, concerns were expressed that scientists working on the same species in different laboratories were having difficulty in agreeing on the staging and identification of larvae. Now whilst the concept of disagreement between scientists may seem difficult to comprehend, I understand that it *was* the case. Members, the general feeling may be that larval researchers are an insensitive cabal with binocular vision whose lifeblood is buffered formalin. However, I am given to understand, this is not so. I have been assured they have the souls of poets, the perspective of artists and the hearts of lions (I. Suthers, pers. com.). Yet they disagree!

In order to resolve some of this disagreement the idea for this workshop was born. Not unlike a minute *Lovettia sealii* with indistinct myomeres initially, it quickly developed a functional reality in the disturbed mind of Iain Suthers. For Suthers, you see, had "volunteered" to organise the workshop. I am sure you would agree with me, members, he has done an outstanding job.

Dr Suthers was also instrumental in arranging for our keynote speaker, Dr Rob Murdoch of the New Zealand Oceanographic Institute, to participate. The Society is also indebted to Dr Don Robertson, who has come from New Zealand to present an important contribution on behalf of his colleague Dr John Zeldis. Dr Murdoch and Dr Robertson will be speaking first, and they will be followed by a full day of sessions covering panel presentations and discussions on Larval Biology, an evening session on the Taxonomy of Temperate Australasian Fish Larvae, and on Friday morning for the enthusiasts, a Larval Fish Drawing Techniques Workshop. I have no doubt that the day's proceedings will prove to be an important milestone in the Society's objective of focussing on a topic of National fisheries significance.

Dr Murdoch knows no Australian (transtasman) jokes, has no interest in cricket or football and has never visited (nor has an interest in settling in) Bondi. He is an authority on fish larvae and will today address the biology of larval hoki in New Zealand. Members, would you welcome Dr Rob Murdoch.

KEYNOTE ADDRESS
A REVIEW OF THE ECOLOGY OF HOKI, *MACRURONUS NOVAEZELANDIAE* (HECTOR), LARVAE IN NEW ZEALAND WATERS

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Abstract

Studies of the ecology of hoki* (*Macruronus novaezelandiae*) larvae in New Zealand are reviewed. To date field studies of hoki larvae in shelf waters off the west coast of South Island, the predominant spawning grounds for hoki in New Zealand, have examined aspects of larval diet and prey selectivity, patch dynamics, and physical environment.

Hoki larvae feed during daylight hours and appear to be selective feeders. Copepods of the *Calocalanus* genus are a particularly important component of their diet, especially for first feeding stages. Aspects of larval diet, morphology, and estimates of mortality and growth from patch studies, are compared with those of the larvae of other hake species. The likely importance of starvation as a source of mortality is assessed.

Distribution patterns of hoki larvae and eggs off the Westland coast and Cook Strait, both in the horizontal and vertical, are analysed in relation to the physical oceanography. The possible effects of mixed layer dynamics, upwelling, and coastal jets on the distribution of hoki eggs and larvae are discussed.

* Blue grenadier

Introduction

Hoki (*Macruronus novaezelandiae*) is a demersal fish belonging to the hake family Merlucciidae, and is found on the continental slope throughout New Zealand (Shuntov 1971; Kuo and Tanaka 1984a), and southern Australia (Last *et al.* 1983). In New Zealand it dominates trawl catches at 200-800 m depths, and much of the commercial catch is fished around South Island, especially off the Westland coast during the winter spawning season (Sullivan and Livingston 1988). In 1988, for example, an estimated 230 000 tonnes of the 250 000 tonne Total Allowable Catch (TAC) was caught off the Westland coast (Hurst 1988). The TAC for hoki within New Zealand's 200 mile Exclusive Economic Zone is presently set at 200 000 tonnes.

The major spawning sites for hoki (Figure 1) are off the Westland coast (Patchell 1982). Concentrations of spawning hoki also occur off the east coast of South Island, predominantly in Cook Strait, and off the Kaikoura coast and Banks Peninsula (Livingston 1990). Japanese reports infer that hoki also have spawning grounds on the west Chatham Rise and Puysegur Bank (Kuo and Tanaka 1984a). Although juvenile hoki have been recorded from a number of locations around southern New Zealand, the

greatest biomass of juveniles occurs over the Chatham Rise (Sullivan and Livingston 1988) and this appears to be the major nursery ground for juvenile hoki (Figure 1).

Until recently, studies of hoki in New Zealand waters have been primarily concerned with aspects of the fishery or adult ecology (e.g. Blagodyorov and Nosov 1978; Patchell 1982; Kuo and Tanaka 1984a; 1984b; Livingston 1990), and there have been relatively few studies of their early life history other than a description of the eggs and larvae (Patchell *et al.* 1987). This paper reviews studies of hoki larval ecology within shelf waters off the Westland coast concerning larval diet, prey selectivity, and patch dynamics. The importance of starvation as a source of mortality is assessed, and a possible survival strategy for hoki larvae suggested. The physical environment of hoki larvae is also briefly described, and its significance to the vertical and horizontal distribution of larvae is discussed.

Hoki larval diet

In common with most larval fish, early stage hoki larvae are visual feeders. Observations were made of feeding incidence in relation to time of capture for hoki larvae collected from Cook Strait in 1987. These larvae were predominantly 3-4 mm standard length (SL). Mean gut fullness increased during the day to reach a maximum after sunset, and decreased during the night to reach a minimum at dawn (Figure 2; Guo and Murdoch unpub. data). A similar feeding pattern has been observed for many other species of fish larvae, and is considered to be indicative of a visual feeding behaviour (Hunter 1981).

The diet of hoki larvae collected from Westland (Murdoch 1990), and Cook Strait (Guo and Murdoch unpub. data), consists primarily of the adults and copepodites of copepods, and is similar in composition to the diets of larvae of other hake species (Table 1). The maximum size of prey consumed is similar for all of the larval size classes examined (3-17 mm SL; Figure 3). This is presumably related to the fact that hoki larvae have a large mouth (similar to other species of hake larvae) relative to the larvae of other fish species (see Hunter 1981). First feeding larvae feed on a diverse range of small prey, particularly phytoplankton (coccolithophorids), tintinnids, and copepod nauplii, whereas larger larvae consume almost solely copepod adults and copepodites (Figure 4). Despite the numerical dominance of small prey types in the diet of small larvae these small prey contribute only about 2% of the total prey volume consumed (Murdoch 1990). It is therefore doubtful that such small prey items are nutritionally significant, and it is likely that the presence of calocalanids in the diet of small larvae, although low in number, are probably necessary to meet their nutritional requirements. It is possible, however, that small soft-bodied organisms such as naked dinoflagellates and non-loricate ciliates are nutritionally significant, since larvae may be consuming large numbers of them. These organisms would have been visually undetectable in the gut analysis using dissection, and detailed histological work is required to establish whether such organisms are an important dietary component for hoki larvae. These organisms are known to be extremely abundant within the mixed layer off Westland in winter (Chang 1990).

Food selectivity

An assessment of prey selectivity by first feeding stages of hoki larvae (3-4 mm SL) was made by comparing the proportions of different potential prey species in the environment with the proportions of the different species in the larval diet (Figure 5; Murdoch unpub. data). Diatoms and thecate dinoflagellates were numerically dominant (55% and 34%, respectively) in the environment but were not recorded in the diet of hoki larvae. These organisms were clearly avoided by hoki larvae, and were not included in

further analysis. Results indicated that the most actively selected prey species were copepods of the genus *Calocalanus* and *Paracalanus*, and the tintinnid *Dictyocysta*. *Calocalanus* was clearly the most important component of the diet of early stage hoki larvae.

The size, visibility, swimming speed, and general morphology of potential prey are the factors most likely to influence prey selectivity by hoki larvae. The apparent negative selection by larvae of many of the smaller organisms, such as diatoms and tintinnids, is presumably because of their shape and palatability, since many possess spines or hard outer shells. The largest organisms consumed by larvae were all copepods. The size of these copepods does not appear limiting, since their width is well below the mouth width of the larvae. The low numbers of the larger copepods, such as *Clausocalanus*, in the diet of early feeding hoki larvae but dominance in the diet of larger larvae, is presumed to relate to the swimming ability of the larvae. The larger copepods and species such as *Oithona* appear to be able to avoid capture by small larvae. The relatively low numbers of *Oithona*, for example, in the diets of larvae smaller than 4 mm (SL) compared to larger larvae (Figure 4), suggests that its swimming and behaviour minimises predation by the small, less experienced, slower swimming larvae. In a study of cod and haddock larval diet, Kane (1984) similarly concluded that only the larger "more experienced" larvae could utilise *Oithona similis*. Kane attributed this to the fact that *O. similis* has a defence that maximises predator avoidance. This has been achieved primarily by adopting an erratic zig-zag swimming pattern, and increasing its width by holding its antennae perpendicular to the body, rather than along the carapace as in most other copepod species.

Patch study

Estimates of mortality and growth of newly hatched hoki larvae (2.0-4.5 mm SL) were obtained from 5 days of sampling a patch of hoki eggs tracked with a radio drogue off the Westland coast in 1987 (Murdoch unpub. data). Larvae within the patch were sampled approximately every 12 h using a plankton pump and an obliquely towed 80 cm diameter ring net. Modal analysis of size frequency distributions of larvae collected indicated the presence of up to 6 cohorts within the patch at any one sampling time. The mean standard lengths of each cohort were approximately 0.2 mm apart (Figure 6). Larval growth was assumed to be linear (Bailey 1982; Thresher *et al.* 1989), and at the same rate over the size range of larvae examined, and linear regressions were fitted to plots of cohort mean length versus time to estimate the mean growth rate of larvae within the patch (Figure 7). This analysis gave a daily growth estimate (0.21 mm SL) similar to the difference between the cohort mean lengths recorded at any one sampling time.

These results indicated that distinct daily cohorts of larvae occurred in the patch, this suggesting that hoki have synchronised, diel spawning periodicity. Analysis by Zeldis (in press) of hoki egg counts in plankton samples taken at two hourly intervals over 4 days, in the vicinity of a school of spawning adult hoki off Westland, also suggested that hoki exhibit diel spawning periodicity. Young eggs were found only in a 6-8 h period centred around 0200 h each day showing this to be the time of spawning. The growth rate for hoki larvae was remarkably similar to that estimated by Thresher *et al.* (1989) for larvae collected off Tasmania (0.24mm (SL) per day for small larvae).

To calculate the weight specific growth rate of hoki larvae, SL was transformed to weight using the length-weight relationship for Pacific hake larvae (Bailey 1982), since larval size and morphology of these two species is quite similar. The weight specific growth coefficient for hoki larvae was estimated to be 0.021.

An approximate estimate of larval mortality within the patch was determined from changes in total larval abundance over the 5 day period of sampling. The total abundance of larvae

within the patch showed an exponential decline over the sampling period, and the daily mortality coefficient was estimated to be 0.19. Recruitment of newly hatched larvae to the patch was low, and therefore considered insignificant. This was reflected by the abundance of hoki eggs sampled in the patch. Egg abundance was low and decreased during the course of the study (Figure 8), indicating that adult fish had ceased spawning in the region of the patch. Dispersion of larvae from the patch was also not considered in the estimate of mortality, although two grid surveys of the patch region, one before and the other after the patch study, indicated that the patch of larvae had dispersed (Figures 9 and 10). The 0.19 daily mortality coefficient is therefore likely to be an over-estimate of the larval mortality.

Physical environment

The effects of various physical oceanographic processes on the vertical and horizontal distribution of hoki eggs and larvae are reviewed below. Three different processes are considered; mixed layer dynamics, upwelling, and coastal jets.

The mixed layer in hoki spawning areas off the Westland coast in winter is relatively deep and ranges from approximately 75 m to depths in excess of 200 m (Bradford 1983; Murdoch unpub. data). A numerical model of the mixed layer off this region predicts that the maximum depth of mixing varies considerably from year to year and can be explained by local meteorological forcing and a general southward flow in the region (Rahmstorf in press). The depth of the mixed layer is biologically important, since regions with a deep mixed layer off Westland in winter generally have low chlorophyll biomass and productivity (Chang and Bradford 1985). The depth of mixing is therefore likely to be important for hoki larvae, not only because primary productivity levels will directly determine the abundance of their prey, but also because it may influence their vertical distribution.

Results of two series of plankton net tows in a patch of hoki larvae off Westland in 1987 suggest that early stage larvae (<4 mm SL) live near the bottom of the mixed layer (Figure 11; Murdoch unpub. data). These results were obtained from oblique net tows to different depths at the same site, and the abundance of larvae between depth strata calculated by subtraction. Although this is not an ideal technique for determining vertical distribution patterns, it does indicate that hoki larvae occur deep in the water column at the bottom of the mixed layer (approximately 200 m at the patch site). Small Pacific hake larvae similarly appear to be aggregated at the base of the mixed layer (Ahlstrom 1959; Bailey 1980; 1982). Bailey (1981) hypothesised that vertical density changes in the water column could directly determine the vertical distribution of hake eggs and larvae; eggs and larvae appeared to be neutrally buoyant at the pycnocline in a stratified water column, but occurred much closer to the surface when the water column was less stratified. Water column structure may also influence the vertical distribution of hoki larvae. *Macruronus novaezelandiae* larvae collected off Tasmania by Thresher *et al.* (1989) were found to be most abundant between 20 and 90 m which is a much shallower distribution than that found in New Zealand waters. In the Tasmanian study, however, the total water depth was also relatively shallow (100-120 m), and there was no mention of the vertical water column structure.

Periodic wind-induced upwelling is known to occur along the Westland coast (Stanton in press). Unlike some upwelling coasts in other parts of the world, off Westland there is no upwelling season or period of persistent upwelling, and upwelling is episodic and interspersed with periods of down-welling. Such upwelling events off Westland would, however, be expected to influence the horizontal distribution of hoki larvae, since the deep vertical distribution of eggs and early stage larvae would tend to promote inshore transport. In upwelling conditions, eggs at the base of the deep mixed layer in slope waters would tend to be protected from

offshore Ekman transport, but transported inshore by subsurface waters. This hypothesis is supported by observations of the horizontal distribution patterns of hoki eggs and larvae in Cook Strait during an upwelling event (Murdoch *et al.* 1990). Hoki eggs were found to be most abundant within the Cook Strait Canyon region (Figure 12), a site where large concentrations of adult hoki were known to be spawning at the time of the survey (Livingston 1990). The maximum abundance of newly hatched hoki larvae (2.0-3.9 mm SL) corresponded with sites of high egg abundance in the Canyon, but were also abundant at the shallow near-shore stations off Cape Campbell where hoki eggs were either absent or in low numbers (Figure 13). These stations were sites where water had upwelled from the Cook Strait Canyon (Figure 14). These results indicated that eggs spawned at depths of at least 200 m within the Canyon had been advected by upwelling into the shallow coastal region off Cape Campbell where they had subsequently hatched (Murdoch *et al.* 1990).

Detailed hydrographic observations off Westland recently have identified seaward-directed plumes of inshore waters which resemble the filaments associated with jets or "squirts" of offshore flow in the upwelling system off California (Flament *et al.* 1985; Kosro and Huyer 1986). These surface plumes of dilute nearshore waters extend well beyond the shelf edge in regions which are important hoki spawning sites. They appear to be transient and associated with topographic features, particularly the southern flank of the Hokitika Canyon. The plumes stratify the water column, thereby reducing vertical mixing, and are evident as regions of shallow mixed layer depth (Figure 15; Moore and Murdoch unpub. data). These plumes are possibly important to hoki larvae, not only because they stabilize the water column and appear to enhance productivity, but also because their associated jet may influence the onshore/offshore transport of larvae. A plot of the geostrophic velocities along a transect through the plume observed in 1987 shows that both strong onshore and offshore flows are connected with the plume. Distribution patterns of larvae in the region of the plume in 1987 show that early stage larvae (<5 mm SL; Figure 16) are found predominantly along the shelf edge over adult spawning sites, whereas older larger larvae (>5 mm SL; Figure 17) are found predominantly closer to shore. Off the west coast of Tasmania, larvae also appear to be most abundant in nearshore regions (Gunn *et al.* 1989; Thresher *et al.* 1989). Coastal jets, in addition to upwelling, may therefore serve as a mechanism for transporting larvae into the productive nearshore waters off Westland.

Discussion and conclusions

The feeding ecology of hoki larvae off Westland is similar to that of larvae of other hake species. Hoki larvae feed in daylight hours on a relatively narrow range of prey species, primarily copepods. The maximum size of prey is similar for all sizes of hoki larvae, and only the early first-feeding stages feed on a range of small prey. These small prey appear to be nutritionally insignificant. It is likely that large prey, such as copepods, are required to meet the nutritional requirements of young larvae, although the contribution of small soft-bodied organisms to the diet of these larvae is unknown. Copepods of the genus *Calocalanus* appear to be actively selected and a particularly important prey species for early stage larvae.

Mortality during the early life history stages of marine fish can be high and variable. The source of this mortality is generally attributed to predation and/or starvation. The importance of starvation as a source of mortality of larval fish has been assessed by a number of authors through analysis of published data from laboratory, field, and enclosure studies (e.g. Hunter 1981; Houde 1987; 1989; Miller *et al.* 1988). Comparisons of the vital rates and energetics of marine fish larvae in relation to temperature were used by Houde (1989) to discern possible life history strategies. Houde noted that for fish species of temperate seas (i.e. regions of high latitude and

low temperatures), spawning was often temporally and spatially confined, the daily mortality, growth and ingestion rates of the larvae were low, and the duration of the larval stage was long and potentially very variable. He hypothesised that for species with these characteristics, density-dependent mechanisms are likely to determine the abundance of early life history stages; the long and variable duration of the larval stage, caused by changes in temperature and food availability, would tend to regulate growth by competition for food, and mortality by predation rather than starvation. Larval morphology has also been shown to be a suitable predictor of the vulnerability of marine fish larvae to starvation-induced mortality (Hunter 1981; Miller *et al.* 1988). These authors recognised that larvae which hatched with a relatively large mouth and body size were likely to be less vulnerable to starvation because they could feed directly on a wide size range of prey.

Based on these assessments and the known ecology of hoki larvae in New Zealand waters, I hypothesise that hoki larvae may not require dense patches of food for successful feeding and that predation is likely to be a more important source of larval mortality than starvation. Hoki spawn at specific sites around South Island over a few months each winter in waters with relatively low surface temperatures (11-13°C). Larval patch studies off the Westland coast indicate that larvae have low coefficients for weight specific growth (0.021), and daily instantaneous mortality (probably less than 0.19). There is no information on the duration of the larval stage in New Zealand waters, although this is presumed to be relatively long. Data on larvae collected in waters around Tasmania suggest that duration of the larval stage is in excess of 65 days (Bruce 1988; Thresher *et al.* 1989). The size of hoki larvae at hatching is average (Miller *et al.* 1988), but the mouth size relative to larval length and the size of prey at first-feeding are particularly large compared with larvae of other species (Hunter 1981). The vital rates, general morphology and feeding characteristics of hoki larvae all therefore suggest that hoki larvae are unlikely to suffer starvation-induced mortality, and that other density-dependent mechanisms may regulate larval abundance.

The similarity between the feeding characteristics and vertical distribution of hoki and Pacific hake larvae supports the hypothesis that predation, rather than starvation at first-feeding, may be the most important factor influencing hoki larvae survival. Larvae of Pacific hake similarly begin feeding on large prey, their growth rate is lower than that of other species, and they generally occur at or below the pycnocline (Bailey 1982). Bailey suggested that this feeding strategy may be a survival tactic associated with living at the bottom of the mixed layer in relatively cold water. He concluded that predation pressure on hake larvae may be high, because of their slow growth and development rates, and that starvation at first-feeding was likely to be less important as a source of mortality. It would appear that hoki larvae have a similar survival tactic (Murdoch 1990).

Hoki eggs and larvae occur in a highly dynamic physical environment where they are subjected to advective processes such as coastal jets and upwelling. Such processes appear to affect the distribution patterns of larvae and may be important transport or retention mechanisms. There is a clear need to further examine the vital rates and energetics of hoki larvae in order to better understand how these processes influence their survival off Westland. Future studies on the vertical distribution of larvae relative to their prey, predators, and structure of the water column will be an important first step for providing an insight into the early life history strategy of hoki in New Zealand waters.

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Table 1. Predominant copepod prey of the larvae of hoki (*Macruronus novaezelandiae*), Pacific hake (*Merluccius product*), and hake (*Merluccius merluccius hubbsi*) off Argentina

Hake species	Predominant copepod prey	Reference
Macruronus novaezelandiae	Calocalanids *Clausocalanus* spp. *Paracalanus indicus* *Oithona* spp.	Murdoch (1990)
Merluccius productus	*Calocalanus* spp. *Clausocalanus* spp. *Paracalanus* spp. *Mecynocera clausi* *Oithona* spp.	Sumida and Moser 1980
Merluccius merluccius hubbsi	*Clausocalanus brevipes* *Paracalanus parvus* *Drepanopus forcipatus* *Oithona* sp. *Oncaea* sp.	de Ciechomski and Weiss (1974)

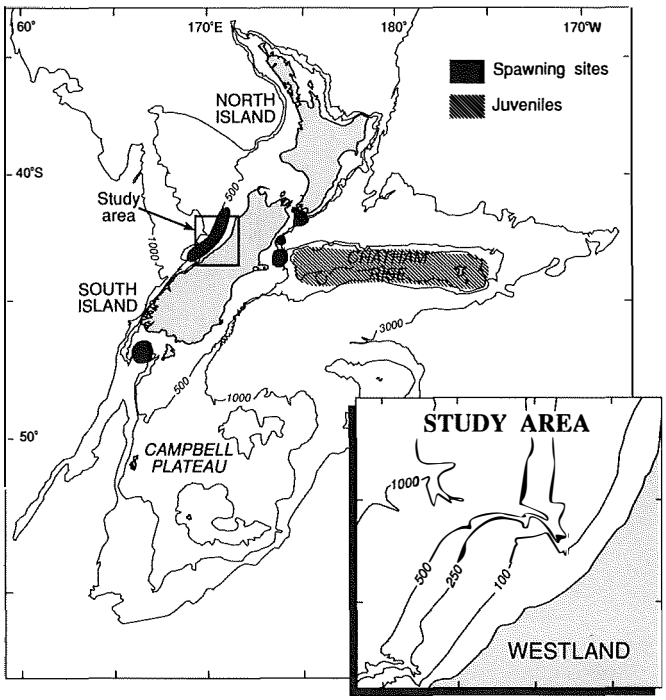

Figure 1. Map of New Zealand showing associated sub-marine platforms, study area, and known hoki spawning sites and juvenile nursery grounds.

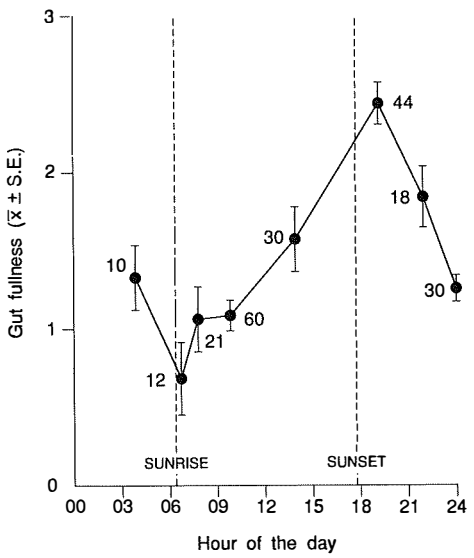

Figure 2. Diel variation in gut fullness (arbitrary units) of hoki larvae (n listed for each data point) collected from Cook Strait, September 1987 (Guo and Murdoch in prep.).

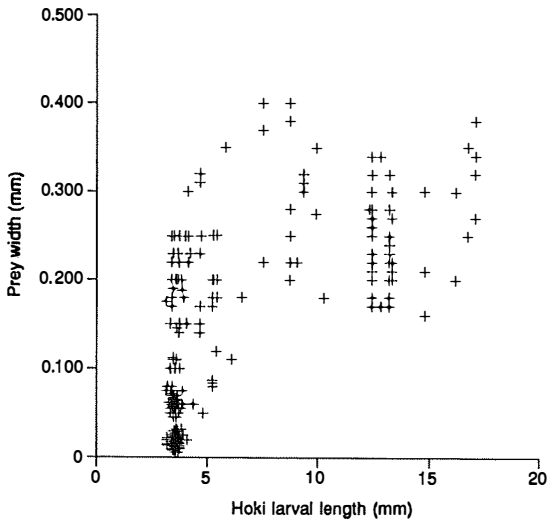

Figure 3. Prey width (n=348) in relation to hoki larval length (SL) (n=105; from Murdoch 1990).

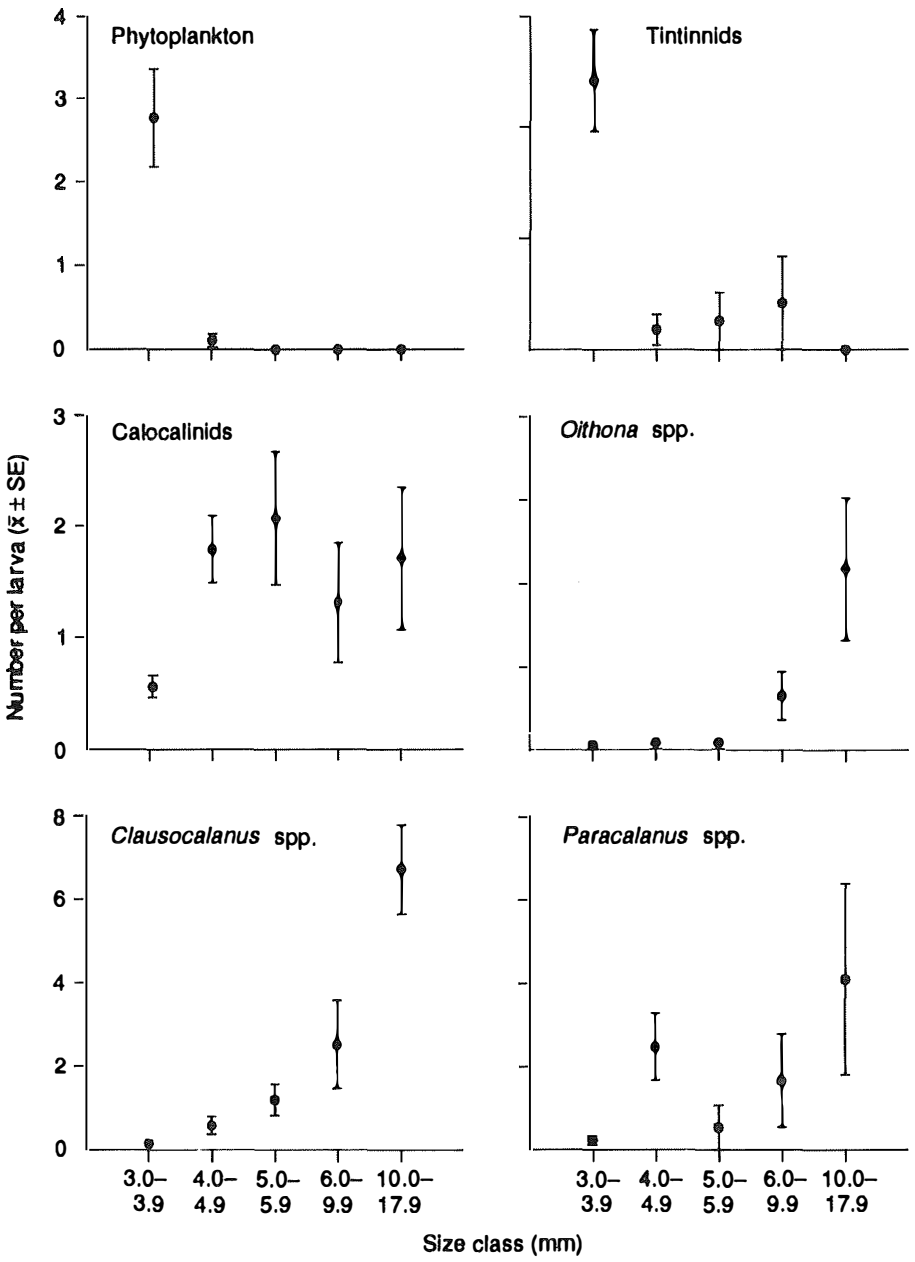

Figure 4. Mean number of selected prey types, approximately in order of increasing size, per hoki larva for the different size classes examined. The numbers of larvae for each size class were 130, 52, 19, 12, and 12, respectively. (from Murdoch 1990).

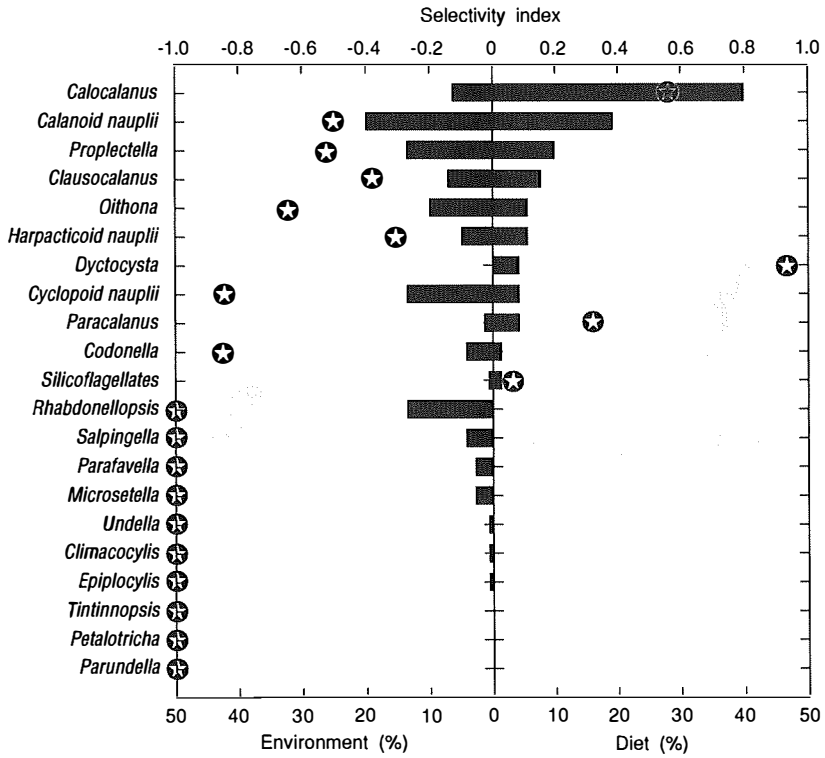

Figure 5. Percentages of different planktonic species in the environment (left) and diet (right) of hoki larvae. The value of the Alpha selectivity index (Chesson 1978) for each species is denoted by a star; a 0 value indicates random feeding, values greater than 0 positive selection, and values less than 0 negative selection. (Thecate dinoflagellates and diatoms have been excluded).

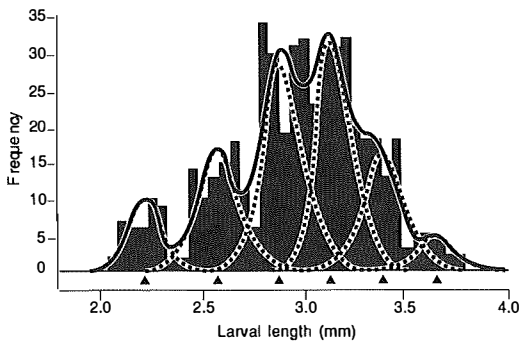

Figure 6. Histogram of the size frequency distribution of hoki larvae from one sample collected within the patch. Results of the modal analysis are also shown, indicating the position of the normal distributions associated with each cohort (dotted lines), the estimated mean length of each cohort (triangles), and the modal estimate of the total sample distribution (solid line).

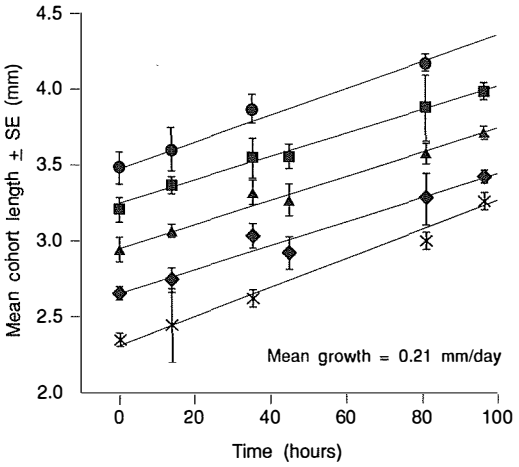

Figure 7. Growth of hoki larvae cohorts based on length frequency data of six different sampling times within the patch study. Mean growth was estimated as the average of the slopes of the linear regressions calculated for mean cohort standard length versus time for each cohort.

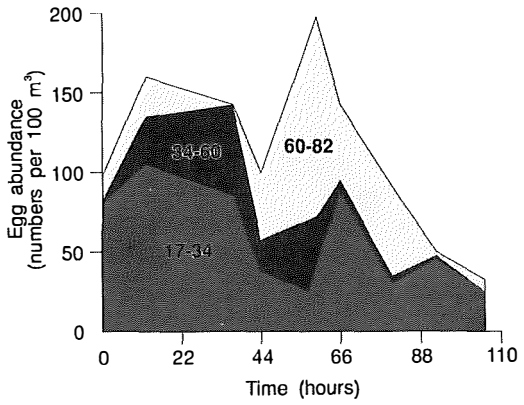

Figure 8. Total hoki egg abundance by age (17-34 h, 34-60 h and 60-80 h), over the duration of the patch study.

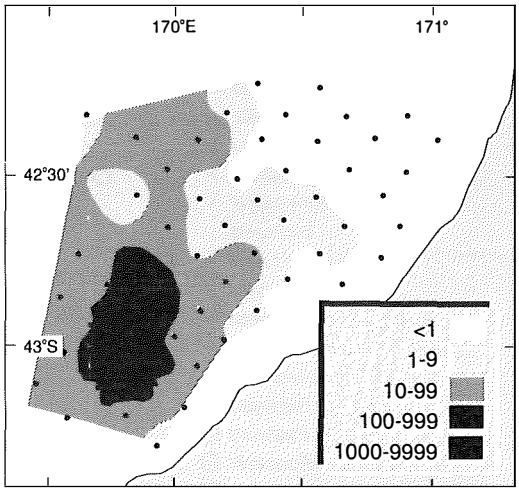

Figure 9. Distribution of hoki larvae (numbers per 100 m³) off Westland, 19-30 July, 1987.

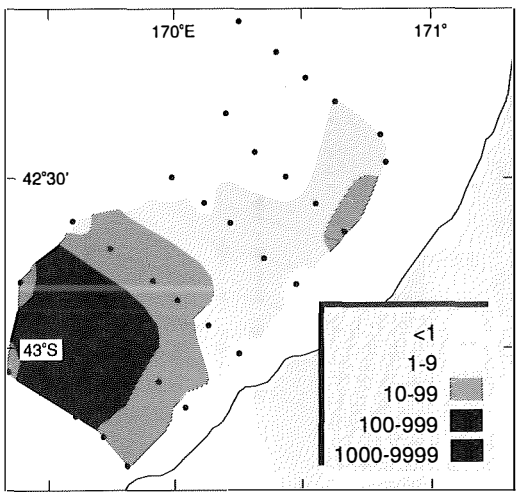

Figure 10. Distribution of hoki larvae (numbers per 100 m³) off Westland, 4-8 August, 1987.

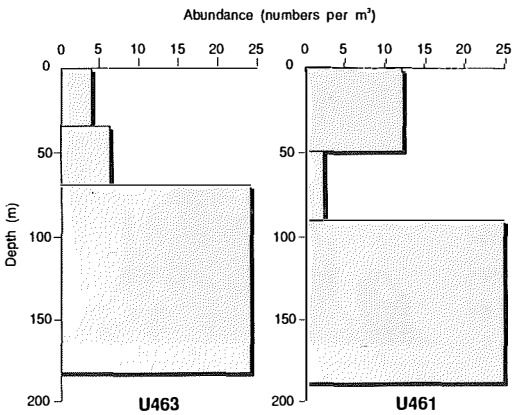

Figure 11. Vertical distribution of hoki larvae in the upper 200 m of the water column from two plankton net tow series at the patch site.

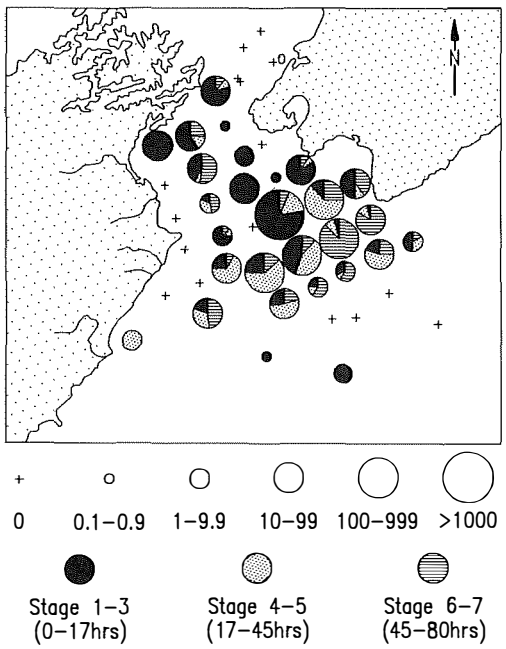

Figure 12. Distribution of hoki eggs (numbers per 100 m^3) in Cook Strait, September 1987. Pie graphs show the proportion of egg developmental stages (from Murdoch *et al.* 1990).

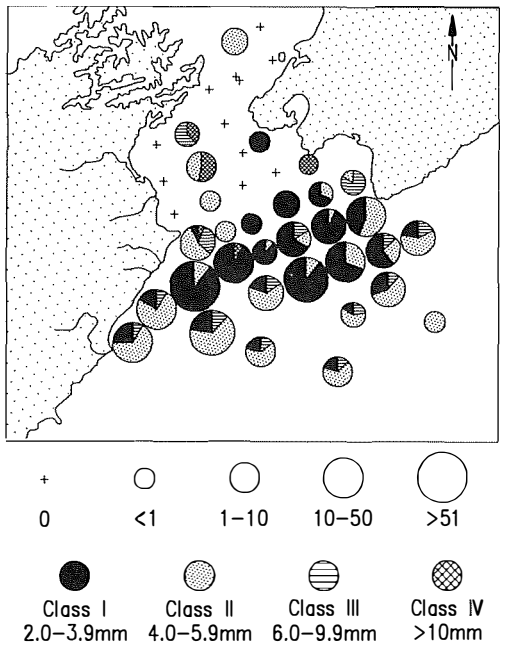

Figure 13. Distribution of hoki larvae (numbers per 100 m^3) in Cook Strait, September 1987. Pie graphs show the proportion of each larval size class (I-IV) (from Murdoch *et al.* 1990).

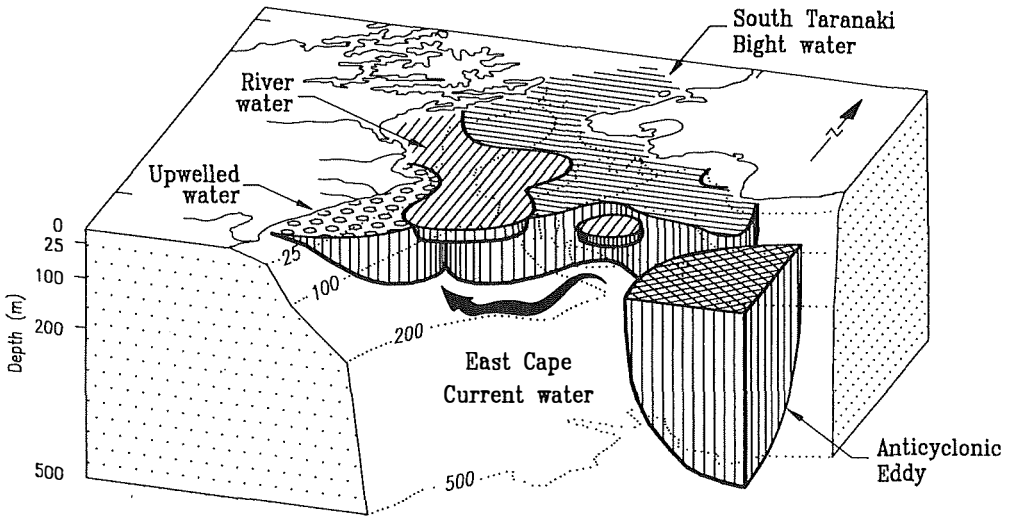

Figure 14. Diagram showing schematic representation of the hydrographical conditions of Cook Strait in September 1987, and proposed advection path of hoki eggs from the spawning site within the Cook Strait Canyon (arrow) (from Murdoch *et al.* 1990).

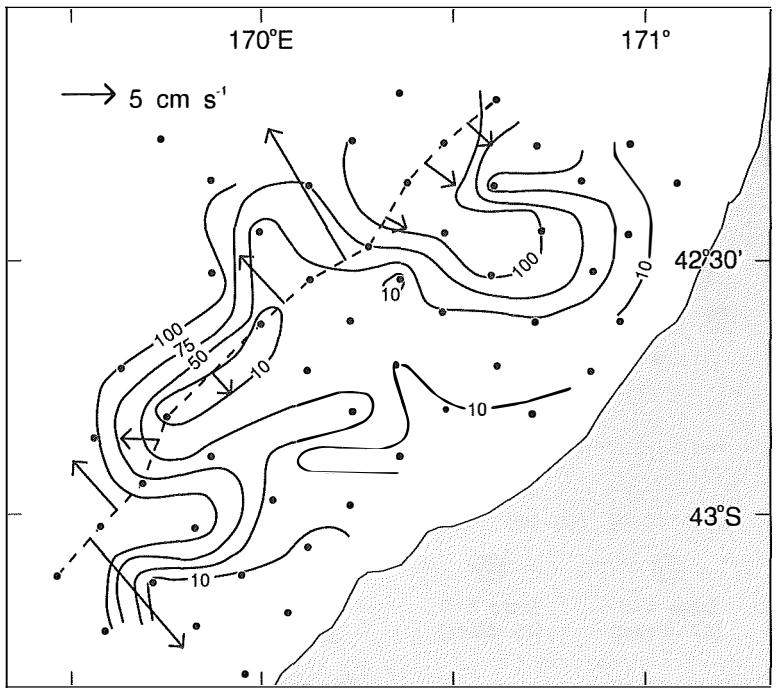

Figure 15. Mixed layer depth (m) off Westland, July 1987, showing presence of a coastal plume. Arrows represent onshore/offshore surface flow velocities, derived from dynamic height, along a transect (dashed line) through the plume feature.

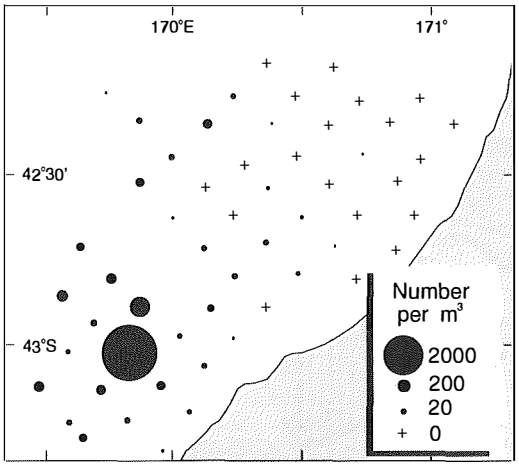

Figure 16. Abundance of hoki larvae <5 mm standard length off Westland, July 1987.

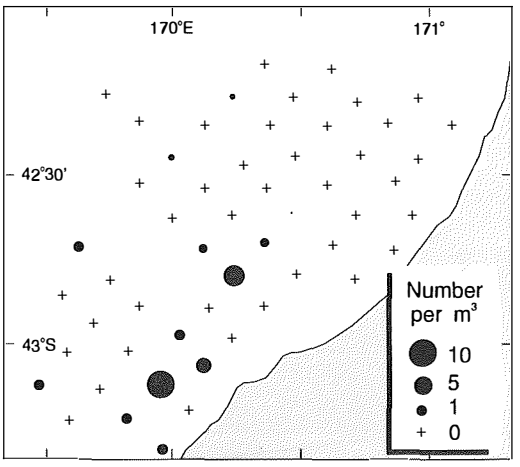

Figure 17. Abundance of hoki larvae >5 mm standard length off Westland, July 1987.

DISCUSSION OF KEYNOTE ADDRESS

Recorded by I.M. Suthers

School of Biological Sciences
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A number of general models of the timing and location of fish spawning have been proposed, such as Harden Jones' (1968) conceptual model of the triangular circuit of migration, and the member/vagrant hypothesis (or the larval retention hypothesis) of Iles and Sinclair (1982) and Sinclair (1988). Mike Sinclair asked if there were any similar general models for hoki. Rob Murdoch replied that hoki have a propensity for spawning in canyon systems [unlike the Australian equivalent, blue grenadier, off the Tasmanian west coast] , and the water masses involved may be variable; sub-tropical or sub-Antarctic. Thus the reasons for spawning time and location are unclear, but upwelling appears important. Current systems do transport larvae through the Cook Strait, but then the juveniles must swim to the [presumed] Chatham Rise nursery areas. Rob Murdoch was equivocal on the process of larval retention, due to upwelling and coastal jets. However the largest larvae occur near land, and do appear to persist there.

Ron Thresher compared and contrasted hoki on the N.Z. west coast with blue grenadier on the Tasmanian west coast, which also spawn in mid-winter in seemingly inhospitable areas. From stable carbon isotope technology, they found that the larvae indirectly fed on detritus swept out from nearshore seagrass beds, via the microbial food chain and tintinnids. Rob Murdoch replied that his NZ larvae did not feed on tintinnids to the same extent - usually only 1-2 per larva. He argued that there was no shortage of nutrients due to intermittent upwelling, and therefore the larvae fed on the usual copepod assemblage. He also noted that while tintinnid concentrations were unknown, there was no particulate (detrital) material in the coastal jets of nearshore water.

Fish larvae have a diurnal feeding periodicity, and Peter Gehrke enquired whether the smaller larvae fed only during the day, while larger larvae could feed over a longer period. Unfortunately, the larger larvae were rare in their samples. Fish larvae sometimes exhibit diel vertical migration and Rob Murdoch noted that while hoki larvae generally occurred deep, larger larvae tended to eat *Paracalanus* which are found at shallow depths around 20 m - suggesting that these larvae migrate to the surface to feed.

Jeff Leis suggested that since larvae were abundant on only one cruise, perhaps regular spawning may occur elsewhere. However despite sampling most of the west coast fishing grounds, they consistently found many eggs and few larvae, suggesting very low survival of the early larvae. Rob Murdoch said they also sampled inshore and offshore of the sampling grid with little success. Hoki do spawn farther north later in the season which they did not examine. Jeff Leis then asked if the eggs and larvae were rapidly advected out of the area contributing to the apparent low survival, but there is only a small residual northerly flow along the west coast. The drogue that Rob Murdoch deployed in the canyon tracked slowly north, but no larvae

were advected with it. Jeff Leis suggested that if the early hatch larvae had poor survival, then a year class should be missing - but Don Robertson replied that these cohorts had not yet recruited to the fishery and it is still unknown if year-class(es) are missing.

From the diet of hoki larvae, Peter Doherty wondered why there was selection against the copepod *Oithona*. He cited Alan Mitchell's MPh. thesis (AIMS, Griffith University) showing size appeared to be the only selection criterion, and was perhaps a general phenomenon. Rob Murdoch replied that *Oithona* is a fast swimmer in jerky movements which precluded larval feeding, although larger larvae can and do eat *Oithona*.

Barry Bruce noted that spawning off Tasmania is often delayed, which may explain the low abundance of larvae off NZ relative to the cruise period. Rob Murdoch replied that while delayed spawning also occurs off the South Island, and may occur off the North Island west coast, their sampling occurred throughout July and August during the peak spawning period.

John Glaister thanked Rob Murdoch for an excellent review of hoki larvae, and the ensuing discussion on comparisons with the Australian blue grenadier.

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ICHTHYOPLANKTON STUDIES FOR FISHERIES RESEARCH

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(Presented by D.A. Robertson)

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A primary goal of fisheries research is the estimation of past, current and future yields of fish. This paper will discuss how the study of fish eggs and larvae - the ichthyoplankton - bears on this priority issue. The topic is approached from both a conceptual standpoint, and by using some examples from current research in New Zealand and elsewhere.

There are two main avenues of ichthyoplankton research that are directly relevant to yield estimation (Figure 1). The avenues are joined at the egg stage and bifurcate from there. On the one hand, one can project back in time from the egg stage to estimate spawning biomass, and on the other hand one can study recruitment processes by projecting forward in time from the egg stage, through the larval and juvenile phases, to the age where recruitment levels become predictable.

The two approaches yield different amounts and types of information. Most obviously, the backward projection produces 'current', nearly real-time information on the spawning stock size and reproductive condition, while the forward projection produces information on the status of the stock a few years into the future. Another important difference is related to the time scales over which the projections operate. Projecting back to the spawners usually involves only a few days (the incubation times of the eggs). The processes which control egg abundance (eg., stock fecundity, egg mortality) can generally be accounted for, and to an extent, are related to the abundance of the parent stock (density-dependent; Rothschild 1986, p.135). On the other hand, forecasting recruitment by projecting forward usually involves months to years and a multidimensional biophysical array of processes, which are very difficult to account for. These include predator-prey interactions with growth, advection, and passage through various life stages with different population dynamics. As a result, successful predictions of recruitment are often impossible until the end of the larval period or beyond. To a larger extent, especially in the larval transition, these processes determine abundance independently of density (Houde 1987).

We will first consider the back projection of biomass from egg surveys. Prior to 1980, the only method for estimating biomass using egg surveys involved estimation of egg production by the stock using a number of surveys through the spawning season, and fitting a curve to the points. The integrated area beneath the curve (the annual planktonic egg production), divided by the annual fecundity of the females and the sex ratio, constitutes the spawning biomass estimate (Saville 1963).

This method was supplemented during the 1980's by the development of the daily egg production method (Lasker 1985). By using

reproductive data from the adults on the proportions of the females spawning per day and the batch fecundity, the 'daily fecundity' of the stock can be estimated. The adult survey for these data is done coincidentally with a single planktonic egg production survey. The spawning biomass then can be estimated by dividing the planktonic production by the daily fecundity of the stock and the sex ratio.

We are researching a variation of this method (Zeldis in press), for possible application to orange roughy (*Hoplostethus atlanticus*). Orange roughy aggregate to spawn on deep water banks and pinnacles at various places around New Zealand during winter. During surveys of these spawners, a decline in the proportion of 'actively spawning' fish (fish destined to spawn that year) is detected (Figure 2). In this method, the average fecundity of the female population on a given day during the spawning season is estimated as the proportion of actively spawning females, times the average number of advanced oocytes per female. The rate that this average fecundity declines during the season equals the 'daily fecundity' of the stock, or the rate that the stock is producing eggs into the plankton. This is divided into the daily egg production, estimated by a plankton survey coincident to the trawl survey, to estimate spawning biomass.

Our biggest problems with this at the moment are related to estimation of planktonic egg production. We know virtually nothing about orange roughy egg development stages and rates of development through these stages; this knowledge is required to account for egg mortality in the estimation of egg production from egg abundance data. We also know little about vertical and horizontal distributions of eggs. Vertical distribution knowledge is required for estimating egg age, because of the dependence of development rate on incubation temperature. Knowledge of horizontal distributions is required for estimating survey size, in terms of geographic survey area size, and sample number. The study of planktonic egg production could provide the focus for future orange roughy ichthyoplankton research.

We are also very interested in estimating hoki (*Macruronus novaezelandiae*) biomass. Hoki are merluccid hakes which spawn widely along the slope of the South Island west coast and Cook Strait, during winter. We believe that the daily egg production method is probably not useful for estimating absolute biomass of these spawners, because individual hoki migrate into the west coast area, spawn and leave over a period considerably shorter than the overall population spawning period. As a result, a 'snapshot' survey, such as a daily egg production survey, will produce an underestimate of unknown magnitude. For that reason, we are researching the use of the *annual* egg production method for this fishery, because it integrates total egg production over the whole spawning season and accounts for all fish that spawn in the area.

Because this method involves very intensive use of ship time over multiple surveys, we have estimated the dimensions of a sampling plan that would produce an annual hoki egg production estimate precise enough to be useful for fishery management (Zeldis in press; Hauser and Sissenwine 1991). We used historical hoki egg abundance data from grid surveys from 1978 to 1981 over the west coast spawning area (Figure 3), to describe hoki spawning season length and sampling variability. From these results, we simulated the precision of annual egg production estimates that would be produced by variable numbers of surveys per year, each with variable precision of the within-survey egg production estimate (Figure 4).

We found that the effect of using multiple surveys to take samples of egg production through the spawning season is to substantially improve the precision over the individual survey precision (Figure 4). For example, with 5 surveys (at 16 day intervals over the 80 day season), and a within-survey CV (coefficient of

variation) of 27.1%, the CV of the annual egg production estimate will be about 13.5%. The sampling variability of the historical data showed that each survey would require about 200 plankton stations to achieve the 27.1% CV. The same annual estimate of CV is achieved with 4 surveys, each with 250 stations. It would seem that the preferred option would be to make more surveys, each with fewer samples, in order to better describe the spawning curve shape. Thus, these results provide pointers for optimal survey design and, in general, show that it is logistically feasible to use the annual egg production method to gain estimates that are precise enough for management of the hoki fishery.

I would like now to turn to the other avenue that ichthyoplankton research can take in a fisheries setting, that is, the forward projection of recruitment and the study of recruitment processes.

First, we can note that although stock-recruitment relationships are at the basis of management of fisheries, they do not explicitly take into account the myriad biophysical environmental effects on eggs, larvae and pre-recruits which occur between the egg stage and recruitment. It is thought that these effects are the main reason for the 'noise' in stock-recruitment relationships. While it is generally accepted that some sort of curved stock-recruitment relation must exist (in order that populations remain 'relatively' stable or at least not go extinct), it is clear that events in the pre-recruit biophysical environment do much to obscure stock-recruitment relationships (see Rothschild 1986 pp.71, 103 and 100 for a discussion of these points).

However, another way of looking at this is to ask 'why is recruitment to fish stocks relatively stable?' Although stock-recruit relationships seem noisy, the ranges of recruitment are usually within one order of magnitude of their mean value (see Rothschild 1986 p. 34). The answer must be that there exist mechanisms for stabilizing recruitment toward the order of magnitude of mean replacement abundance.

Although much of this control probably occurs in the postmetamorphic phase, there is evidence that coarse control on abundance also occurs in the larval phase. For example, the abundances of larval northern anchovy from 1951 to 1982 off California (Figure 5; Lo 1985) are all within one order of magnitude of each other, except for 3 low years at the beginning of the time series. Another example is provided by a time series of larval abundance data from North Sea plaice (see Table 5 in van der Veer 1986). During the precipitous decline in abundance during the larval phase there is great *potential* for wild fluctuations in abundance to occur (over several orders of magnitude), due to subtle variations in growth and mortality rates and the exponential nature of these processes (Houde 1989). Indeed, one can ask why abundances of larvae do not vary far more than they actually seem to do.

Perhaps the answer is that by the time the larvae approach metamorphosis, they have already experienced a strong averaging effect on their abundance. Imagine that the larval environment is structured as a time-space mosaic of growth and mortality conditions (Smith 1985). As the larvae age and pass through different parts of the mosaic, their abundance will be winnowed to a level circumscribed by the range of environmental conditions they have experienced. It seems that these biophysical environments *usually* have a pretty finely tuned set of conditions, which prevent late larval abundances from being much more variable than they are. These adjustments on larval growth and mortality seem to have the effect of rectifying abundance toward the order of magnitude range from which post-metamorphic processes eventually determine year class strength.

The implication of having heterogeneous survival conditions arranged as a mosaic is that mortality rates will be variable during the larval period and for different geographic sectors of the larval distribution. I am testing this possibility using data from a large study of environmental effects on survival of larval snapper in the

Hauraki Gulf, New Zealand. Snapper eggs and larvae were collected over three summer spawning seasons (Figure 6). It was found that egg abundance varied less than larval abundance between summers. This suggested that variability in larval survival operated between years. I will be studying the mortality rates involved in generating these larval cohort abundances, by ageing the larvae and back-calculating to their abundance as eggs by using the egg abundance curves. I will investigate how the mortality rates varied among larval cohorts and geographic areas of the Gulf, with respect to the biophysical environment.

The biophysical environment *did* vary markedly during these three summers. In the first two summers, phytoplankton concentrations in the mixed layer of the Gulf were much lower than in the third summer, when larval abundances were highest (Figure 7). Also, in the first two summers, massive salp blooms occurred in the Gulf, but not in the third summer. These salp blooms dominated meso-zooplankton biomass. We are proposing that salp grazing essentially destroyed the food supply of first-feeding snapper, by grazing out the autotrophic and micro-heterotrophic portion of the pelagic trophic web and precipitating it to the bottom in large faecal pellets. We are currently investigating this further with studies of phytoplankton and microzooplankton species composition and biomass. Also, physical data that were collected coincidentally suggested that the salps were 'seeded' into the Gulf by intrusions of offshore, shelf, water. These intrusions appeared to have been set up by the westerly winds which prevailed in the early parts of the first two summers.

Fishery and temperature data suggest that the environment exerts a strong effect on abundance of adult snapper and this effect occurs during the first year of life (Figure 8). We do not yet know to what extent this correlation is caused by environmental effects on snapper larvae, and, in general we do not yet know when in their early life history the abundance of snapper is determined. For that reason, coincident with the egg and larval study just described, other MAF Fisheries staff have run studies of snapper juvenile ecology and trawl surveys for pre-recruits. Our attempt is to approach the problem in a comprehensive manner, involving all life stages of the species over a number of years.

In the snapper larval study, we are hypothesizing a biological mechanism (salp grazing) for the destruction of larval food and reduced larval survival. If this hypothesis turns out to be true, it represents a contrast with predictions from Lasker's stable ocean hypothesis (Lasker 1975), which relates the destruction of the larval food directly to physical breakdown of stratification. More recent work relates the degree of physical turbulence in the feeding environment to contact rates between predator and prey and larval cohort success (Rothschild and Osborn 1988). Again, however, measurements of physical turbulence, alone, may not explain results from the snapper study. To generalize, all that can be safely said is that the well being of larval fish is tied to the 'match or mismatch' of their production and development in time and space with processes in the biophysical environment. However, under this rubric, many diverse mechanisms may exist. It is not clear how addressable the question of larval survival may be by generalized theory; a recent and exciting approach can be found in Rothschild (1991). There are, of course, other avenues in the study of ichthyoplankton that are important to fisheries research. Examples of these would be stock distributions and interactions, species identification, and aquaculture. However, by describing some recent work in two of the larger areas of ichthyoplankton study, I hope I have set a stage for other papers at this workshop.

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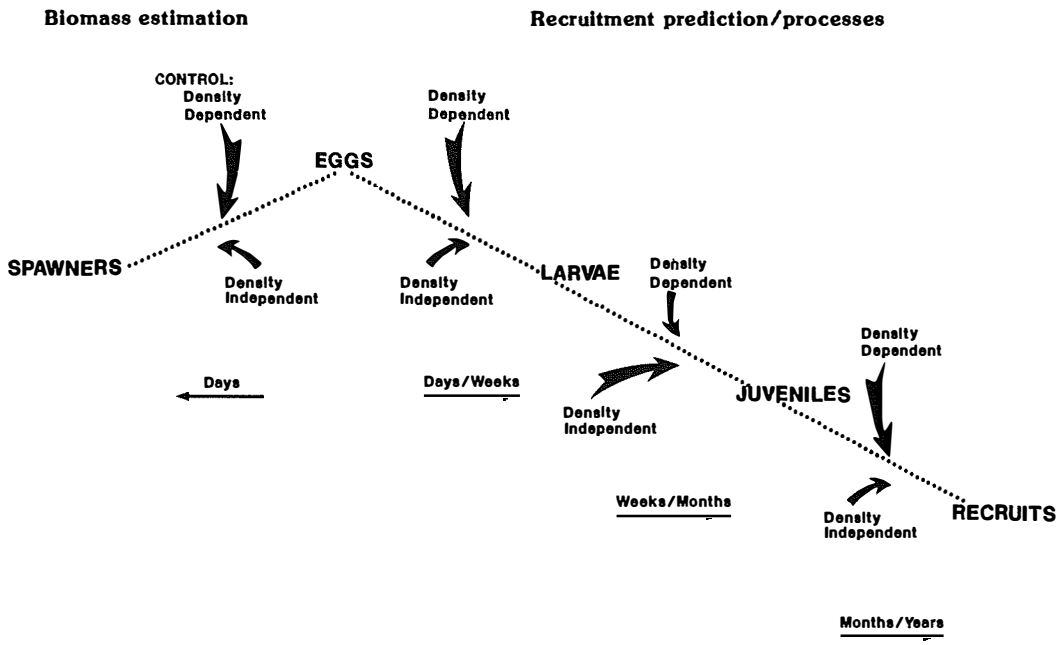

Figure 1. Two main avenues of ichthyoplankton research relevant to yield prediction. Shown are strength of control by density dependent and independent processes (arrow size) and time scales over which processes operate.

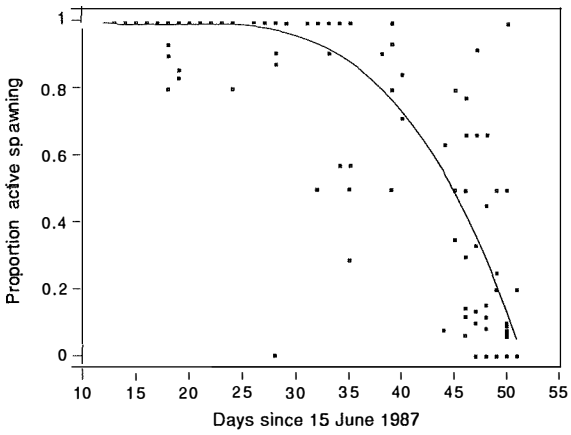

Figure 2. Decline in the proportion of 'actively spawning' orange roughy during the 1987 north Chatham Rise trawl survey. Shown are proportions of late vitellogenic, hydrated and ovulated stages combined, relative to all fish destined to spawn that year, from trawl catches.

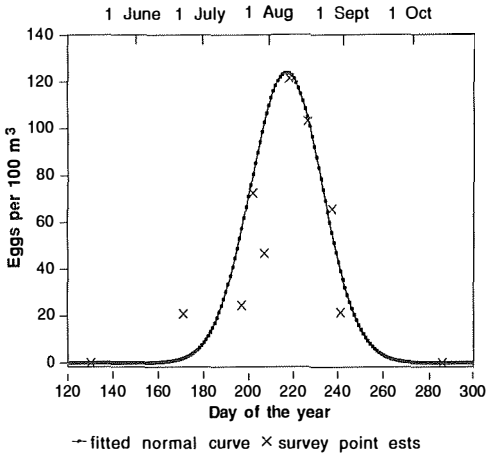

Figure 3. Hoki egg abundances during South Island west coast grid surveys done from 1978 to 1981, combined from all years (MAF Fisheries, unpublished data). Tows were double oblique hauls to 210m. Normal curve was fitted to data (mean = day 217, 1 sd = 16.0 days) to illustrate seasonal spawning curve.

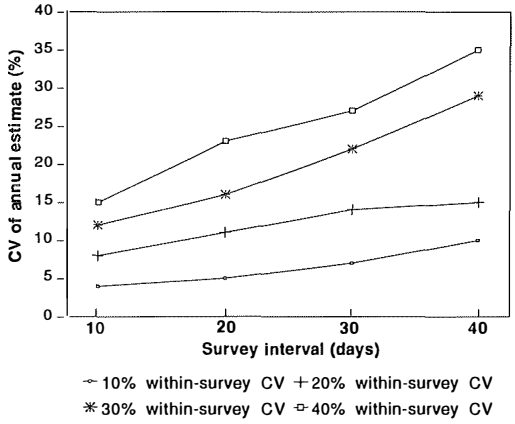

Figure 4. Coefficients of variation (CVs) of annual egg production estimates (as CVs of 100 ratios of input to estimated annual egg production) at various survey intervals and within survey CVs.

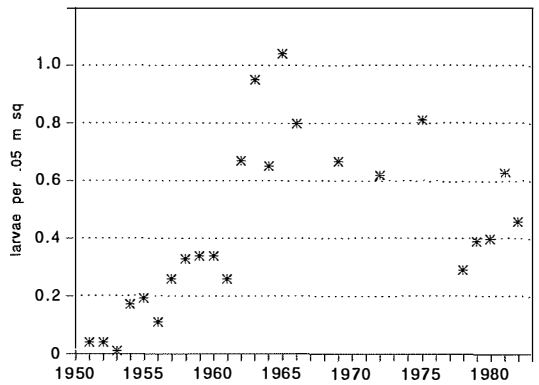

Figure 5. Northern anchovy larval abundance (per 0.05 m^2) off California from CalCOFI data from 1951-1982 (adapted from Table 3 in Lo 1985).

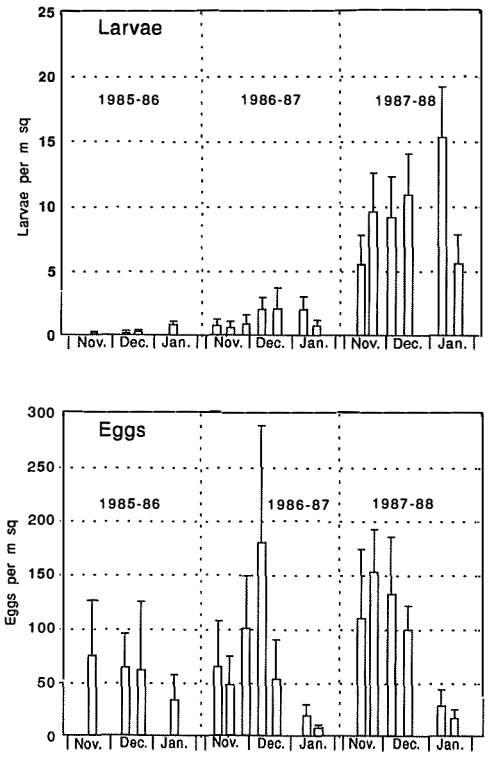

Figure 6. Hauraki Gulf snapper larval and egg abundances over 3 summer spawning seasons 1985-86 to 1987-88. Each bar indicates mean and 95% confidence interval for abundance estimate from a grid survey (average survey station number = 53, 1 sd = 7.6).

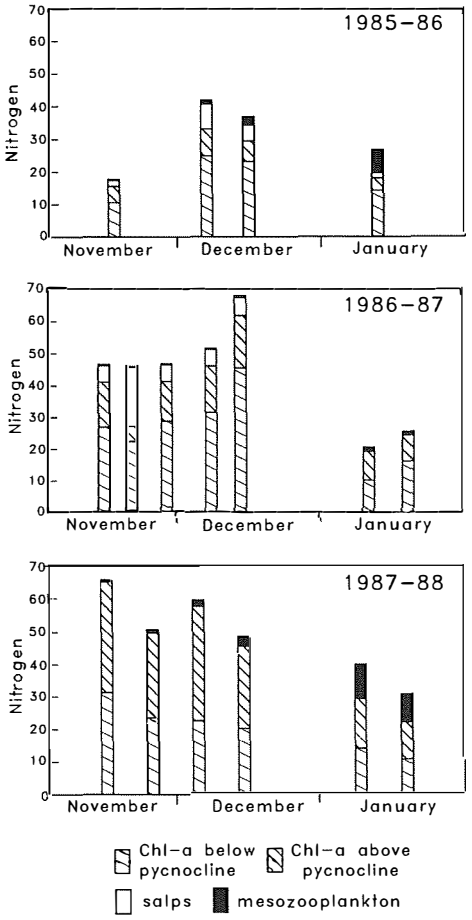

Figure 7. Biomass (in $\mu g.l^{-1}$ units of nitrogen) of chlorophyll-a, salps and other mesozooplankton for each grid survey in the Hauraki Gulf over 3 summers 1985-86 to 1987-88. Chlorophyll-a is divided into biomass above and below the pycnocline. Salp and mesozooplankton biomass are integrated over the water column.

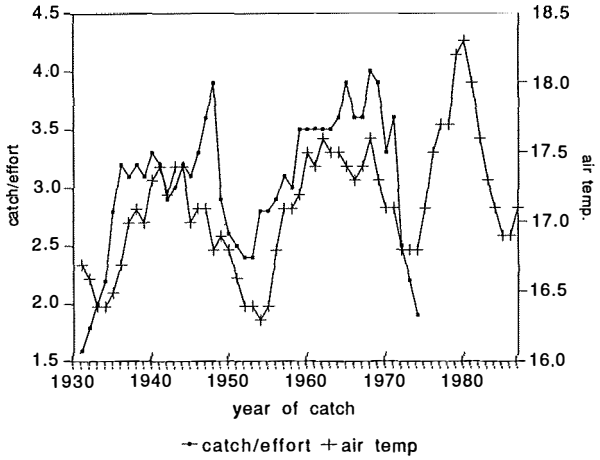

Figure 8. Relationship between snapper catch per unit of effort and air temperatures in the Hauraki Gulf. Air temperatures are means for spring and summer and are lagged forward 6 years; 6 years is the average age of fish in the catch (Paul 1982).

SESSION 1

FEEDING ECOLOGY AND CONDITION OF LARVAE

Session Chairperson:	G. P. Jenkins
Session Panellists:	J. W. Young
	D. J. Gaughan
	N. P. Preston
	G. P. Jenkins
	I. M. Suthers
	M. J. Milicich
Rapporteurs:	H. M. May and B. D. Stewart

CHAIRPERSON'S INTRODUCTION

G.P. Jenkins

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Welcome to the session on feeding, growth and condition of fish larvae. We will try to make the session as relaxed and informal as possible. The format will consist of talks of about 5 minutes duration with discussion at the end of each and, if time allows, a general discussion at the end of the session. Those with pertinent questions are welcome to interject if they wish.

Today's talks are really a precursor to the workshop on recruitment over the next two days. Today we are talking about the factors which lead to recruitment variability, that is, factors which affect mortality of larvae. Feeding, growth and condition are all important factors in larval mortality. The other important factor which we will not talk about much today is predation. We must remember that there is probably an interaction between feeding, growth and predation in that poorly fed, slow growing larvae will spend longer in the larval phase of high predation mortality.

One observation today is that the average age of the panellists is probably much lower than the average age of fish biologists in general. This may be due to the fact that this area of research has only become popular in Australia in the last ten years or so. Therefore there is now a vanguard of young fish biologists working in this area.

Without further ado, we'll begin the session.

FEEDING ECOLOGY OF MARINE FISH LARVAE: AN AUSTRALIAN PERSPECTIVE

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Abstract

Information on the diets of marine fish larvae found in Australian waters is scarce, particularly when we consider that of some 3000 species of fishes in the waters of the Australian Fishing Zone, there are published data on feeding for fewer than twenty species. In the larvae studied so far, diets are dominated by the various life history stages of copepods, although other taxa (including bivalve veligers, appendicularians, tintinnids and other fish larvae) dominate the diets of some species. Generally, feeding success, prey size and prey diversity all increase as the larvae grow. Nevertheless, flexibility and opportunism in feeding are important characteristics of larval behaviour. Larvae generally feed during the day, with feeding peaks in the morning and afternoon, although some species feed throughout the day and some feed only at night. Gut evacuation rates range from 2 to 6 h. Larvae eat between 10 and 30% of their body weight (or 5 to 100 prey) per day, depending on prey type and availability. Larvae in tropical oligotrophic waters can affect the abundance of their prey, which results in competition for food and subsequent density-dependent reduction in growth rate. This contrasts with larvae from temperate waters, which do not appear to be food-limited. Present studies indicate that marine fish larvae in Australian waters have similar feeding strategies to their counterparts elsewhere in the world. However, with so few larval species examined in detail, such generalisations are premature. Future research should aim to 1) collect larval feeding data on more species and 2) examine further the relationship between feeding ecology, recruitment success and seasonal and interannual variations in plankton production.

Introduction

In 1914 Hjort proposed the 'critical period hypothesis' that food availability is critical to larval survival. This hypothesis has been strongly debated (e.g. May 1974), but it has generated considerable research into the feeding ecology of marine fish larvae. Until recently all that was known on this subject came from studies in the northern hemisphere. With increased interest into the early life history of marine fishes in Australian waters over the last decade, this imbalance has begun to be redressed. Local studies have supported overseas findings. However, some noticeable exceptions have been found, which should encourage us to explore this area of research further.

Larval feeding studies in Australian waters, although few in number, reflect the wide variety of marine environments encountered by newly-hatched larvae. However, of some 3000 species of marine fishes identified from Australian waters, the feeding ecology of very few of their larvae has been studied in any detail (Table 1). This obviously limits the breadth of

this review. Nevertheless, an appraisal of research to date, and of areas in which future research is needed, may benefit future studies.

Diet

As in the northern hemisphere, the diets of marine fish larvae in Australian waters are typically based on the various life history stages of Copepoda, as in *Trachurus declivis* (Young and Davis in press) and species of *Thunnus* (Uotani *et al.* 1981; Young and Davis 1990). Similarly, Gaughan (Murdoch University, unpublished data) found that the diets of five species of estuarine fish larvae were dominated by copepods. However, there are some notable exceptions. Larval flounder (family Pleuronectidae) feed largely on bivalve veligers (Jenkins 1987). First-feeding larval blue grenadier, *Macruronus novaezelandiae*, feed on algae and tintinnids (Murdoch 1990; Thresher *et al.* in preparation), although their diet shifts very quickly to copepods. Piscivory in several larval scombrids has been reported (Jenkins *et al.* 1984; Young and Davis 1990).

Dietary shifts are common: the larvae of the tropical atherinid, *Hypoatherina tropicalis*, which mainly feeds on copepods, will at certain times feed entirely on tintinnids (Schmitt 1986). Larval *Trachurus declivis* eat cladocerans and larval euphausiids when they are available as prey (Young and Davis in press). Larval *Thunnus maccoyii* shift from a diet of copepod nauplii through cyclopoid and calanoid copepods to other fish larvae with increasing size (Young and Davis 1990). This shift in diet to larger prey appears to be largely a function of mouth size, and may be an adaptation to maximise the energetic value from each prey (Hunter 1981). Notwithstanding this shift to larger prey, many larvae continue to eat very small prey as they grow (Murdoch 1990; Young and Davis in press; D. Gaughan unpublished data, Murdoch University). Prey characteristics such as colouration, swimming speed and nutritional quality may also contribute to a prey's suitability (Mitchell in press). For example, Mitchell (in press) found that tropical larvae selected the most pigmented nauplii and copepods.

There is some evidence to suggest that larvae are capable of partitioning their food resources (Jenkins 1987; Young and Davis 1990; D. Gaughan unpublished data). For example, the diets of co-occurring species of larval flounder are increasingly divergent as they grow, thus avoiding competition for food (Jenkins 1987). Similarly, preliminary comparisons of the diets of five species of estuarine larvae from southwestern Australia show evidence of food partitioning (D. Gaughan, Murdoch University, unpublished data). Govoni *et al.* (1983) suggested that such partitioning may be 'a behavioural adaptation which mitigates periods of low food supply'.

The feeding patterns of the larvae of some species appear to be consistent over vast distances. For example, the larvae of species of *Trachurus* have a very similar diet, regardless of where they are found (Arthur 1976; Sinyukova 1964). Crustacean microzooplankton are their most common prey, even to the extent that certain genera (e.g. the harpacticoid copepod *Microsetella* spp.) are an important prey item for the larvae from both hemispheres (Sinyukova 1964; Arthur 1976; Young and Davis in press).

Prey selection

Selection for both prey size and prey type appears to be a common trait of most fish larvae. Schmitt (1986) found that larval *Hypoatherina tropicalis* selected for copepods in a higher proportion than they occurred in the plankton and that this selection was size-dependent. Jenkins (1987) found that co-occuring species of larval flounder selected for different prey types and that this divergence increased as the larvae grew. Larvae of *Thunnus alalunga* and *T. maccoyii* selected for corycaeids and against calanoids (Uotani *et al.* 1981; Young and Davis

1990). In contrast, tropical pomacentrid larvae selected in favour of calanoids and against the cyclopoid copepod *Oithona* spp. (Mitchell in press). However, prey selection must be tempered by prey availability. For example, larval *Trachurus declivis* selected for cladocerans and larval euphausiids when they were present in the plankton (Young and Davis in press). Schmitt (1986) proposed that flexibility and opportunism in feeding behaviour may increase a larva's chances of obtaining adequate nutrition when prey levels are low. The question has been raised as to whether prolonged and differential rates of digestion of prey by larvae may bias or confuse results (Govoni *et al.* 1986).

Assessment of prey selection in fish larvae is dependent upon adequate sampling of the larva's food. Frank (1988) stressed the importance of using appropriately-sized mesh in nets used to capture microplankton. The scale of sampling is also important in determining the distribution and abundance of microplankton. Jenkins (1988) found that abundance in a single sample of microplankton could be as much as three times greater than the mean abundance of pooled samples over a scale of metres.

Timing of feeding

Generally, marine fish larvae are visual feeders (Hunter 1981) and hence feed during the day (Last 1980; Watson and Davis 1987), as do most of the larvae in Australian waters. For example, larvae of *Trachurus* and *Thunnus* appear to feed in two pulses; in the morning and late afternoon (Young and Davis 1990; Young and Davis in press). However, this is not the case for all larvae. Jenkins (1987) reported that larvae of *Rhombosolea tapirina* fed over a 24 h period. Invertebrate eggs were more prevalent in the diet during the night, indicating a shift in prey to easily caught food. Larvae of *Macruronus novaezelandiae* (R. Murdoch, N.Z. Oceanographic Institute, unpublished data) appear to feed continuously through the day, peaking at sunset. A similar pattern was also found for two species of pomacentrid larvae (Mitchell in press).

Digestion and food consumption

Studies in the northern hemisphere indicate that digestion generally takes between one and four hours, although longer and shorter times have been reported (Govoni *et al.* 1982). This seems to be the case for larvae in Australian waters, although data are very few. Larval flounder fed to satiation in the laboratory evacuated their food in 4 h (Jenkins 1987). Similar digestion times were calculated from wild larvae collected at short time intervals from immediately after sunset (Young and Davis 1990; Young and Davis in press). The prey consumed ranged from ~10 prey per day in larval *Thunnus* spp. (Young and Davis 1990), 70 per day in larval flounder (Jenkins 1987), to more than 100 in the pomacentrid larvae *Amphiprion polymnus* (Mitchell in press). The variation in numbers of prey eaten is dependent on prey type, prey size and digestion time.

Impact of larval fish on their prey

We are beginning to understand that there is great variability in larval feeding ecology, largely because we have access to both tropical and temperate species and can contrast and compare them. An example is that generated by Cushing's (1983) paper, which concluded that larvae, at least in the early stages, are too few to affect the abundance of their prey. Much support has been given to this idea both in northern hemisphere studies (e.g. Peterson and Ausubel 1984) and local studies in southern temperate waters (Jenkins 1987). However, a recent simulation of dynamics of fish larvae and their prey suggested that larvae were capable of depleting prey numbers (Bollens 1988). In a recent study of tropical tuna larvae we examined this idea more closely.

Larval *Thunnus maccoyii* are spawned in the oligotrophic waters of the eastern Indian Ocean. From an examination of gut evacuation rates, numbers of prey eaten per day and the abundance of microzooplankton prey, we concluded that these larvae could affect the abundance of their prey (Young and Davis 1990). Consequently, larvae were competing for food, leading to a density-dependent reduction in growth rate (Jenkins *et al.* 1991). Using the same techniques, we found that larval *Trachurus declivis* had little impact on prey levels in the temperate waters off eastern Tasmania (Young and Davis in press). Such contrasts are noteworthy, as they point to the problems of extrapolating conclusions from one area to another.

The critical period concept

Much work has been done in the northern hemisphere to address the notion of a critical period, when larvae switch from endogenous food reserves to exogenous feeding. Cushing (1975) presented the match-mismatch hypothesis, in which the success or failure of a year class is dependent on the timing of spawning and plankton blooms. Lasker (1975; 1981) developed this idea further to the 'stable ocean hypothesis', which proposed that fish larvae (in particular *Engraulis mordax*) are dependent upon food patches that develop during periods of low mixing intensity. A recent investigation in the Derwent estuary on settlement in larval clinids (*Heteroclinis* spp.) found that pulses of settlement were invariably preceded by brief, irregularly occurring peaks of phytoplankton production (Thresher *et al.* 1989). Their findings were consistent with a 'critical period' in which settlement rates were determined by irregular variation in the availability of food for new-born larvae. This study, however, did not extend to the diets of the larvae, so the interaction of the microzooplankton and the plankton blooms has yet to be investigated. However, Murdoch (1990) found that algae are an important component of the diet of first-feeding larval blue grenadier. The whole question of the relationship of spawning and larval production to seasonal changes in nutrient production is not well understood. We have a good knowledge of when most marine fishes spawn in Australian waters and therefore when larvae are likely to be found, but the link with seasonal pulses of production has yet to be examined in detail.

Finally, although I have tried in this review to cover all of the published material on feeding in larval fishes from Australian waters, there may be inadvertant omissions. Nevertheless, this summary may help to encourage debate on past results and future directions of research in this field.

Acknowledgements

This review benefited from the comments made by D. Gaughan (Murdoch University, W. A.) and A. Mitchell (Australian Institute of Marine Science, Qld.).

Table 1. A summary of research on feeding in larval fishes from Australian waters

Species	Source	Study area
	Tropical	
Scomberomorus semifasciatus	Jenkins *et al.* 1984	Barrier reef
S. queenslandicus	" "	
S. commerson	" "	
Hypoatherina tropicalis	Schmitt 1986	Barrier reef
Thunnus maccoyii	Uotani *et al.* 1981	Indian Ocean
	Young and Davis 1990	
	Jenkins *et al.* 1991	
Thunnus alalunga	Uotani *et al.* 1981	Indian Ocean
	Young and Davis 1990	
Katsuwonus pelamis	Uotani *et al.* 1981	Indian Ocean
	Young and Davis 1990	
Amblyglyphidodon aureus	Mitchell in press	New Guinea
Amphiprion polymnus	" "	" "
	Temperate	
Rhombosolea tapirina	Jenkins 1987	Port Philip Bay
Ammotretis rostratus	" "	" "
Trachurus declivis	Young and Davis in press	SE Tasmania
Macruronus novaezelandiae	Thresher *et al.* in prep	SE Tasmania
	Murdoch 1990	New Zealand
	Estuarine	
Pseudogobius olorum	Gaughan [Murdoch Uni. unpublished data]	SW Australia
Favonigobius lateralis	" "	" "
Favonigobius suppositus	" "	" "
Urocampus carinorostris	" "	" "
Parablennius tasmanianus	" "	" "

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FEEDING BY ESTUARINE AND MARINE FISH LARVAE

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Fish larvae are basically selective plankton samplers. They select plankton according to size and type, where type refers to different taxa or species with varied shapes, colours and/or behaviours. The diets of an assemblage of fish larvae in an area will probably reflect the plankton composition within a certain size range in that area. So, differences in the diets of larval fish between two areas can be expected if the two areas have different zooplankton communities. This also applies to a single area in which zooplankton communities change through time. Moreover, since various species and sizes of fish larvae may select different types of prey, diets may differ between two areas which have similar zooplankton communities but different fish larval assemblages.

When diet items are described to the species level, comparisons between areas do indeed often show considerable differences. However, when broader taxonomic categories are used, the diets of fish larvae between different areas are often very similar. This includes comparisons between different estuaries and between estuarine and marine systems. Hence, copepods are an important prey type of most marine and estuarine fish larvae (see listed references marked *), and dietary differences at the species level of copepods between areas reflect (1) the differences in occurrence of these copepod species and (2) prey preferences of the individual species of fish larvae in each assemblage.

Despite the predominance of copepod prey for most fish larvae there are some which concentrate on other food sources. Regardless of where they occur, fish larvae can be divided into three broad categories based on their preferred prey types (Figure 1). These are (1) copepodivores, the largest group, (2) chordativores and (3) others. Each of these categories can then be further subdivided.

Copepodivores include those that (1) concentrate only on copepods and (2) those that also regularly eat other plankton taxa such as tintinnids, bivalve larvae, polychaete larvae, invertebrate eggs and phytoplankton. Copepodivores form the largest category because copepods are usually the numerically dominant form of zooplankton in the size range suitable for fish larvae to eat.

Chordativores are the main non-copepod eating group and can be divided into those that eat (1) appendicularians, (2) fish larvae, and (3) a combination of appendicularians and fish larvae. This group provides the main difference between estuaries and oceans since appendicularians and piscivorous fish larvae are not common in estuaries. I found only one example of an estuarine fish larva which predominantly ate larval fish, a cottid, *Hemitripterus americanus* (Laroche 1982); and none which ate appendicularians. Larvae of a marine *Hemitripterus* sp. from the Japan Sea are also piscivorous (Okiyama and Sando 1976, *cit.*

Laroche 1982). The scombrid, *Scomber scombrus*, mainly eats copepods until 6-7 mm in length and then eats larval fish. This pattern was evident both in the estuarine Long Island Sound (Peterson and Ausubel 1984) and in the Gulf of St Laurence (Ware and Lambert 1985), which is marine.

Most of the marine examples of chordativores are larvae of scombrids or pleuronectiforms (Shelbourne 1957; Last 1978; Gadomsky and Boehlert 1984; Jenkins *et al.* 1984 and references therein). The pleuronectiforms in this category concentrate their feeding on appendicularians rather than larval fish. Of the scombrids, some mainly eat larval fish and others eat a combination of larval fish and appendicularians. Note that for both the pleuronectiforms and the scombrids there are also species, sometimes co-occurring with the chordativores, with diets based on copepods or other invertebrate plankton (Gadomski and Boehlert 1984; Last 1978; Young and Davis 1990).

The third category (others) consists of fish larval species which prey heavily on a suitably sized zooplankton taxon which is more abundant than copepods at the time. Examples of important non-copepod types of prey include bivalve larvae, barnacle larvae, cladocerans, polychaete larvae and tintinnids (e.g. Last 1980; Rajasilta and Vuorinen 1983; Jenkins 1987; Watson and Davis 1989). Many fish larvae in this category are probably "closet" copepodivores and are eating the most abundant suitably sized zooplankton which, contrary to typical marine and estuarine systems, are not copepods. Several studies, both in estuaries and in the ocean, have found larvae which were feeding primarily on copepods until these decreased in abundance and then another taxon became the dominant food (Marak 1960; Laroche 1982; Rajasilta and Vuorinen 1983).

In an area of the Baltic Sea, cladocerans were the main prey type only when the abundance of the preferred copepod was low (Rajasilta and Vuorinen 1983). Laroche (1982) found that copepods dominated the diets of three species of cottids for two months and then in the following month barnacle nauplii became the main food. Several authors have concluded that variations in the abundance of plankton, either seasonal or spatial, play an important role in determining the diets of larval fish (e.g. Marak 1960; Rajasilta and Vuorinen 1983; Whitfield 1983; Ware and Lambert 1985).

In conclusion, when differences in the diets of fish larvae between different estuaries and between estuarine and marine waters occur, they are due to (1) differences in the abundances and types of suitable sized prey and (2) differences in prey selection by the species of fish larvae which occur in each system.

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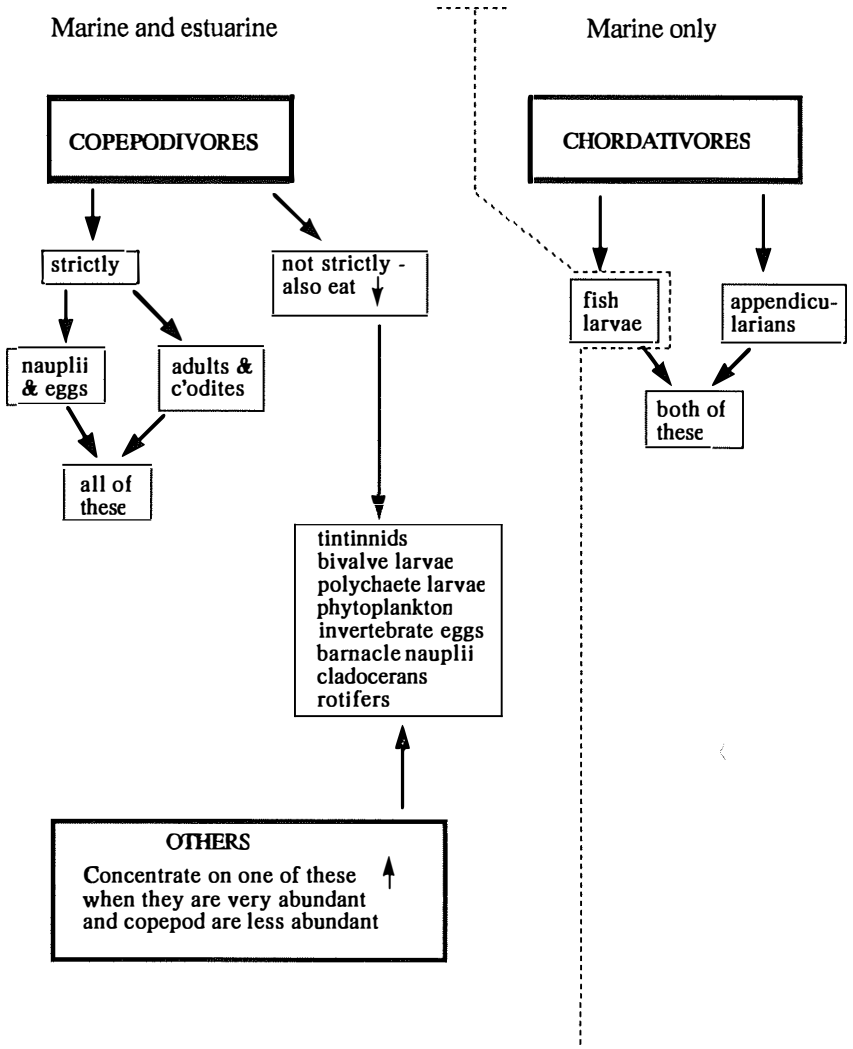

Figure 1. Diet categories of fish larvae based on predominant prey types.

IN SITU REARING OF PRAWN LARVAE - TESTING THE STARVATION HYPOTHESIS

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One of the major problems facing larval biologists is obtaining quantitative estimates of mortality due to factors such as starvation, predation or advection to an unfavourable environment. In fisheries biology, it is well established that variation in the survival of planktonic larvae is an important determinant of year class strength (Cushing 1975). The need to determine causes of larval mortality is most urgent for those species which show little apparent relationship between adult stock size and recruitment.

Some species of tropical penaeid prawns well illustrate the mismatches that can occur between reproductive output and subsequent recruitment to fisheries (Staples 1991). This mismatch is particularly pronounced in the banana prawn (*Penaeus merguiensis*) in the Gulf of Carpentaria, Australia (Rothlisberg *et al.* 1985; 1987). A relatively small number of larvae in the spring are responsible for the major pulse of recruitment to the fishery; conversely the major peak of larvae in autumn gives rise to a disproportionately small number of adults (Table 1). One possible explanation for this is seasonal differences in larval advection (Rothlisberg 1982) but other sources of larval mortality such as predation or starvation could also be important.

In a review of food limitation of planktotrophic marine invertebrate larvae, Olsen and Olsen (1989) proposed that crustacean larvae are sensitive to starvation. This has rarely been tested *in situ* and little is known about the natural diet of prawn or other crustacean larvae. *In situ* rearing of larvae in enclosures can provide information about natural diets and indicate the importance of starvation. This type of approach has often been successfully used for larval fish studies (e.g. de Lafontaine and Leggett 1987). Early attempts to rear crustacean larvae *in situ* using simple mesh enclosures met with little success (Thorson 1946). More recently, after some modifications in enclosure design, quantitative estimates of the survival of crab larvae (Epifanio *et al.* 1991) and prawn larvae (Preston *et al.* in press a and b) have been obtained. The studies of prawn larvae also revealed qualitative aspects of larval diet. The aim of this paper is to describe the methodology and illustrate the advantages and disadvantages of *in situ* rearing of crustacean larvae using examples from a recent study in Albatross Bay, Gulf of Carpentaria (Preston *et al.* in press a).

Enclosures alter the natural environment and this will always result in some artifacts. The most serious of these are the interruption of the normal flow of water and the restriction of the movements of larvae and their prey. These limitations have to be weighed against the major benefits of excluding predators whilst allowing larvae access to their natural food. Furthermore, controlling the location and water depth of caged larvae can provide detailed information about temporal and spatial variations in supplies of

natural food. Such information cannot be gained from studies of net plankton alone because the previous origin and feeding history of the larvae is unknown.

In designing enclosures, care has to be taken to select the most appropriate mesh size and overall dimensions. Pilot studies are required to determine the most suitable mesh size for excluding predators, preventing entanglement of the larvae and allowing natural food to enter the enclosure. The Albatross Bay study demonstrated low survival of *P. merguiensis* larvae in enclosures with a mesh size 250μm; this was probably due to the entanglement of larval limbs. Reducing the mesh size to 140μm significantly improved survival. A comparison of the gut contents of caged larvae with larvae captured in plankton nets indicated no reduction in the range of food items ingested by caged larvae.

In determining the overall dimensions of the enclosures, factors to be considered include the depth of water to be sampled and the ease of deployment and recovery of enclosures at sea. The enclosures used in the shallow waters of Albatross Bay (Figure 1) extended the total depth of the water column (9 m). Pilot studies in which larvae were placed in enclosures for one hour revealed pronounced variation in recapture rates in relation the total length of the enclosures. Recovery rates ranged from <40% in 9m enclosures with no internal partitions to >95% when the same enclosures were subdivided into 3 m lengths. The low recovery rates from the unpartitioned enclosures were due to the trapping of larvae in folds of the flexible enclosures during handling.

In situ rearing studies are well suited for short term studies of the natural diet and nutritional state of larvae. For very small larvae, such as prawn protozoeae, many individuals may be required in order to obtain sufficient material for biochemical analysis. Enclosures offer the means to rear large numbers of individuals at many different locations in a short space of time; this is a distinct advantage over capturing larvae with nets or pumps. *In situ* rearing studies provide a rapid method of identifying the appropriate diet for rearing larvae in captivity. The technique can also provide a sensitive assay of water quality in aquaculture ponds (Preston *et al.* in press b).

In Albatross Bay estimates of survival were obtained over a period of four days (one moult stage). The survival rates obtained in enclosures were similar to published estimates of survival based on the decrease in abundance of prawn larvae in the plankton (e.g. Jones *et al.* 1970). The potential for obtaining estimates of survival in longer term experiments (over several moult stages) remains to be established. However, problems will be encountered in reproducing natural conditions due to fouling of enclosures and because of progressive changes in the diet of larvae from herbivory to omnivory. Increasing the overall dimensions of cages, regular cleaning of the mesh and and/or supplementary feeding with natural zooplankton may help to overcome these problems. However, the most appropriate application of enclosures for studies of prawn larvae is in short term (one or two moults) experiments to determine interactions between larvae and their nutritional environment during early herbivorous stages.

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Table 1. The relative importance (mean percentage over 4 years) of the two generations of *Penaeus merguiensis* in Albatross Bay, Gulf of Carpentaria, Australia

Unpublished data compiled by CSIRO Division of Fisheries, Cleveland. (CL - carapace length).

Life stage	Autumn	Spring
Zoea	99	01
Mysis	90	10
Planktonic post-larvae	40	60
Benthic post-larvae	38	62
Juveniles >10mm CL	25	75
Emigrants 10-20mm CL	04	96
Adults >25mm CL	<1	>99

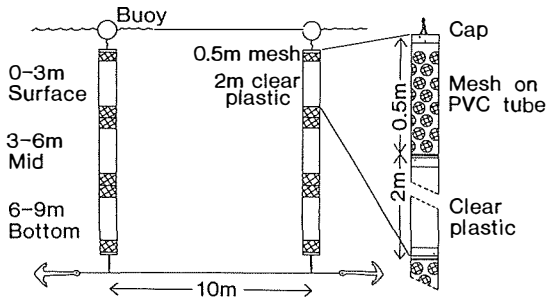

Figure 1. Schematic of enclosures used for *in situ* rearing of *Penaeus merguiensis* larvae in Albatross Bay.

WHAT CAN GROWTH TRAJECTORY TELL US ABOUT THE NUTRITIONAL STATE OF FISH LARVAE?

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Abstract

The growth trajectory of marine fish larvae may vary in a predictable way depending on nutritional state. Using examples from Australian research; greenback flounder (*Rhombosolea tapirina*) and jack mackerel (*Trachurus declivis*) which were apparently not food limited, showed exponential growth. In contrast, southern bluefin tuna (*Thunnus maccoyii*) larvae, from a concentrated patch where density dependent limitation of feeding and growth was apparent, often showed linear to reducing growth over time. Southern bluefin larvae collected away from the patch, however, showed exponential growth. Furthermore, larvae of long-snouted flounder (*Ammotretis rostratus*) from the field showed strong exponential growth; however, when reared in the laboratory under inadequate conditions (poor survival), growth was linear. Thus, it appears that growth trajectory may be a useful gross indicator of larval condition. The importance of growth rate in the determination of larval survival rate and recruitment success is still open to question. For example, in some species such as King George whiting (*Sillaginodes punctatus*) maximising the chance of finding a suitable habitat for settlement through flexible larval duration may be more important than maximising growth rate in older larvae.

Growth is considered to be a major factor in larval survival through its interaction with size selective predation (Shepherd and Cushing 1980; Smith 1985). That is, slower growing larvae will spend longer in the vulnerable stages (Bailey and Houde 1989). Growth trajectory may be examined using daily increments on a population basis or for individual larvae by backcalculation (Jenkins and Davis 1990). This paper discusses, with examples from Australian research, the use of the shape of the growth trajectory as an indicator of larval growth and condition as an alternative to a detailed comparative study of growth rates.

Work on southern bluefin tuna larvae in oligotrophic waters off the northwest of Australia indicated that there was a 25% reduction in growth inside a concentrated patch compared with outside the patch due to competition for food (Jenkins *et al.* 1991). This was reflected in growth trajectories determined from backcalculation; growth trajectories of larvae within the patch were approximately linear, in some cases negative, whilst outside the patch growth was exponential (Figure 1). This suggests that the linear growth trajectory of larvae within the patch was indicative of poor growth.

In another example from Australian research, population based growth of flounders, *Rhombosolea tapirina* and *Ammotretis rostratus*, in Port Phillip Bay was exponential (Figure 2). These species have also been reared in the laboratory under conditions of excess food by Crawford (1984). Growth of *R. tapirina* over the first 30 days in ambient seawater was exponential and the rate was similar to that of larvae from

Port Phillip Bay (Jenkins 1987). In contrast, larvae of *A. rostratus* grew very slowly in the laboratory relative to the field, and the growth trajectory was approximately linear. While the majority of *R. tapirina* larvae survived, very few *A. rostratus* larvae survived (Crawford 1984). This suggests once again that exponential growth in this species is indicative of good condition while linear growth is indicative of poor condition. These results also suggest that field-collected larvae were not strongly food limited. Larvae of jack mackerel collected off the east coast of Tasmania in 1989 were also apparently not food limited (A. Jordan, pers. comm.), and once again growth was exponential (Figure 3). Exponential growth trajectories may be accentuated in areas with high predation such that slow growing larvae are rapidly removed.

Overseas research supports the contention that larval growth is typically exponential (eg. Bolz and Lough 1983; Fives *et al.* 1986; Fukuhara 1986; Comyns *et al.* 1989; Palomera *et al.* 1988) probably because mobility and ability to capture prey increases rapidly in the early larval stage (Hunter 1981). In fact growth from the early larval stage is typically best described by a Gompertz curve because larval growth is exponential (Zweifel and Lasker 1976). Where linear models have been fitted to growth data, the variability in the data is usually such that the true shape of the growth trajectory would be impossible to determine (eg. Cowan 1988). It is likely that only in extreme cases of food limitation in the laboratory or the field will true linear growth be detected. Where food limitation is present, but not extreme, it will be expressed as temporal or spatial variation in the rate of exponential growth. Detecting this variation will require relatively large sample sizes for sufficient statistical power. However, simply by examining the backcalculated growth trajectories of a few larvae, the shape of the growth trajectory (ie linear vs exponential) may indicate whether severe food limitation is occurring.

Linear, rather than exponential growth trajectories may also occur when larvae experience low water temperatures relative to the normal range. For example, Methot and Kramer (1979) determined growth trajectories of northern anchovy, *Engraulis mordax*, larvae from the field and laboratory, and growth trajectories ranged from linear at the lowest temperatures to moderately exponential at higher temperatures. Temperature effects will have to be taken into account if growth trajectory is to be used as a measure of condition. In the case of southern bluefin tuna larvae, temperature conditions were relatively constant over all samples (Jenkins *et al.* 1991)

The importance of growth rate to survival of larvae is still under question. While early growth in most larvae appears to increase exponentially, in a number of larvae there is a marked reduction in growth at the end of the larval stage. For example, King George whiting, *Sillaginodes punctatus*, larvae show an exponential increase in daily increment width, which would be proportional to growth rate (B. Bruce, personal communication; B.D. Stewart, unpublished data), in early stages (Figure 4). However there is a marked decrease in growth at the end of the larval stage before a rapid exponential increase upon settlement (Figure 5). This pattern has also been observed in a number of labrid species (Victor 1986; Cowan 1991). It is possible that high growth rate is particularly important in the youngest stages due to vulnerability to size-selective predation. For example, Brothers *et al.* (1983) found that young juvenile bluefin tuna, *Thunnus thynnus*, were derived from the fastest growing fraction of larvae. However, particularly in benthic fishes, factors relating to successful settlement may become more important in later stages, i.e. the flexibility to remain in the plankton at the optimal size and stage of development for settlement until a suitable juvenile habitat is found.

In summary, we may not need to know the full range of potential growth rates to determine if larvae are severely food limited; simply determining the shape of the growth trajectory may tell us this. Such severe food limitation may be more likely in species such as southern bluefin tuna where larvae occur in concentrated patches

in oligotrophic/oceanic waters. Australian research on larval fish ecology has yet to detect such severe food limitation in coastal waters. Further research is needed into the relationship between growth rate and stage-specific survival so that knowledge of larval growth rate can be translated into probability of survival.

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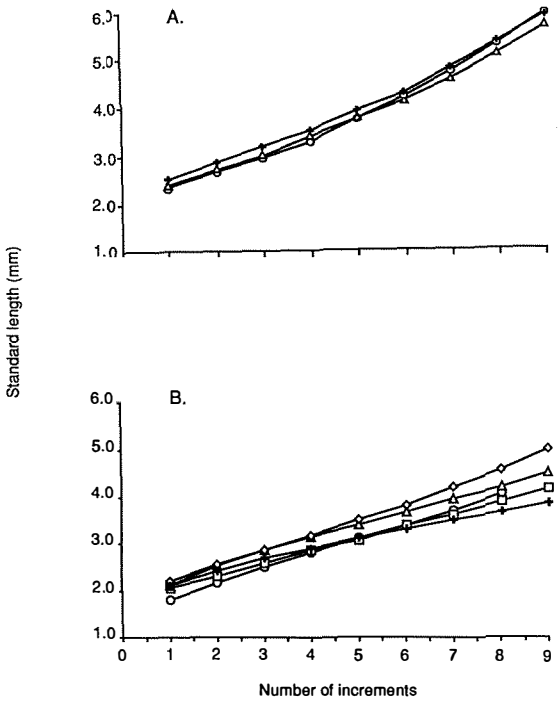

Figure 1. Examples of individual growth trajectories of *Thunnus maccoyii* larvae, (A) Individuals from a station outside the larval patch, (B) individuals from a station inside the patch.

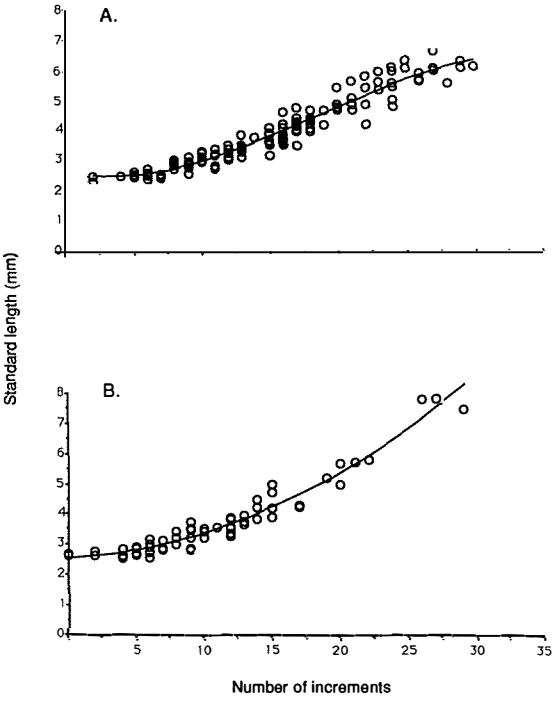

Figure 2. Populations based growth curves of (A) *Rhombosolea tapirina* and (B) *Ammotretis rostratus* larvae collected from Port Phillip Bay.

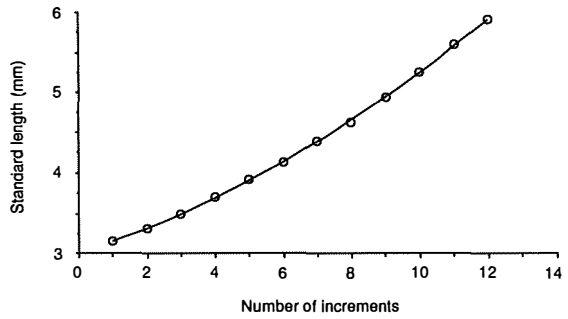

Figure 3. Backcalculated growth trajectory of an individual *Trachurus declivis* larva collected off the east coast of Tasmania.

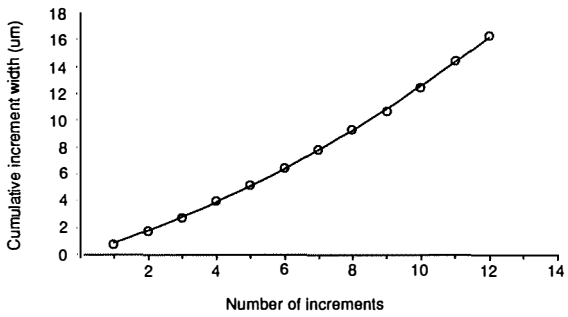

Figure 4. Relationship between cumulative increment width and number of daily increments in the early larval phase of an individual *Sillaginodes punctatus* collected from Port Phillip Bay.

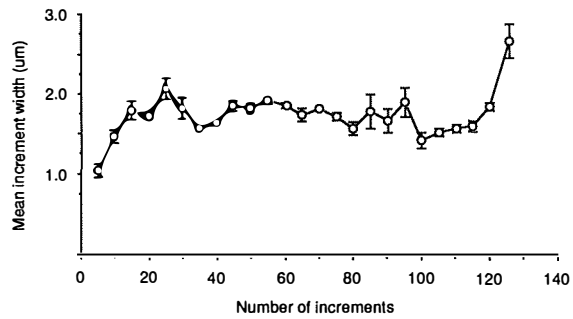

Figure 5. Relationship between mean (± 1 s.d.) increment width and number of daily increments up to the settlement phase of a sample of early post-settlement *Sillaginodes punctatus* collected from Port Phillip Bay.

THE USE OF CONDITION INDICES IN LARVAL FISH

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Abstract

Mortality of larval fish and invertebrates may potentially be estimated from indices of larval condition or health, on the assumption that larvae in poor condition grow slower and are subject to the cumulative effects of starvation, predation or disease. Larval condition integrates feeding success of the previous few days and, to the extent this influences growth and mortality, may ultimately determine not only recruitment but also the structure of adult assemblages. This paper briefly reviews morphological, biochemical, otolith and histological condition indices, with specific reference to a comparison of dry weight, lipid and otolith indices of pelagic juvenile cod (*Gadus morhua*). Morphological indices such as body depth or dry weight are simple, but are often insensitive, and require shrinkage correction for the early larvae. Biochemical indices such as RNA/DNA ratio appear to be equivalent across species, but require sorting of the larvae at sea before rapid freezing. The peripheral increment widths of the otolith are a simple measure of recent growth, while histological measurements of the gut epithelium or muscle cell diameter represent a direct index of starvation mortality.

Validation of indices is necessary, but caution is advised when extrapolating from reared larvae to the field. The within-larva correlation of many indices is low or not significant probably due to varying temporal responses to starvation of each index. In general, condition indices must be tailored to the species and the size (or stage). There are very few Australasian studies of larval condition. The relative high diversity and low density of Australian fish larvae, requires indices to be equivalent across species to assess the impact of oceanographic features or events.

Introduction

Starvation has been proposed as a major source of larval mortality, but is rarely observed in the ocean (e.g. Strasburg 1959). Indices of larval condition - such as health and growth - are a relatively new technique to objectively assess the impact of oceanographic conditions (or aquaculture techniques) on prey distribution and abundance, and ultimately on potential survival. Since the initial studies of larval condition by Ehrlich *et al.* (1976), and O'Connell (1976; 1980), who showed evidence that up to 8% of wild clupeid larvae were in starving condition, many studies have since confirmed that food, or feeding opportunity, is a limiting factor for larval survival (Setzler-Hamilton *et al.* 1987). Consequently the recruitment limitation hypotheses in fisheries that invoke larval survival as determining either year-class strength or adult community structure (Doherty and Williams 1988) may now be tested. Such an approach is attractive given that obtaining robust estimates

of larval mortality in the field is highly unlikely (Taggart and Leggett 1987). Most condition indices probably reflect the feeding environment over scales of 2-7 days.

Condition indices involve the assessment of a starvation sensitive variable, which then must be standardised by a starvation insensitive variable (Table 1). The morphometric variables indicate a heavier or fatter larva per unit length. Ash weight may increase in larvae in poor condition due to relative increase in skeleton and skin, and osmotic influx of salts (Ehrlich 1974), but other studies have shown ash to decrease due to decreasing ossification of the skeleton. The amount of RNA is directly proportional to the amount of protein synthesis, which is standardised by the number of cells (DNA content). The triacylglycerol (TAG) index indicates the amount of storage fat standardised by the amount of structural fat (cholesterol is a component of cell membranes). The otolith index shows the amount of recent (or peripheral) otolith growth relative to larval length. Finally the histological index may be a summed score estimated from a number of target tissues, or simply a measurement of cell size (either gut epithelium or muscle cell diameter).

A major assumption is that an index is positively correlated with larval survival, such that larvae in good condition will continue to feed well, and be less susceptible to predation and disease due to spending less time in the larval phase (e.g. Shepherd and Cushing 1980). Condition indices cannot account for unfavourable advection which could operate regardless of larval condition.

The uses and limitations of condition indices are still being explored, and some major questions in this field are as follows:

1) are the various indices correlated?;
2) are condition indices comparable between different developmental stages?;
3) is variation within an individual larva greater than between individuals?;
4) and what are the limitations of the various indices?

In this report I wish to address these issues from published information on larval condition, and illustrate my case with data on pelagic juvenile cod >12 mm standard length (*Gadus morhua*) from the N.W. Atlantic (Suthers *et al.* 1992). The data are unique because 3 different indices of condition (morphological, biochemical and otolith) are compared from the same individual.

Materials and methods

Pelagic juvenile cod were collected off southwestern Nova Scotia in the northwest Atlantic during May and early June of 1987 (cruises 87-1, 87-2 respectively). Each larva was freeze-dried (DWT), had the otoliths extracted (OTO), and then was lipid extracted (TAG). Details may be found in Suthers *et al.* (in press). The outer 14 daily growth increments and otolith radius were measured using an image analysis system (Campana 1987; Suthers *et al.* 1989). These growth increments were assumed to be a conservative index of recent growth, reflecting the environmental conditions at capture. During 1985, measurements were made to a resolution of $\pm$0.04 mm; anal body depth (ABD), pectoral body depth (PBD), eye diameter (EYED), and head length (HL), after Koslow *et al.* (1985). Condition indices were then calculated as residuals of univariate regressions of the starvation dependent variables on SL. Also, for each cruise a principal component analysis of the starvation dependent and independent variables was performed.

Results and discussion

1. Correlation of TAG, DWT and OTO.

After discarding the first (size) component, the plots of principal components PC2, PC3, and PC4 show that OTO varied differently relative to the other variables (Figure 1a). PC2 (<7% of

the total variance) was a contrast between OTO and all other variables, while PC3 (<4%) represented a contrast between TAG and SL. PC4 contrasted CHOL and DWT with TAG and SL (<1% of total variance).

Similarly for cruise 85-1,2, PC2 (5%) also contrasted OTO with all other variables and PC3 (1%) contrasted the 2 body depths with head length (Figure 1b). PC4 contrasted head length with eye diameter - a result found in morphometric studies of herring (Ehrlich *et al.* 1976; McGurk 1985a).

Not surprisingly therefore, from 16 pairwise index comparisons (including a variety of cruises), the correlation of OTO index with either TAG or morphometric indices was often zero, or not significant (Suthers *et al.* in press). The DWT and ABD indices were usually significantly correlated and particularly the TAG and DWT indices.

Why is OTO telling a different story? The answer may lie in the fact that otolith growth is generally correlated with somatic growth, which is fundamental to larval survival. It is unlikely therefore that pelagic juveniles will store excess TAG in preference to growth (Ehrlich 1974). Note however that these conclusions are species specific - for example cod have approximately triple the TAG content of capelin which may swamp any variation in lipid levels. Some larval bivalves and crustaceans need a lipid reserve for settlement or metamorphosis, and TAG versus CHOL may be a useful index in these species (Fraser 1989). The conclusions may also be size specific - the importance of TAG as a condition index in larval cod is unknown. Finally, note that otolith growth tends to be very conservative relative to body growth, and under poor growth the otolith will still lay down a narrower daily growth increment, ultimately producing a heavier or larger otolith relative to fish size (Reznick *et al.* 1989; Secor and Dean 1989). This problem is ameliorated, as in this study, by considering only short (14 d) time intervals.

Martin *et al.* (1985) compared the condition of striped bass larvae from samples taken over 8 weeks using 4 measures of condition, each derived from separate larvae. The histological score (of a number of target tissues) and RNA/DNA ratio fluctuated similarly (no correlation statistic provided), and a morphological score showed a roughly similar pattern (Figure 2). Content of free fatty acids declined through the sampling period, and appeared to be an unsatisfactory index (free fatty acids are the physiologically mobile lipids, and are the breakdown product of TAG and phospholipids). As low correlations between indices occur even when values are derived from the same individual, it appears that each index, for each species, at each size, may operate at a different response rate to the starvation event (or not at all!). Martin and Wright (1987) concluded that RNA/DNA ratios respond the most rapidly (1-2 d), morphology the most slowly (5-7 d) and histology at an intermediate rate.

2) Condition in larval vs. juvenile fish

It is generally believed that pelagic juveniles are less susceptible to starvation than larvae, presumably due to the inertia of having larger body reserves and liver, and due to selection against slow growing larvae. In general, pre-flexion larvae do more frequently exhibit emaciation than post-flexion larvae, or are more easily discriminated as starved or moderately starved from both laboratory and field studies (Martin *et al.* 1985; Powell and Chester 1985; Grover and Olla 1986; Yin and Blaxter 1986; Clemmesen 1989). In particular, Theilacker (1986) showed the proportion of dying/starving larvae changed dramatically from <3.5 mm larvae to 3.5-4.0 mm larvae. However, authors who have examined condition in pelagic juveniles in the wild have also found evidence of food limitation. Bailey (1989) found that 50-60 mm walleye pollock grew significantly faster at a station with ten times the biomass of zooplankton,

based on the outer ten daily growth increments of the otolith. Karakiri *et al.* (1989) found that variation in the width of the peripheral ten daily increments in juvenile plaice (10-40 mm), was attributed to food supply. Peterman (1987) concluded for Pacific salmon that most of the density dependent component of mortality occurred in the first 12-18 mo (during the initial marine phase, and not in the natal streams), and that the zooplankton prey abundance was the proximal factor. Rearing larvae to the pelagic juvenile stage in the laboratory for validation of condition indices is difficult, but it would seem that starvation mortality in even the later stages occurs but is often overlooked.

3) Is variation within larvae greater than between?

Despite the surprisingly low correlation of indices from the same larva, variation in condition at large spatial scales appears to be the dominant signal. To address this, four nearshore and four offshore stations were randomly selected from the 1985 data set (Suthers *et al.* 1992), and four larvae were selected from within each sample which had DWT, ABD and OTO measured. The studentised residuals (to homogenise the variance) of each index were nested within fish (as replicates), in a fully nested 3 factor ANOVA (Underwood 1981; Table 2). There were large significant differences in condition between the inshore and offshore (due to the low zooplankton biomass inshore, Suthers *et al.* 1989), but of importance to this issue - the condition of larvae within a sample were not significantly different (and the MS of the error term was the smallest).

4) Limitations of each index?

Morphometric indices are simple, and require no special preservation but the results are often insensitive - particularly for larvae - unless the effects of shrinkage due to time since death and preservation are taken into account (Theilacker 1986). This entails careful laboratory calibration, and dedicated short plankton tows. Multivariate measurements may moderate the shrinkage problem (particularly the apparent contrast between EYED and HL in cod and herring). Pelagic juveniles >10 mm are less susceptible to this shrinkage, and ABD seems to be a simple technique. All such measures are species specific.

Biochemical indices require rapid freezing of the larvae at sea, which poses difficulties in trying to identify larvae and separate them from the zooplankton. The main advantage of the RNA/DNA method is that it appears to give a consistent relationship across species (Buckley 1984; Clemmesen 1987). Protein growth rate may therefore be calculated from the ratio of RNA/DNA and water temperature. Recently these relationships have been questioned and in fact exhibit considerable subdaily variation (A. Ferron, pers. comm.). For larvae >3 mg DWT (approximately 12 mm), RNA/DNA ratios also increase with size, but this has not been examined in detail. The persistent use of ratios in this technique is disturbing as a large ratio may be due to a large numerator, or a small denominator. The TAG/sterol ratio appears to successfully identify nutrient-stressed anchovy larvae (Håkenson 1989a; b) and pollutant stressed crab, lobster, and herring larvae (Fraser 1989).

The otolith index was first used by Methot (1981), in comparing the otolith growth of larval anchovy with a myctophid from 13 samples off Oregon, covering 4° of latitude. Remarkably there were no spatial trends in recent growth, and nor did the 2 species co-vary, possibly due to uniform environmental conditions (range 1°C), and to the method of analysis. Of particular concern with this technique is the fidelity of the otolith in recording daily changes in growth. Recent studies show that the metabolic lag between a starvation event and its record in the otolith may be of the order of 1-4 days (Govoni *et al.* 1985; Bailey and Stehr 1988; Maillet and Checkley 1989).

By examining the width of the outer daily growth increments (e.g. 7-14), one can circumvent the effect of larger otoliths in slower growing fish (e.g. Secor and Dean 1989; Reznick *et al.* 1989). A great advantage is to back-calculate periods of 7d growth - up to 4 week precapture - as a natural tag of the pelagic juvenile's past feeding environment (Suthers *et al.* 1989). There can be considerable effort to obtain these data - unless one is ageing the larvae anyway.

Histological indices are laborious, requiring special preservation procedures and short tow duration, and required a specialist to consistently score the target tissues. In response, Theilacker and Watanabe (1989) developed a robust technique to measure epithelial gut cell height. The histochemical determination of liver glycogen (O'Connell and Paloma 1981) supported previous histological work (O'Connell 1980), but was not recommended as a simple technique. The advantage of histological examination is the ability to discriminate larvae in increasing condition versus decreasing condition (Theilacker 1986), and it is truly an index of starvation mortality rather than growth rate.

Conclusion

Larval feeding studies often make the valid point that feeding rates could not have a significant impact on their prey density - or larvae may not compete for food (e.g. Jenkins 1987) - thereby implying that food levels are not limiting survival. However it is not the absolute food abundance but the relative food abundance that is limiting (*sensu* Andrewartha and Birch 1954, p. 489); the availability of food relative to the larva's vision and mobility. Only recently have we become aware of small-scale turbulence and contact rates contributing to feeding incidence (Rothschild and Osborn 1988; Sundby and Fossum 1990). Persistent suggestions by a few members at this workshop, that starvation may be a minor component of larval and pelagic juvenile mortality, are ignoring a solid body of evidence that shows declining condition with declining prey abundance. The Australasian data are sparse in this area, and we should aim to fill this void, particularly as the Australian marine environment is relatively nutrient-poor. If larval food limitation can limit recruitment and ultimately alter adult community assemblages, then the Australian marine environment should provide examples.

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Table 1. The various types of condition indices

Type of index	Starvation dependent variable	Starvation independent variable
Morphometric	dry/ash weight	standard length
	body depth	
Biochemical	ribonucleic acid (RNA)	deoxyribonucleic acid (DNA)
	triacylglycerol (TAG)	sterol/cholesterol
		standard length
	tripsen content	
Otolith	peripheral daily increment widths	standard length
		otolith radius
Histological	target tissues e.g. gut, liver muscle	–
	cell height/diameter	?

Table 2. Results of a nested 3 factor ANOVA, using the studentised residuals of DWT, ABD and OTO as within fish replicates, to determine if variation in condition index within larvae is greater than that between larvae

Data collected in May 1985 off southwestern Nova Scotia, Canada, and re-analysed from Suthers *et al.* (in press). **, $p<0.01$; *, $0.01 < p < 0.05$

Source	df	SS	MS	F	P
Inshore/ offshore	1	27.17	27.17	11.49	**
Sample	6	14.19	2.37	2.68	*
Larva	24	21.17	0.88	1.62	-
Error	64	34.83	0.54		

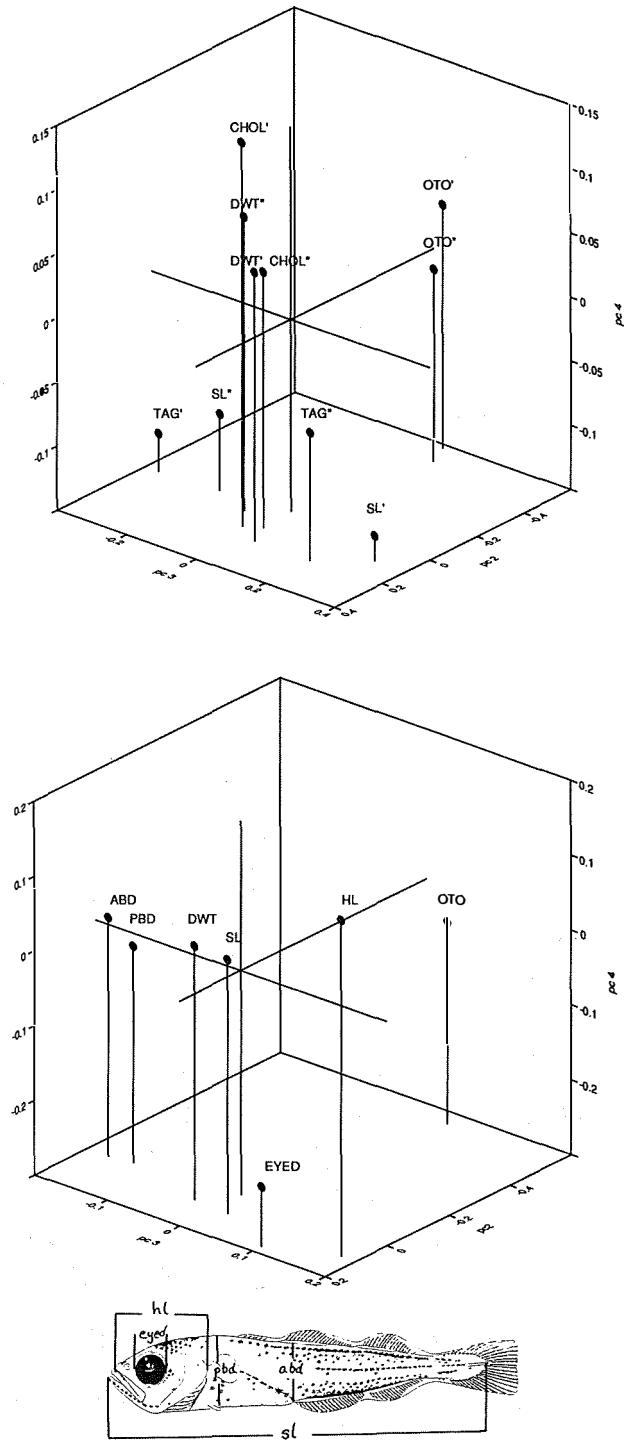

Figure 1. Three dimensional plot of principal components 2, 3 and 4 of a) cruise 87-1 (') and 2 (") combined, and b) cruise 85-1. CHOL, cholesterol; DWT, dry weight; OTO, peripheral width of daily growth increments; SL, standard length; TAG, triacylglycerol. Note how both plots show the otolith condition index to load alone on PC2, and how TAG is contrasted with SL on PC 3 in a), and ABD is contrasted with SL in b). From Suthers *et al.* in press.

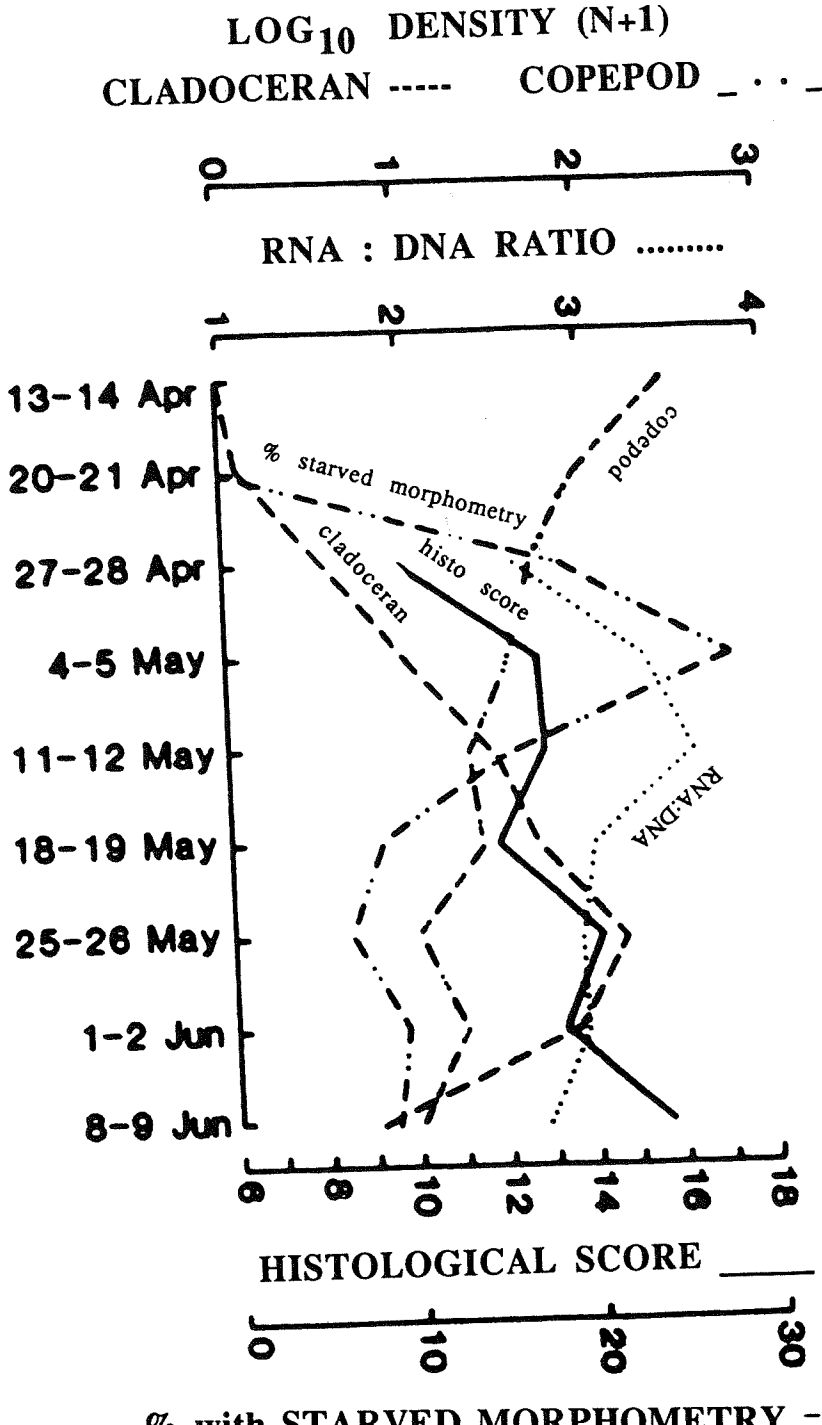

Figure 2. Comparison of RNA/DNA ratio, histological score, and percent starving striped bass larvae from the Potomac River, with their primary food resource - copepod and cladoceran density (from Martin *et al.* 1985).

DO OTOLITHS RECORD CHANGES IN SOMATIC GROWTH RATE? - CONFLICTING EVIDENCE FROM A LABORATORY AND FIELD STUDY OF A TEMPERATE REEF FISH, *PARIKA SCABER*

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Otolith increment widths in a temperate reef fish, *Parika scaber* (Pisces: Monacanthidae) have been shown to vary in different months and correlate with changes in somatic growth rate (Kingsford and Milicich 1987). Fish that were slower growing had narrower spacings between rings than those with a higher average growth rate. Thus, the relationship between otolith length and fish length remained constant for all fish sampled despite differences in monthly somatic growth rate. These data imply that variations in the pattern of ring spacing may be a reliable repository of past patterns of growth for an individual.

Similar documentation of a close correlation between otolith size and fish size has been described for a range of other species (e.g. Lough *et al* 1982; Ralston and Miyamoto 1983; Nishimura and Yamada 1984) and this evidence has been used to rationalise the backcalculation of prior somatic growth in larval and juvenile fish (e.g. Penney and Evans 1985; Victor 1986; Thorrold and Williams 1989).

However, few studies have carried out the necessary verification to show that otolith growth responds causally to changes in somatic growth; this evidence is critical if reconstructed growth trajectories are to be believed.

The aim of the present study was to subject presettlement juveniles of *Parika scaber* to a range of temperature and food regimes in order to induce changes in growth rate. It was hypothesised that these changes in growth rate were related to concomitant changes in otolith microstructure during the 10 day duration of the experiment.

Juveniles were subjected to two regimes of temperature (19-21°C and 24-26°C), and three feeding levels (fully-fed, partially-fed, and starved) of a diet consisting of larvae of *Opifex fuscus*, an endemic mosquito. Fish were individually tagged to ensure that changes in growth rate and any associated changes in otolith microstructure could be accurately determined for any individual.

Growth rates in untagged fish that were fully-fed were not significantly different to growth rates in tagged fish ($t=0.97$, $p>0.05$). This result suggests that any effects of tagging on *P. scaber* juveniles were minimal. The growth rate of fish prior to the experiment was estimated from field collections to be 0.5mm standard length (SL) (±0.05 S.E.) day^{-1} ($n=60$). This was higher than the maximum growth rate recorded for fish from the experiment (0.2mm SL ±0.01 S.E. day^{-1}). Controlled feeding levels

affected the growth rates of fish, but the two different temperature levels in isolation or in combination with feeding levels, did not (two-way ANOVA). Fish that were fully-fed grew the most (0.2mm SL +/- 0.01 day^{-1}), whilst fish that were starved did not grow at all. Partially-fed fish exhibited a size-hierarchy effect with larger fish increasing body size at the expense of smaller individuals.

In conflict with the field study, otoliths of fully-fed fish continued to increase at the same daily width despite the induced alteration in growth rate. Thus, otoliths were disproportionately large compared to estimates from the field. However, otoliths of starved fish were not as large as predicted from a continual production of daily rings at a constant width. Daily ring deposition probably ceased at different times during the experiment for the starved fish, dependant on body size.

From measurements of increment spacing and otolith size it is clear that although the growth rate of fish changed for all food treatments, this was not reflected by such predictable changes in increment spacing. Other studies where otolith growth has been shown to be uncoupled from somatic growth argue that factors such as temperature, photoperiod or changes in life-history may be responsible for the pattern of change in increment spacing (e.g. Volk *et al.* 1984; Campana and Neilson 1985; Mosegaard *et al.* 1988; Wright *et al.* 1990). Thus, increment spacings may not always change in a direction predicted by changes in somatic growth.

This is in direct contrast with other studies, where increment spacings have responded to environmental changes and the associated alteration of growth rate. Temperature, photoperiod, food availability, time and frequency of feeding, pH, and some interactions between these factors, have been shown to affect increment spacings in otoliths over 2-8 week periods (e.g. Wilson and Larkin 1982; Volk *et al* 1984; Neilson and Geen 1985; Eckmann and Rey 1987; Hovencamp 1990; Maillet and Checkley 1990). However, no study has yet demonstrated a daily response of increment spacing to growth rate for any species (see also Campana and Neilson 1985).

The most surprising and unique result from this study is the failure for increment spacings to track manipulated changes in somatic growth, despite strong indications from field collections (Kingsford and Milicich 1987) to the contrary. Evidence of a significant correlation of otolith scaling, even if accompanied by a description of how this may change with natural fluctuations in growth rate, is not sufficient evidence to allow growth parameters to be backcalculated at the daily or even at a weekly level of precision. Before the otolith can be used as a tool to reconstruct the growth histories of individual fish, some form of validation is required, and since responses of fish otoliths to environmental parameters and somatic growth changes are species-specific, validation must be conducted at this level.

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DISCUSSION OF SESSION 1

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Each panel presentation was followed by time for discussion, which is reported in sequence here.

In response to *Jock Young's* recommendation that much further work on larval feeding ecology is needed, Jeff Leis pointed out that information on feeding was available in a thesis by Lou Hock Chark from James Cook University. Jock Young then referred to work on feeding of larvae which was proposed in NSW in the near future. Peter Gehrke pointed out that there are already several studies in progress, such as those by NSW Inland Fisheries. Jock Young acknowledged that there is probably a backlog of work about to be published and predicted that there will be a dramatic increase in future studies in this area.

In response to a question by Don Hancock, Jock Young defined the "critical period hypothesis" as relating to the time period between the transition from endogenous to exogenous feeding. The availability of food at this time influences the level of mortality by starvation. Iain Suthers mentioned that an extension of this theory is the match/mis-match hypothesis; for example mixing of the water column in spring brings nutrients to the surface layers which results in an increase in the availability of food. If this event coincides with larval hatching then it is known as a match; if not, the events are mismatched.

Jeff Leis suggested that food limitation is more likely in the tuna species spawning in the tropics due to the highly patchy distribution of larvae. He further suggested that this situation may be the exception rather than the rule in the tropics. Jock Young agreed that work on other tropical species would be of great interest.

Pancho Neira questioned Ron Thresher on the application of the critical period hypothesis to live bearers such as clinids. Ron Thresher responded that the situation is the same except that larvae do not have a yolk-sac. As an example he referred to his own work in Storm Bay, where recruitment by clinids to rock platforms corresponded to phytoplankton blooms 6-7 weeks prior. It appears that survival to recruitment largely depends on the occurrence of a phytoplankton bloom at the time the larvae are released.

Daniel Gaughan was asked whether there were any general studies on freshwater fish diets. He replied that there are no specific examples but suggested that, like marine fish, they would feed on the most abundant species present which would include rotifers, cladocerans and cyclopoid copepods.

Iain Suthers suggested that it may only be necessary to examine size structure, as opposed to classifying individual species, to answer questions relating to food limitation. Jeff Leis pointed out that the nutritional value, behaviour and

pigmentation (and hence visibility to predators) of prey are equally as important as size in determining the diet of larvae. If just size frequency was analysed the nutritional value of each species would have to be assumed to be equal. He went on to suggest that confining the size groups to within classes, such as Crustacea or Chordata, would overcome this problem. Iain Suthers agreed that although there are some problems with such a model, it would have some use in bulk-sorting of larvae when investigating feeding rates. Mike Sinclair commented that the data required would depend on the question being asked, for example for some species you may only need size data but for other, more selective, species more detailed data may be required.

Ron Thresher believed that the fundamental problem in gut content analysis is bias created from variability in retention rates; for example, the importance of copepod and tintinnid tests in blue grenadier larvae may be overestimated due to the relative length of time retained in the gut. Recent work has also shown the importances of ciliates in these diets which were previously overlooked due to inadequate preparation techniques. He stressed the importance of accurate tests of clearance rates and the usefulness of stable isotope analysis which should be run in conjunction with gut analysis studies. Peter Gehrke suggested that the importance of rotifers to freshwater larvae may be overestimated if the difficult-to-resolve mouth-parts are overlooked. Greg Jenkins made the point that bivalve veliger shells may be visible in the gut for a relatively longer period than other plankters while naked ciliates are not well preserved in straight plankton samples!

Barry Bruce asked *Nigel Preston* why penaeids in the Gulf have two spawning periods when the recruitment from one event is much more successful than the other. Nigel Preston, in the spirit of the workshop, put the question over to Peter Rothlisberg, who replied that reproduction of penaeids appears to be conservative; studies throughout the Indo-Pacific have shown that penaeids consistently have two distinct spawning periods, but the output from these spawnings is variable. In Malaysia the two spawning periods coincide with two wet seasons, and there is significant recruitment from both. In a much harsher environment such as the Gulf of Carpentaria where there is only one wet season, the two peaks are still evident. He argued that this reproductive strategy allows great flexibility in adapting to new or changing environments. The Gulf is < 6000 years old, yet penaeids have coped with this environment very well, albeit differently to other places.

Maria Milicich questioned *Greg Jenkins* as to whether patterns of growth with larval age may be developmentally determined rather than a result of feeding success etc. Greg Jenkins agreed that you would probably get a species-specific growth trajectory based on development pattern but pointed out that in the case of southern bluefin tuna larvae the pattern appeared to be significantly different inside and outside the patch, suggesting an environmental factor was operating. John Gunn pointed out that because the tuna were only studied for an 8-9 day period they may not have reached the inflection point of increased growth which was observed in the growth trajectories of other species mentioned in the talk. Ron Thresher found that blue grenadier showed an initial linear growth period of variable duration before 'launching' into exponential growth. This was interpreted at the time as variation in the onset of successful feeding. Greg Jenkins responded that even at the eight day point of growth, differences were noticeable between growth trajectories inside and outside the patch, ie larvae inside the patch had mostly linear trajectories, in some cases negative, whilst larvae from outside the patch already showed a tendency to exponential growth. He agreed that later exponential growth was probably likely for many larvae from within the patch.

Following *Iain Suther's* contribution, Mike Sinclair proposed that the larval stage may not be the most vulnerable stage (maybe a myth

started by Hjort and Cushing!) and that many studies suggest food is not a limiting factor. Iain Suthers disagreed and stated that only three papers (Peterman, Suthers and Bailey) have looked at the pelagic juvenile stage (supposedly the all-important stage) and all concluded that food availability is important in explaining growth and presumably survival. Mike Sinclair responded that in the paper by Peterman on pelagic juvenile salmon, there was an impact of food limitation on larval survival but not on year-class size. Greg Jenkins further questioned the importance of the early larval stages by pointing out that the majority of work has been on these early stages and that more work needs to be done on the later larval, early juvenile, and juvenile stages which may perhaps be of greater importance.

Bryce Stewart began the discussion on *Maria Milicich's* panel presentation by pointing out that in a study he conducted on juvenile King George whiting, where the fish were on a cycle of 15 days of food and then 5 days of no food, the otoliths responded by forming 15 wide rings followed by 5 narrow rings. He also achieved accurate results when back-calculating. Maria Milicich responded that such results may indicate that the utility of this method varies between species and should be validated for each species. She suggested that in her case there may have been a lag effect exceeding the duration of the experiment, but suggested that if this were the case it would limit the application of the method anyhow. Greg Jenkins made the point that it is now well known that the relationship between otolith-size and increment size varies with growth rate and that you could have similar increment spacings in fish growth at different rates due to differences in this relationship. If this difference is accounted for, back-calculation may still work. Maria Milicich responded that in such cases it would then be reasonable to proceed with back-calculation. She suggested that a lag in the response of otoliths to changes in somatic growth may explain her results but that it would have to be a lag of at least 10 days and such a lag would make back-calculation difficult.

From his own experience, Ron Thresher warned against generalising from the results of laboratory-based studies because increment formation was often abnormal in the laboratory. However, by the same token, he suggested that when laboratory studies gave negative results it would usually be put down to laboratory artefacts and the studies would not be published, with the published literature being biased towards positive results. He also mentioned that the fish size / otolith size relationship in Maria Milicich's experiment was not strictly linear and therefore the experimental results would depend on the part of the curve you were working with. Tony Fowler questioned how it was known that increments were laid down in starved fish at all. Maria Milicich responded that increment deposition in these treatments had been verified using tetracycline marking. Bryce Stewart mentioned that starved whiting had increments so narrow as to be barely detectable with the light microscope. Greg Jenkins suggested that scanning electron microscopy is often needed to resolve increments in slow growing fish.

Barry Bruce commented that his work on larval whiting indicated almost no lag between the decrease in ring spacing and reduction in food. Greg Jenkins responded that otolith growth in young larvae may respond more quickly to change in food intake than older individuals which would have larger energy reserves. Iain Suthers then asked Ron Thresher how validation studies could be designed to overcome these problems and suggested mesocosms as a possible solution. Ron Thresher responded that while mesocosms may be an answer, field-based studies were the ideal solution (i.e. tracking cohorts etc.), but these were difficult to conduct.

In a final general question, Peter Doherty asked if Greg Jenkins would reconsider his earlier statement that coastal fish larvae were generally not food limited, particularly in light of the examples given by the keynote speakers. Greg Jenkins responded by saying that he was basing his comment on the small amount of work done in coastal waters of Australia (mainly Victoria and Tasmania) and work from overseas on highly productive bays and estuaries. He suggested that he was not trying to generalise to all coastal waters, and agreed that there would be many coastal situations were food limitation would probably occur.

SESSION 2

EXTENSIVE LARVAL REARING

Session Chairperson:	S. C. Battaglene
Session Panellists:	S. J. Thurstan
	J. B. Burke
	R. B. Talbot and S. C. Battaglene
	P. C. Gehrke
	F. P. Ruwald
	M. Daintith
Rapporteurs:	C. A. Hair and C. A. Gray

CHAIRPERSON'S INTRODUCTION

S.C. Battaglene

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In extensive aquaculture systems, larvae are stocked at relatively low densities in earthen ponds and feeding is based mainly on the natural food in the pond (Figure 1). Extensive culture of fish, particularly freshwater fish like carp, dates back to the Romans. Extensive culture today is still practised at a semi-subsistence level in underdeveloped countries using methods developed thousands of years ago. John Lake pioneered the practice of extensive culture in Australia, with golden perch and silver perch, at the Inland Fisheries Research Station at Narrandera in the 1960's and 70's.

Extensive culture has been recently adopted for marine larvae in Israel (eg mullet, tilapia, milk fish) the USA (eg striped bass, red drum) and Australia (eg barramundi and Australian bass). Significantly, studies in Australia have shown that species such as barramundi and bass, traditionally reared in intensive systems, can be more productively and economically produced in extensive systems.

During this session we will restrict ourselves to the extensive rearing of 'marine type' larvae, ie those small poorly developed larvae with small yolk and oil reserves. There will be examples of larvae reared in saltwater, brackish water and freshwater. We will look specifically at the factors which determine larval survival and growth in ponds, namely: food reserves, water quality, predation and diseases.

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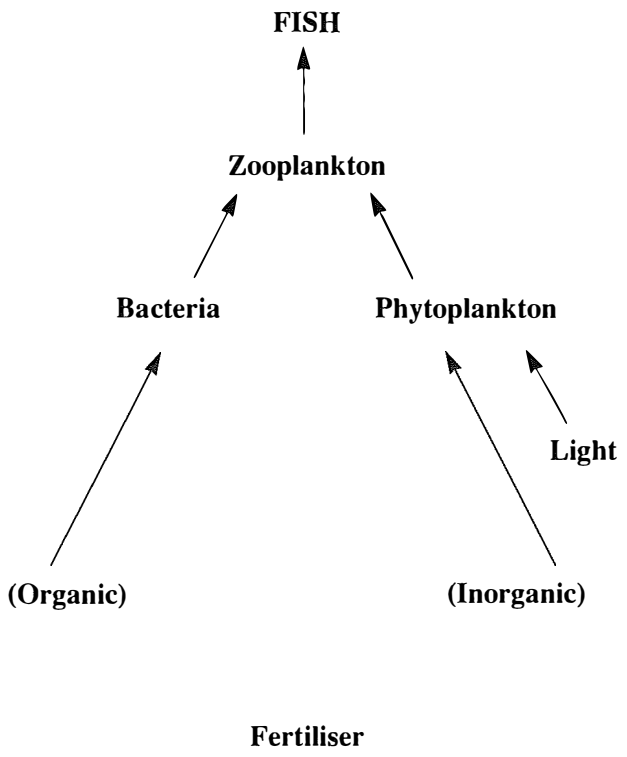

Figure 1. The aim of extensive rearing is to produce planktonic food organisms by fertilising water in a closed system (a pond) to produce blooms of unicellular algae and bacteria which provide food sources for zooplankton, which in turn are food for the fish larvae (from Rimmer and Rutledge 1991).

COMMERCIAL EXTENSIVE LARVAL REARING OF AUSTRALIAN FRESHWATER NATIVE FISH

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Introduction

The establishment of Australian native fish hatcheries was made possible with the development of efficient hormone-induced breeding and extensive pond rearing techniques for Murray cod (*Maccullochella peeli*), golden perch (*Macquaria ambigua*), and silver perch (*Bidyanus bidyanus*) in the late 1970's (Rowland *et al.* 1983; Rowland 1986a; Rowland 1989).

Extensive larval rearing involves fertilizing large earthen ponds to promote a plankton bloom which becomes the food supply for the fish larvae. The conditions in the ponds imitate the plankton rich environment of inundated floodplains, thought to be important nursery grounds for young fish (Geddes and Puckridge 1989).

Many key factors play an important part in the survival and growth of fish larvae in the rearing ponds. An understanding of fish growth and development, behaviour, diet, plankton ecology, fish diseases, predators and critical water quality parameters, enable pond management practices that will ensure good growth and survival rates essential for viable commercial production. This paper outlines how these factors relate to rearing Murray cod, golden perch and silver perch.

Larval growth, development, behaviour and diet

There are some important differences between the larvae of Murray cod, golden perch and silver perch that warrant different rearing conditions.

Murray cod larvae are large, 12mm total length (T.L.), and well developed when they commence feeding 9 to 11 days after hatching (Lake 1967; Rowland 1989). At this early stage they are capable swimmers, easily capturing small zooplankton and showing a preference for crustaceans and chironomid larvae (Lake 1967; Rowland 1985).

Rowland (1985) showed that first feed larvae were able to withstand a delay of over 10 days without food, without a significant increase in mortality (mortality was always less than 20%) as long as the larvae were then offered food at high concentrations. He also showed that survival in aquaria was over 80% for Murray cod larvae fed on a low level of zooplankton of 250 organisms/litre. Survival for larvae fed at higher food concentrations was not significantly higher. The highest value was 89%.

These features of large size, efficient prey capture and ability to survive at low food levels ensure that survival of Murray cod in the rearing ponds is consistently high (Figure 1).

Golden perch and silver perch larvae are similar to many species of marine fish larvae, being small and poorly developed at first feed. The concept of a "critical period" is described for this type of fish larvae when sufficient prey must be encountered or heavy mortality results (May 1974; Pitcher and Hart 1982; Leggett 1986). At the commencement of feeding, golden perch and silver perch larvae are only 5mm total length.

At this stage they are poorly developed, weak swimmers that are inefficient at capturing food (Lake 1967; Arumugam and Geddes 1987). Rowland (1989) describes the importance of having dense blooms of suitable zooplankton in the rearing ponds for the first few days of feeding as being vital for obtaining high survival rates.

The type of plankton suitable for high survival rates in the rearing ponds differs for golden perch and silver perch. First feed silver perch larvae are limited to smaller prey having a smaller mouth gape of 0.4mm compared with 0.5mm in golden perch (Arumugam and Geddes 1987). Gut analysis of early feeding larvae shows that silver perch start feeding on small rotifers, algae, chironomid larvae and small crustaceans.

In contrast, golden perch larvae feed mainly on small crustaceans and insect larvae, rarely ingesting rotifers or algae (Lake 1967; Arumugam 1986b). The highest survival rates for silver perch larvae at Inland Fisheries Research Station (IFRS) have occurred when they were released into ponds with a dense bloom of rotifers, *Brachionus sp.* For golden perch, high rates of survival have occurred in ponds with blooms of cladocerans, *Moina sp.* (S.J. Thurstan, unpublished data).

Visual stimuli are important for golden perch larvae and fry for locating their prey and initiating an attack (Arumugam 1986b). This helps explain why they rarely eat algae or slow moving rotifers and are attracted to larger, more obvious prey as found for bluegill (*Lepomis macrochirus*) (Wetterer 1989). Golden perch of less than 20mm in length tend to select the largest prey available, and often attack prey that is too large to ingest (Arumugam and Geddes in press). As golden perch increase in size, their impact on larger species of zooplankton also increases. Arumugam and Geddes (1987) describe the relationship between mouth gape and fish length for golden perch as linear, which gives an indication of the size of prey, fish of different lengths are able to consume.

Data on growth collected from fry rearing ponds at IFRS over six years show a linear increase in length for Murray cod, golden perch and silver perch during the rearing period (Figure 2). In contrast, Arumugam and Geddes (1987) found that golden perch length and weight increased exponentially with respect to time in a single rearing pond. The different results are best explained by the greater variability in conditions affecting fish growth experienced in the many ponds comprising the IFRS data.

The presence of structures that provide some form of cover or shelter have been shown to be important for the growth and wellbeing of golden perch reared in laboratory conditions. Once the larvae reach 10mm in length they seek cover and defend a territory from other fish. Fish that have cover competed more successfully for food, grow faster and are able to withstand longer periods of starvation (Arumugam and Geddes 1987). Similar cover seeking behaviour has been observed for Murray cod. Silver perch, however, rarely use cover, spending more time actively swimming, usually in groups. The importance of cover in rearing ponds has not been studied, but it may play an important role in fry production.

Plankton ecology and insect predation

The plankton blooms that develop in rearing ponds normally follow a predictable succession of dominant species with a tendency for the average size of the zooplankton to increase over time (Arumugam 1986b). Detailed descriptions of plankton succession in IFRS rearing ponds are given by Arumugam (1986b); Arumugam and Geddes (1986); Geddes and Puckridge (1989).

A typical succession of dominant zooplankton species in a newly filled rearing pond at IFRS starts with rotifers such as *Brachionus* sp , followed by cyclopoid copepods and *Moina* sp, then calanoid copepods and finally *Daphnia carinata* (Arumugam 1989). The length of time before the start of the rotifer bloom and the period which each species dominates depends upon pond water temperature. Pond temperature can vary more than 10°C over the breeding season, and may change dramatically overnight. At 18°C the first rotifer bloom will take ten to fourteen days to develop and may last for one week. At 28°C the rotifer bloom may occur after four days and last for only two days.

The unpredictable nature of the weather which influences the temperature of rearing ponds presents a problem of coordinating the release of golden perch and silver perch larvae into a rearing pond with an ideal zooplankton bloom. Artificially bred golden and silver perch larvae require feeding seven days after the broodstock are induced to spawn and there can be no guarantee that the zooplankton species abundance will be ideal. This uncertainty may account for the high variability of golden perch and silver perch survival in rearing ponds , shown for golden perch in Figure 1.

To reduce the high rates of golden perch mortality caused by unsuitable zooplankton in the rearing ponds, Arumugam (1986a) proposed feeding golden perch in the hatchery on *Artemia salina* nauplii for a few days until pond conditions are suitable. This practice has been tried at IFRS with some success (Author, unpublished data).

Post and McQueen (1987); Arumugam and Geddes (1986); and Arumugam and Geddes (1988) showed that as fish grow they have an increasing effect on the size, composition and biomass of the zooplankton populations in enclosures, resulting in marked reductions in the abundance of preferred prey species and blooms of non-prey species of zooplankton. Rearing ponds are harvested when predation pressure reduces the food organisms to levels that can no longer support fish growth. The mass of fish normally harvested from the 0.4 ha rearing ponds at IFRS normally ranges between 20 and 40 kg, with a maximum recorded value of 160 kg.

Many species of aquatic insects inhabit the rearing ponds, and often develop large populations. Several species have the potential to be serious predators of fish larvae (Arumugam 1986b) but they pose a greater problem in the later stages of rearing fry when they compete for the limited resource of plankton for food (Geddes 1986; Arumugam and Geddes 1986). Routine control of aquatic insects takes place in fish rearing ponds in Malaysia (Arumugum 1989) but as yet it is not common practice for rearing Australian native fish.

Water quality and disease

The eutrophic conditions of rearing ponds lead to considerable variations in water quality factors such as dissolved oxygen, pH and ammonia which affect fish growth and survival. Routine monitoring of water quality is required to maintain favourable conditions (Rowland 1986b).

Thermal stratification commonly occurs in rearing ponds, forming a cooler, oxygen deficient (concentrations less than 2ppm) layer up to 1 m deep on the bottom of the pond. These conditions may retard fish growth by:

1. reducing the bottom cover available to Murray cod or golden perch:
2. concentrating the fish and zooplankton into a smaller volume, which subjects the plankton to heavier grazing pressure (Arumugam 1989):
3. reducing the availability of benthic food organisms that are important prey items to the fish (Arumugam 1989):
4. the production of toxic metabolites such as ammonia and sulphides in anaerobic conditions (Avnimelech and Zohar 1986).

Low oxygen conditions in ponds can be remedied with aeration equipment or by exchanging water.

Protozoan parasites, such as *Chilodonella* sp., *Ichthyophthirius multifiliis, Trichodina* sp. and *Ichthyobodo necator*, are the only disease organisms that have been recognized as causing significant mortality of native fish in rearing ponds (Rowland and Ingram 1991). Regular inspections of fish must be carried out to identify the onset of the diseases, which can then be treated by applying malachite green to the pond.

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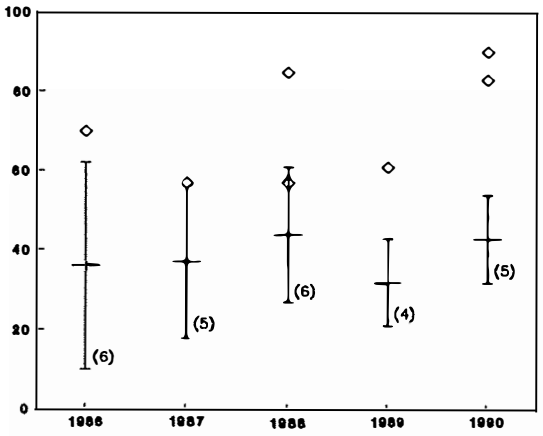

Figure 1. Survival rates of golden perch (Ŧ) ± s.d. and Murray cod (◊, points represent single points). Sample numbers of golden perch in parenthesis.

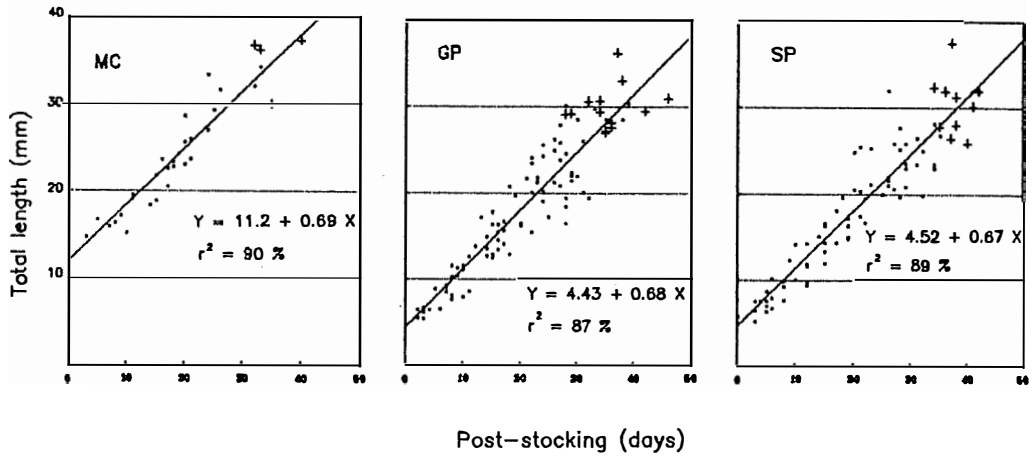

Figure 2. Growth of Murray cod (MC), golden perch (GP), and silver perch (SP) in rearing ponds. Each point (.) is a mean length from 3-5 fish from a pond or 10-20 measured at harvest (+).

THE EFFECT OF SALINITY IN THE EXTENSIVE REARING OF AUSTRALIAN BASS *MACQUARIA NOVEMACULEATA*

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The Australian bass is a euryhaline catadromous fish requiring salinities of at least 14gl^{-1} for successful spawning (Llewellyn and Macdonald 1980; van de Wal 1985). Adult fish undertake a downstream migration in early winter with adults and juveniles returning upstream in winter and early summer. Langdon(1987) postulated that juvenile bass need to remain in estuarine waters until they develop the ability to osmoregulate in fresh water because energy losses due to osmoregulation are minimised within the confines of the estuarine habitat where isosmotic conditions are most likely to be found. Thus the timing of this ability to osmoregulate is critical in the transfer to fresh water of artificially reared juvenile bass.

Commercial production of Australian bass in Queensland (Qld) commenced in 1988, almost ten years later than in New South Wales (NSW), where some excellent research had been conducted into the larval biology of these animals by a number of workers. However, two commercial hatcheries in Qld claimed significant larval survival when transferred to fresh water within a few days of hatching. This was in direct contrast to the findings of Battaglene *et al.* (1989), who found that larvae could not survive in fresh water before the age of three weeks. Subsequently, a research programme was initiated to compare NSW and Qld stocks reared under identical conditions in a cooperative effort between the Brackish Water Fish Culture Research Station at Port Stephens and the Department of Primary Industries, Fisheries Branch, hatchery at Deception Bay.

Larvae from NSW and Qld were held in two different acclimation salinities, 15 gl^{-1} and 28 gl^{-1}, at a temperature of 20±1°C. For each trial, survival over 48 h of three replicates of thirty larvae was tested against salinities of 0, 2, 5, 15 and 28 gl^{-1} at the ages of 4, 7, 11, 14, 17, 21 and 28 days. The results were analysed using two 4-way ANOVA comparing two blocks of results. Block 1 compared all ages of larvae for two salinities (2 and 5 gl^{-1}) against acclimation and stocks. Block 2 compared larval ages 14, 17, 21 and 28 days for three salinities (0, 2 and 5 gl^{-1}) against the same acclimations, salinity and stocks.

Survival at 0 gl^{-1} was significantly reduced for all larvae irrespective of source or treatment up to the age of 21 days. However, by 28 days, all larvae had developed the ability to cope with fresh water. It should also be noted that at least 80% of the larvae survived 2 gl^{-1} by the age of 7 days or over. The effect of acclimation salinity was very evident on Day 4 when fry acclimated at 15 gl^{-1} showed significantly better survival at 2gl^{-1} than those fry acclimated at 28 gl^{-1}. Beyond that age, the effect of acclimation was not significant.

Although the early survival claims have not been able to be repeated at one of the two Qld hatcheries, the other hatchery continues to claim success. One possible explanation of this

situation is suggested by the laboratory results which show a vast improvement in early larval survival with a low salinity of 2 gl^{-1} as well as a positive effect of acclimation on survival. The hatchery claiming these early larval survivals draws water from Stockyard Creek which is known to have a high mineral content with a measured salinity level of 1.4 gl^{-1} in mid-winter (a normally dry period in South East Qld). By way of contrast, the other Qld hatchery draws water from Ringtail Creek which has a low mineral content.

Thus it is possible that yolk-sac fry reared in 15 gl^{-1} salinity for one week and transferred to well prepared ponds with a residual salinity in the vicinity of 2 gl^{-1}, may survive, depending on their ability to find suitable food sources and to avoid possible predators. This may well be the basis for the apparently anomalous results in the Qld hatcheries.

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THE EFFECT OF TEMPERATURE IN THE EXTENSIVE REARING OF AUSTRALIAN BASS, *MACQUARIA NOVEMACULEATA* (STEINDACHNER)

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Introduction

The Australian bass (*Macquaria novemaculeata*) is a catadromous percichthyid fish native to the coastal drainages of south-eastern Australia (MacDonald 1978). Its renowned angling and eating qualities have created a demand for the commercial production of bass fingerlings for stocking into farm dams and public impoundments. In comparison to other commercially important native freshwater fish (Rowland *et al.* 1983), only relatively small and irregular numbers of Australian bass have been produced to date.

Two major problems have limited the success of large scale breeding of Australian bass. In early research, a high proportion of larvae failed to develop functional swim bladders, resulting in slow growth and increasing mortality over the latter stages of intensive larval rearing. Similar difficulties have also been reported in the intensive culture of several species of marine fish (Spectorova and Doroshev 1976; Al-Abdul-Elah *et al.* 1983; Chatain 1987). Australian bass are physoclistous, inflating their swim bladders 6-11 days after hatch at a temperature of 19_1°C (Figure 1). Some of the factors affecting the development of swim bladders in cultured Australian bass larvae were experimentally determined by Battaglene and Talbot (1990). A high percentage (>70%) of larvae with functional swim bladders can now be produced by culturing larvae for the first ten days after hatch, in conditions of darkness, salinities above 25 ppt and low to zero aeration.

The second major constraint to the large scale breeding of Australian bass is an apparently nutritionally based metabolic disorder (Battaglene *et al.* 1989a). This disorder has been particularly troublesome, causing high mortality of intensively reared larvae at around 30 days of age. Affected larvae exhibit symptoms such as erratic swimming, fainting, constipation, failure to digest food, pale colour and copious mucous production. Possible causes of this disorder include hepatic and renal dysfunction due to nutritional deficiencies in fatty acids and/ or vitamins (Battaglene *et al.* in press).

The low survival of bass larvae in intensive systems prompted the initiation of experimental work on extensive pond culture based on the methods used to rear the closely related golden perch *Macquaria ambigua* (Rowland *et al.* 1983). In the period 1987-91 more than 30 pond stockings have been undertaken during experiments designed to appraise and improve extensive rearing techniques. Ponds at the Brackish Water Fish Culture Research Station (BWFCRS) and freshwater and saltwater ponds in the Clarence River region of NSW have been used.

The experimental stocking of freshwater ponds with 21-day-old larvae resulted in low and variable survival (0-17%) to metamorpho-

sis (Battaglene *et al.* 1989b). This was possibly due to the restricted ability of larvae to tolerate transfer from saltwater to freshwater. Survival of 21-day-old larvae in saltwater ponds was more consistent (3-15%) but yolk-sac larvae did not survive (Battaglene and Allan 1990). Poor food availability appeared to cause low survival in some extensive rearing experiments run at ambient temperatures. Supplementation of wild zooplankton in ponds with newly hatched brine shrimp substantially increased survival to 12.3±8.8%, n=8 (Battaglene *et al.* in press).

Australian bass spawn in winter, when ambient temperatures in some experimental ponds drop as low as 9°C. Van der Wal (1985) reported an optimum temperature range of 16-20°C for survival of seven-day-old bass larvae, with significantly reduced survival and growth at 12°C. This range of 16-20°C corresponds with the September/October water temperatures in most NSW estuaries (Wolf and Collins 1979). Temperature is considered the major growth rate-controlling force for fish fed a suitable ration (Brett 1979; Shepherd and Bromage 1988). At ambient winter pond temperatures bass larvae are slow growing in comparison with many other extensively reared fish. Ponds covered by greenhouses store solar heat (Ogle 1980) and have been used to increase winter pond temperatures (Parker 1989) and subsequent growth rates of prawns and fish (Juan *et al.* 1988; Seidman and Issar 1988; Paessun and Allison 1984).

The following summarises the results of experiments carried out in passively-heated greenhouse covered ponds and uncovered ponds, to observe the effect of increased pond temperatures on the growth and survival of Australian bass larvae.

Methods

Experiments were conducted during the winters of 1989 and 1990 using eight saltwater prawn nursery ponds (250 m^2, 1 m deep), located at Palmers Island on the Clarence River. Four of these ponds were enclosed within a plastic greenhouse. An uncovered saltwater pond at BWFCRS (1000 m^2, 1 m deep) was also used. Eight experimental stockings were carried out in the uncovered Palmers Island ponds, eight in the greenhouse covered ponds and one in the pond at BWFCRS (Table 1).

Temperature, salinity, pH and dissolved oxygen (DO) were measured every 1-7 days. The larvae, obtained from hormonally induced broodstock, were intensively reared at BWFCRS using techniques described by Battaglene *et al.* (1989a). Larvae were stocked into the ponds at 2-3 weeks of age at a density of one million per hectare. At stocking, the larvae had developed swim bladders, absorbed their yolk-sac and oil globule, and started exogenous feeding. The extensive culture methods used are described by Battaglene and Allan (1990). In addition, 1 hp paddle wheel aerators were used to increase morning dissolved oxygen levels. For all ponds, natural zooplankton was supplemented by adding newly hatched brine shrimp as described by Battaglene *et al.* (in press). Larvae were sampled every 1-7 days and ponds harvested when the larvae were fully metamorphosed at approximately 20 mm total length. Results are given as mean±SD.

Results and discussion

Temperatures during the experimental trials in the passively heated greenhouse ponds ranged from 18-23°C. Under these conditions larvae took from 48-59 days to reach metamorphosis from hatch with an average survival of 51-23.4% (Table 1). In contrast, temperatures in the uncovered ponds in the Clarence River and at BWFRCS ranged from 9-24°C with metamorphosis occurring at 88-118 days of age and survival averaging 14.7-11.3%. Survival among ponds for all trials was highly variable ranging from 0-80.8%. Salinities in and among ponds ranged from 7-25 ppt, dissolved oxygen from 5.2-16.9 ppm and pH from 6.7-9.8.

The average daily larval growth rates (to metamorphosis) in the passively heated greenhouse ponds were markedly higher (194-231%) than the uncovered ponds (Table 1 and Figure 2). They are also equal to, or greater than, those recorded for intensively reared larvae (Battaglene *et al.* 1989a), with more than twice the average survival rate.

The high degree of variability experienced in survival among pond trials was, in part, due to mortality caused by protozoan parasite epizootics. In some ponds ciliates of the genus *Trichodina* were found on moribund fish. Formalin (15 ppm) or malachite green (0.5 ppm) were used to treat ponds with infected fish. Both treatments reduced parasitic ciliates to undetectably low levels. Regular prophylactic treatments for protozoans in the latter stages of rearing may further increase survival.

Another problem that can reduce survival in fish ponds is water quality deterioration due to sudden mortality of phytoplankton blooms (Boyd *et al.* 1975). The shorter rearing period achievable in greenhouse ponds may reduce the number of disease epizootics and water quality problems.

The ponds at Palmers Island used during these trials are prawn farm nursery ponds. Prawn farms in NSW and South East Queensland usually only produce one prawn crop per year, making them comparatively less profitable than those in tropical climates (Hardman *et al.* 1991). Bass fingerlings were suggested as a potential winter crop for prawn farmers by Battaglene and Allan (1990). The use of passively heated greenhouse nursery ponds can allow the production of two prawn crops in temperate climates (Juan *et al.* 1988). In addition, the faster growth rates achieved in the greenhouse ponds during this study indicate that two crops of bass could be produced before post larval prawns become available in spring.

Extensive larval rearing experiments with barramundi (*Lates calcarifer*) have recently been carried out in tropical Queensland. These demonstrated that compared with established intensive rearing techniques, equivalent numbers of barramundi can be produced more quickly and far more cheaply (Rimmer and Rutledge 1991). During the experiments summarised in this paper over 161,000 juvenile Australian bass were produced from 17 pond stockings. The results of this study indicate that commercially important advantages can be gained by extensively rearing Australian bass larvae in greenhouse ponds rather than by conventional intensive hatchery techniques.

Acknowledgements

We thank Glen Searle for the use of his ponds and help in the design and running of the Palmers Island extensive rearing trials. Paul Beevers and Mel Lockhart assisted with the intensive rearing of bass larvae and during transport and harvest. We also thank Stuart Rowland and Kevin Clark for the use of the Eastern Fish Hatchery and for their assistance during the trials.

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Table 1. Results of Australian bass (*Macquaria novemaculeata*) extensive rearing experiments in greenhouse covered and uncovered ponds

All larvae were intensively reared at BWFCRS for 10-20 days post hatch (average length 4.5-5.8 mm) and stocked into ponds at a density of 1 million per hectare

Site *	No. of ponds stocked	Average % survival	Age at harvest (days)	Growth/day (mm)	Temperate range (^{0}C)
I	8	51-32.4	48-59	0.37-0.44	18-23
II	8	12-9.0	88-118	0.17-0.30	12-24
III	1	35	103	0.19	9-24

*I = Palmers Island greenhouse ponds

II = Palmers Island uncovered ponds

III = BWFCRS uncovered pond

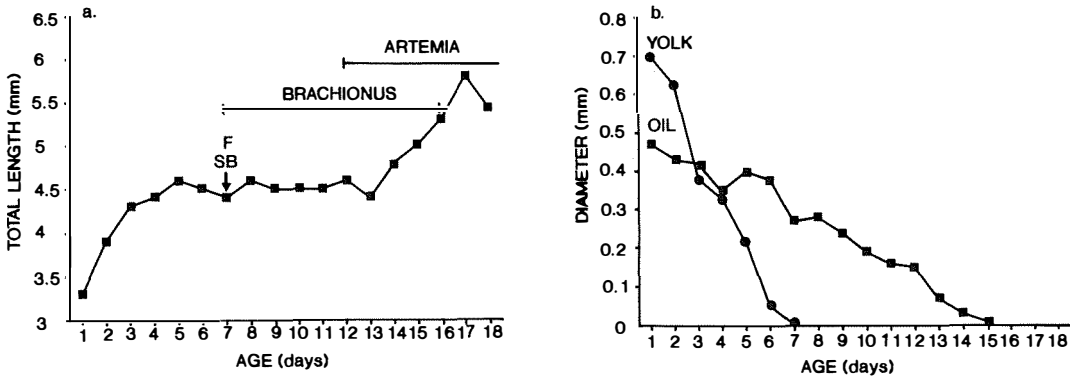

Figure 1. a. The growth of Australian bass (*Macquaria novemaculeata*) during the first 18 days of intensive rearing showing the time of exogenous feeding (F) and swim bladder inflation (SB). Larvae were fed on *Brachionus* (7th-16th day) and *Artemia* (from 12th day). **b.** Absorption of the ● yolk-sac and ■ oil globule.

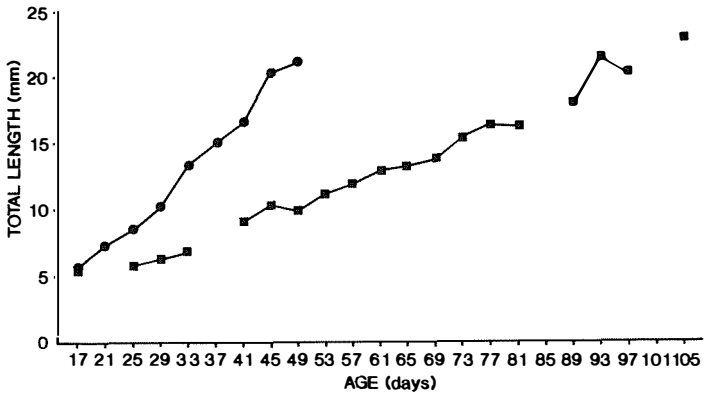

Figure 2. The growth to metamorphosis of extensively reared Australian bass (*Macquaria novemaculeata*) under two individual temperature regimes, ■ 9-24°C and ● 18-22°C. Each point represents the mean length (TL) of 3-10 fish at that age.

IMPLICATIONS OF WATER QUALITY FOR LARVAL FISH METABOLISM, ACTIVITY AND GROWTH IN EXTENSIVE REARING CONDITIONS

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Introduction

The principal objectives in rearing larval fish are survival and growth of the larvae. Under extensive rearing conditions, these objectives are pursued with relatively low capital, technical and labour inputs when compared with increasingly intensive operations.

It is possible in rearing conditions to achieve excellent survival but poor growth, or alternatively, poor survival and excellent growth, but from a physiological perspective at the level of individual organisms, unfavourable environmental conditions initially cause reduced growth, and further environmental deterioration leads to death. In this context, good growth implies survival at one extreme, and death of the individual represents the other extreme on a continuum of responses to the environment. Survival, therefore, is implicit in the following discussion of factors affecting larval metabolism and growth, and only sublethal responses to water quality are considered.

Energetics of growth

Growth is only one of several processes competing for an allocation of energy ingested by fish larvae. Not all ingested energy is assimilated, a portion of ingested energy being excreted. The assimilated portion is allocated to metabolism and growth. Excretion in adult teleost carnivores typically accounts for 27% of ingested energy (Brett and Groves 1979), but when food is readily available, excretory losses may approach 60% (Gehrke 1988). The larvae of marine fish are less efficient at assimilating energy from their diet, and may excrete between 30 and 39% of ingested energy. Larval metabolism, however, accounts for only 31% of dietary energy compared to 44% in adult teleost carnivores, but variability in larval excretion rates dictates whether any metabolic savings can be partitioned into accelerated growth (MacKenzie *et al.* 1990). Growth, then, relies on surplus energy left over from excretory and metabolic losses.

Metabolic rates are profoundly influenced by both water quality and exercise levels, implying that it is possible, in theory, to increase the amount of energy available for growth by reducing the proportion of ingested energy consumed by metabolism.

Enhancing growth by manipulating energy usage

Fish larvae derive their initial energy from their yolk supply, and require no locomotor activity to obtain that energy. Once the yolk is con-

sumed, however, all energy requirements must be met by ingested energy, which involves activity to forage and capture prey.

The most important factor affecting metabolic rates of fish is body size, which accounts for over 80% of the variation in both standard and active oxygen consumption (Thurstan and Gehrke 1991). After body size, the next major factor determining metabolic energy requirements is activity level (Blaxter 1969; Brett 1970; Rombough 1988) which accounts for 12.95% of fish oxygen requirements after size effects have been removed (Thurstan and Gehrke 1991). By adding effects due to temperature, oxygen and salinity, up to 30% of the variation in metabolic intensity can be explained. The remaining variation is due to effects between species, different experimenters, and chemical or biological factors which are not usually published.

Potential exists for improving growth of larvae by maintaining conditions which minimise larval activity and metabolism. How might this be achieved? Larvae of many species are not capable of sustained activity, but rather, alternate between periods of burst activity and inactivity (Rombough 1988). Burst activity relies on anaerobic metabolism which accumulates an oxygen debt and is energetically less efficient than aerobic pathways. Thus, where adverse water quality dictates that larvae avoid unfavourable habitats (Gehrke 1990; Gehrke in press) affected larvae may be forced to swim relatively large distances at considerable energetic expense. By maintaining water temperature and oxygen tension within ranges which do not elicit avoidance behaviour, larval activity may be reduced.

The most direct way to increase the amount of energy available for growth is to increase energy intake. Not all of the additional energy ingested will be allocated for growth: losses through excretion and metabolic energy consumption will both rise, but the absolute amount of energy available for growth will increase. At normal rearing densities of larvae, it may not be possible to maintain the increased ration without eventually depleting the food supply in the pond before fish are large enough to transfer. In ponds at Narrandera, fish effectively consume the plankton in a pond within 4 to 8 weeks, feeding *ad libitum*. Fertilising ponds after stocking may prolong plankton production, but can also cause oxygen tensions to deteriorate, so the relative benefit needs to be assessed.

If food density is in excess of requirements, as normally occurs when larvae are stocked into rearing ponds, it might be assumed that larvae are consuming a maximum ration, in which case attempts to increase that ration further may prove fruitless. Importantly, MacKenzie *et al.* (1990) indicate that ingestion rates of fish larvae, when standardised for effects of size and temperature, do not increase any further when food density exceeds 185 $\mu g\ l^{-1}$, and that maximal ingestion rate is 75 $\mu g\ d^{-1}$ for a standard larva of 125 μg (all weights measured as dry weight) at 18.7°C. In rearing ponds at IFRS, total plankton densities frequently reach or exceed 3000 $\mu g\ l^{-1}$ around the time of stocking, which is well above the critical prey density, so that food availability does not limit ingestion of energy. Presumably, however, the benefit of maintaining high plankton density is that larvae forage less and metabolise less energy for activity.

Water quality in extensive rearing facilities

One of the major differences between extensive and intensive approaches to fish rearing is the effort invested in controlling water quality. At one extreme, extensive operations may not attempt to control water quality at all, and perhaps not even monitor environmental conditions. At the other extreme, intensive water engineering and process controls now enable water quality to be controlled independent of climatic influences. Water quality in extensive rearing ponds tends to follow climatic conditions closely, and management techniques are based upon anticipating weather patterns and avoiding extremes by sensible location of ponds and pond design.

Within the realm of normal pond water quality variables, temperature and oxygen most frequently reach undesirable levels and it is by working with this minimal combination of factors that pond water quality is managed during the rearing period. This selection of factors is not merely coincidental, but is of fundamental importance because temperature and oxygen exert a greater influence on larval metabolism and activity than most other physical and chemical factors.

Direct effects of water quality

Growth and metabolism both operate more efficiently as temperature tends toward an optimum, making it desirable to minimise the effects of rapid temperature changes in a pond. Sudden changes in temperature of only a few degrees Celsius can have dramatic effects on growth. At 16°C, spangled perch (*Leiopotherapon unicolor*) metabolise 41.5% of their energy intake. This figure increases to 72.2% at 14°C, and to a phenomenal 201.5% at 13°C (Gehrke 1988). Thus, a drop in temperature of only 3°C can influence a change from normal growth rates to fish which lose weight rapidly. Sudden bouts of cold weather could therefore result in reduced or negative growth in rearing ponds until the return of warmer weather.

Deficiencies in oxygen availability have different effects depending upon the size of the larvae and fingerlings. Newly-hatched larvae expend little or no energy in ventilation because they obtain a significant proportion of their oxygen requirements by diffusion across the external body surface. Before metamorphosis, the gills become the dominant site of respiratory gas exchange, and ventilation contributes from 5 to 30% of the standard metabolic oxygen requirement.

As environmental oxygen tension declines, the scope for activity or growth declines until oxygen uptake is barely adequate to maintain standard metabolism. At this point, 100% of assimilated energy is devoted to maintaining essential metabolic processes, and any further decline in oxygen availability below this critical oxygen tension forces a reduction in metabolic rate. Larvae and fingerlings may survive in ponds where dissolved oxygen is maintained above the critical oxygen tension somewhere between 20-40% of air saturation, but growth is likely to be restricted under such conditions. To reduce growth restrictions due to oxygen availability, oxygen tension in rearing ponds should be maintained as high as possible. Certainly, minimum oxygen concentrations recommended by convention may be adequate for short term survival, but caution is advised in accepting any such minimum concentration where growth of larvae is desired (Doudoroff and Shumway 1967).

Conclusions

Growth of fish larvae can, in theory, be enhanced by increasing surplus energy, or by increasing the efficiency of converting energy into growth. In extensive rearing facilities, options for increasing energy ration are limited and possibly of little benefit. Alternatively, additional energy for growth can be obtained by minimising metabolic energy consumption by managing water quality to reduce larval activity.

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LARVAL FEEDING TRIALS WITH STRIPED TRUMPETER, *LATRIS LINEATA*

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Abstract

The striped trumpeter, *Latris lineata*, is an esteemed table fish and highly suited to the sashimi market, and therefore holds considerable commercial value. Due to the absence of empirical data on the lifecycle of *L. lineata*, a research project was initiated to investigate the reproductive biology and various developmental (embryonic - larval - juvenile) stages of the species. The baseline information obtained could then be utilised for both assessing the aquaculture potential of *L. lineata*, and for application to the effective management of the wild fishery.

Results to date have shown striped trumpeter to be highly fecund, producing small pelagic eggs (1.31 $\pm$ 0.11mm) with a single oil droplet (0.27mm). Fertilisation rates of approximately 97% have been repeatedly achieved from the artificial fertilisation of hand-stripped ova. Newly hatched larvae are small (3.34 $\pm$ 0.26mm), poorly developed and have a relatively large yolk sac.

Hatchery produced larvae were obtained over two successive breeding seasons (1989 and 1990), and trialled on a variety of larval diets. These included (i) a microencapsulated pelleted diet, (ii) a combined microencapsulated - live food diet (iii) a live food diet consisting of *Brachionus plicatilis* and *Artemia sp.* (iv) a combined *Brachionus plicatilis* and mixed zooplankton diet, and (v) a mixed zooplankton diet.

Growth and development were significantly higher for those larvae fed on the combined *Brachionus plicatilis* and mixed zooplankton diet. Flexion was observed from Day 23 post hatch, and the tail, dorsal and anal fins were developed by Day 44 post hatch. For those larvae fed on *Brachionus plicatilis* and *Artemia sp.* development tended to be suppressed, and by Day 45 post hatch there was no visible sign of flexion. Growth and development of larvae reared on the microencapsulated diet was negligible.

Feeding trials, experimental results and inherent problems will be presented at the Workshop, together with future research directions for the 1991 breeding season.

COMPARISON OF INTENSIVE AND EXTENSIVE CULTURE OF THE TASMANIAN WHITEBAIT *LOVETTIA SEALII* (JOHNSTON)

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History of the whitebait fishery

The fishery dates back to the early 1930's. Large scale commercial fishing began in the early 1940's and reached a peak catch of 515 tonnes in 1947. The fishery could not sustain this kind of pressure and declined dramatically the following year. Subsequent to this the catches remained severely depressed (< 50 t) and the fishery was closed in 1974.

The whitebait runs consist of six species of fish:

Tasmanian whitebait	*Lovettia sealii*
Jollytail	*Galaxias maculatus*
Spotted galaxias	*G.truttaceus*
Climbing galaxias	*G.brevipinnis*
Tasmanian mudfish	*G.cleaveri*
Smelt	*Retropinna tasmanica*

The Tasmanian whitebait and Jollytail are the predominant fish and the Tasmanian whitebait is especially at risk since the fishery collects adults before they spawn.

Biology

Lovettia sealii (Sub-order Salmonoidei, family Aplochitonidae) is represented by a single genus, found only in Tasmania.

Lovettia is anadromous and adults collect in estuaries during winter and in early spring move up the rivers to spawn. At this stage they are known as whitebait. Mature fish are 1 year old, 45-49 mm long and weigh 0.8 to 0.9 g. Females carry up to 350 eggs and spawn in rivers at the upper reaches of tidal influence. The eggs, 1.1 mm diameter, are adhesive and attached to submerged logs, stones and branches, below low water mark and located in areas of high flow. Following several spawns per fish they progressively deteriorate and die. *Lovettia* are essentially a one year fish and less than 0.01% of fish survive for two years. Larvae hatch about 20 days later and are carried downstream into the estuaries, returning one year later as adults (Blackburn 1950; Fulton and Pavuk 1988).

Little is known about the life history of *Lovettia* between hatch and maturity. Work by Fulton and Pavuk (1988) using isozyme electrophoresis indicates that there are at least five genetically distinct populations in Tasmania. This suggests that *Lovettia* move only short distances in the sea.

Aquaculture investigations

Aquaculture investigations of *Lovettia* began in 1987 as a private venture by Frish Pty. Ltd. on the east coast of Tasmania, near Triabunna. At the time of writing (1991) fish have been reared through three generations.

The low individual weight of fish means that a large number of larvae must be reared to achieve a commercially useful harvest. The labour and infrastructure requirements for growing large amounts of rotifer and *Artemia* make this kind of culture uneconomic. As a result of this a new approach has been developed. Live zooplankton are harvested from local estuaries using a vessel designed for this purpose. A description of the presently accepted technique of intensive marine fish culture, together with the new approach, follow.

Intensive culture

Adult *Lovettia*, when fully mature, spawned and deposited eggs on the sides of fibreglass hatching troughs. Spawning was stimulated by increased flow and lowered salinity.

Eggs were incubated in freshwater using recirculating or flow through systems. Dead eggs readily become infected with *Saprolegnia*. Since the small adhesive egg is not easy to remove, the *Saprolegnia* can rapidly overcome the surrounding live eggs. Treatment to successfully control the spread of the fungus involved increasing the salinity in the hatching troughs to 25 ppt for 30 minutes daily. Turbulent flow also assists in controlling the fungus.

Newly hatched larvae, 5 mm long, were removed to 4 m^3 fibreglass tanks where they were acclimatised to marine water of 34 ppt over a period of 2 days. The larvae were active swimmers and began feeding in the first 24 hours at 12-14°C. A recirculating system including a high pressure sand filter and biological filter was used to maintain water quality in the tanks.

Feeding - standard method

Brachionus plicatilis was used for initial feeding. Levels of highly unsaturated fatty acids in the rotifer were boosted using emulsified marine oil for direct enrichment (Watanabe *et al.* 1983). Uneaten rotifers were flushed out of the system overnight. Observations of food in the gut indicate that *B.plicatilis* is readily digested leaving only traces of the mastax in recognisable form. Eggs of the rotifer however, remain intact throughout the digestive tract. Mean time to 90% gut evacuation following feeding to satiation with rotifers is 3.5 hours at 12°C in fish 7.7 mm long and 18 days old.

Feeding with rotifers continued for 20 days. At this time *Artemia* instar II nauplii were introduced. Instar I nauplii remain almost intact during their passage through the gut suggesting that they are not well digested, whereas this is not the case for the instar II nauplii. *Artemia* instar II were enriched with marine oil in a similar manner to the rotifers.

After day 30, *Artemia* were the sole food. Fish were weaned onto salmon starter crumble at day 45. Following weaning, fish were fed standard salmonid pelleted food up to 2 mm in diameter.

Feeding - live zooplankton

Live natural marine zooplankton was the sole food source for *Lovettia* from hatch to adult.

The zooplankton was harvested daily from local estuaries and split into different size fractions. Initial feeding commenced with zooplankton in the size range 63 to 250 μm. This was increased to 500 μm at day 50.

Feeding with live zooplankton has benefits in terms of water quality in the larval rearing tanks. Compared to feeding with *Artemia* and pellets, there are no *Artemia* cysts, turbidity is increased, surface film is not present and ammonia levels remain very low. As a consequence daily feeding and maintenance including syphoning and screen cleaning is reduced from 3 hours per tank per day for the standard method to 45 minutes per tank per day for the new approach, which includes harvest time on the zooplankton harvester.

Extensive culture

Lovettia were spawned and eggs incubated as described for the intensive technique.

Just before hatch the hatching troughs were drained of water, covered and transported to culture ponds. Culture ponds were partially filled with fresh water filtered to 500 µm to exclude predators. Larvae were introduced to the ponds and the ponds progressively filled with seawater, filtered to 500 µm, over a period of several weeks. Fish were fed by adding live zooplankton daily to the pond. Systems are now in place to provide nursery ponds and tanks at the culture ponds so that larvae can be acclimatised to fully marine before they are placed in the ponds. Ponds can then be manipulated to produce a bloom of zooplankton prior to larvae entering. Fish are fed additional zooplankton as required.

Harvesting of live zooplankton

Harvesting of live zooplankton in commercially useful quantities has been made possible due to the development, by Frish Pty. Ltd., of a special boat designed for this purpose, illustrated in Figure 1. The trailerable vessel is 7.5 m long, 2.5 m wide, weighs 475 kg and has a minimum operating depth of 0.8 m.

The patented device harvests and concentrates zooplankton in the upper waters by scooping them onto a primary dewatering screen then size sorting through a series of sieves. The stainless steel mesh for the sieves and primary screen may be changed to accommodate different screening requirements. Harvested and concentrated zooplankters are stored in 700 L wells on board the boat and unloaded by pumping directly into ponds or a transport tank. The device is operated by one person and powered by an outboard motor and auxiliary petrol engine which provides power for pumps and hydraulic rams.

Results and discussion

Zooplankton

The harvesting boat is presently operated on local estuaries, primarily Little Swanport and Spring Bay, Triabunna.

Primary screen size is 63 µm mesh (Swiss Screens, stainless steel, dutch twill) when feeding larval fish. This is increased to 105 µm as fish grow. The water filtering rate is 200 L per second using the 63 µm mesh, and 300 L per second with the 105 µm mesh.

Zooplankton harvest rates in open systems such as estuaries vary according to time of day, state of tide and season. Monitoring of zooplankton catches indicates the most favourable times to harvest. Harvest rates at present (spring, 1991) in Spring Bay are :

63 - 250 µm size fraction 2.4 - 3.0 x 10^6 zooplankters/hour

250 - 500 µm size fraction 1.8 - 2.4 x 10^6 zooplankters/hour.

About 10% of harvested zooplankton are damaged during harvest and die. The remaining organisms stay active in the water column for at least 24 hours. Zooplankton are not fed to fish after 24 hours.

Future developments include the construction of specialised zooplankton ponds filled with filtered sea water to exclude predators of zooplankton. This is expected to increase harvest rates by a factor of 10 to 1000 times.

Zooplankton from the estuaries contains predominantly copepods, including the calanoids *Acartia tranteri* and *A.danae* and the cyclopoid *Oncae media*. For short periods in summer the zooplankton may consist almost entirely of oyster (*Crassostrea gigas*) larvae in the estuaries that support an oyster industry. These are readily consumed by *Lovettia*.

Copepods may be important in the early life history of marine fish. Copepodites and adult copepods are, in general, the main food of

marine fish larvae (Hunter 1980). Copepods have high levels of free amino acids (Dabrowski and Rusiecki 1983) which are absorbed directly by the morphologically simple gut of newly hatched fish larvae and may potentially provide a valuable source of energy (Fyhn 1989). Copepods also have high levels of n-3 highly unsaturated fatty acids even when feeding on foods low in these fatty acids (Robin *et al.* 1984). Highly unsaturated fatty acids are essential for most marine fish larvae.

Zooplankton from Spring Bay, 2 day old *Artemia* and adult *Lovettia* whole fish have been analysed for metals by Division of Sea Fisheries , Hobart. Metal levels in harvested zooplankton are higher than in *Artemia* nauplii (Table 1). Data on maximum acceptable levels of metals in feed for marine fish larvae are not available in literature searches. The concentrations found in the *Lovettia*, which had been fed entirely on the harvested zooplankton for 7 months prior to analysis, did not show an excessive accumulation of the metals (Table 1). Cadmium and zinc levels in pelleted feed, of 1.02 and 161 µg/g dry weight respectively produced levels of 0.11 and 7.6 µg/g wet weight respectively, in the flesh of farmed salmon on Hawaii (Fast *et al.* 1990). This also suggests that accumulation of metals from feed is not excessive. Growth of *Lovettia* fed the zooplankton was not significantly different from *Lovettia* fed on rotifers, *Artemia* and pellets, and survival was significantly better in the zooplankton fed fish. This suggests that the levels found in the zooplankton are not detrimental to larval development. Levels of metals in *Lovettia* were lower than maximum permissible levels in fish flesh for human consumption (Table 1).

Intensive culture

There was no significant difference in growth between the fish fed on rotifers, *Artemia* and pellets (1989-90) and the fish fed entirely on harvested zooplankton (1990-91). Growth in cultured *Lovettia*, measured as total length, is almost linear from hatch to maturity. Mean weight of cultured fish at harvest, 1.1 g, is larger than wild fish (0.8-0.9 g).

Major mortalities occurred in the 1989-90 season with peaks occurring at 15 and 37 days accounting for 70% losses. Overall mortality was greater than 90%. During the 1990-91 season no mortality peaks occurred and overall mortality was less than 50%. This suggests that zooplankton is nutritionally more competent than the standard diet of rotifers, *Artemia* and pellets.

Extensive culture

Culture of *Lovettia* in a pond has been attempted once to date (September 1991). Final biomass in the pond will be determined at harvest. Recent sampling of the pond has shown that many fish are small and immature compared to the larger fish in the pond and those in the intensive culture system. Previous samplings were done at night by attracting fish to a light and it is possible that only the larger fish were sampled by this method.

The most likely cause of the underdeveloped fish is food limitation, which can be a significant problem in extensively reared fish. In general extensively reared fish are more difficult to sample and are not graded. This can give rise to faster growing fish that outcompete others and leads to a greater range of sizes compared to intensive culture.

However, the advantages of extensive systems are such that these problems are worth pursuing. Advantages include:

- using natural productivity to produce fish
- diversity of prey species should promote improved growth and survival especially in larval stages
- mechanical failures do not have immediate and potentially catastrophic consequences as they may in intensive culture
- low infrastructure costs

- lower skill level of work force
- lower work time input per fish produced
- lower cost of fish produced.

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Table I. Metal concentration (μg/g) in harvested zooplankton, *Artemia* nauplii 2 days post-hatch, adult *Lovettia* and maximum permissible levels in fish flesh for human consumption (Control)

Metal	Concentration (μg/g)				
	Zooplankton[a]		*Artemia*	*Lovettia*[b]	Control[c]
	wet wt.	dry wt.	wet wt.	wet wt.	wet wt.
Cadmium	0.15	1.22	0.02	0.04	0.2
Copper	3.02	24.9	6.5	1.4	10.0
Zinc	57	473	19.6	19.9	150
Mercury	0.01	0.08	n.d.	n.d.	0.5

n.d. not determined

[a] single mixed zooplankton sample, Spring Bay, August 1991.

[b] adult whole *Lovettia* grown entirely on harvested zooplankton.

[c] National Health and Medical Research Council (1985) recommendations.

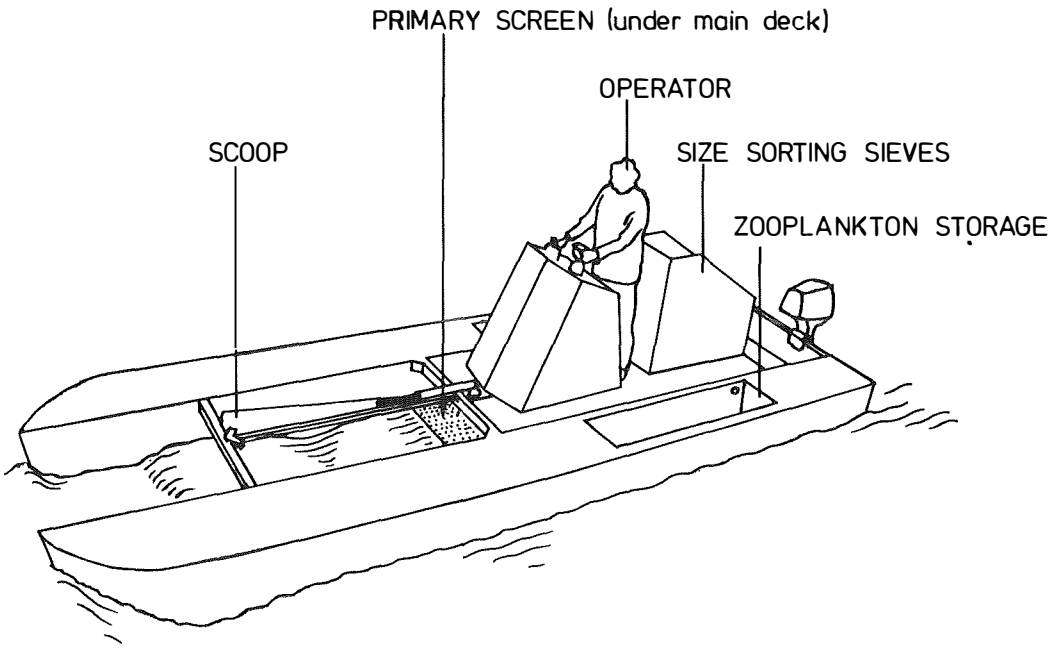

Figure 1. The zooplankton harvesting vessel.

DISCUSSION OF SESSION 2

Recorded by C.A. Hair and C.A. Gray

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Each panel presentation was followed by a time for quesions, after which the session was opened for General Discussion.

Following *Paul Brown's* panel presentation Jim Tait asked how closely the succession of plankton recorded in ponds paralleled that in the wild. Peter Gehrke replied that it was fairly similar but you generally see a greater diversity of plankton in and between isolated billabongs than in ponds. Jim Tait then asked if breeding of native freshwater fish was aimed to coincide with any particular environmental cue. Paul Brown said he would be looking at this more closely next year. Stephen Battaglene added that golden and silver perch are both cued to spawn on floods, and floods increase the flood plain and presumably the amount of food and space available to larvae.

Campbell Davies wanted to know from *John Burke* whether larval bass are stocked back into the same stream from which the broodstock were collected. John Burke indicated that most stocked bass came from broodstock collected from the Noosa River System. He added that electrophoretic studies of bass from different drainages have not been quite completed, but seem to indicate there is not a lot of variation in stock from stream to stream.

John Glaister quesioned *Bill Talbot* as to whether the 'Texas method' of using naturally occurring plankton in ponds with red drum had been tried with bass. Bill Talbot replied that this was tried initially with bass of various ages but they grew slower and there was higher growth and survival in ponds supplemented with *Artemia*. He pointed out that in brackish water ponds, unlike freshwater ponds, it is harder to get good pond preparation and you must make sure that you are getting food to the larvae during early development. Hence the value of supplementary feeding. Stephen Battaglene referred to the fact that in Texas, red drum larvae are stocked into ponds as yolk-sac larvae, and while this has also worked for barramundi it has not worked with bass. He suggested that this may have something to do with differences in the succession of plankton in summer ponds used with barramundi and red drum versus winter ponds for bass. He also pointed out that yolk-sac larvae may be less tolerant of poor water quality in under-prepared ponds.

The process of initial swim bladder inflation was suggested by Stephen Battaglene as another possible reason for the low survival of yolk-sac bass larvae stocked into ponds, in particular the role of light was mentioned as inhibiting inflation. Iain Suthers asked whether the larvae have to gulp air at the surface to inflate their swim bladders. Bill Talbot said this was the case with bass and that a surface skimmer to take the oil off the top of the water surface increased swim bladder inflation rates in intensively reared bass. Other species which have similar inflation mechanisms were then mentioned and included golden perch, snapper, striped bass and European

sea bass. Stephen Battaglene emphasised that factors influencing swim bladder inflation were species specific.

Jim Tait wanted to know from *Peter Gehrke* whether any studies had looked at the physiological cost of larvae having to regulate trace metal concentrations. Peter Gehrke was not aware of any such studies.

Following *Frances Ruwald's* presentation, Maria Milicich asked what wild zooplankton had that rotifers and *Artemia* did not. Frances Ruwald suggested it may be essential fatty acids. The general aim of the striped trumpeter program was then discussed. Frances Ruwald hoped that ultimately striped trumpeter will be farmed in the same way as Atlantic salmon are today and highlighted the almost total lack of information available on the species.

Nigel Preston suggested that there was an opportunity to put larvae in enclosures and examine their diet. Frances Ruwald mentioned some early pond trials which had been run to look at natural diet. There was then considerable discussion on the value of enclosure studies to determine what larvae ate in the wild. Bill Talbot doubted that the density of food would be high enough in enclosures for larvae to survive. Stephen Battaglene supported these remarks by pointing out the patchy nature of food in the wild and the very low survival rate of larvae in the wild. The value of extensive larval rearing as a means of determining what larvae may prefer to eat was then discussed. Peter Doherty made the point that marine fish larvae in a laboratory may require high densities of food, but this was not necessarily the case for larvae in the wild, a view shared by Mike Sinclair. This point raised considerable discussion.

In general the aquaculture representatives thought food density was a critical factor determining survival in reared larvae and extrapolated this to the survival of larvae in the wild. Mark M^{c}Cormick spoke about experiments with juvenile goat fish where two different types of net enclosures were tried in a very high current area. He thought this would ensure a large quantity of zooplankton but the fish were starving within ten days. He indicated that the larvae in the laboratory also starved within ten days and questioned the use of cages with young larvae (<20 days).

Iain Suthers mentioned the problem of determining what a larva eats from its stomach contents, particularly things like rotifers. Bill Talbot who has looked at the stomach contents of bass larvae explained that the lorica of rotifers usually stays intact. Frances Ruwald indicated that no work had been done on striped trumpeter larvae in the wild.

Iain Suthers wanted to know whether tropical fish larvae were starving because of high water temperature? Mark M^{c}Cormick said no – and the temperature was about 26-27 ^{0}C.

Mike Sinclair asked *Martin Daintith* why the whitebait fishery declined. Martin Daintith replied that it was due to overfishing and had been very slow to recover.

The *General Discussion* on Session 2 commenced with debate on the importance of swim bladder inflation as a possible factor influencing larval mortality. Aldo Steffe thought swim bladder inflation was very important as an energy conservation mechanism at night and pointed out that different species have different inflation strategies depending on where they are in the water column. Stephen Battaglene asked whether there was a diurnal pattern to swim bladder inflation. Aldo Steffe said there are two main patterns; some fish have totally deflated swim bladders by day and inflate by night, the others have inflated swim bladders both day and night but increase the volume of their swim bladders at night.

Johann Bell asked whether nutrition affected swim bladder inflation in reared larvae. Stephen Battaglene replied that some recent studies have linked high levels of highly unsaturated fatty acids (HUFA) and thyroid hormone to improved swim bladder inflation rates. Aldo Steffe discussed the phylogenetic principle that

more primitive fishes have a connection from the swim bladder to the alimentary canal throughout their entire life. The more advanced fishes have the connection only in early life, flat fishes have no swim bladder, and some fish have developed a closed gas gland.

Barry Bruce wanted to know whether snapper needed to go to the water surface to inflate their swim bladders and suggested that turbulence might affect larval mortality. Stephen Battaglene replied that reared snapper had similar requirements to bass with regard to inflation; only the strongest larvae are probably capable of swimming to the water surface.

Peter Doherty asked the panel if they had any advice on appropriate measures to determine larval fitness. Stephen Battaglene suggested stress tests. John Burke described stress testing as a useful tool and listed air exposure, salinity shock and temperature shock as tests which appear in the literature. He mentioned that these techniques are not commonly used in Australia. Stephen Battaglene mentioned the shortcomings of using larval length as an index of condition. Iain Suthers asked if larvae were more fragile to handling at various stages in their development. Stephen Battaglene said this was the case with larvae he had reared and cited studies with sea bream and sea bass in France which showed that larvae are most delicate during weaning from live food to pellets.

Peter Gehrke put up a slide of the daily ration of food in relation to prey density. He cited a study by McKenzie where the critical prey density was around 180 mg per litre of prey. He pointed out that no matter how much you increase the prey density above this point there was no apparent effect on daily ration. He went on to explain that at NSW Inland Fisheries Research Station (IFRS) they aimed for about 3000 mg of prey per litre, not to have a large amount of prey at the start of a trial but to ensure enough food was available by the time they harvest some 3 months later. He suggested the energetics, prey density, and foraging ability of larvae are important considerations when examining the question of food limitation.

Stephen Battaglene said that larvae in a tank often band together in a very tight mass, and wondered if this was the case in the wild. John Burke said this was also his experience with cultured barramundi and bass. Peter Gehrke asked them if there was even distribution of food in cultured fish, but they did not think the clumping behaviour was related to food distribution. Greg Jenkins made the point that collection techniques in the wild are not sophisticated enough to detect spatial changes on this scale. He indicated that larvae can have a depth preference on a particular day and be quite concentrated (22 larvae per cubic litre).

The role of disease as a possible factor affecting larval survival was raised by Stephen Battaglene who said that disease, in particular ectoparasites, in both fresh and salt water, are a limiting factor in extensive rearing. Martin Daintith asked what diseases caused problems and what treatments were used. Bill Talbot replied that protozoans such as *Trichodina* and *Scyphidia* caused problems and he treated ponds with malachite green 0.5 ppm or formalin 15 ppm.

Aldo Steffe commented on the energetic arguments put up by Peter Gehrke earlier. He said that the larvae are not just passive drifters and there was a trade off between the time where the larvae can spend feeding and the time when they would avoid being swept away into an unfavourable area. He therefore suggested that the energetic constraints are going to be very different in the wild to those derived in the laboratory. Peter Gehrke agreed with this comment.

SESSION 3

BIOLOGICAL EFFECTS OF OCEANOGRAPHIC PROCESSES

Session Chairperson:	I. M. Suthers
Session Panellists:	S. R. Thorrold and A. D. McKinnon
	A. S. Steffe and M. Westoby
	A. J. Jordan
	B. D. Bruce and D. A. Short
	J. D. Booth and R. A. Stewart
Rapporteur:	L. J. Worland

CHAIRPERSON'S INTRODUCTION

I.M. Suthers

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The importance of measuring physical variables in conjunction with biological sampling of the ocean has been emphasized by many, and reviewed by Legendre and Demers (1984). For example Frank and Leggett (1985) showed that reciprocal oscillations in gelatinous predators and larval fish prey were the result of water mass replacement, driven by onshore/offshore winds, and were not the result of classic Lotka-Volterra dynamics. Similarly, the pursuit of a simplistic grid of stations to determine the distribution and abundance of ichthyoplankton may be misguided and prone to high variance, due to aggregation processes that occur around flotsam, fronts, eddies, shear zones and other linear oceanographic features (Wolanski and Hamner 1988; Kingsford 1990). The aim of this session is to examine some of the interactions between physical features and larval ecology.

One of the first Australian studies to consider the interaction of biota with oceanographic features was the transport of larval phyllosoma of the western rock lobster (reviewed in Phillips 1981). Another early study was on the effects of a mesoscale eddy of the East Australian Current (EAC), by Brandt and Wadley (1981). Today, with satellite imagery we are now far more aware of the nature of large scale features such as the EAC and its eddies, the Flinders Current, the Leeuwin Current and the impacts of El Niño-Southern Oscillation (ENSO) events (Jeffrey *et al.* 1990). There have been other notable Australasian studies on the effects of oceanographic processes on larval distributions, which include larval prawn transport in the Gulf of Carpentaria (e.g. Vance *et al.* 1985), the seasonal distribution of larval fish off the north-west shelf (Young *et al.* 1986), and the distribution of larval blue grenadier off the west coast of Tasmania (Thresher *et al.* 1989), and the west coast of New Zealand (e.g. Murdoch *et al.* 1990). We should give greater recognition to the fundamental contribution of these and other recent larval studies (see summary of literature on fish larvae by Miskiewicz this meeting) to the management of our coastal fisheries. The recent shift in some quarters from larval research to strictly adult fish biology is as short-sighted as ignoring environmental considerations in order to create jobs. A major new frontier in larval biology and fisheries management is the spatial and temporal distribution of spawning effort in Australia's temperate fisheries, and the influence of sporadic upwelling (Jeffrey *et al.* 1990) or run-off.

On the Great Barrier Reef, physical and biological oceanographers are investigating the effects of circulation and riverine inputs on the larvae of the Crown-of-Thorns starfish. Are outbreaks of the starfish due to nutrient inputs or altered circulation features? In a similar vein, Simon Thorrold and David McKinnon report in this Session on the coastal boundary layer off Townsville, where consistently high abundances of larval fish are observed. They also discuss the effects of massive riverine inputs from Cyclone

Joy in January 1991 on the larval distributions in this boundary layer, and on primary and secondary production.

On the east coast of the north island of New Zealand, John Booth and Robert Stewart show the influence of the East Cape Current, and the role of hydrographic features assisting larval retention and settlement of lobster puerulus.

Off eastern Tasmania, Alan Jordan discusses the role of the East Australian Current and the influence of the 1988/89 ENSO event, which may have altered not only the distribution of spawning effort by jack mackerel, but also reduced the trophic links in this area, and resulted in the low production of a variety of fish larvae.

The Spencer Gulf of South Australia supports a valuable fishery for King George whiting; however we know little about the distribution and transport of the larvae. The circulation features are complicated during the summer by a strong front across the mouth of the Gulf, generated by the net evaporative loss at the head of the Gulf (an "inverse estuary"). Barry Bruce in his presentation discusses the age and growth of whiting larvae in the Spencer Gulf, and summarises how the front acts as a barrier to the exchange of larvae with the ocean. He shows a remarkable diversity of larvae in the area, and how the distribution of larvae around the front appears sometimes to be taxon-specific - showing yet again that there are no generalised larval models of dispersal.

At a much finer scale, Aldo Steffe and Mark Westoby examine the effects of an estuarine eddy on the horizontal and vertical distribution of larval fish in Botany Bay, and focus our attention on the ontogenetic development and subsequent behaviour of larvae, and the critical role of the swim bladder. How do fish larvae maintain their distribution in a tidally mixed estuary with a net outflow?

The Workshop's keynote addresses by Rob Murdoch and John Zeldis, and the summaries by the five panellists of this session, as well as other on-going larval research by the Australian oceanographic community (such as on reef fishes, abalone, prawns, scallops, spanner crabs, estuarine plumes and sewage plumes), all highlight the importance of hydrographic features in influencing the distribution of larvae and ultimate recruitment success. During this session, and the discussion, we shall be reminded of the inadequacy of most physical, numerical models in describing larval transport. This is due to unrealistic assumptions of larvae as passive particles, and to our preference for 2-dimensional, depth-averaged models. Mike Sinclair has speculated privately that Australia's relatively small fish-landings may be due not only to general nutrient impoverishment, or to the narrow continental shelf, but perhaps to the lack of topographic and hydrographic features that provide larval retention areas. Hopefully, with new ideas (and new technologies), this workshop should stimulate many of us to address the importance of hydrographic features in larval ecology.

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BIOLOGICAL SIGNIFICANCE OF THE COASTAL BOUNDARY LAYER OFF TOWNSVILLE, NORTH QUEENSLAND

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Abstract

We sampled across a hypothesized coastal boundary layer off Townsville, North Queensland, over the summer (October-March) of 1990/91. Physical (temperature and salinity) and biological (chlorophyll *a*, zooplankton abundance and copepod egg production rates) variables were measured at fixed stations 8, 16 and 24 km from the coast. Temperature and chlorophyll *a* gradients were observed across the presumed front, with the inshore station having consistently higher values than offshore stations. Plankton abundances showed greater variability, with no consistent trend through time. The physical environment during the sampling period was dominated by a large input of low salinity water associated with Cyclone Joy in January 1991. This plume moved 30 km offshore during January, with concomitant increases in both plankton numbers and productivity. Oscillations in the position of chlorophyll-rich coastal waters, caused by variations in wind-stress and the strength of the East Australian Current, may lead to enhanced plankton production at the boundary between coastal and offshore water masses.

Introduction

Over the past three years, Australian Institute of Marine Science staff have used light traps to monitor larval and juvenile fish distributions across the central Great Barrier Reef lagoon. A consistent peak in the abundances of both reef and pelagic fish species has been observed at a station 16 km from the coast. Modelling studies (King and Wolanski 1990) and satellite imagery suggested that this position corresponded to a zone where coastally trapped, nearshore water becomes decoupled from offshore water under the influence of the East Australian Current. The aim of this study was to determine if the observed aggregations of small fish may be explained by enhanced biological activity at this frontal zone.

Methods

Sampling was conducted in the central Great Barrier Reef lagoon, off the coast of Townsville. We visited fixed stations (numbered 3, 2, and 1 respectively), 8, 16 and 24 km from the coast, approximately once a month from October 1990 to May 1991. At each station, triplicate water samples were collected, at the surface, mid-water and bottom, using a Niskin bottle. Temperature and salinity were measured from each cast, and the water from each set of three depths was pooled to provide replicate depth-integrated samples for chlorophyll *a* analysis. Chlorophyll samples were analysed by fluorometry.

At each station, three vertical plankton hauls using a 150 mm plankton net (diameter 0.5m) were made, and preserved in 5% formalin/

seawater. Then a gentle sub-surface horizontal tow was made to collect live copepods for egg production experiments. Copepod egg production provides a convenient method of estimating copepod secondary production. Several species of copepod were initially trialled. *Acrocalanus gibber* was chosen as it was abundant and easy to both recognise and handle. Nine 250 ml pyrex bottles were filled with water collected from each station, which had been passed through a 100 µm filter to remove most juvenile copepods. The live plankton sample was condensed, and live specimens sorted. A single adult female was then placed in each of the bottles, and incubated on a plankton wheel for 24 hr. After incubation, the eggs and nauplii in each bottle were counted to determine the egg production rate of each female. Since no acclimation period was allowed, we reasoned that the egg production in the laboratory woud reflect the feeding conditions encountered in the field by the copepods prior to capture.

Results

Sea-surface temperature showed a steady upward trend during summer (Figure 1), peaking in January before cooling off through March and May. Surface waters showed a gradient across the sampling stations, with warmer waters at the inshore stations, and cooler water offshore (Station 1). This trend appears to be reversed in May, with cooler waters inshore. A sharp rise in temperature at all stations on January 23, was associated with similar drops in salinity. This was due to a shallow lens of less saline water (approximately 20 ppt) moving rapidly offshore (at least 8 kilometres in 4 days). This lens of low salinity water was the result of cyclone Joy hovering off the coast of Townsville, bringing with it the wettest January on record. Streamflows of the Burdekin River, approximately 100 km south of Townsville, recorded levels of 18000 megalitres per day during February (Figure 2), and monthly totals in both January and February of over 10 000 gigalitres.

Chlorophyll *a* numbers showed remarkably little variation throughout the sampling period, varying between 0.2 and 0.7 mg l^{-1} (Figure 3). The inshore station (3), 8 km from the coast, had consistently higher chlorophyll values than either of the offshore stations, which were similar. Again the effect of the freshwater plume is apparent. Although chlorophyll values at the 8 km station actually dropped during this period, a sharp increase in chlorophyll *a* at both the 16 and 24 km stations was apparent as the less saline water moved offshore.

Plankton abundances showed no apparent trend through time across the stations (Figure 4). Generally, the inshore station had higher plankton numbers than the two offshore stations. This was however, variable, and at different times the 16 and 24 km stations had the highest numbers. Abundances increased dramatically at all stations in January, with numbers at the inshore station peaking on January 18. Numbers at the 16 km station did not peak until March, while the 24 km station showed high abundances on January 23 and in March. Plankton numbers dropped dramatically in May, and returned to similar values recorded before January. Thus abundances were maintained after the chlorophyll maxima recorded in January. Flow records from the Burdekin River (Figure 2) suggested, however, that there was a prolonged period of freshwater input during both January and February, and enhanced chlorophyll values may have occurred throughout this period.

Copepod community composition at all stations was coastal/neritic in character, though the 24 km station often included oceanic species (*Clausocalanus spp.*, Calocalanidae), which were less abundant or absent at the 8 and 16 km stations. There was less evidence of a resident "coastal" community, though some species, such as *Acrocalanus gibber*, were more abundant inshore.

Egg production rates of *A. gibber* are compromised by our inability to collect enough *A. gibber* in plankton tows in November or De-

cember to conduct the egg production experiments. The data we do have suggest that daily egg production increased markedly during January, compared with October, March or May (Figure 5). Mean daily egg production increased from approximately 10 female^{-1} day^{-1} in October to 30 female^{-1} day^{-1} in January, before dropping down again in March. The highest value we obtained was 41 female^{-1} day^{-1}, at the 24 kilometre station, on January 23.

Discussion

The presence of a frontal zone between coastal and offshore water in an oceanographic model of the area developed by King and Wolanski (1990), provided a convenient explanation for observed distribution patterns of juvenile fishes in the central Great Barrier Reef Lagoon. We hypothesized that enhanced production at a frontal zone, between nearshore water trapped along the coast and offshore water moving under the influence of the East Australian Current, may aggregate small fish and their prey. Our results do not, however, support this hypothesis. We were unable to to detect consistently higher standing stock of chlorophyll *a*, plankton abundances or secondary production of *A. gibber*, at the frontal zone.

Cyclone Joy gave us a unique opportunity to study the effects of large amounts of low salinity (and presumably high nutrient) water on the coastal plankton community. Chlorophyll *a* values did not increase at the inshore station during this period, but did increase at both 16 and 24 km stations. Both plankton abundances and egg production rates of *A. gibber* were, however, enhanced at all stations during this time. While we have no information on the composition of the phytoplankton community, this suggested that the phytoplankton species that responded to the freshwater event were of a high food quality for herbivorous copepods. Garcia-Soto *et al.* (1990) noted that large diatoms, especially *Skeletonema costatum*, developed rapidly after nutrient input from freshwater runoff in the Bay of Biscay. Furnas (1989) also found that growth rates of diatoms were extremely fast immediately after Cyclone Winifred crossed the north Queensland coast in February 1986.

Temperature and chlorophyll distributions across the sampling transect suggested that there was some separation between nearshore and offshore waters in this region. Our inability to detect an "inshore" copepod community indicates, however, that there may be considerable leakage of water across this boundary zone. This is not surprising, given that the exact position of the separation zone is likely to change under the influence of both meteorological and hydrological forcing events (King and Wolanski 1990). For instance, King and Wolanski's model suggests that under increasing SE winds, the separation zone moves offshore, before breaking down entirely as wind speeds approach 7-10 ms^{-1}. High secondary production may be occurring at the frontal zone due to this "leakage" of coastal water across the boundary layer. Our results suggest that herbivorous copepods such as *A. gibber* are capable of rapid responses to the input of chlorophyll-rich coastal water. The variability in zooplankton numbers we have found across our sampling stations may, then, reflect the dynamic nature of this frontal system. If so, sampling will have to be conducted on smaller spatial and temporal scales to gain a full understanding of the biological significance of this feature.

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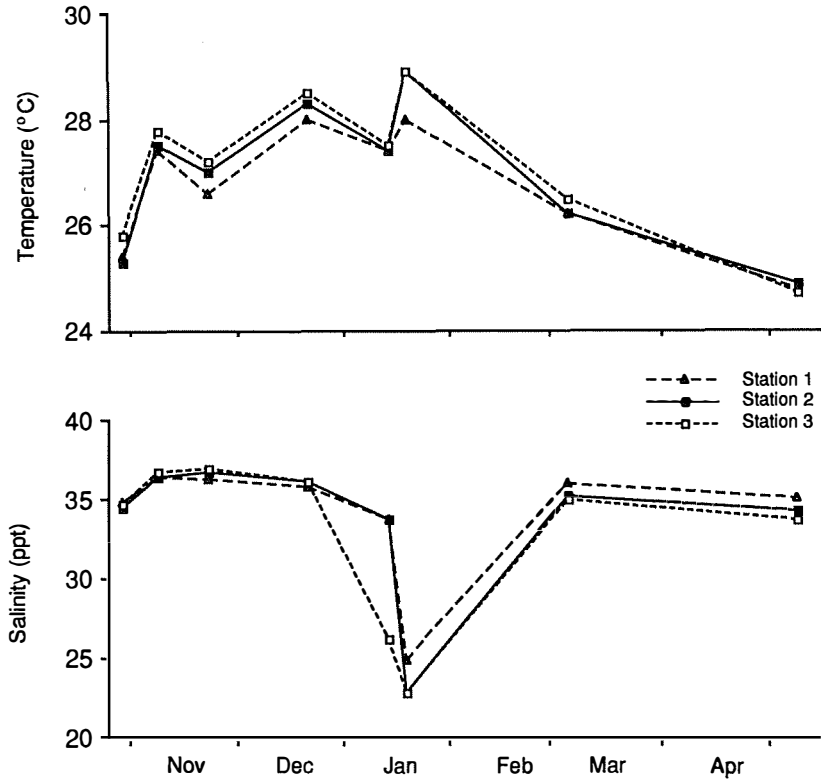

Figure 1. Sea-surface temperatures (top) and salinities (bottom) at sampling stations, October 1990-May 1991. Stations 1, 2 and 3 are respectively 24, 16 and 8 km from the coast.

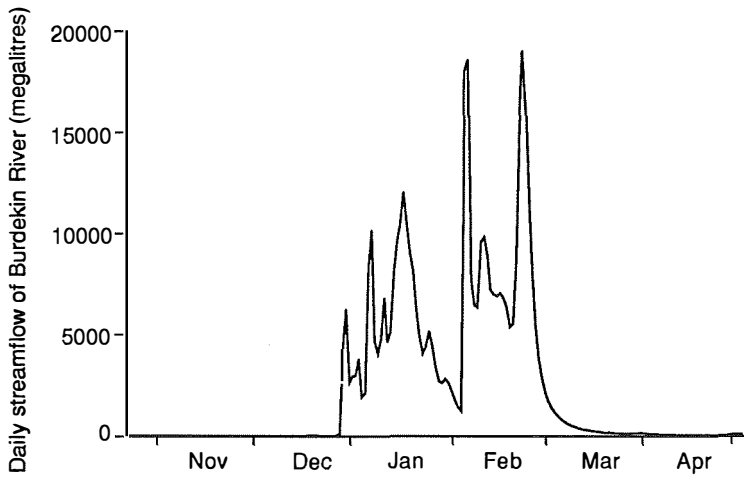

Figure 2. Daily streamflows (megalitres) of the Burdekin River at Clair, October 1990-May 1991.

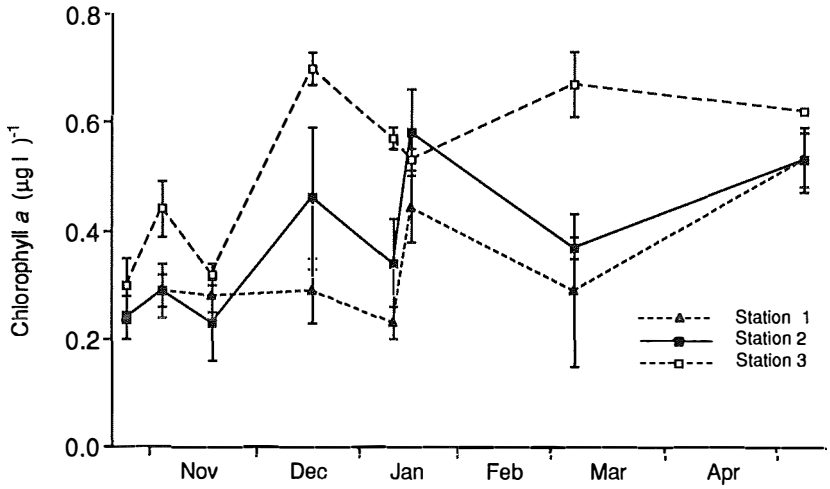

Figure 3. Total chlorophyll *a* concentrations (mg l^{-1}) at sampling stations, October 1990-May 1991.

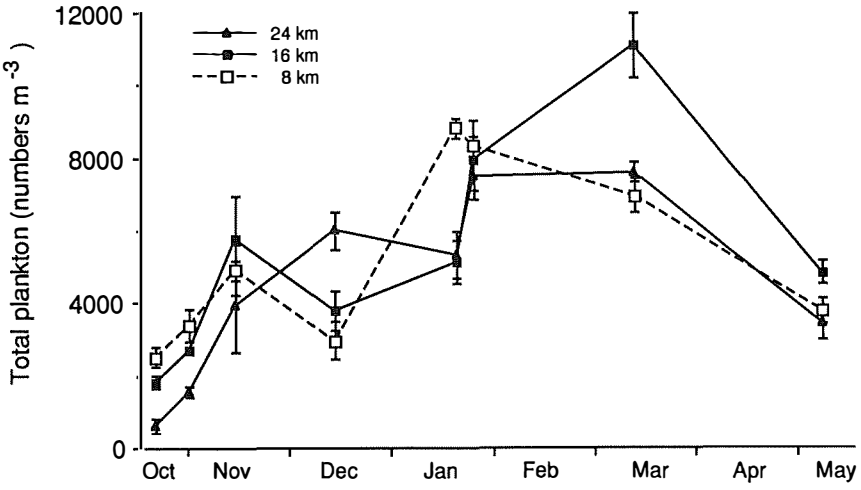

Figure 4. Total plankton numbers (nos. m^{-3} at sampling stations , October 1990-May 1991.

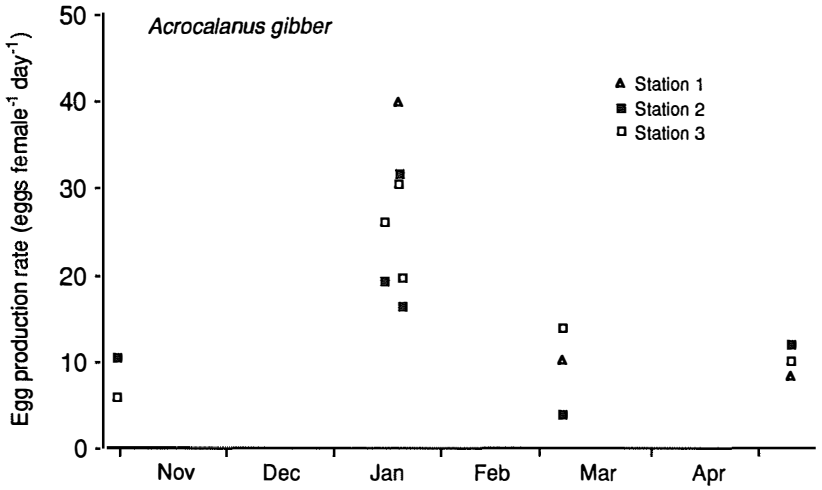

Figure 5. Daily egg productions (eggs $female^{-1}$ day^{-1}) of *Acrocalanus gibber*, October 1990-May 1991.

TIDAL CURRENTS, EDDIES AND ORIENTATED BEHAVIOUR BY LARVAL FISHES

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General background

Australian marine embayments, lagoons and estuaries are important nursery areas for many species which spawn at sea, and also for resident species which can complete their entire life cycle within estuarine areas (State Pollution Control Commission of New South Wales - SPCC 1981: Bell *et al.* 1984; Middleton *et al.* 1984; Bell *et al.* 1988; Potter *et al.* 1990; Ferrell *et al.* 1990). Larvae originating at sea may be transported towards estuarine entrances by seasonal winds (e.g. Nelson *et al.* 1977; Pietrafesa *et al.* 1986; Taggart and Leggett 1987), estuarine fronts (Govoni *et al.* 1989; Kingsford 1990), convergences associated with internal waves (Kingsford and Choat 1986), coastal trapped waves (Church *et al.* 1986), or the vagaries of offshore eddy movements in the East Australia Current (Boland and Church 1981; Creswell *et al.* 1983; Louis 1989). These larvae must then negotiate[1] tide-swept entrance channels prior to entering the estuarine system. Once within an estuary, a common problem for larvae is how to avoid being flushed out to sea during ebb tides. This is true for the larvae of both ocean spawned and resident species. Finally, larvae competent to settle must find suitable nursery habitats. Throughout this entire migration process larvae must balance the necessity to feed and avoid predators against the risk of not finding suitable nursery habitat.

Weinstein *et al.* (1980) proposed that orientated vertical movements by larvae, in response to changes in tide and photoperiod, allowed larvae to use the residual landward flow near the bottom to avoid seaward transport and to aid their recruitment into nursery habitats within a stratified estuarine system. This mechanism has often been invoked in subsequent studies examining estuarine recruitment of larval fishes (Norcross and Shaw 1984; Robison 1985; Boehlert and Mundy 1988). However, it is still unclear how ocean-spawned larvae are able to initially reach these upper estuarine areas in which density-driven bottom currents can be used to assist their upstream movement towards preferred nursery areas. The mechanism(s) by which larvae achieve this are poorly understood (Miller *et al.* 1984; Norcross and Shaw 1984; Boehlert and Mundy 1988; Miller 1988).

[1] The authors elected to express larval behaviour in such terms as "negotiate", "use" etc. For other comments on Passive Particle and Orientated Behaviour models, the reader should refer to the various reports of discussion. Ed.

Here we summarize the conclusions arising from an intensive sampling program designed to describe larval fish distributions at two sites which are characterized by different current regimes and are near the entrance of a large marine-dominated bay - Botany Bay, NSW (34°01'S, 151°11'E - see Figure 1). Analysis of variance techniques were used to assess variation in larval fish concentrations due to vertical position in the water column (surface vs epibenthic), developmental stage (preflexion and flexion stages vs postflexion stages), tidal (mid-flood vs mid-ebb) and diel (day vs night) factors. Detailed methods and results of this study are presented in Steffe (1991).

We ask two main questions : (1) Can larval distributions at each site be explained solely by localized circulation patterns without recourse to effects of larval motility or behaviour? (2) If not, can larval distributions at each site be better understood in terms of behaviours which enhance the probability of larval retention and recruitment within estuarine systems? These questions are addressed by initially constructing a null model predicting the consequences if larvae act as passive particles. Finally, a model based on orientated larval behaviours is proposed to explain the observed larval distributions. We also discuss the potential of this model for predicting larval distributions in other coastal and estuarine areas, and hence the model's potential for ultimately predicting relative settlement patterns of juvenile fishes into seagrasses or other nursery habitats.

Larval assemblage

More than 29,000 larval fishes were caught and 144 larval fish taxa recorded during the sampling period. The larval assemblage was dominated numerically (>61%) by taxa which have demersal reproductive strategies and which presumably spawn within Botany Bay, such as gobies, blennies and syngnathids. Taxa which spawn in nearshore marine habitats, and also taxa which spawn pelagic eggs within the Bay were important components of the larval assemblage both taxonomically (>57%) and numerically (>37%). Although taxa of offshore and tropical origin comprised nearly 16% of the taxa caught, their numerical contribution (0.5%) was relatively unimportant.

Passive particle null model

The sampling sites had very different physical characteristics although they were located at similar distances from the Bay entrance (Figure 1). These physical differences between sites can be expressed as different flow environments at each site (see Nowell and Jumars 1984). The Tidal Stream (TS) site was located away from the shoreline in an area dominated by strong tidal currents and exposed to the prevailing wind and ocean swell conditions (Figure 1). The Port Area (PA) site was located near the shoreline in an area dominated by a complex of relatively slow moving eddies (Figure 1). Also, the Port Area site was located within the dredged Port Botany shipping channel, which runs perpendicular to the direction of the main tidal current stream and has steep banks, thus creating similar flow conditions to those described for flows over depressions (see Nowell and Jumars 1984). A null model which assumes larvae act as passive particles did predict different larval distributions at each of these sites. However, the larval distributions we recorded at each site did not conform to these predictions. Thus, the null model was shown to be a poor predictor of larval distributions at these sites.

Orientated behaviour model

A larva's behavioural responses to its perceived environment are strongly dependent upon the presence or absence of directional stimuli. It seems that larval behaviours have structured larval distributions within Botany Bay, given that a passive particle null model based solely on the prevailing circulation patterns was a poor

predictor of larval distributions. Thus, we propose that larval recruitment into and retention within Botany Bay, and other marine dominated bays, estuaries and lagoonal areas, can be explained in terms of larval orientation (or disorientation) interacting with circulation patterns.

Our model describes larval recruitment and retention processes as being active orientated behavioural responses to environmental stimuli during the day. At night the orientated behaviour model predicts that the precision of larval responses is reduced, rendering nocturnal behavioural responses largely passive. This scenario, of course, can be expected to change depending on larval ontogeny and behavioural differences between species. That is, individual species, and even different developmental larval stages, may use different behaviours to solve the problem of estuarine recruitment.

We hypothesize that the following behavioural processes, either individually or in concert, were important in structuring the observed larval distributions in Botany Bay:

1. Larval use of the reduced current flow within the epibenthic layer, particularly during ebb tides
2. Behavioural plasticity
3. Disorientation at night
4. Nocturnal gas bladder inflation strategies.

Larvae located in areas having strong tidal currents were found to use the reduced flow associated with the epibenthic layer, particularly during ebb tides, to enhance their recruitment into Botany Bay. It is likely that innate rhythmic behaviours having tidal and diel periodicities are used by larvae to aid their recruitment into estuaries. Although these types of rhythmic behaviour are apparently important for larvae attempting to negotiate tide-swept areas it seems that flexible behavioural traits which allow larvae to take advantage of localized favourable conditions may quickly override previously entrained behavioural patterns.

Many larval behaviours such as feeding (Hunter 1981; Blaxter 1986), schooling (Bond 1979; Partridge and Pitcher 1980), and orientation to currents (Arnold 1969; 1974) are largely dependent on vision. Consequently, it should be expected that orientated responses by larvae should be best during daylight and larval disorientation should be greatest at night when visual acuity is reduced. The degree to which nocturnal disorientation occurs can be expected to vary ontogenetically and also between species. Thus, we regard day-time distributions as a measure of a larva's preferred position in the water column. This selected position may be influenced by constraints imposed by current speeds or the location of food patches. However, at night a larva that is not in contact with a fixed reference point such as the seabed may experience passive drift interspersed with bouts of unorientated swimming. Nocturnal gas bladder inflation strategies aimed at conserving energy (Hunter and Sanchez 1976; Steffe 1991) may also lead to changes in vertical distribution at night thereby exposing these larvae to passive drift. At dawn the daily cycle is completed as larvae quickly move back to their preferred positions in the water column.

Implications

The orientated behaviour model describes processes which occur during the planktonic phase of larval fishes. These processes are greatly influenced by larval behaviours and ultimately they structure the distribution of larvae that are competent to settle. Thus, the orientated behaviour model is also important in explaining settlement patterns of juvenile fishes within marine bays, coastal lagoons and estuaries. The model predicts that settlement rates may vary between similar nursery habitats because some larvae consistently tend to accumulate in some areas but not in others. We believe eddy-dominated sites tend to accumulate larval fishes and that larval survival may also be enhanced in these areas. Also, the model predicts that the effects of

stochastic events should be mitigated within nursery areas located near to sites favouring larval accumulation, whereas stochastic effects should greatly influence the structure of juvenile fish assemblages in nursery areas associated with 'average' larval sites, such as in tide-swept entrance channels.

Epibenthic flows and eddy circulation patterns appear to be important to larval recruitment and retention processes. If the relationship between orientated larval behaviours and hydrography is correctly understood, as we have argued above, it should be possible to predict, based on localized hydrography, which sites should have consistently high recruitment and also which sites should have variable but usually low recruitment. Therefore, it should be possible to implement sampling designs for use in both larval surveys and settlement studies which select replicate sites according to local hydrography, and hence the predicted potential of a site for larval recruitment success, rather than by only using a simple randomized design. The orientated behaviour model, though descriptive rather than quantitative, provides many testable hypotheses pertinent to estuarine and nearshore recruitment processes for fishes.

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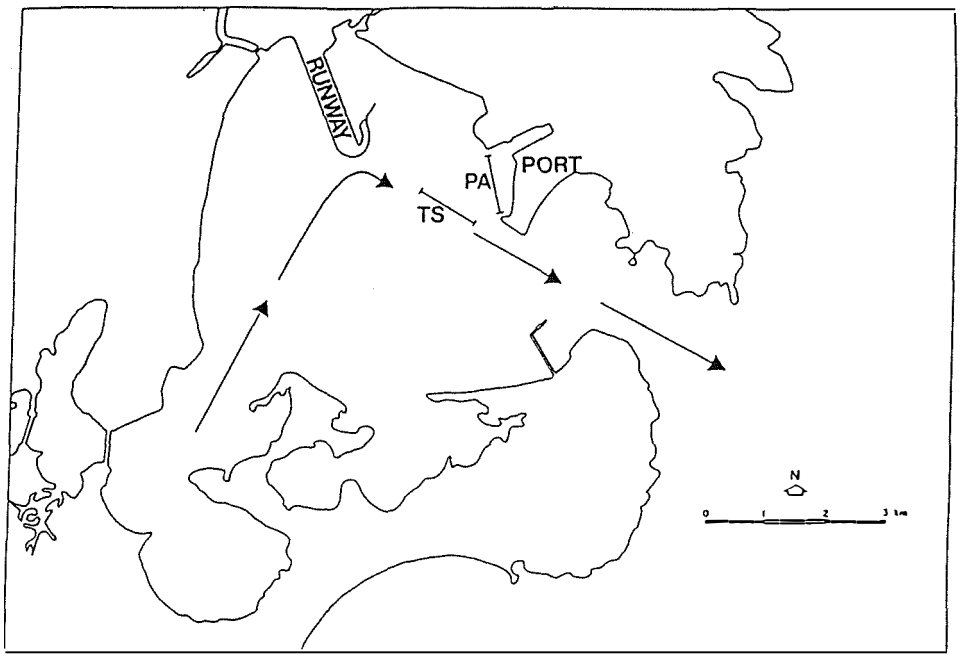

Figure 1. Map of Botany Bay showing location of sampling sites. Note - TS = Tidal Stream site, PA = Port Area site. Arrows indicate location of main tidal current stream.

INTERANNUAL VARIABILITY IN THE OCEANOGRAPHY OF THE EAST COAST OF TASMANIA AND ITS EFFECTS ON JACK MACKEREL (*TRACHURUS DECLIVIS*) LARVAE

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Introduction

While the actual mechanisms responsible for El Niño events around the world are not completely understood and may vary with latitude and between events, the oceanographic conditions that occur during such events are well documented. It is clear that El Niño events result in warm sea surface temperatures and a deepening of the thermocline. Changes in wind driven Ekman transport also result in reduced coastal upwelling (Mysak 1986).

During the summer of 1988/89 the east coast of Tasmania experienced a period of ocean variability, known as a La Niña, that has been linked to the large scale ocean/atmosphere coupling in the southern hemisphere associated with an El Niño/Southern Oscillation (ENSO) event (Harris *et al.* 1991). The regional oceanography of this area is determined firstly by the local westerly wind stress and secondly by the large scale oceanographic circulation dominated by the warm, nutrient poor East Australian Current (EAC) and cool, nutrient rich water of subantarctic origin. During summer the shelf on the east coast is episodically flooded with EAC water, while westerly winds occasionally move subantarctic water up onto the east coast (Harris *et al.* 1987). The boundary that separates these two water masses is defined as the subtropical convergence, the position of which shows significant interannual variability (Harris *et al.* 1987).

The summer of 1989 saw an increase in subtropical influence resulting from a reduction in the westerly wind stress and increasing influence of EAC water from the north. This situation led to a range of physical processes on the shelf break, such as warm sea surface temperatures (Figure 1a) and strong thermal stratification (Figure 2a). Whilst no data are available, it is likely that the reduced westerly wind stress also decreased Ekman transport, while onshore transport may have increased due to the dominance of the EAC on the shelf. The past two years have seen a much greater influence of subantarctic waters with resultant cooler sea surface temperatures (Figure 1b,c) and less stratification (Figure 2b). However, given the dynamic nature of mesoscale eddies and fronts on the east coast, intrusions of warm EAC water have episodically occurred.

Harris *et al.* (1991) provided a detailed analysis of the effects of the 1988/89 La Niña event on the water column stratification, nutri-

ent cycling and production and structure of the food chain in south East Tasmanian waters. They detailed a general decline in nutrient conditions of the shelf waters up to the summer of 1988/89 with an associated shift in community structure. There was a reduction in algal biomass, and almost total elimination of large zooplankters (principally the euphausiid *Nyctiphanes australis* and salps *Thalia democratica* and *Salpa maxima*) from shelf waters. These conditions led to populations of small copepods dominating, which are less affected by levels of production as they can switch from herbivory to omnivory (Cushing 1989). This appreciable compositional change in the zooplankton community in oligotrophic conditions is similar to that found in the California current region (Smith 1985) and indicates a differential response to ENSO events by different members of the pelagic food web.

The variability in both physical and biological processes experienced in these waters during the La Niña year of 1988/89 and subsequent 'normal' years is likely to impact on the spawning behaviour and survival of eggs and larvae in these waters. Physical processes likely to have an impact include changes in temperature, horizontal advection, vertical stability and turbulence. While data on physical processes are sparse for the shelf region of the east coast, the presence in summer of EAC eddies, shelf fronts and wind driven transport and turbulence makes this area highly variable. Biotic factors which are important include changes in the abundance and distribution of predator and prey communities, and the amount of food available for energy storage and mobilization for reproduction.

The larval sampling program conducted on the east coast of Tasmania between January and April 1989-91 has provided an opportunity to assess the impact of the oceanographic variability on the spawning and early life history stages of jack mackerel (*Trachurus declivis*). The purpose of this paper is to discuss the potential impact of this variability on both spawning adults, eggs and larvae, and what factors may have influenced interannual variability in egg and larval abundances. The range of possible effects on jack mackerel spawning, and eggs and larvae resulting from such variability is summarised in Table 1.

Effects on spawning population

Spawning time and distribution

Analysis of three years of jack mackerel egg and larval distributions, and backcalculated spawning dates from otolith ageing suggests that neither the spawning area, time or duration for jack mackerel on the east coast of Tasmania were affected by the La Niña event of 1989. Spawning in all three years began in late December and continued till late February with the bulk of spawning occurring in January in all years. Spawning was continuous throughout the sampling area with highest egg densities at shelfbreak stations, and no evidence of a major concentration and shift in spawning area. The data suggest that the response of adult jack mackerel to the La Niña event was to move from the shelf waters onto the shelfbreak/slope area, their normal site of spawning.

Several workers have identified a shift in spawning time in response to interannual differences in water temperature. Gunn *et al.* (1989) estimated that spawning of blue grenadier on the west coast of Tasmania differed between years by a month and suggested that such changes resulted from interannual differences in water temperature. Spawning distribution however was unaffected. Ware and Lambert (1985) also related timing of peak spawning of Atlantic mackerel to changes in water temperature which they concluded is a regulator of spawning activity and oogenesis.

Other species may respond to warm water conditions by changing their spawning distribution. Such changes during El Niño years are well documented for a number of pelagic species. Spawning distributions of several species shifted

polewards during such years, including anchovy in the Benguela current region (Le Clus 1990), and anchoveta (Walsh *et al.* 1980) and sardines (McCall 1979) off South America. There is also some evidence that some South American clupeoid populations migrate into deeper water during strong El Niño events (Arntz 1986). It is also possible that changes in spawning time and location are an adaptive response to spawn in an area and time which makes best use of the seasonal and spatial patterns of ocean stability to provide suitable feeding conditions and favourable transport (Lasker 1981; Shelton and Hutchings 1989). The fact that jack mackerel spawning time, area and duration were consistent in all three years suggests that this may be an adaptive response to spawning in an area with high physical and biological variability.

Energy available for reproduction

The influence of an El Niño event on gonad condition and egg production has been documented for several species with the most immediate effect being a decline in reproductive output (De Martini 1991; Hay and Brett 1988; Lenarz and Echeverria 1986). Experimental and observational studies have demonstrated that naturally occurring food limitations may result in fluctuations in fecundity (Hay and Brett 1988; Hunter and Leong 1981). Variability in egg production may result from decreased batch fecundity in serial spawners (De Martini 1991), changes in mean egg weight (Tanasichuk and Ware 1987), or changes in the duration of the spawning season (Hunter *et al.* 1985). The link between food abundance and reproduction however depends on the dynamics of the prey communities and the spatial and temporal pattern of fat storage and mobilization for spawning.

As previously mentioned, El Niño events almost always result in decline in zooplankton production (McGowan 1985). The situation is no different on the east coast of Tasmania, with the largest decrease occurring in the larger sections of the plankton (Harris *et al.* 1991). The principal food source of jack mackerel late in summer and autumn is the krill species *Nyctiphanes australis* (Webb 1976) resulting in fat reserves up to 12% by April. In the summer of 1989 *N. australis* disappeared from southeast Tasmanian waters (Harris *et al.* 1991) and a subsequent decrease in fat reserves was evident during this year. The bulk of spawning the following year is known to occur before the peak in feeding so it is likely that most of the energy available for reproduction is controlled by the amount of fat stored in the previous summer, as suggested by Hunter and Leong (1981) for *Engraulis mordax*. This may have a direct impact on batch fecundities through a process of folicular atresia (Hay and Brett 1988), and could result in a decrease in egg production in the summer of 1990.

Effects on eggs and larvae

Abundance and distribution of prey

The change in the structure of the zooplankton community in the summer of 1989 identified by Harris *et al.* (1991) in southeast Tasmanian waters clearly affected the abundance of prey available to jack mackerel larvae. Distribution of prey may also have been affected due to the strong stratification throughout the spawning season. Young and Davis (in press) analysed the diet of jack mackerel larvae from that year and identified that although there was a shift in prey taxa between years, with the exclusion of calyptopid stage *N. australis* in the guts in 1989 mirroring their absence in the plankton, there was no evidence of food limitation during the year.

Abundance and distribution of predators

Predation on fish eggs and larvae appears to be a major source of mortality (Hunter 1981), although its dominance appears to change through different early life history stages (Hewitt *et al.* 1985). Hunter (1981) lists crustaceans,

chaetognaths, medusae, ctenophores and planktivorous fish as known predators of fish eggs and larvae. Whilst we have no data on the likely predators or predation rates of jack mackerel eggs and larvae, the large compositional change in the plankton during the La Niña year of 1989 suggests that the level of predation may have been significantly reduced.

Horizontal advection

Several studies have suggested that interannual differences in advection of eggs and larvae can result in significant mortalities and subsequent recruitment variability (Bailey 1981; Nelson *et al.* 1977). In several species this advection is responsible for cross shelf transport of eggs and larvae to inshore nursery areas (Cowan and Shaw 1988; Parish *et al.* 1981) with offshore advective losses controlled by the local hydrographic conditions. The shelf waters of the east coast of Tasmania show significant interannual variability in local hydrography dominated in summer and autumn by the interaction of EAC eddies, shelf fronts and subantarctic water masses (Harris *et al.* 1987). The Maria Island area, the area of highest egg and larval densities in 1989, was defined by Harris *et al.* (1987) as a region of large scale advective processes with episodic effects of mesoscale physical processes superimposed.

Obviously trying to interpret patterns of advection of eggs and larvae in such a dynamic area is a difficult task, with current reversals possible on the shelf over a few days (Pearce 1981). With the reduction in the wind stress and increased influence of EAC water in the La Niña year of 1989, patterns of shelf advection would have been affected. There is clearly some mechanism of onshore advection of eggs and larvae from spawning sites on the shelf break/slope region to inshore waters. It is also clear that such interannual variability in shelf transport may be an important source of mortality for jack mackerel eggs and larvae. While we are presently analysing the age distribution of larvae sampled on cross shelf transects to investigate possible patterns of larval advection, assessing possible offshore advective losses is impossible due to the lack of offshore stations and suitable physical data.

Vertical stability

The hypothesis that ocean stability influences food aggregations for larvae and hence larval survival (Lasker 1981) has been supported by a number of workers (Peterman and Bradford 1987; Walsh *et al.* 1980). The reduction in the westerly wind stress during the summer of 1989 resulted in greater vertical stability during the spawning period (Figure 2a), compared with 1990 (Figure 2b). It is possible that the stability experienced in 1989 resulted in lower larval mortality rates than during the windier and less stable summer of 1990. The lack of data on the vertical distribution of microzooplankton in these years precludes any assessment of its importance in interannual differences in larval survival.

Interannual differences in egg and larval densities

While it is difficult to assess the impact of interannual variability in the range of physical and biological processes outlined on spawning and egg and larval survival, it is clear from the data that there were large interannual differences in egg and larval densities. Jack mackerel pre-flexion density was down from 53.8 per 100 m^{-3} in 1989 to 2.8 per 100 m^{-3} in 1990 (Table 2a). This relates to a pre-flexion larval density in 1990 only 5.2% of that in 1989. Jack mackerel egg density showed a similar decrease between years, with the density in 1990 only 8.6% of that in 1989 (Table 2a). While the egg and larval densities are not directly comparable due to estimates of each stage resulting from different cohorts, the magnitude of the decrease in densities is similar for both stages. This suggests that the interannual variability in larval densities did

not result from differences in larval mortality but resulted from either differences in egg mortality (due to predation, anomalous transport, or both) or differences in the level of egg production. Given the decrease in densities seen in all larval taxons between years (Table 2b), the processes driving interannual variability in larval production must have affected a wide range of spawning taxons.

While it is possible that the variability in jack mackerel egg and larval abundances may result in variable year class strength, understanding what processes are driving this variability will obviously involve a greater understanding of the physical oceanography of the area as well as concurrently measuring survivorship and recruitment, together with population fecundity and condition.

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Table 1. Summary of effects on jack mackerel spawning, and eggs and larvae resulting from physical and biological variability experienced during the La Niña conditions of 1989

Variable	Effect
Effects on adults	
Spawning time/duration	xx
Spawning area	xx
Condition factor/fat	+
Fecundity	?
Effects on eggs/larvae	
Prey abundance/distribution	xx
Predator abundance/distribution	?
Horizontal advection	?
Vertical stability	?

xx – no effect

\+ – effect

? – unknown

Table 2. Comparison of 1989 and 1990 mean densities (number per 100 m^3). (a) Jack mackerel egg and larval stages. (b) All other larval taxons

	Years	
	1989	1990
(a). Jack mackerel		
eggs	18.6	1.6
pre - flexion	53.8	2.8
flexion	2.7	0.5
post-flexion	0.5	0.3
(b). Larval Taxons		
Scorpaeniformes	5.6	0.5
Pleuronectiformes	1.4	0.1
Gadiformes	0.3	0.0
Tetraodontiformes	1.5	0.3
Perciformes	1.1	0.1
Clupeiformes	0.2	0.1
Unidentified	1.1	1.7

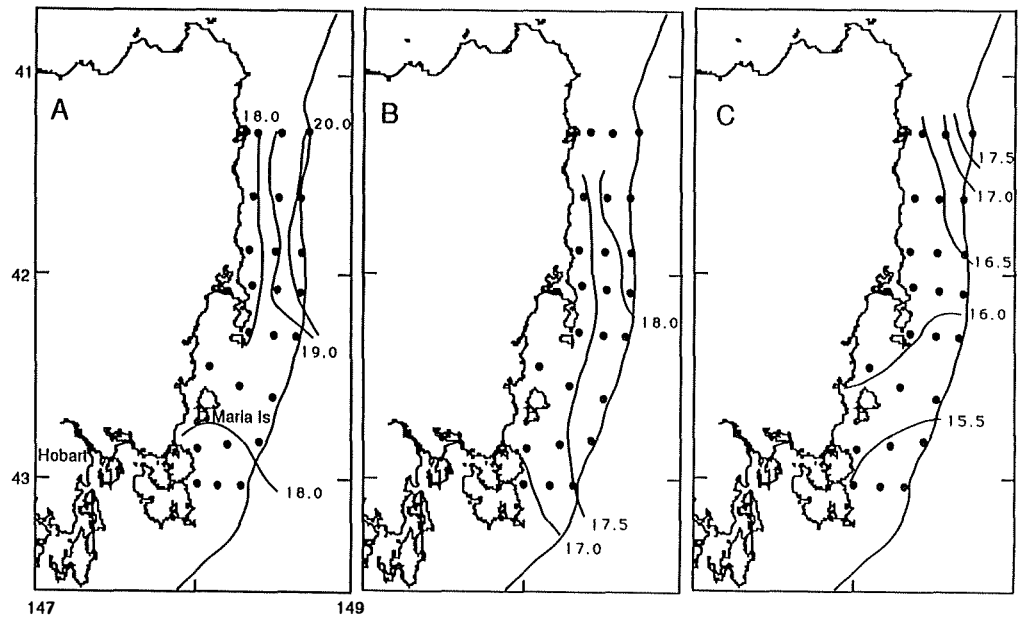

Figure 1. Plots of sea surface temperature for the east coast of Tasmania during February 1989-91 based on data taken during research cruises. *indicates sampling stations. A. February 26-28th, 1989. B. February 18-20th, 1990. C. February 18-28th, 1991.

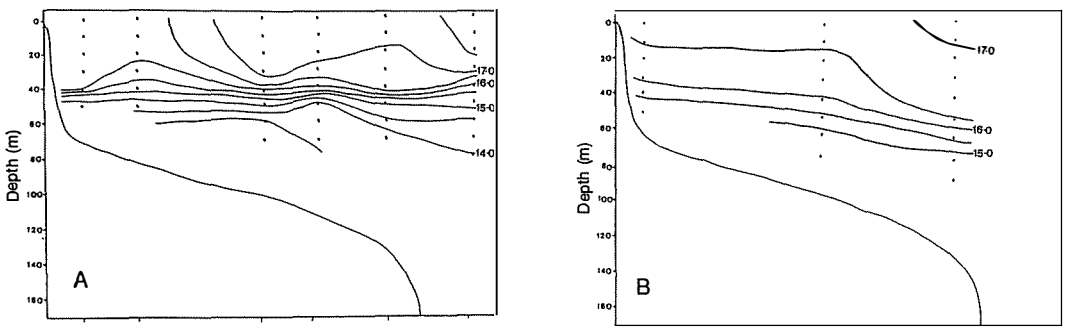

Figure 2. Profiles of water temperature across the shelf break on transect due south of Maria Island (see Figure 1). A. Profile taken 24th Jan 1989. B. Profile taken 23rd Jan 1990.

OBSERVATIONS ON THE DISTRIBUTION OF LARVAL FISH IN RELATION TO A FRONTAL ZONE AT THE MOUTH OF SPENCER GULF, SOUTH AUSTRALIA

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Abstract

The Gulfs of South Australia present oceanographers with an interesting set of features resulting from the interaction of local climate and geography. The area is dominated by a net evaporative loss due to arid conditions in the north that produces a net circulation which is the reverse of that found in normal estuaries. Salinities increase from normal seawater at the mouth of the Gulfs to over 48ppt at their heads. Additionally, due to the near equality of the principal solar and lunar constituents of the tidal cycle when they are apposed, tidal movement virtually ceases for periods of approximately 1-2 days. These features impart particular patterns of circulation that influence the distribution of larval fish in the region. Of particular interest is the development of a frontal zone at the mouth of Spencer Gulf during summer and autumn that results in a significant reduction in Gulf-shelf exchange. A pronounced discontinuity in larval distribution is apparent across the frontal zone consistent with such a reduction in exchange. Both larval diversity and concentration peak within the frontal zone. The concentration and retention of larvae at the frontal zone prior to its breakdown may produce a staging area for the subsequent advection of larvae into Gulf waters when Gulf-shelf exchange is resumed. It is suggested that interannual variations in the timing of frontal breakdown may influence the advection of King George whiting larvae from coastal spawning areas into Gulf waters and thus influence localised recruitment patterns.

Introduction

The concept that interactions between larval biology and hydrographic processes may be a determining factor in larval fish survival and hence recruitment (Kiorboe *et al.* 1988) has been considered since Hjort's critical period concept was suggested in 1914 (Hjort 1914) and has stimulated considerable interest in the patterns of larval fish distribution, processes of advection and the implications of biological interactions in coastal waters. The non-random nature of such distributions is well documented in both tropical and temperate regions (Williams *et al.* 1988; Gorbunova *et al.* 1985; Leis 1982; Richardson *et al.* 1980; Richardson and Percy 1977; Leis and Miller 1976). However the mechanisms determining the existence (and persistence) of such patterns are less well known. Biological factors believed to influence the structure of coastal assemblages include the spawning mode and location of adults , the timing, duration and extent of spawning, the size and motility at hatching, the duration of the larval stage, behaviour of larvae, biological processes

(eg predation) and the availability and concentration of suitable prey (Suthers and Frank 1991; Minami and Tamaki 1980; Richardson *et al.* 1980; Richardson and Pearcy 1977). Physical aspects of the environment such as temperature, wind stress and current patterns influence many of these factors by providing relevant cues or determining the extent of advection and concentration of larvae, prey and nutrients (Corten 1986; Lasker 1981 and references within).

Frontal zones ie the meeting of two dissimilar water masses, are common, ephemeral features in coastal waters and can produce dramatic changes in the distribution of a variety of planktonic organisms by mechanically limiting exchange and dispersal (Owen 1981), concentration via convergent processes (Pingree *et al.* 1974; Richardson *et al.* 1986) and increased productivity via nutrient enhancement (Kiorboe and Johansen 1986; Longhurst 1981). Although fronts are common in Australian coastal waters, little research has been undertaken to examine their biological significance and in particular the ecological implications for ichthyoplankton.

The coastline of South Australia is dominated by two large shallow embayments. The larger of the two, Spencer Gulf, extends some 320 km northwards, is 130 km at its widest point and averages aproximately 21m in depth. Due to high evaporation and low rainfall, salinity increases from oceanic values at the mouth to more than 48 psu (percentage salinity units) in the north. The Gulf is thus regarded as an inverse estuary (Nunes and Lennon 1986). Seasonal heating reduces the magnitude of the horizontal density gradient in summer and, combined with wind driven upwelling of fresher, cooler, ocean water on the shelf, produces a density minimum at the mouth of the Gulf. Convergent flow in the lower layers contributes to the formation of a frontal zone in the region of the mouth that facilitates a summer time reduction in Gulf-shelf exchange (Sherringham 1990). The cooling of saline waters in autumn, and the reversal of wind stress, results in the breakdown of the frontal zone and subsequent discharge of saline waters in the lower layers and inflow of shelf water in the upper layers (Lennon *et al.* 1987).

The purpose of this paper is to examine whether the observed frontal zone has an effect on distribution of larval fish, to highlight the possible implications of any such effects, and to thus suggest directions for further research in South Australian waters.

Methods

Data on the distribution of larval fish were extracted from samples collected from Spencer Gulf and adjacent shelf waters by the South Australian Department of Fisheries (SADF) from 1986 to 1991 to provide a composite picture of summer and autumn patterns. Samples were collected primarily to investigate the spawning and early life history of King George whiting (*Sillaginodes punctata)* rather than an assessment of distribution in relation to the frontal zone, but still serve to illustrate potential effects. A cross shelf transect through the frontal zone was sampled on three cruises in 1989 and 1990 (stations A to J - Figure 1). Additional distributional data for northerly sections of the Gulf were extracted from transect stations occupied during summer and autumn in 1986 and 1987 (stations T1 to T4 - Figure 1). The combination of cruise data from different years presents some analytical difficulties and limits much of the present discussion to a descriptive nature. However the frontal zone is a seasonally consistent feature of the region and although the exact timing of formation and dissolution may well vary, it is assumed for present purposes that when it is present the effects on larval distribution are likely to be similar.

Larvae were sampled using a 70 cm diameter bongo system (500 μm mesh) fitted with Rigosha 1020B flowmeters. Oblique tows were made at each station to within 5 m of the bottom or to a maximum depth of 150 m. Depth of tow was controlled by monitoring wire out and wire

angle. Tow depth was recorded using a Tekna maximum depth meter attached to the frame of the net. All sampling was performed at night.

Samples from each station were selected at random and fixed in either 10% formaldehyde (for initial identification) or 95% ethanol (otolith analysis). Samples were sorted under a stereomicroscope where larval fish were removed, enumerated and identified. As the primary emphasis of the work was on the larval ecology of whiting species (Sillaginidae), in many cases the identification of other larval taxa was not taken beyond family level. Results were standardised to the number of larvae per 1000 m^3 to enable comparison of concentrations between stations.

Vertical profiles of conductivity, temperature and depth were collected at each station prior to ichthyoplankton sampling using a Seabird Seacat CTD profiler. Details of data processing are discussed by Sherringham (1990).

Results and discussion

The frontal zone was particularly evident in temperature and salinity profiles during the January and March cross shelf cruises between stations B and G (Figures 2 and 3). The location of the frontal zone varied between cruises with a more northerly displacement occurring during March 1989. Variability in the location of the frontal zone has also been reported by Sherringham (1990), but could not be attributed to any specific mechanism. The temperature profile of the late May transect (Figure 2) featured comparatively less structure, with Gulf and shelf waters approaching similar temperatures and the cooler oceanic water having commenced moving off the shelf. A halocline was still present in late May between stations D and F; however the inclination of isolines suggested that frontal dissolution and bottom water discharge was imminent. Late May or early June are typically periods when frontal breakdown and a resultant increased level of exchange have been previously reported (Lennon *et al.* 1987).

A pronounced discontinuity in larval taxa was apparent across the frontal zone in all three cruises (Tables 1, 2 and 3). Both the concentration of larvae and the number of taxa peaked within the region of the frontal zone during both January and March, and to a lesser extent in late May (Figure 4). In fact the numbers observed were the highest for any section of Spencer Gulf with the exception of the most northerly regions where gobiid larvae were extremely abundant. Such increases in concentration and diversity are consistent with the juxtaposition of water masses with different fauna where the frontal zone may possess elements of both regions (Owen 1981). This is particularly evident in the March transect (Table 2) where predominantly shelf taxa such as morids, mullids, serranids and the gempylid (*Thrysites atun*) overlapped with the variety of Gulf taxa. The discontinuity of larval taxa across the frontal zone supports physical observations of reduced exchange between shelf and Gulf waters during the period (Nunes *et al.* 1990; Sherringham 1990). Interestingly, some taxa were found almost exclusively within the frontal zone (eg pegasids and leptoscopids). Brandt and Wadley (1981) reported a similar situation with respect to certain midwater fish species at the boundary of an eddy in the Tasman Sea and described such areas as ecotonal zones. Narrow ecotonal zones separating inshore and offshore larval assemblages have also been reported off the coast of Oregon in the north-east Pacific (Richardson and Pearcy 1977; Richardson and Stephenson 1978; Richardson *et al.* 1980).

Physical concentration of larvae via convergent processes may account for the observed peak in concentration within the frontal zone. Sherringham (1990) reported convergent cells on either side of the Spencer Gulf frontal zone and similar concentrating effects with respect to larvae and zooplankton have been identified in other frontal systems (eg Sakamoto and Tanaka 1986; Pingree *et al.* 1974).

Productivity enhancement in the region of the frontal zone is also possible given the reported upwelling events associated with its formation (Sherringham 1990). There is some evidence of a discontinuity in nutrient concentration across the front (P. Petrusivics, South Australian Department of Fisheries pers. comm,); however, no productivity measures are available for the area.

The location of the frontal zone at the mouth of Spencer Gulf and the associated frontal feature in Investigator Strait may have important implications for the early life history stages of King George whiting and in particular their recruitment to Gulf waters. It is interesting to note that the area over which the frontal zone oscillates in lower Spencer Gulf coincides with a believed spawning area for King George whiting and that the timing of peak spawning from back-calculated spawning dates utilising daily ageing (Bruce 1989) coincides with the mid to late Autumn period when the frontal zone is strongest (Sherringham 1990). Whether thepresence of the frontal zone or the presumed increase in productivity in the area has any cueing effect on spawning has yet to be demonstrated, but considering that whiting are also known to spawn in coastal waters west of Spencer Gulf that are not under the influence of the frontal zone, such a cueing effect is less likely. The significance of the frontal zone may be more related to the extent to which it serves to limit physical exchange (presumably including larvae) between shelf and Gulf waters. This is suggested by comparing the March and May distribution of King George whiting larvae. During March, whiting larvae were largely restricted to within the frontal zone. However in May, when the front was in the process of breaking down, the distribution of whiting larvae extended much farther north (Tables 2 and 3). Both Spencer Gulf and Gulf St Vincent contain major nursery areas for King George whiting. Given that most larvae originate from spawning outside of Gulf waters and must cross the frontal zone to enter the Gulfs, the timing of breakdown and subsequent increased exchange may have the potential to either facilitate or obstruct the advection of larvae into the Gulfs and subsequent recruitment to such nursery areas. Interannual recruitment variability has been reported by Jones *et al.* (1990) for both Gulf and coastal nursery areas and although recruitment trends appear to be linked between these areas there is sufficient variability to suggest that in some years, recruitment to Gulf waters is not linked. Information regarding interannual variability in the timing of frontal breakdown is not available but considering the close ties to meteorological conditions (that are known to vary) it is reasonable to suspect that this does occur and if so could affect the timing and strength of recruitment.

The occurrence of King George whiting larvae within the frontal zone in March prior to the breakdown of the front suggests that an additional hypothesis regarding the significance of the frontal zone is also possible. If convergent processes result in the accumulation and retention of larvae within the frontal zone then this may serve as a staging area for the subsequent transport of larvae into Gulf waters when Gulf shelf exchange is resumed. Such a staging area was suggested by Govoni *et al.* (1989) for *Brevoortia patronus* and *Leiostomus xanthurus* larvae with respect to the Mississippi plume front. In this alternative hypothesis, the suspected increase in productivity at the frontal zone may have important ramifications if it results in enhancing the feeding environment and hence survival of larvae. Retention of *Clupea harengus* larvae within a frontal region in the North Sea was reported by Kiorboe *et al.* (1988). They found that peaks in both larval abundance and copepod production coincided in the frontal region. In spite of this, Kiorboe *et al.* found that larval growth in the region was sub-optimal and suggested that competition for food was contributing to density dependent growth and survival. Feeding or condition indices for larvae within the frontal zone in South Australia have not yet been investigated but present logical future research topics.

Conclusions

Although the physical processes accounting for the formation, seasonal persistence and subsequent breakdown of the frontal zone in lower Spencer Gulf have been extensively studied, the biological implications of the zone have not been documented. The apparent discontinuity in larval distribution across the zone coupled with possible enhanced productivity suggests that these processes have an important structuring effect on larval assemblages within the area. In addition, the seasonal limitation of exchange between Gulf and shelf waters and the timing of frontal breakdown may be a determining factor in the advection of larvae of King George whiting from coastal spawning grounds to nursery areas within the Gulf and thus subsequent recruitment. Given the predictability of its occurrence, the frontal zone in Spencer Gulf affords a good opportunity to investigate the relationship between frontal dynamics and larval distribution, advection and ecology.

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Table 1. Summary of the distribution of taxa in Spencer Gulf and shelf waters during January

(T1-T4 1988; A-J 1989. Stations shown in Figure 1)

		frontal zone												
		<———>												
					Station									
Taxa	T1	T2	T3	T4	A	B	C	D	E	F	G	H	I	J
Blenniid		*												
Atherinid	*		*											
Hemirhamphid	*		*		*									
Sillago schomburgkii	*	*												
Theraponid	*	*	*											
Apogonid	*	*	*	*										
Syngnathid	*	*	*	*										
Tetraodontid	*	*	*	*					*					
Carangid		*	*	*	*	*	*	*	*	*	*	*	*	*
Callionymid	*	*	*	*	*	*	*	*	*		*	*		*
Clupeoid	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Gobiid	*	*	*	*	*	*	*	*	*		*			
Monacanthid	*	*	*	*	*	*	*	*	*	*	*	*		
Mugiloidid	*	*	*	*	*	*	*	*	*					
Platycephalid	*	*	*	*	*		*	*	*	*				
Pleuronectiform	*	*	*	*		*		*			*	*	*	*
Labrid		*	*	*	*	*	*	*	*	*	*	*		
Clinid			*	*				*	*					
Gobiesocid			*	*					*					
Creedid			*	*	*	*	*	*	*		*	*	*	
Scorpaenid			*	*					*				*	*
Sparid			*	*					*					
Triglid			*	*							*		*	*
Pempherid			*	*				*	*					
Gerreid				*	*	*	*	*	*					
Mullid					*		*	*	*	*	*	*	*	*
Pegasid									*	*				
Sillago bassensis				*	*	*	*	*	*					
Serranid											*	*		
Percophidid					*	*	*	*	*	*				
Leptoscopid								*	*					
Argentinid									*					
Thrysites atun										*	*	*	*	*
Cepolid											*			
Cheilodactylid											*			*
Morid											*	*	*	*

Table 1. continued

Taxa	Station T1	T2	T3	T4	A	B	C	D	E	F	G	H	I	J
Myctophid											*	*	*	*
Berycid													*	
Gonostomatid													*	*
Astronesthid														*
Carapid														*
Paralepedid														*

Table 2. Summary of the distribution of taxa in Spencer Gulf and shelf waters during March

(T1-T4 1988; A-J 1989. Stations shown in Figure 1)

frontal zone

<——————>

Taxa	Station T1	T2	T3	T4	A	B	C	D	E	F	G	H	I	J
Hemirhamphid			*											
Tetraodontid			*										*	
Apogonid		*												
Gobiesocid		*		*						*				
Syngnathid	*	*	*	*										
Blenniid	*	*		*										
Clinid	*	*	*	*				*	*	*				
Callionymid	*	*	*	*	*	*	*	*	*	*	*	*	*	
Clupeoid	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Gobiid	*	*	*	*	*	*	*	*	*	*	*			
Monacanthid	*	*	*	*		*	*	*	*	*				
Scorpaenid	*		*	*			*	*	*	*			*	
Mugiloidid	*			*	*	*	*	*	*	*		*		
Triglid	*				*	*	*	*	*	*			*	
Platycephalid				*			*	*	*	*		*		
Sillaginodes punctata						*	*	*	*	*				
Pleuronectiform					*		*	*	*	*				*
Carangid					*	*	*	*	*	*		*		
Creedid					*	*	*	*	*	*		*	*	
Gerreid					*		*	*	*	*		*		
Percophidid					*	*	*	*	*	*				

Table 2. continued

Taxa	Station T1	T2	T3	T4	A	B	C	D	E	F	G	H	I	J
Sillago bassensis					*		*	*	*	*				
Labrid							*	*	*					
Leptoscopid							*	*	*					
Pegasid							*	*	*					
Pempherid							*	*						
Morid								*	*	*	*	*	*	*
Mullid								*	*		*	*		
Serranid								*	*	*				
Thrysites atun								*	*	*	*	*	*	*
Cheilodactylid											*	*	*	*
Gonostomatid											*		*	*
Myctophid											*	*	*	*
Berycid												*	*	
Macrorhamphosid												*		
Tracichthyid												*		
Cepolid													*	*
Trichiurid													*	*
Leptocephalid														*
Paralepedid														*

Table 3. Summary of the distribution of taxa in Spencer Gulf and shelf waters during late May

(T1-T4 1988; A-J 1990. Stations shown in Figure 1)

								frontal zone <- - - ->					
	Station												
Taxa	T1	T2	T3	T4	A	B	C	D	E	F	G	H	I	J
Clinid	*	*	*	*		*	*	*						
Gobiid	*	*	*	*	*	*	*	*				*		
Monacanthid	*	*	*	*			*	*						
Pleuronectiform	*			*				*						
Scorpaenid	*	*	*	*			*	*						
Syngnathid	*	*		*			*	*						
Clupeoid		*	*	*	*	*	*	*		*	*	*	*	
Sillaginodes punctata		*	*	*		*	*							
Gobiesocid			*	*		*		*						
Platycephalid				*		*								
Pegasid				*										
Triglid				*										
Mugilid				*				*						
Callionymid					*	*	*			*				
Creedid					*	*	*	*		*				
Gerreid					*	*		*						
Cheilodactylid										*				
Myctophid										*		*	*	*
Berycid												*		
Cepolid												*		
Idiacanthid												*	*	*
Leptocephalid												*	*	*
Morid													*	
Gonostomatid														*
Paralepedid														*
Scomberesox														*

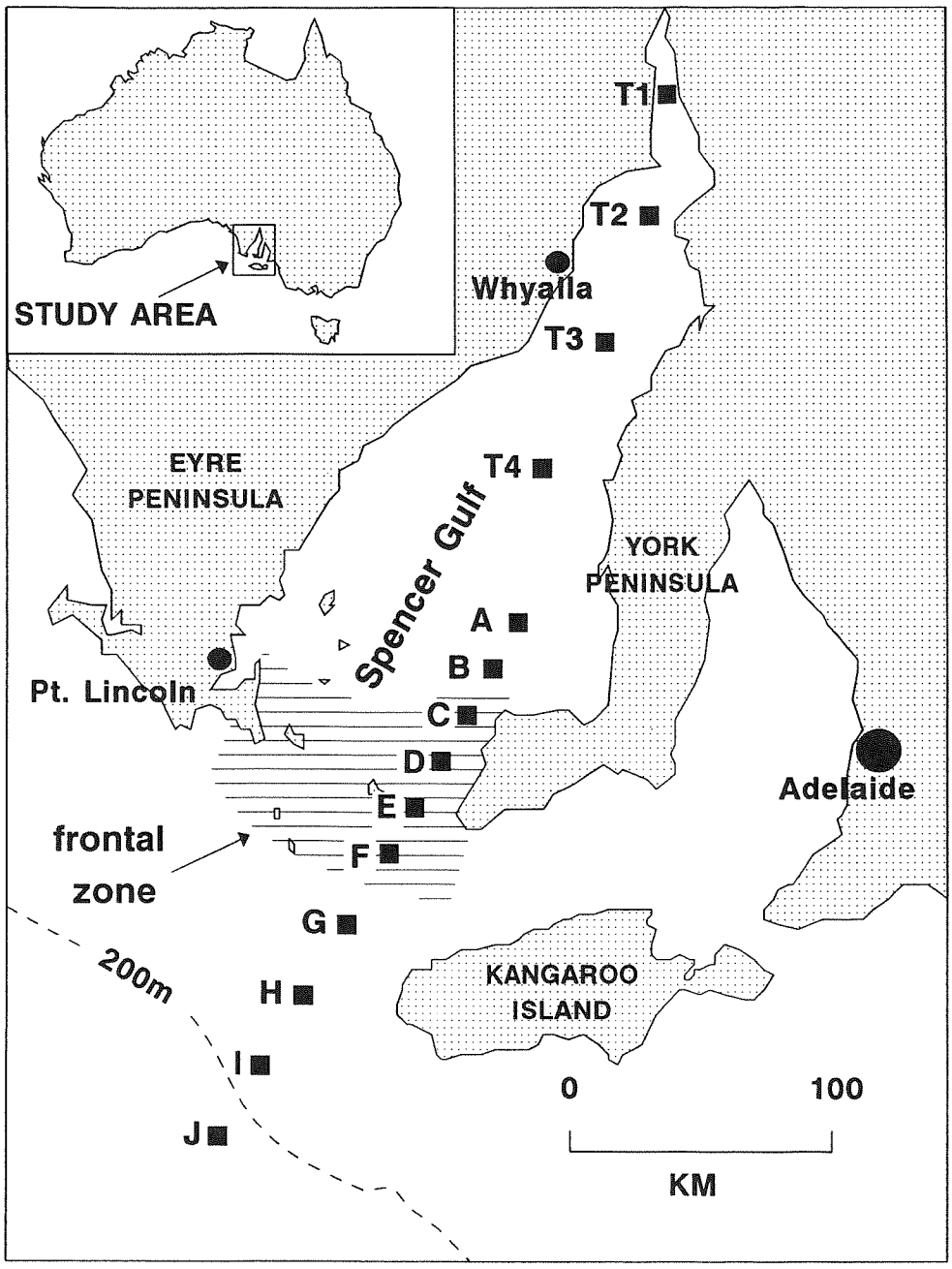

Figure 1. Locations of stations used for analysis. Hatching denotes the area within which the frontal zone is generally located.

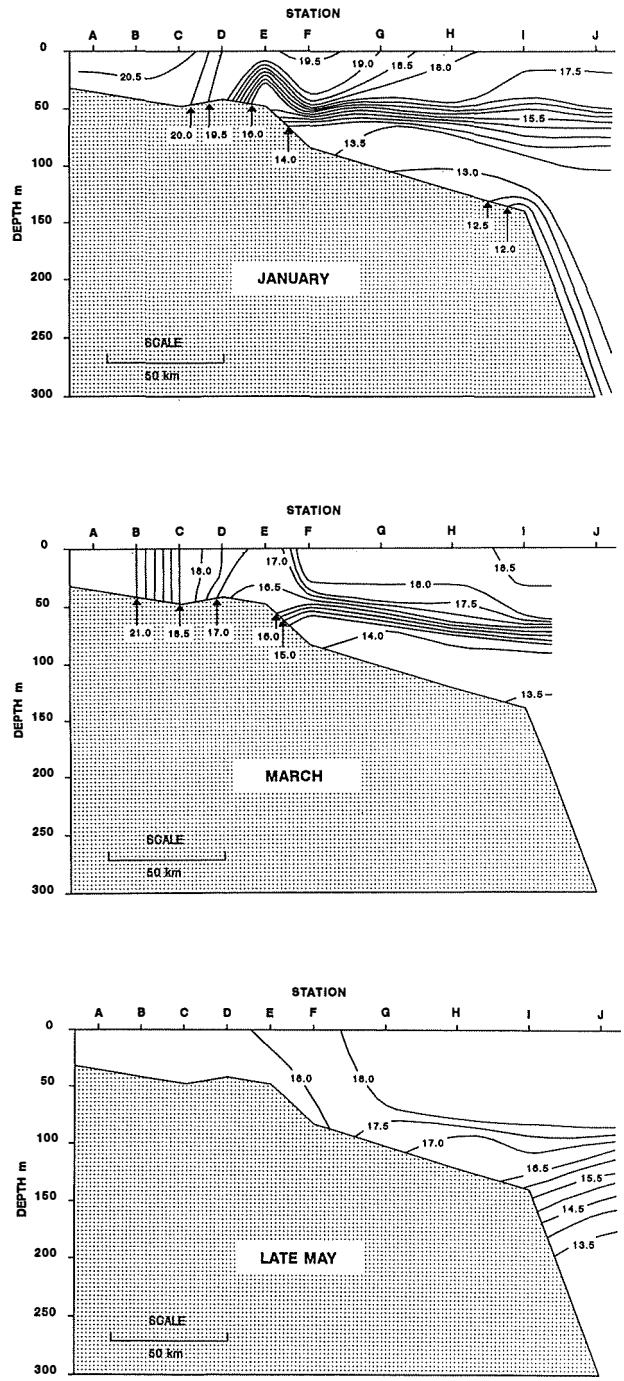

Figure 2. Temperature profiles across the frontal zone and adjacent shelf during summer (January 1989) and autumn (March 1989 and late May 1990) (0.5°C isotherms). Stations as per Figure 1.

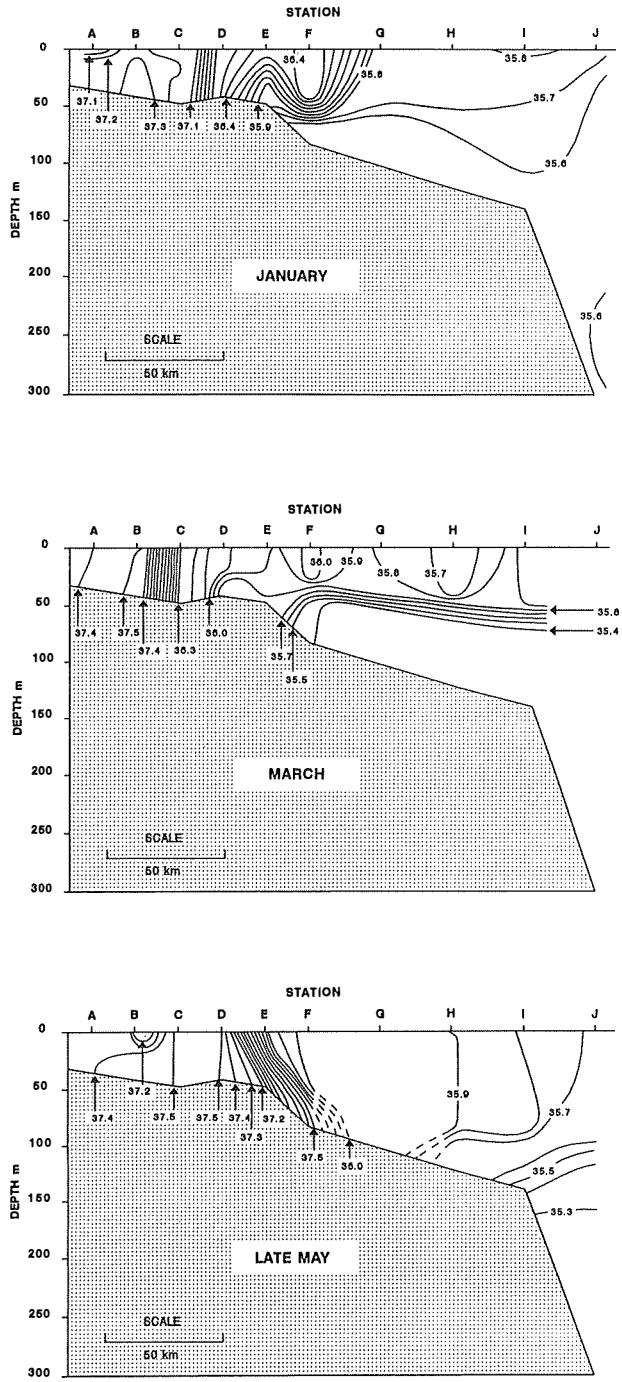

Figure 3. Salinity profiles across the frontal zone and adjacent shelf during summer (January 1989) and autumn (March 1989 and late May 1990) (0.1 psu). Stations as per Figure 1.

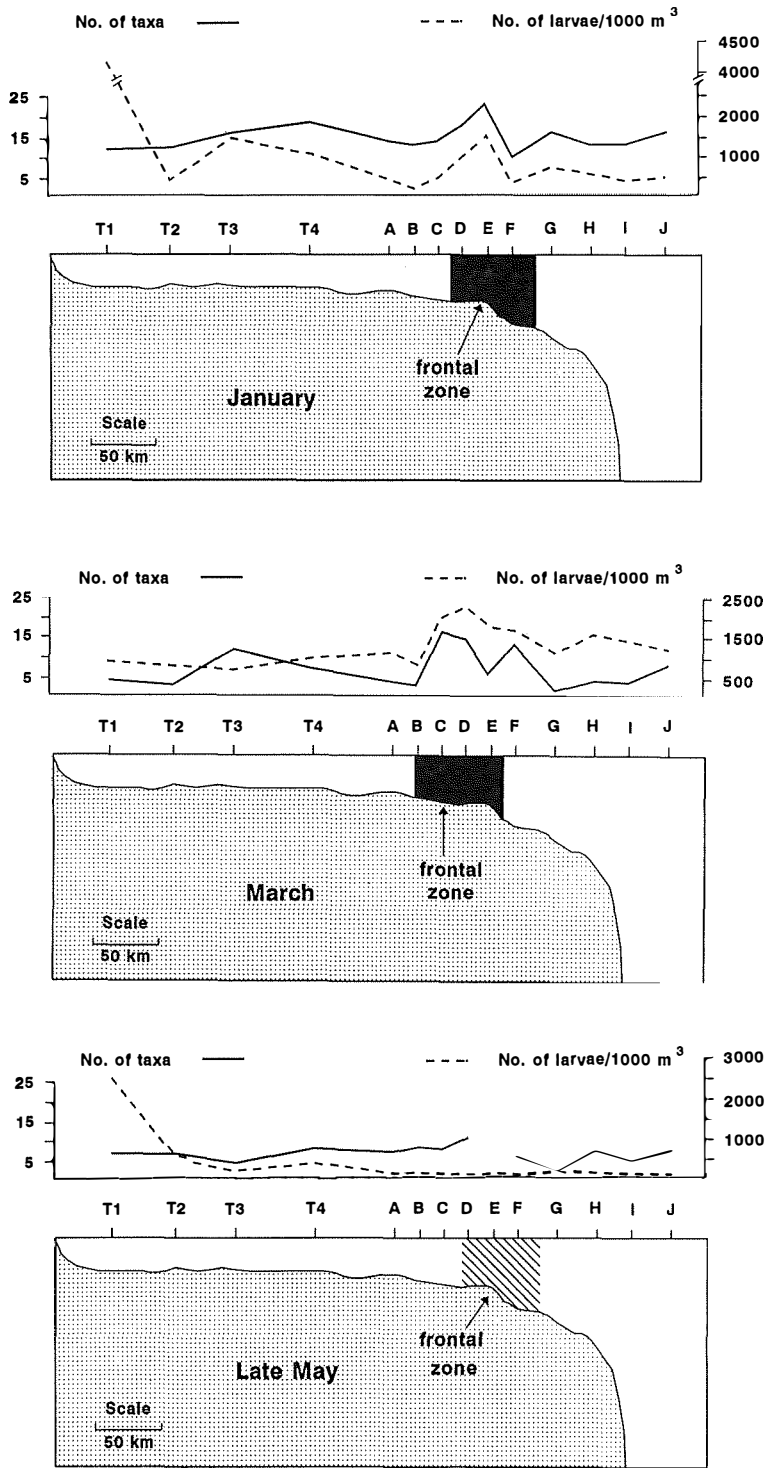

Figure 4. Concentration of larvae and number of taxa in Spencer Gulf and adjacent shelf waters during summer (January 1989) and autumn (March 1989 and late May 1990). Stations as per Figure 1.

DISTRIBUTION OF PHYLLOSOMA LARVAE OF THE RED ROCK LOBSTER *JASUS EDWARDSII* OFF THE EAST COAST OF NEW ZEALAND IN RELATION TO THE OCEANOGRAPHY

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Abstract

In plankton samples taken during 1987-88 from the east coast of New Zealand south of East Cape, mid- and late-stage phyllosomas of the rock lobster *Jasus edwardsii* were much more abundant off the North Island than off the South Island. Larvae were sampled seasonally at night beyond the continental shelf edge with a fine-meshed midwater trawl, and occurred to a distance of at least 600 km from shore. The high larval abundance off the North Island was probably determined by several factors including high levels of local larval production, larval behaviour, and the oceanography. The latitudinal position of the larvae broadly coincided with that of the East Cape Current system, the most conspicuous area of circulation and eddying present off the east coast of New Zealand. Off the South Island, there are no similar oceanographic features to retain larvae near shore, and the numbers of phyllosomas caught were low. Low larval production south from Banks Peninsula may have contributed to this result. The high abundance of phyllosomas off the south-east of the North Island is probably of considerable significance to the fishery, contributing not only to high puerulus settlement in the region, but possibly also leading to juvenile migrations to other areas.

Introduction

In most shallow-water palinurid lobsters, eggs hatch and larvae are released near shore. The leaf-like phyllosoma larva passes through a number of instars (grouped and referred to as stages) over several months in offshore waters before metamorphosing to the settlement stage, the puerulus. Phyllosoma larvae are reported to be poor swimmers (Phillips and Sastry 1980), and their body form appears suited to passive drift. This, together with the long larval period offshore, means that oceanographic features, particularly currents and eddies, may play an important role in the dispersal and subsequent return to shore of larvae.

The red rock lobster *Jasus edwardsii* (Hutton) (Decapoda: Palinuridae) supports one of the most valuable fisheries in New Zealand. In recent years about 60% of the 3500-5500 t annual landings of this species have come from the east coast of the country (MAF Fisheries data). A knowledge of larval recruitment processes is important to management of this major resource.

Female *J. edwardsii* breed annually, with egg-hatching taking place during spring (mainly September and October). There is large geographic variation in larval production because

size at onset of breeding (Annala *et al.* 1980; unpublished MAF Fisheries data), breeding female abundance (based on recent fishery landings), and egg-per-recruit (Annala and Breen 1989) vary markedly with locality. Annual larval production is high along the east coast of New Zealand from East Cape to Motunau, in the southwest of the South Island from Jackson Head to Foveaux Strait, and at the Chatham Islands; moderate in the northeast of the North Island north of East Cape; and it is low elsewhere.

Lesser (1978) described 11 phyllosoma stages; those at stage V and beyond (=advanced larvae in this paper) occurred beyond the edge of the continental shelf and to the end of his 185 km long transect. Later sampling (Booth unpublished data) confirmed this pattern, with most of the advanced phyllosomas being found at distances at least 20 km seaward of the shelf edge. At night, advanced phyllosoma larvae were found mainly in surface waters (down to about 60 m), and they dispersed to greater depths during the day. Duration of the larval period is at least 12-23 mo (Lesser 1978; Booth 1979; unpublished data).

This paper describes the distribution and abundance of advanced phyllosoma larvae of *J. edwardsii* sampled seasonally along a series of transects off the east coast of New Zealand south of East Cape, and examines how the nearshore oceanography might have influenced the result.

Flow patterns along east coast of New Zealand

New Zealand lies in a general west to east oceanic drift zone (Heath 1985) (Figure 1). Flowing south of East Cape, on the western side of the Hikurangi Trough, is the inshore arm of the East Cape Current (ECC) system. Near the head of the Hikurangi Trough the direction of flow is reversed, mainly because of constraints of the bottom topography. Part of the flow of the inshore arm of the ECC does not join the eddy thus formed, but moves northeast along the eastern side of the Hikurangi Trough and the Kermadec Trench as the outer arm of the ECC system (Heath 1975a; 1980) (Figure 2). The rest of the flow meanders generally east to contribute to the Subtropical Convergence.

South of Cook Strait, the flow along the east coast of the country is generally from the south as the Southland Current (Figure 1). The primary flow of this current departs eastward near Banks Peninsula, but some water flows as far north as about Cape Turnagain, where it turns east and combines with the south-moving ECC water.

The most conspicuous water circulation off the east coast of New Zealand is within the ECC system. The southward flow of the ECC may take the form of eddies (Ridgway 1970); there is sometimes continuity at about 39.5°S between the north and south flows (eg., Heath 1975a; Figure 8); and there is possibility of some recirculation of the ECC system as a whole (Garner 1969). There is a 'permanent' eddy centred near the head of the Hikurangi Trough around 41° S, 178°E, and others long-lived have been reported over seamounts to the north (Bradford *et al.* 1982). A small, persistent eddy lies off the eastern approach to Cook Strait, and variable eddy patterns are common as far south as Banks Peninsula (Barnes 1985). A weak, anticyclonic flow 50-100 km wide has been reported in the southwest corner of the Bounty Trough (Heath 1975b).

Methods

Phyllosoma larvae were sampled along six transects off the east coast of New Zealand approximately 3-monthly during June 1987-March 1988 (Figure 3). Some transects had to be altered or omitted because of heavy sea conditions. Some additional transects between Cape Runaway and Cook Strait were sampled in order

to define more clearly the boundaries of high larval abundance (Figures 3 and 4). Sampling was carried out with a fine-meshed midwater trawl (FMMWT) similar to that used by Robertson *et al.* (1978). The trawl had a mesh size reducing from 150 mm (stretch measure) near the mouth to 12mm in the codend. The effective mouth area of the trawl was much less than the nominal mouth area (about 70 m^2) because of the large meshes and because phyllosomas cannot be 'herded'. Nevertheless, catches were comparable because all tows were made in a similar manner. Coefficient of variation (CV) values for 3-6 tows made in rapid succession in the same direction at the same station were determined 7 times on the Mahia transect.

Most transects started from points 20-30 km seaward of the edge of the continental shelf and extended generally eastward a further 110 km. Each transect usually consisted of 6 half-hour tows of the FMMWT, each tow separated by 18 km, made in the course of one night. Sampling started at least one hour after sunset and ended at least one hour before sunrise. The headline of the mouth was set at 30m depth, and the tows were made at 1.0-1.3 m sec^{-1}.

Phyllosoma larvae were identified and staged according to Lesser (1978). Mid-stage larvae were those at Stages V-VII; late-stage larvae at Stages VIII-XI.

Results

Just over 1200 (940) advanced (late-stage) phyllosomas (and 3 pueruli) of *J. edwardsii* were taken in the seasonal sampling in Figure 3 and Table 1. In June 1988, a further 600 and 170 advanced phyllosomas (but no pueruli) were caught in the nearshore and offshore sampling respectively (Figure 4).

In the seasonal sampling, advanced phyllosomas were most abundant along the Mahia transect (Table 1). CV values on this transect for consecutive tows at the same station were mostly 35-45%. The mean catch of larvae per tow was significantly lower each season for the Castlepoint transect compared with Mahia (Mann-Whitney U-test, $P < 0.05$), and only a single phyllosoma was caught south of Cook Strait. Within transects, there was high variability between stations in the phyllosoma catches (Table 1). The highest catches of mid-stage larvae were made in late summer/early autumn and winter, and the highest catches of late-stage larvae in spring and early summer, indicating that phyllosoma development takes at least about 12 months.

The northern boundary (at least in inshore waters) of the area of high phyllosoma abundance was near to but south of East Cape; the southern boundary was near the Castlepoint transect (Figures 3 and4; Table 1). In June 1988, phyllosomas were equally abundant from Tolaga to Castlepoint (one-way ANOVA; probability, P, of phyllosoma densities being the same on all transects = 0.520) (Figure 4).

Both mid- and late-stage phyllosomas occurred along the entire lengths of transects, including the Offshore transect in Figure 4. In June 1988, the mean catch of advanced larvae per tow for the Mahia transect was not significantly different to that for the Offshore transect (Mann-Whitney U-test, $P >> 0.05$) (Figure 4).

Discussion

In all seasons, the only significant catches of phyllosomas made along the east coast of New Zealand south of East Cape were from off the North Island (Figures 3 and 4; Table 1). This was in the region of the ECC system, the most conspicuous area of strong circulation, eddying and water retention off the east coast of the country. Eddies and fronts are well known for their mechanical ability to limit dispersal, and collect individuals and conserve concentrations of species (Owen 1981). Only a single phyllosoma was taken off the South Island.

Catches from occasional other FMMWT sampling off the east coast of New Zealand were consistent with the present results. Transects were sampled off the northeast (November 1979) and southeast (seasonally, 1979-81) coasts of the North Island, and off the southeast of the South Island (May 1985 and June 1990, including offshore samples from the southwestern part of the Bounty Trough); only samples off the southeast of the North Island contained phyllosomas (Booth 1980; unpublished data).

The pattern of phyllosoma abundance is consistent with levels of puerulus settlement. Along the east coast of New Zealand, settlement of pueruli on collectors over the last 10 years has been several times higher in the North Island south of about East Cape than elsewhere (Booth and Tarring 1986; Booth 1991).

Phyllosomas were widespread along North Island transects, and were taken almost 600 km from shore. The outer arm of the ECC system lies offshore between 150 km and at least 400 km, depending on season and latitude (Heath 1975a), and was probably traversed by the Offshore transect. However, most transects off the North Island probably sampled only the inner arm of the ECC system, where high variability between stations within transects (high SD values and high variance to mean ratios from Table 1) indicated a contagious distribution of larvae. The eddy indicated at 41°S in Figure 1 was not sampled.

Factors influencing phyllosoma abundance along the east coast of New Zealand include local larval production, survival (in turn linked to food and predator abundance) and behaviour, and the oceanography. Larval production is high between East Cape and Motunau, and lower to the south. Nutrient levels and productivity are moderate to high off the entire east coast (Bradford and Roberts 1978).

Components of the oceanography influencing larval abundance include currents which bring larvae into the area; features such as eddies which retain larvae in the area for long periods; and currents which return larvae after transport offshore. It seems likely that some larvae are carried into the study area by the East Auckland Current from the north and by the Southland Current from the south (Figure 1). The obvious difference between the oceanography of the southeast of the North Island and the east of the South Island is the presence off the North Island of a large pattern of strong circulation and eddying which may provide an effective mechanism for larval retention and shoreward transport of larvae. In contrast, eddies are weaker and more variable off the east coast of the South Island, and water flows are more direct, running to the north (as the Southland Current) and east (as the West Wind Drift).

The ECC system may not be the only oceanographic system important in the larval recruitment process off the North Island. The eastward extent of the area of high larval abundance is unknown, and larger scale patterns of offshore transport and return of larvae may exist, similar to that for *Panulirus cygnus* off Western Australia (Phillips and McWilliam 1986).

Phyllosoma larvae may be able to exert some control over their horizontal transport by altering their vertical distribution so as to exploit currents flowing in particular directions or at different speeds (Phillips and McWilliam 1986). The high abundance of advanced *Jasus* larvae in the general area of adults revealed in sampling of southern waters (Booth and Grimes 1991) is consistent with larvae having some control over their horizontal position. It is unclear for the present study what role larval behaviour played in determining the pattern of phyllosoma abundance off the North Island because the degree of recirculation of water within the ECC system is unknown. Southward flow in the inner arm of the ECC system is about 0.5 m sec^{-1}; the rate in the north-moving outer arm is somewhat less (Hydrographic Department 1958; Heath 1975a); and it is 0.2-0.5 m sec^{-1} near the southern part of the eddy off Castlepoint (Sdubbundhit

and Gilmour 1964; Barnes 1985). Using an average drift rate of 0.35 m sec^{-1}, larvae would be held in the ECC system for as few as 40 days unless a) significant overall recirculation of the ECC system were taking place; b) larvae were retained for long periods in eddies and meanders within the ECC system; or c) larvae through their behaviour influenced their horizontal distribution.

In conclusion, advanced phyllosomas were present in high numbers throughout the year off the east coast of the North Island in a region which coincides in latitudinal position with the ECC system, a conspicuous area of strong eddying and circulation. Off the South Island, numbers of advanced phyllosomas were low, and there are no oceanographic features similar to the ECC system to retain larvae nearshore. Levels of larval production (high in the north; low south of Motunau) probably contributed to the disparity in larval abundance. Further work is required to determine the mechanism and duration of larval retention in the ECC system and the degree to which these are influenced by larval behaviour, and whether any other oceanographic systems are important in the retention and return of larvae. Examination of sea surface temperatures from satellite imagery in relation to puerulus settlement patterns on shore may lead to improved understanding of the larval recruitment process. The high abundance of phyllosomas off the southeast of the North Island is probably of considerable significance to the fishery, contributing not only to high puerulus settlement in the area, but possibly also leading to juvenile migrations to other areas (Booth 1983).

Acknowledgements

Thanks to colleagues at MAF Fisheries who assisted in the sorting out of phyllosomas at sea, and to the master and crew of RV *James Cook* for their cooperation in the sampling. We thank Don Robertson and Paul Breen, both of MAF Fisheries, for valuable suggestions on an earlier version of this paper, and to Graeme Mackay for efficient production of the Figures.

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Table 1. Numbers of mid-stage (Stages V-VII) and late-stage (Stages VIII-XI) phyllosoma larvae of *Jasus edwardsii* per station taken in seasonal sampling off east coast of New Zealand, 1987-88

n, total number of larvae for the transect; SD, standard deviation.

			Mid-stage larvae				Late-stage larvae				Total larvae			
Transect	Date		n	Mean	Range	SD	n	Mean	Range	SD	n	Mean	Range	SD
Runaway	Dec	87	0				0				0			
East Cape	Feb	88	0				0				0			
Tokomaru	Sep	87	6	1.5	0-6	3.0	112	28.0	0-112	56.0	118	29.5	0-118	59.0
Mahia	Jun	87	42	8.4	0-21	8.4	112	22.4	8-44	13.4	154	30.8	8-48	15.8
	Sep	87	18	3.0	0-5	2.3	388	64.7	29-182	57.9	406	67.7	34-186	58.5
	Dec	87	11	1.8	0-4	1.7	229	38.2	10-75	24.0	240	40.0	10-75	24.0
	Feb	88	167	27.8	0-107	41.9	44	7.4	0-16	6.6	211	35.2	0-123	47.0
Castlepoint	Jun	87	1	0.3	0-1	0.5	2	0.5	0-2	1.0	3	0.8	0-2	1.0
	Sep	87	1	0.2	0-1	0.4	30	5.0	0-20	8.2	31	5.2	0-20	8.3
	Dec	87	1	0.2	0-1	0.5	20	4.0	0-10	3.7	21	4.2	0-11	4.2
	Mar	88	10	1.7	0-6	2.1	6	1.0	0-6	2.5	16	2.7	0-11	4.3
Kaikoura	Jul	87	0				0				0			
	Sep	87	0				0				0			
	Dec	87	0				0				0			
	Mar	88	0				0				0			
Banks	Jul	87	0				0				0			
	Sep	87	0				0				0			
	Dec	87	0				0				0			
	Mar	88	0				0				0			
Otago	Jul	87	0				1	0.2	0-1	0.4	1	0.2	0-1	0.4
	Sep	87	0				0				0			
	Dec	87	0				0				0			
	Mar	88	0				0				0			
Foveaux	Jun	87	0				0				0			
	Dec	87	0				0				0			

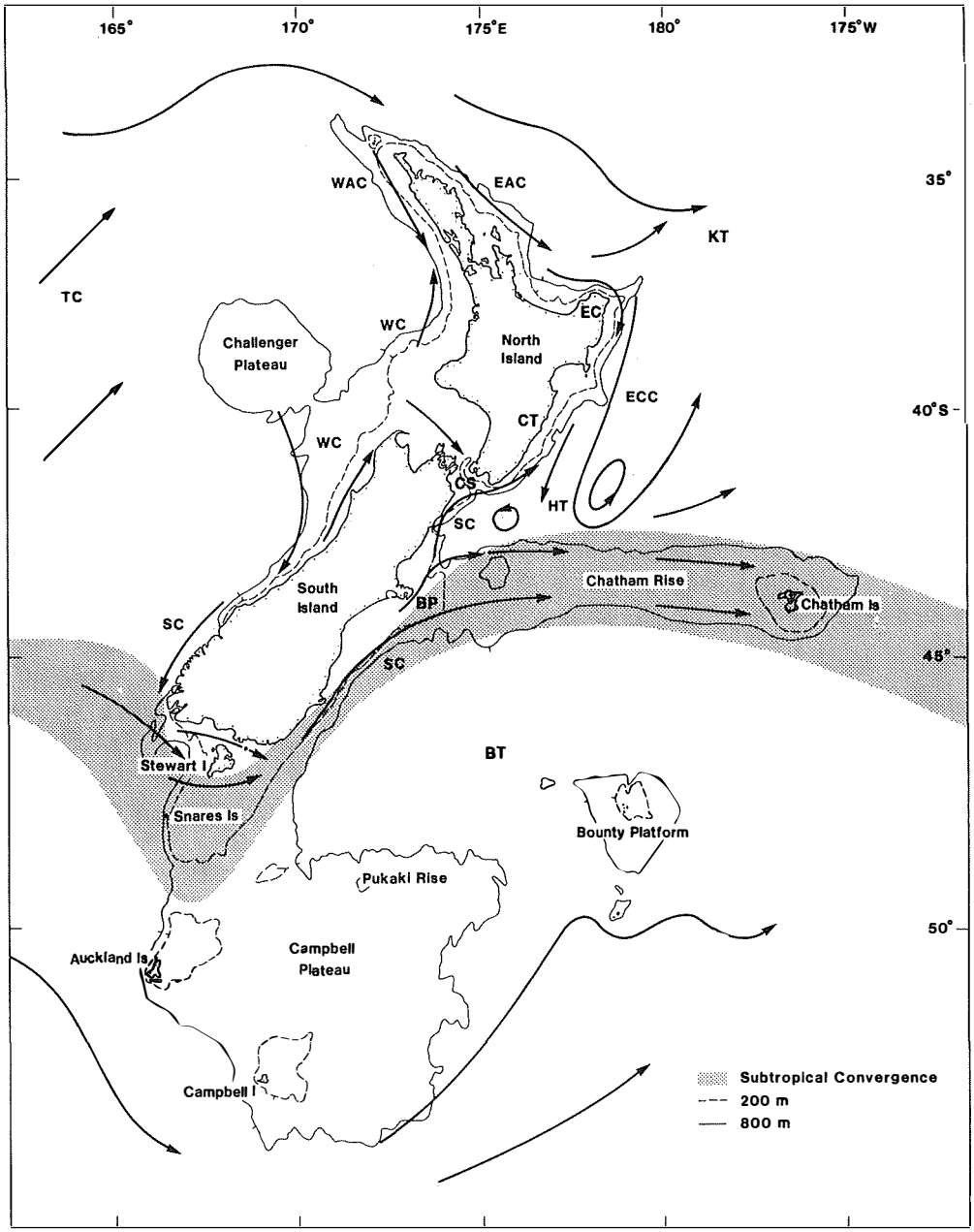

Figure 1. New Zealand region, showing major surface currents (based on Heath 1985, Fig 2), other oceanographic features, and localities mentioned in text in relation to the oceanography. Bathymetry in metres. BP, Banks Peninsula; BT, Bounty Trough; CS, Cook Strait; CT, Cape Turnagain; EAC, East Auckland Current; EC, East Cape; ECC, East Cape Current; HT, Hikurangi Trough; KT, Kermadec Trench; SC, Southland Current; TC, Tasman Current; WAC, West Auckland Current; WC, Westland Current.

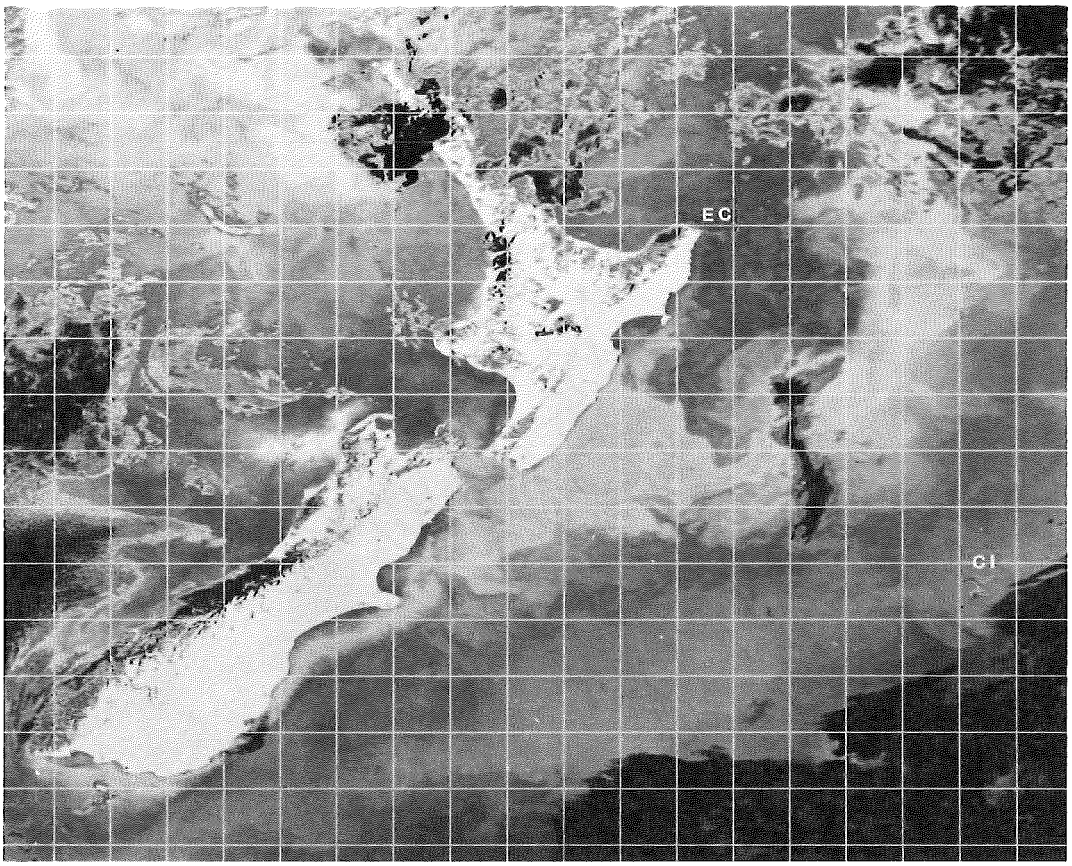

Figure 2. Sea surface temperature image for New Zealand, 14 November 1985, showing flow of warm East Cape Current water (dark) south from East Cape, and presence of mixed East Cape Current – Southland Current Water further south off the North Island (light). Cold Southland Current Water off the East Coast of the South Island also shows as dark in this image. Data received by N.Z. Meteorological Service and the image processed and kindly provided by E.J. Barnes, DSIR Physical Sciences. Black is cloud cover; EC, East Cape; CI, Chatham Islands.

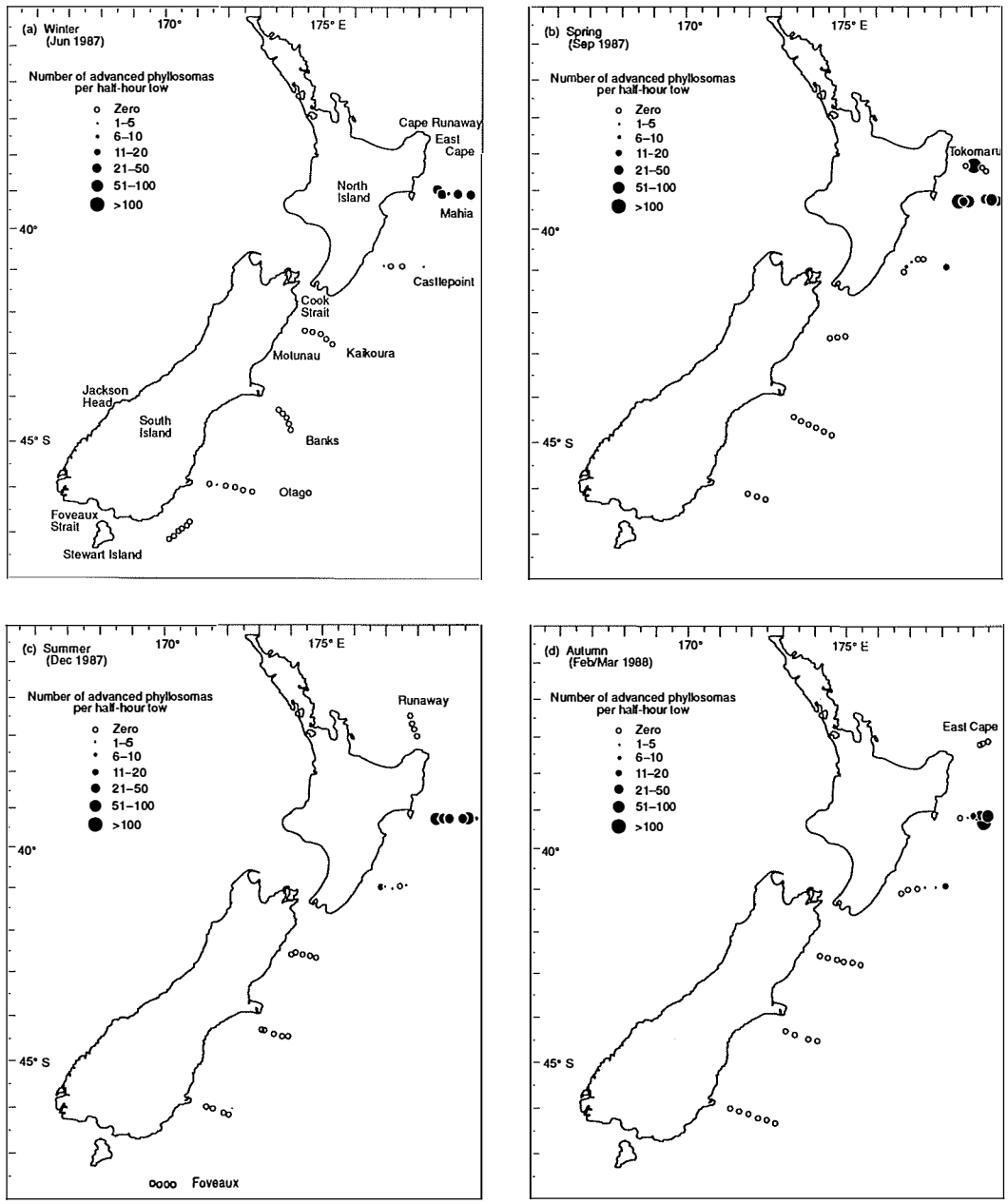

Figure 3. Catches by season of *Jasus edwardsii* phyllosoma larvae in half-hour tows along transects off the east coast of New Zealand, 1987-88. Localities mentioned in text in relation to biological data are given.

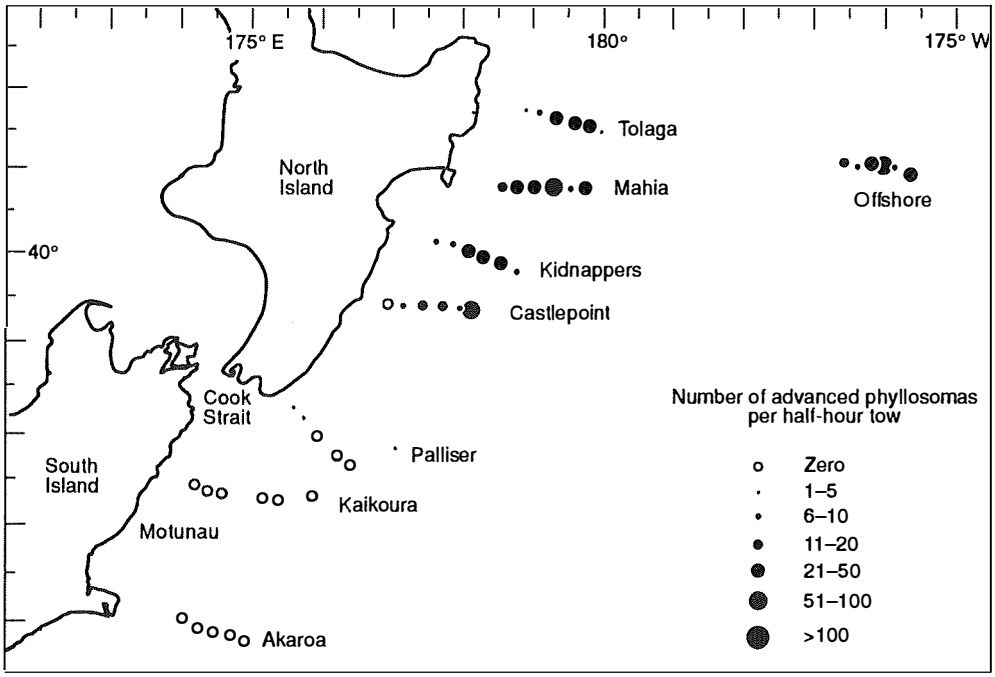

Figure 4. Catches of *Jasus edwardsii* phyllosoma larvae in half-hour tows along transects off the east coast of New Zealand, June 1988.

DISCUSSION OF SESSION 3

Recorded by L.J. Worland

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Following *Simon Thorrold's* panel presentation Nigel Preston wondered if the invertebrate zooplankton that was also collected in the light traps was analysed. However, these samples are still unsorted. Interestingly, there appeared a large biomass in the traps, yet little appeared in the net plankton.

Peter Doherty questioned the interpretation of advection processes between the 5 and 15 nm stations. Rather than a distinct lag in the freshwater pulse between the two stations, had the same body of water simply aged as it moved offshore? Simon Thorrold felt that the plume was advected across the stations, but the biological effect depended upon the composition of the inshore versus offshore copepod community. The offshore community appeared to respond to a greater level than nearshore areas.

Cathy Hair asked how often the samples were taken, and what may have happened between samples? Simon Thorrold advised that samples were once per month over 6 months, with increased sampling during the flood event. Biological effects of the magnitude during the flood could not have occurred between the monthly samplings.

Rick Fletcher asked if data exists for other, perhaps drier summers when there was not a cyclone and huge influx of water, but was told there are none, and Simon Thorrold is waiting for a drier 1991/92.

David Williams asked if there was any relationship between larval fish and copepods? Simon Thorrold found enhanced levels of ichthyoplankton inside the plume and at the front compared to the ocean - similar to that found by Govoni *et al.* (1988) around the Mississippi plume, although Simon Thorrold noted that these frontal larvae were actually in poorer condition (Powell *et al.* 1991).

Iain Suthers commented that the larval fish community, and zooplankton, appear therefore to be food and nutrient limited, to which Simon Thorrold agreed, especially the offshore community, while the nearshore 5 nm station changed the least in response to the flood/nutrient event.

Mike Sinclair pointed out to *Aldo Steffe* that by using a physical oceanography model, and then comparing the actual larval distributions, one can infer larval behaviour - but only if the physical model accurately describes the circulation. Aldo Steffe replied that the circulation of Botany Bay is well studied due to the many port and runway developments (with even the construction of a large-scale replica). He consulted extensively with fishermen who use the eddy to set their trawls, the same eddy predicted from physical models. Strong horizontal and vertical gradients in larval distribution are apparent, despite reduced current velocities in the area. Some species appear bottom-oriented in the main current, yet 150 m away the same species

may be at the surface. These distributions are blurred during the night, but are restored during the day.

Barry Bruce made the interesting point that early larvae may be passive in response to the eddy, but with development (size) may exhibit oriented behaviour (which would vary from species to species). Aldo Steffe defined young larvae as preflexion and flexion stages, which indeed for some taxa did not exhibit oriented distributions as post flexion larvae. At flexion the caudal fin and gas bladder develops, necessary to maintain their distributions (the standard length at flexion varies from species to species).

Bill Talbot agreed with Aldo Steffe, that even a one day old fish larva may be at the surface in the dark, but in the light they rapidly return to the bottom. In Botany Bay, Aldo Steffe argued, these oriented behaviours may actually modify drift.

Jeff Leis noted that there are indirect indications that larval behaviour is important (e.g. Leis 1982a) but we lack direct observations of this. Iain Suthers also noted that larval behaviour is instrumental in the larval retention hypothesis which requires larvae to migrate across a velocity shear. Yet the vertical migration involved across a velocity shear may only be several metres which is impossible to detect even with an opening/closing plankton net.

Ron Thresher returned to the validity of a null physical model and argued that independent data on eggs/pre-flexion larvae (which function as passive particles) are required to support the null model. In response Aldo Steffe said that he used 500 micron mesh (too coarse for eggs/early larvae), and argued that we also need to know the larval source. Some species are derived from outside the estuary and migrate to estuarine nursery areas. Jeff Leis agreed with Ron Thresher that physical oceanographers feel confident with 2-dimensional/depth integrated models which will produce different results from real samples. However, Iain Suthers noted that Botany Bay is well-studied hydrographically due to the many port/airport departures. Barry Bruce recalled Jeff Leis' work on stage-specific egg drift of creediid species off Hawaii (Leis 1982b), and wondered if any oriented behaviour of larvae were evident - however he was told that too few post-flexion larvae were collected.

When *Alan Jordan* had completed his presentation, Don Robertson observed that jack mackerel are fast swimming and are sensitive to water temperature. Perhaps the abundance difference described, is in fact an availability one. Alan Jordan acknowledged that they are sampling a portion of the overall distribution, and perhaps spawning occurred farther south. However the decrease in mackerel larval abundance occurred across all taxa, and there seemed to be an ecosystem response to low productivity, and thus low egg production.

Paul Brown referred to *Barry Bruce's* statement that the back-calculated spawning time was calculated from daily ageing of new recruits, and asked if the dates and sizes corresponded with the physical circulation model and known spawning sites. Barry Bruce replied that spatially, there is a broad-scale spawning pattern, but temporally the back-calculated dates and actual spawning did correspond, although the spawning dates differed between years.

Tony Fowler commented on the difference in ichthyofauna across the front in the summer. Inside the front there is a variety of inshore species, yellowfin bream, whiting, blennies and hemiramphids, while offshore he found similarities to the frontal group, although leptoscopids were found only in the front. Barry Bruce emphasized that grouping larval fish at the family level (thus possible multi-species groups) can obscure specific differences.

Rick Fletcher asked *John Booth* whether the recruits on the west coast of the South Island are from Australia. John Booth replied that there was evidence of an easterly drift from Australia, as significant numbers of *Jasus edwardsii*

phyllosoma occur across the south Tasman Sea, but it is probably not the only source of larvae. Lobster recruitment to the west coast is problematic.

Rob Lewis noted that in the cool temperate southern hemisphere, the six species of *Jasus* are generally found on isolated islands - but how are the larvae retained? John Booth replied that is wasn't initially obvious that the larvae were retained, but from samples made on the delivery voyage of the new N.Z research vessel from Norway (through the south Atlantic and across the south Indian and Southern Oceans), larvae were generally found within 1000km of land - near to the distribution of adults. Few were found beyond this distance, suggesting that altered vertical migration by the phyllosoma maintained their larval distribution.

There was discussion on the possible age of phyllosoma larvae (which cannot be aged). The duration of the larval phase is 10 months for most *Jasus* species, but the New Zealand species is at least 22 months (and possibly 34 months). As the Western Australian and Californian spiny lobsters have durations of 6-11 months, Mike Sinclair speculated as to whether the larval duration was a function of the size of oceanographic features associated with the larval retention.

John Booth replied to a question from Maria Milicich, that the inter-annual variability in lobster settlement is quite high, possibly linked to El Niño events. There was a high ENSO event during August 1991, which appears to be associated with high settlement on the east coast, North Island. ENSO events could affect the eddy system, which could be examined from (expensive) satellite images during the time of puerulus settlement onshore.

Peter Doherty suggested the larvae 1000-800km east of the west coast adult distribution may not return. All of John Booth's transects were less than 400km, and the fate of well-offshore larvae is not known.

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GENERAL DISCUSSION AND SUMMING UP

Chairperson: J. S. Gunn
Rapporteurs: L. T. Worland and I. M. Suthers
Summing up: J. M. Leis

GENERAL DISCUSSION

Chairperson: J.S. Gunn

Recorded by L.J. Worland and I.M. Suthers

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Sampling design

Neil Loneragan asked what are the appropriate sampling strategies so that "hotspots" are not missed. He suggested using a grid design to find oceanographic features and larval patches, before zeroing into the patch to determine limiting biological processes. For example, Greg Jenkins discovered such a larval tuna patch using a grid, that was missed by the Japanese. However, John Gunn suggested that the Japanese may have used the wrong net for *Thunnus* larvae. Tim Davis acknowledged that sampling design is a dilemma, but depends upon the questions being asked. Jeff Leis added that as larval tuna in Greg Jenkin's patch were growing more slowly than the background, then perhaps patch studies are irrelevant. Greg Jenkins considered that the number of patches, and the relative background may be very important, but logistically difficult to determine.

Ron Thresher raised the issue of small spatial and temporal scales that can confound any sampling programme. For example, his sampling of clinid larvae in Storm Bay along transects less than 100 m apart and parallel to shore, revealed a linear patch that passed through a transect and "disappeared" - i.e. the spatial scale at 100 m was still too coarse. Temporal patchiness of larvae can occur over only a few days or weeks, which is incompatible with the constraints of ship time. Barry Bruce extended these two problems into a third; time and space scales relevant for snapper larvae may be irrelevant for another species.

Greg Jenkins suggested that more biological and physical oceanographic data are used to help design our sampling although he conceded this would not have helped to discover the tuna larval patch. Ron Thresher warned that physical oceanographers worked at much coarser scales than are relevant for fish larvae. For example a massive chlorophyll pulse near the Straits of Gibraltar lasting four days was only detected from ship by chance - which was then related to satellite information.

Larval behaviour

Dave Williams noted that earlier discussion on feeding had considered the tropical environment to be a more difficult one for fish larvae, and yet bluefin tuna go to extraordinary lengths to place larvae in such an environment. Perhaps our understanding is missing something here, although he agreed that tropical waters are too warm and too low in oxygen for skipjack spawning. Greg Jenkins suggested that tropical spawning by bluefin tuna may be optimal for developmental rates, or for the circulation and transport, but Iain Suthers warned of such optimality arguments. Jeff Leis suggested that apparent non-optimal spawning may be a result of phylogenetic drag, such that adults now survive in temperate waters but not the larvae.

Peter Rothlisberg stated his maxim "larvae are flexible, larvae adapt, larvae behave in a variety of ways". He suggested that larval behaviour is conservative and limited, but conforms to the particular hydrographic regime by marrying the local physics to the biology. Planktonic larvae are given too much credit in their orientation, (such as discussed for Botany Bay and Storm Bay), and we seem to have downplayed the role of physics. For example, epibenthic prawn larvae may orient to currents and to tidal pressure waves, but if holoplanktonic there is no frame of reference. Not that larvae are passive particles, but we should determine their swimming and behavioural capacities.

Aldo Steffe countered this with the question of scale - at 100s of km physical processes are important, but at 100s of m within an estuary, an orientated behaviour to these gradients would be expected. Iain Suthers suggested that larvae may well be able to detect a tidal pressure wave regardless - we really don't know larval capabilities and tend to consider them as passive particles. Similarly, while Ron Thresher agreed with Peter Rothlisberg, he repeated that we really do not know what larval capacities are - just as with current physics, bumble bees shouldn't fly! A surprising result from a study by Maria Milicich (and Simon Thorrold), shows night vision of pre-settlement pomacentrid larvae is as good as ours, and cautioned treating larval sensory abilites too naively. Maria Milicich also noted that sensory abilities may change with larval development.

Peter Doherty commented that there is a whole suite of other organisms in the plankton as well to be considered with vertical migration, not just the larvae. He also noted that our traditional plankton sampling methods are totally inadequate for sampling the nekton - another methodological problem! Peter Gehrke cautioned about transferring laboratory -determined orientated behaviours to the field. For example, golden perch and silver perch larvae show strong responses to light quality, amino acids and various organ substances in the laboratory, but even in a simplified pond environment the strongest of these responses (light) is modified greatly. Peter Rothlisberg observed that with penaeid larvae, one knew where they were spawned and where they settled. Thus to invoke the process one must simplify the mechanism so that it may apply in other situations - and not create more complex models. Aldo Steffe replied that passive particle and orientated behaviour models will give the same predictions of where larvae settle, but using orientated behaviours larvae may complete the journey quicker, which has advantages for survival.

Jeff Leis raised the issue of the null physical model. Physical oceanographers are not working at scales of larval biologists, and all too often we accept their overview from 2D models. Physical oceanographers must be invited to participate in recording simultaneous physical and biological measurements.

Larval mortality

John Gunn raised the issue of food limitation on survival in the ocean. Tim Davis commented on their patch study of tuna larvae over a four day period. Mike Sinclair discussed 2 studies that attempted to infer larval mortality in relation to recruitment - concerning cod and scallops in the north-west Atlantic. Campana *et al.* (1989) studied cod egg production, larval distribution and abundance, age 1 abundance and followed through with cohort analysis for 3 years. There was no relationship between larval abundance and year class strength, but by age 1, mortality had stabilized, as most of the significant changes happened in the pelagic juvenile stage. Similarly, the early larval abundance of scallops was a poor measure of recruitment, and even at settlement high mortality was still occurring. Iain Suthers noted papers by Taggart and Leggett (1987 a and b), where 40 cohorts of capelin larvae were monitored in a small enclosed cove. Daily mortality ranged from 2-100%, with no relationship to the small-scale microzooplankton abundance. The authors doubted that in the open

ocean robust mortality estimates could ever be obtained, due to the problems of larval immigration and emigration. Iain Suthers recommended study of condition to circumvent estimating larval mortality.

Simon Thorrold raised the issue of scale, when estimating larval mortality. Ed Houde's (1987) recent review on larval mortality concluded M was about 0.3 - but at small time scales M may vary wildly. Alan Jordan raised the sampling problem again, in relation to mortality rates. Post-flexion jack mackerel (10-12 mm) are difficult to sample in standard plankton tows. Larval patchiness may be driven by the spawning patchiness which is seasonally dependent on the particular year-class spawning. Peter Doherty also noted that estimates of M require quantitative samples of each size/age class, but there is a large net-avoidance problem for post-flexion larvae.

Light traps

Light traps are also selective and could not be used to estimate M. The limited success of light traps in temperate waters (Bruce) may be due to their limited use! Jeff Leis stated that light traps are highly efficient to certain stages (usually late stages) of certain taxa. There was some discussion of the relative efficiencies and merits of light traps, bongo nets, Tucker trawls, purse seines, day vs. night sampling, and the relative volumes of water that are sampled by each gear. Hopefully these issues will be addressed in an imminent comparative paper by Choat *et al.*, and the conference presentation by Maria Milicich on light sensitivity of larvae. Bruce Mapstone reasoned that a variety of gear types must be used to sample all stages, but then cautioned on such amalgamations due to the relative efficiency of each gear type. Peter Gehrke also noted the problems of sampling different freshwater habitats: open billabong, snags and weed beds.

Condition indices

John Burke raised the issue of growth variability in one stock of juvenile fish where there are fast growers or "shooters" and slow growers that will not change regardless of tank conditions. Thus we need measures of larval condition, which Iain Suthers suggested as a means of circumventing some of the problems of mortality estimates. Ron Thresher noted the genetic factor here. For example, clinid larvae that were relatively large at parturition were also large at settlement, and there was no correlation with larval duration or growth rate. Iain Suthers noted the paper by Chambers and Leggett (1989), where family lines were carefully controlled and showed that a large egg produced a large larva and early metamorphosis, suggesting genetic pre-programming, rather than any environmental influences such as feeding rate. Steve Battaglene found that most mortality in aquaculture tanks occurs between hatching and first feeding, regardless of fertilisation rates, or environmental conditions such as stocking density.

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SUMMING UP

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Introduction

It is very encouraging to see the way research on the larval biology of aquatic animals has expanded in Australia in the past decade - from a time, when a few isolated individuals were working on the important problems in larval biology to now, when we have enough people working on them not only to be able to hold a dedicated full-day workshop, but also to be able to fill the room to overflowing with participants - and further, to have several contributed papers on larvae in the regular ASFB sessions (one of which won the Whitley Award). Larval biology used to be regarded as a black box that was too difficult or too expensive for the Australian marine science community to prise open. Has this attitude changed, where are we now, what progress have we made, and where do we go from here? I will attempt to assess this by using the session themes as a structure for this summary.

I have provided my own idiosyncratic view of the four disciplines covered by the broad heading of Larval Biology and by this workshop (Table 1). These disciplines all focus on the larval stage, but differ in their goals, orientation, methods, freedom to choose research topics and other factors (Table 1). An understanding of these differences can be helpful in considering the research produced by each discipline, in determining how the disciplines can interact, and in planning future research. I do not mean to imply that individual researchers don't work in or make valuable contributions in more than one of these disciplines. Nor do I intend to imply any hierarchy of value to the disciplines.

One of the great advantages of working at an academically oriented institution is the freedom to choose the subject and area of one's research. This means one can avoid the really messy problems or species, and work in relatively tractable environments. In other words, one can easily choose projects with low risks. At an institution oriented toward applied problems, one often has the research project and species assigned with little consideration for how difficult they are to come to grips with. I suggest this difference alone can go a long way toward explaining the differences among the research priorities and results among the disciplines of larval biology.

Larval taxonomy

We now have a reasonably firm foundation in larval taxonomy, not only for fishes, but also for a number of invertebrates. Consequently, one no longer has to be first a larval taxonomist in order to pursue studies in larval biology. There is now a large pool of knowledge on how to identify the larval stages, and our goal must be to make this more readily accessible. Too often, the would-be larval biologist had to "re-invent the wheel" and work out the identity of a species already identified by someone else who has not

bothered to publish a description or lodge voucher specimens in an accessible collection. This situation is slowly improving with the production of identification guides, and descriptions of individual taxa in journal papers. The possessors of a very large amount of previously unpublished taxonomic knowledge on temperate Australian fish larvae have, as a result of this workshop, generously agreed to make it generally available as an unpublished guide (see Miskiewicz this meeting). An expanded version of this guide should be available in published form in a couple of years. Still, much remains to be done. There are over 3000 bony-fish species in Australian waters (Paxton *et al.* 1989), and while the larvae of most can be identified to the family level, fewer than one-third can be identified to species.

The taxonomy and drawing sessions emphasized the need for high-quality descriptions which meet the minimum standards originally summarized by me in Australian Ichthyoplankton Newsletter a few years ago, and reprinted in revised form in the report of those workshops. More workers need to deposit voucher specimens in accessible collections that have a long-term commitment to curation and to making the material readily available to other investigators: i.e. Museums. Collections at universities and fishery laboratories seldom have the long-term commitment of their administrations, making them poor places to deposit material.

This raises the fate of the collections made in various field studies of larvae. In Australia, these include the blue grenadier studies off Tasmania, the southern bluefin tuna studies off northwestern Australia, the pilchard studies off southwest Western Australia, and the jack mackerel studies off eastern Tasmania. The same concerns apply to the snapper and blue grenadier studies off New Zealand. These studies targeted larvae of single species yet captured a wide variety of species, including many of commercial and ecological importance. The collections were made and sorted at considerable expense, and in most cases only the information on the target species has been extracted. Therefore, the collections are extremely valuable for the information they contain on non-target species. The cost of adequately curating them is small compared with the money already expended on them, but they must be adequately curated in an institution that has a long-term commitment to care of collections. It is essential that these collections be held against future need, and that a small amount of money be made available to compensate the host institution for their conservation. If these collections are viewed as a resource for fishery biology and marine ecology, then perhaps a small committee should be set up to oversee their conservation and use.

The Kiwi connection

Rob Murdoch and Don Robertson (the latter speaking on behalf of John Zeldis) gave us a summary of New Zealand work on larval fishes as performed at the New Zealand Oceanographic Institute (NZOI) and the Ministry of Agriculture and Fisheries (MAF). The NZOI work has focused on hoki (the Kiwi name for blue grenadier), and it is interesting that Rob Murdoch tentatively concludes that predation may be more important than starvation in hoki larvae. The Robertson/Zeldis presentation was more wide-ranging and posed the relevant question: why doesn't abundance vary more than it does? After all, given the fecundities involved, one would expect to see more variation in year-class strength. They concluded that a 'biophysical mosaic' in time and space acts as a filter to dampen fluctuations to within one order of magnitude. More work on the nature of this mosaic will help us understand these fluctuations. The Match/Mismatch vs Member/Vagrant controversy was touched upon and the latter dismissed by Robertson and Zeldis (see also Zeldis 1989). However, the example used by them (snapper in the Hauraki Gulf) seems to me to provide a good example of why such either/or debate is wrong-headed: the Hauraki

Gulf is probably a retention area for snapper larvae (Member/Vagrant hypothesis) within which there can be matches or mismatches of food caused either by injection of salps or other reasons. In other words both processes may operate on the same populations, but at different points in the biophysical mosaic.

Don Robertson asked why biologists seem to have so little influence on management decisions. This theme emerged several times during the workshop. Is the quality of the data upon which we base our recommendations the problem? It seems to me that too much of the data upon which our recommendations are based is fishery-dependent, and our methods of using these often poor data contain too many untested (in the Australian context) assumptions. Are stock size estimates based on eggs and larvae any better? I think they could hardly be worse, and they have the great advantage of being fishery-independent.

Feeding ecology and condition of larvae

Feeding, and more particularly food limitation, always gets a nod as an important factor in larval survival, so it is appropriate that we had a session on feeding. To my mind, this session emphasized how far we have to go in understanding feeding, and how we must be cautious in getting there. There is a general feeling in the literature that larvae must be having a tough time "out there" finding enough to eat, but there is relatively little to back up this feeling. Jock Young and Daniel Gaughan reviewed the Australian work on larval fish feeding. The information they reviewed on gut fullness and diet specialization on such rare items as other fish larvae conveys to me the impression that the larvae we are sampling with plankton nets are getting along very nicely, thank you. Along these lines, Nigel Preston's work on larvae of a commercially important prawn indicates starvation is unlikely to be a major cause of larval mortality in this species. Additional Australian evidence comes from the work of Olson (1987) on the larvae of Crown-of-Thorns Starfish which showed that supplementary feeding in an *in situ* field experiment did not increase survival and only slightly increased developmental rate. It is noteworthy that Olson found food concentrations in his field experiment were below the minimum threshold necessary to support larval development in the laboratory, yet resulted in good survival. Further, these low field concentrations of food resulted in development times shorter than the fastest recorded in the laboratory under any food conditions. Both these findings provide a clear warning against blithely projecting laboratory results to the field.

In one of the few cases where larvae seemed to be constrained by food availability, Greg Jenkins demonstrated that *Thunnus maccoyii* larvae in extremely dense patches of larvae had slower growth than larvae outside of such patches: possible density-dependency, so beloved by modelers. Whether this affects survival or not remains to be seen. Otherwise, most studies conclude larvae are not concentrated enough to affect the density of their prey.

Condition indices are a promising approach to studying feeding and food limitation, and Iain Suthers took the useful approach of measuring and comparing three different indices in cod larvae from the field. His results introduce a note of caution because, although indices usually perform well in the laboratory, in wild cod larvae the indices did not all tell the same story, and correlation between indices was often poor or even negative. Obviously, future work with indices will require careful field-based validation.

The use of otolith-based measures of age and growth for larval fishes has spread widely in the past ten years, and has provided us with much insight into larval biology. Maria Milicich's laboratory-based otolith work strikes another note of caution, and emphasizes the need for validation of otolith-based technique.

It seems unlikely that many larvae die of starvation, but that they are more subject to predation because they are weak or grow slowly. We know very little about predation on larvae in either good or bad condition. Usually, predation mortality is considered that which can't be accounted for by other factors. Efforts are needed to measure predation on larvae directly, and no one in Australia seems to be working on this important problem.

Perhaps, as Iain Suthers tells me, I am being too selective in my view of the evidence on feeding ecology and condition. However, remember that for the purposes of this summation I am confining myself to the workshop presentations or other Australian work (in this regard, Iain Suthers tells me he's finding many empty guts - presumably indicating low feeding success - amongst the field captured larvae he's examining, but this observation is at odds with the published Australian work). I have purposely taken this rather extreme view because I think there is too much uncritical acceptance of the overriding influence of food and feeding conditions in the literature. I hope to generate a bit more critical thinking in this area.

Extensive larval rearing

This session covered recent developments in aquaculture, and of the workshop sessions it is the one about which I know the least and therefore probably have the most uninformed and biased views. The papers served to remind me that freshwater systems differ markedly from marine ones, particularly in terms of larval ecology. In spite of their considerable progress and continued efforts to control conditions and maximize yield, the culturists still have major unexplained fluctuations in survival rates and growth. It is sobering for someone like me who works in "natural" marine systems to realize that even with a large degree of control over what happens in their culture systems, the aquaculturists still have a long way to go before they can count on the kind of predictable yields their terrestrial counterparts take more or less for granted.

The culturists have the distinct advantage of being able to observe their animals alive and to perform manipulative experiments on the larvae, something the field biologists find exceedingly difficult to do (but, see Nigel Preston's work). Observations by the culturists on problems in inflation of larval fish gas bladders, and the large mortalities this apparently causes in culture systems, elicited much excitement amongst the "field types". Perhaps this should be dubbed the Gas/Missed-Gas Hypothesis. However, ever the ratbag, I must throw out a few caveats, and let my biases show.

Observations by aquaculturists have provided us with some of the more enduring paradigms in larval fish biology: the critical period, and the very high levels of food (higher than that normally found in the field) necessary for larval survival. (Most larval biologists think Hjort (1914) originated the idea of and coined the phrase 'critical period'. In fact, as May (1984) points out, this was done by aquaculturists at least 15 years before Hjort's use of the term. Hjort admitted he had no real field data to back up his ideas of the critical period: he apparently developed his ideas from aquacultural observations.) Much energy has been expended in either testing these ideas or in trying to fit field data to them. I suggest that larval fish ecologists have been led astray by these culture-based (=lab-based) observations. There is no good demonstration that there is a critical period in the field, and it seems to me that the evidence on feeding and condition in the field (see above) argues against the need for very high food concentrations for growth and survival. Let's not forget that culture systems (and most laboratory systems) are highly artificial, and that survival rates considered by culturists to be poor are still one to several orders of magnitude above those measured in natural systems. Typically, fishes resulting from culture differ from wild individuals morphologically (e.g. meristically, morphometrically, or in pigment), biochemi-

cally (e.g. higher lipid content) or in taste (e.g. Japanese claim to be able to taste a difference between cultured and wild sea bream): this should warn us that something very different is happening in the culture system than in the wild. Projection of laboratory results into the field is always hazardous, but when, as is the case in culture systems, the laboratory observations are the by-product of either "green-thumb" manipulations or experiments which have the primary or sole goal of increasing yield, one must be doubly cautious.

Our aquacultural colleagues described a number of the experiments they have performed with temperature, food levels, salinity, water quality, and enclosure morphometry with the goals of increasing survival and growth. We field biologists can only admire and envy the ability to perform such manipulative experiments.

Biological effects of oceanographic processes

If the patterns observed by the field biologists are to be properly interpreted and understood, and perhaps, more important, if field sampling is to be conducted at appropriate scales and structured in a meaningful way, there must be input from physical oceanographers. This is now beginning to be the norm rather than the exception, but it is difficult to achieve the necessary blending of biological and physical talent outside of large research organizations such as AIMS and CSIRO. Biologists frequently do not know enough about their animals or about physical oceanography to ask the right questions or to assess if what the physicists offer will be appropriate for the problem. Physical oceanographers frequently are not interested in working at the scale of interest to the biologist, in working in the "noisy" near-shore or on-shelf environments beloved by biologists, or in working on studies perceived to be empirical and descriptive with little generality or application to theory. The papers in this session demonstrate some of the promise of collaboration between biologists and physicsts, and also some of the problems.

Simon Thorrold and David McKinnon, and Barry Bruce, presented case studies of how the physics of frontal zones can influence the distribution of fish larvae. John Booth and Robert Stewart argued that the large-scale circulation off the east coast of New Zealand held rock lobster larvae near the North Island for 12-22 months. Alan Jordan implicated large-scale oceanographic variability in the interannual variability of larval abundance off the east coast of Tasmania, and touched upon the neglected area of the influence of physical and biological factors on fecundity and propagule quality. Aldo Steffe and Mark Westoby inferred behavioural flexibility for fish larvae and its importance for position maintenance in a coastal embayment by comparing observed distributions of larvae with those predicted from a null physical model (which assumed passive larvae). Lack of direct measurements of larval behavioural capabilities is a major problem in larval biology. A number of behaviours have been inferred in other studies, but if the validity of the physical null model is questionable (as is frequently the case), then the inferred behaviour is equally questionable. While interesting and valuable results were obtained, I had the feeling that none of the studies achieved what they might have because they did not have a physical oceanographer dedicated to them. All used "second-hand oceanographic information" from programs not designed to support the biological studies.

Other issues

Although there was not a formal session on sampling problems, they were referred to frequently in questions and discussions. Larval biologists in this country are perhaps leading the world in the application of unconventional sampling techniques including the light trap and plankton purse seine. This is to be encouraged,

but there must be more effort at cross-calibration of methods and validation of the unconventional ones. In North America, there is a big move toward using multinets such as Mocness with real-time readout of physical variables and remote opening-closing abilities. This move is not evident here, in spite of the presence of one such net on R.V. Franklin.

It is noteworthy that the stock-size assessment discipline of larval biology which has taken up so much time and resources overseas, is virtually ignored in Australia. Perhaps this is a function of the relatively short time that larval biology has been seriously studied here: maybe we just don't have the biological underpinning necessary to pursue this larval biology discipline. The emphasis, particularly in the USA, seems to be on hindcasting population size using the egg production method developed for the California anchovy. Our own fishery biologists seem only now to be awakening to the need for the fishery-independent data on population size that egg and larval surveys can provide. The Robertson/Zeldis presentation can perhaps give us some guidance here, as will the proceedings of a symposium on such methods held in June 1991 as part of the 15th annual Larval Fish Meetings in Los Angeles (to be published in Contributions in Science of the Natural History Museum of Los Angeles County).

Another result of our short time in the larval business is the lack of long time-series of data on abundance and distribution of egg and larval stages. Few studies in Australia have produced data for more than the duration of a PhD thesis study. For much of our coast, and for many of our commercial species, there are no larval data at all.

The issue of regional differences was raised several times. Temperate/tropical, shelf/oceanic, and Australian/N. Atlantic differences in larval biology were postulated. Some may even be real, but clearly some are due to our thin data base or our reliance on text-book generalities about tropical (or other) systems. Tropical shelf systems are as different from the "oligotrophic deserts" of the central oceanic gyres as terrestrial deserts are from rainforests, so any attempt to contrast marine tropical and temperate systems is confounded from the start. However, it is true that we have no major upwelling areas such as the California Current system, and that the classic North Atlantic picture of the short, sharp spring and autumn 'blooms' in primary and secondary production does not apply in most Australian waters. Many of the paradigms in larval biology were derived from work in the North Atlantic and California (especially those on feeding), so we should be on the look-out for differences between these northern hemisphere systems and our own.

Conclusion

I was impressed by the high quality of the work presented at the workshop. We know a lot more about Australian larvae than we did ten years ago, and although this sheds some light into the black box, it serves primarily to show how much more we have to find out. At least there is a recognition that larval studies must be an integral part of our marine research agenda. We have concentrated on questions of taxonomy, distributional ecology and aquaculture thus far. Without neglecting these, it is now time to build on this base and look at additional aspects of larval ecology. It is an exciting time to be working on larval biology in Australia and lots of possibilities present themselves, but to take advantage of them we need a more secure career structure for our larval biologists. Too few of them have permanent positions from which to pursue their studies. Without this, I fear much of the enthusiasm demonstrated here in Hobart for larval studies will be lost.

Acknowledgements

I thank Iain Suthers for inviting me to sum up the Larval Biology Workshop, and emphasize that the views expressed are solely my own. I hope this Summary will serve to stimulate some

thought and debate, and make no pretence of presenting a balanced view. My thanks to Suzanne Bullock for editorial assistance, and Iain Suthers and Tom Trnski for comments on the manuscript.

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Table 1. Characteristics of the four disciplines of larval biology

	DISCIPLINE	
Characteristic	1) Taxonomy & Systematics	2) Ecology
Goals	Identification & relationships	Determination of pattern & process
Orientation	Academic	Academic
Methods	Rearing, size series, cladistics, phenetics, etc.	Field Sampling, ANOVA, correlation; rarely lab and *in situ* experiments
Input from other disciplines	1) - 2) yes, specimens 3) no 4) yes, specimens	1) yes 2) - 3) no 4) yes
Use of physical data	Rarely in meristic variation or biogeography	In sample design; to interpret observed distributions
Latitude of choice of subject or area	Moderate to high	Moderate to high
Characteristic	3) Stock Size Assessment	4) Aquaculture
Goals	Forecasting or hindcasting population size	Commercial; increase yield
Orientation	Applied	Applied
Methods	Field sampling, calibration	Manipulative experimentation, selective breeding
Input from other disciplines	1) yes 2) yes 3) - 4) no	1) little 2) yes? 3) no 4) -
Use of physical data	prediction of year class strength (eg via upwelling indices)	manipulate culture conditions, and modify if suboptimal
Latitude of choice of subject or area	Low	Low to high

EVENING SESSION

TAXONOMY OF TEMPERATE AUSTRALASIAN FISH LARVAE

Session Chairpersons: A. G. Miskiewicz
F. J. Neira

EVENING SESSION
TAXONOMY OF TEMPERATE AUSTRALASIAN FISH LARVAE

Session Chairpersons: A.G. Miskiewicz
F.J. Neira

Evening workshop for larval fish taxonomists to generate a preliminary guide to families of temperate larvae, a list of names of Australasian workers, and some figures/descriptions of larvae.

The session was well and enthusiastically attended. No formal record was kept of the discussion, but Chairperson Tony Miskiewicz has provided the following situation statement, which includes agreement and support for an *Atlas of Fish Larvae of Temperate Australian Fishes*. This 2-year project commenced in January 1992 and is funded by a grant from the Australian Biological Resources Studies. The principal researcher for the project is Dr F.J. Neira with contributions from a range of workers with expertise in various families.

A REVIEW OF STUDIES OF THE EARLY LIFE HISTORY OF FISH IN TEMPERATE AUSTRALIAN WATERS

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Introduction

An important, but poorly studied, aspect of the life history of fishes in Australian waters is the ecology of their larvae. Fish larvae often bear little resemblance to adults. This leads to problems with their identification and is a major reason for the paucity of ecological studies in temperate Australian waters (Leis and Rennis 1983). It is only in the last fifteen years that the larval development, spawning localities, seasonal variations in abundance and the size range of recruitment to nursery habitats have become known for some species.

The aim of this review is to provide an overview of larval fish studies in the waters of temperate Australia and the present status of these studies. The scope of the review extends from Moreton Bay in southern Queensland to Perth in south-western Australia. As a part of this review, a complete bibliography of larval fish studies in this region is also provided.

Taxonomic studies

A very diverse fish fauna, with a high degree of endemism, occurs in temperate Australian waters. However, the larvae of this fauna are very poorly described. As mentioned in the Introduction, until the past fifteen years there have been few descriptions of larval development of individual species. Associated with the increase in ecological studies, the number of species whose larvae have been identified has also increased (Table 1). However, although the larvae of many species from temperate Australian waters have been identified, the larval development of many of these are still undescribed or are the subject of incomplete descriptions of varying standards (Trnski this meeting).

The first study of fish larvae in Australian waters was by Tosh (1902) who described the development of the eggs and the early larval stages of the sand whiting *Sillago ciliata*. Tosh (1903) figured the eggs and early larval stages of 30 species collected in Moreton Bay. Regan (1916) described and figured the larvae of an Odacid, *Odax balteatus* and a Scorpaenid, *Gymnapistes (Pentaroge) marmoratus*, caught in Port Phillip Bay. Dakin and Colefax (1934; 1940) described the eggs and larvae of the pilchard *Sardinops neopilchardus*. Blackburn (1941) described the eggs and early larvae of the anchovy *Engraulis australis* and the larvae of the maray, *Etrumeus teres*. Bruun (1940) described the larval development of the Schindleriid, *Schindleria praematura*. Munro (1944) described the egg and larval development of the yellowfin bream *Acanthopagrus australis* and black bream *A. butcheri*. Munro (1945) described the larvae and juveniles of *S.*

ciliata, A. australis, tarwhine *Rhabdosargus sarba*, blackfish *Girella tricuspidata*, trumpeter *Pelates quadrilineatus*, stargazer *Ichthyscopus lebec*, and toadfish *Spheroides pleurogramma* from the Brisbane River. As part of a revision of the Fam. Bregamacerotidae, Munro (1950) described the development of larvae of *Bregamaceros*. Munro (1955) described the egg and larval development of the sabretooth blenny *Petroscirtes lupus* (*Dasson steadi*). Thomson and Bennet (1953) described the spawning behaviour and early larval development of the oyster blenny *Omobranchus anolius*. Milward (1966) described the development of the eggs and larvae of the Australian smelt *Retropinna semoni*.

Larval stages of 16 species caught off Port Hacking were figured in Bruce (1982). Miskiewicz (1987) described the development of 32 species including *Monodactylus argenteus* (Miskiewicz 1989) from Lake Macquarie and nearby coastal waters. Neira (1988) described the larval development of 5 species from the Swan Estuary in south-western Australia. Detailed developmental series have been described for the Australian devilfish, *Gymnapistes marmoratus* (Neira 1989), the cardinalfish, *Apogon rueppellii* (Neira 1991), *Lesueurina sp.* (Neira and Gaughan 1989), and the flathead *Platycephalus speculator* (Hyndes *et al.* in press). Crawford (1986) described the egg and larval development of the flounders *Rhombosolea tapirina* and *Ammotretis rostratus* based on hatchery reared specimens. Bruce (1988) described the larval development of the blue grenadier *Macruronus novaezelandiae* from Tasmanian waters. In addition, larval development of several families whose representatives occur in temperate Australian waters have been described by Leis and Rennis (1983), Bruce (1989a; b) and Leis and Trnski (1989).

To consolidate the results of all the taxonomic studies into one volume, a project is underway to produce an *Atlas of Fish Larvae of Temperate Australian Fishes* (Table 1). This two year project commenced in January 1992 and is funded by a grant from the Australian Biological Resources Studies. The principal researcher for this project is Dr F.J. Neira with contributions from a range of workers with expertise in various families.

Ecological studies of marine and estuarine species

Eastern Australia

The earliest ecological studies of fish larvae in southern Australian waters were conducted as part of zooplankton surveys (Dakin 1937; Dakin and Colefax 1934; 1940) and as part of a resources assessment survey for clupeoids (Blackburn 1949; 1950; 1960).

The first survey of estuarine fish larvae was conducted by Helbig (1969) who investigated spatial, tidal and diel variations in the distribution of fish larvae in Moreton Bay over a 15 month period. This study was limited due to taxonomic problems with most taxa identified only to familial level or unidentified.

In the past 15 years, larval fish studies in temperate Australian waters have proliferated (Table 2). Due to the logistical problems and costs, the majority of these studies have been concentrated in estuaries and enclosed bays and many undertaken as part of postgraduate projects.

There are numerous estuaries in southern Queensland and along the NSW coast that support large commercial and recreational fisheries. Several studies have been undertaken in NSW estuaries aimed at assessing the significance of estuaries as spawning and/or nursery habitats for fish, to assess seasonality and size of entry of fish larvae into these systems and the processes by which fish larvae enter and maintain themselves within estuarine habitats.

Pollock *et al.* (1983) described the timing and size at which *Acanthopagrus australis* larvae entered Moreton Bay from samples that were collected for larval prawn surveys. As part of a tagging study of tailor *Pomatomus saltator*,

Halliday (1990) collected plankton samples off Fraser Island to determine the location and timing of spawning.

A three year survey in Lake Macquarie and nearshore coastal waters was conducted by Miskiewicz (1986; 1987). The aims of this study were to determine which species spawn within the estuary and which spawn at sea, the seasonal variation in the species assemblage and the size at which larvae of species which spawn in marine waters enter the estuary. Tidal and diel variations in abundances of larvae moving into and out of the estuary were also investigated. In a complementary study, Marsden (1986) investigated seasonal variations in the species composition and abundance of fish larvae entering Tuggerah Lake located just south of Lake Macquarie.

Powles (1973) investigated the entrainment of eggs and larvae of the anchovy *Engraulis australis* into the cooling water system of a power station in Lake Macquarie. He also investigated the survival of the *E. australis* eggs and larvae in the heated water discharged from the plant.

Botany Bay is a highly urbanised protected embayment located just south of Sydney. The initial study of fish larvae in the Bay was a two year survey associated with assessing the impacts of port development and the construction of a runway (SPCC 1981; Steffe and Pease 1988). This study was limited by the use of small nets with a fine mesh. Steffe (1982; 1989) investigated tidal and diurnal variations in distribution of larvae at two sites over a 24 hour period in Botany Bay. The results of more detailed studies aimed at assessing larval distributional patterns within Botany Bay and the possible mechanisms by which larvae maintain themselves within the estuary are described by Steffe (1990; 1991).

The studies described above were limited to a single estuary and this gives no indications of seasonal and spatial variability in species composition and abundances of larvae between estuaries. A study is presently underway to compare seasonal variations in the species assemblage and abundances of fish larvae in 9 estuaries along the central NSW coast (Suthers *et al.* in progress).

The first seasonal survey of fish eggs and larvae in Sydney coastal waters was conducted by Bruce (1982) who sampled for one year at the CSIRO 50 and 100 metre oceanographic stations off Port Hacking. This study was limited by the low numbers of larvae in the samples and problems with identifications of species.

In recent years, a number of surveys of larval fish have been commenced in the coastal waters of the Sydney region. These studies are associated with a major monitoring programme assessing the impact of the surface sewage effluent plumes from the three major cliff-face outfalls at North Head, Bondi and Malabar and their replacement by deepwater outfalls. A pilot study to determine sampling stations and provide data for a cost benefit analysis was undertaken by Gibbs (1987). The full scale programme began in June 1988 and will run for five years (FRI 1991; Gray *et al.* in press; Gray in progress). In association with this programme there have been two surveys to assess the incidence of deformities in larval fish caught in and out of the surface sewage plumes at Malabar (Kingsford and Suthers 1990) and North Head (Kingsford *et al.* 1991).

Apart from investigating larval distributions around sewage plumes, studies are also underway to investigate the variations in the species composition and abundance and distribution of fish larvae in relation to estuarine fronts and plumes at different times and states of the tide. The initial focus for this work is the front occurring at the entrance of Botany Bay (Kingsford 1990; Kingsford in press; Kingsford and Suthers in prep.). Associated with this work, Druce (1990) investigated the larval and juvenile fish communities occurring in association with drift algae and other floating objects.

Leis and Reader (in progress) have a study underway to determine changes in seasonal abundance and species composition of fish larvae in surf zones near Sydney. The aim of this study is to assess the significance of this habitat for fish larvae.

There have been three studies of larval distributions in coastal waters along the NSW coast. The first resulted from three CSIRO plankton surveys for larval squid, undertaken in January, March and May 1983, in coastal and oceanic waters between Sydney and Brisbane. The distribution of selected species was described in Miskiewicz (1987). Plankton surveys in northern NSW coastal waters were undertaken in August and September 1985 (Gorman and Graham 1985) and August and September 1986 (Gorman *et al.* 1987) to determine the spawning times and locations of gemfish (*Rexea solandri*). The aim of the third survey, conducted between Coffs Harbour and Newcastle, was to collect whiting larvae *Sillago spp.* as part of a population discrimination study (Dixon and Miskiewicz in progress). Work is continuing to identify the remaining larvae in the samples from these three studies.

Victorian waters

The Gippsland Lakes are a major estuarine system in south-eastern Victoria that supports a large commercial and recreational fishery. Arnott and McKinnon (1985) described the seasonal abundance of anchovy *E. australis* eggs and larvae in the system. Associated with a survey of juvenile fish distribution patterns in the Gippsland Lakes, Ramm (1986) detailed the distribution and seasonal abundance of eggs and larvae of *E. australis* and eggs of the black bream *A. butcheri*.

Langly (1984) described the summer ichthyoplankton community occurring in seagrass beds in Port Phillip Bay. As a precursor to detailed studies on ageing, diets and growth rates of larvae of two flounder species, *Rhombosolea tapirina* and *Ammotretis rostratus* in Port Phillip Bay (Jenkins 1987a; b; 1988), Jenkins (1986) conducted a one year survey to determine spatial patterns of larval distributions within the Bay and seasonal patterns of abundance. Fancett and Jenkins (1988) described the impact on fish larvae of predation by scyphomedusae in Port Phillip Bay. As part of a study of fish communities in seagrass beds, Jenkins (in progress) investigated the distribution and seasonality of pre-settlement larvae in Swan and Port Phillip Bays.

Willis (1991) investigated the diet of larval and juvenile *A. butcheri* in the Hopkins River estuary in western Victoria. Newton (in prep.) undertook a seasonal survey of the species assemblage, abundances and spatial distribution of fish larvae in the Hopkins River estuary in relation to hydrology and distribution of zooplankton.

As part of a programme investigating the ecology of neustonic Pontellid copepods, Holdway and Lanzing (in progress) collected neuston samples in Bass Strait waters in which numerous neustonic fish larvae were also collected. Work is ongoing to identify the larvae in these samples.

Tasmanian waters

Two major surveys of fish larvae have been undertaken in Tasmanian waters. The first was in association with a resource assessment survey and life history study of the blue grenadier, *Macruronus novaezelandiae* (Gunn *et al.* 1989; Thresher *et al.* 1988a; b; Furlani *et al.* in prep.). The second was undertaken as part of a resource assessment survey for jack mackerel, *Trachurus declivis* (Jordan and Marshall in progress). This work has been augmented by a three year study of interannual variations in the diet of *T. declivis* larvae (Young and Davis in press).

As part of a study to assess the factors influencing interannual variations in recruitment of inshore species, surveys have been conducted of several species of weedfishes (Fam. Clinidae) (Gunn and Thresher 1991; Thresher *et al.* 1989).

South Australian waters

As part of a resource assessment survey of pelagic fish in the Great Australian Bight, plankton surveys were conducted on 9 cruises in the Bight between January 1979 and December 1980 (Stevens *et al.* 1984). On each cruise, a transect was sampled in the western, central and eastern Bight. The only species identified from the samples was the pilchard *S. neopilchardus*, larvae of which were only caught in April and May.

Since 1986, the South Australian Department of Fisheries has conducted a major programme of fish larval surveys in Spencer Gulf, Gulf Saint Vincent and in shelf waters (Bruce 1989c). The aims of this study are to describe the development, species assemblage, distribution and seasonality of fish larvae in South Australian marine waters.

Western Australian waters

In south-western Australia there are about 80 estuaries, many of which are only open to the sea on a seasonal basis. This is related to the strongly seasonal rainfall patterns in the region. The first survey of fish larvae in south-western Australia was conducted by Lenanton (1977) in the Blackwood Estuary. However, this study was limited by taxonomic difficulties and the larvae were only identified to familial level. The first major survey investigating the seasonality and distribution of fish larvae was conducted in the Swan Estuary (Neira 1988).

A number of subsequent studies have been undertaken in the Swan Estuary and other estuaries in south-western Australia to investigate the ecology of larvae in this variable habitat (Gaughan *et al.* 1990; Hyndes *et al.* in press; Neira *et al.* 1992; Neira and Potter in press; submitted).

A resource assessment survey of the pilchard, *S. neopilchardus,* fishery is being conducted in the coastal waters of south-western Australia. As part of this programme, plankton surveys are being undertaken to determine the seasonality and distribution of fish eggs and larvae in the coastal waters off Albany (Fletcher in progress). The aim of the plankton surveys is to determine the spawning localities and times of *S. neopilchardus*.

Ecological studies of freshwater species

Compared to estuarine and marine species, there have only been a limited number of ecological studies of freshwater species. These studies have mainly investigated the relationship between floods, spawning cues, behaviour and distribution patterns of larvae and juveniles (Harris 1983; 1986; Geddes and Puckridge 1989; Gehrke 1990a; b; 1991; 1992; in prep; Puckridge and Walker 1990).

Aquaculture

There is a long history of aquaculture studies of freshwater species. These studies have been aimed at inducing spawning and rearing of larvae for restocking programmes in inland waterways. The first work on freshwater species was conducted on the Murray cod *Maccullochella peeli* (Dakin and Kesteven 1938). Lake (1967a; b) described the results of work to induce spawning of *M. peeli*, catfish *Tandanus tandanus*, silver perch *Bidyanus bidyanus*, golden perch *Macquaria ambigua*, western carp gudgeon *Carassiops klunzingeri* and European perch *Perca fluviatilis*. He also figured the eggs and early larvae of these species. The spawning, egg and early larval development of the spangled perch *Madigania unicolour* (Llewellyn 1973) and southern pigmy perch *Nanoperca australis* (Llewellyn 1974) has also been described.

More recently studies have been conducted on Australian bass *Macquaria novemaculeata* (Van der Wal 1985; Van der Wal and Nell 1986; Battaglene and Allen 1990; Battaglene and

Talbot 1989; 1990; in review; Battaglene *et al.* 1987; 1989; in press; Talbot and Battaglene 1991; Battaglene and Allen 1990), Murray cod *M. peeli* (Rowland 1988); silver perch *B. bidyanus* (Rowland 1984) and golden perch *M. ambigua* (Rowland 1983; Arumugam and Geddes 1987) and Australian grayling *Prototroctes maraena* (Bacher and O'Brien 1989).

In recent years there have been attempts at culturing a range of marine species with varying degrees of success. The first successful attempts were conducted by Crawford (1984; 1986) who reared the Tasmanian flounders, *Rhombosolea tapirina* and *Ammotretis rostratus,* and described the development of the eggs and larvae. The Tasmanian striped trumpeter *Latris lineata* has been spawned in captivity and early larvae reared to 40 days (Ruwald *et al.* 1991; Furlani and Ruwald in prep.). Attempts at inducing spawning and rearing larvae of a range of species have been made at the NSW Fisheries Brackish Water Research Station (Battaglene and Talbot in review; Table 3)

Conclusions and recommendations

As indicated by the information presented above, there has been a vast expansion in larval fish studies in recent years and with the number of studies currently underway, our knowledge of larval fish taxonomy and ecology will be increased even further.

Although the Atlas will provide a considerable impetus, there is a need for further taxonomic studies and descriptions of larval development of species occurring in temperate Australian waters. This will assist workers in identification of larvae collected during ecological studies. With regard to ecological studies of fish larvae, there is a need for long term (over a number of years) studies covering broad spatial scales along with complementary oceanographic data. Such studies will assist our understanding of the reasons for interannual variations in larval abundances and distribution patterns.

Many studies have been undertaken to collect plankton samples for other reasons, yet the samples contain fish larvae. Efforts should be made to remove these larvae from the samples and if not analysed, the samples should at least be lodged in an appropriate institution for storage.

Finally, there is a need for people working on fish larvae to ensure that their samples are properly curated and lodged in institutions such as the Australian Museum, for long term storage, where they are available for study by other workers.

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Table 1. Families and species of fish whose larval stages will be described and illustrated in the *Atlas of Fish Larvae of Temperate Australian Fishes*

(* indicates commercial and recreationally important species).

ORDER	FAMILY	SPECIES	COMMON NAME
Clupeiformes	1. Clupeidae	*1. Nematalosa vlaminghi**	Perth herring
		*2. Spratelloides robustus**	Blue sprat
		*3. Hyperlophus vittatus**	Sandy sprat
		*4. Hyperlophus translucidus**	Translucent sprat
		5. Herklotsichthys castelnaui	Southern herring
		*6. Sardinops neopilchardus**	Pilchard
		7. Etrumeus teres	Maray
	2. Engraulidae	*8. Engraulis australis**	Australian anchovy
Salmoniformes	3. Galaxiidae	*9. Galaxias maculatus*	Black minnow
		10. Galaxias occidentalis	Western minnow
Gonorynchiformes	4. Gonorynchidae	*11. Gonorynchus greyi*	Beaked salmon
Gadiformesa	5. Gadidae	*12. Gaidropsarus novaezelandiae*	
	6. Merluccidae	*13. Macruronus novaezelandiae**	Blue grenadier
Ophidiiformes	7. Ophidiidae	*14. Genypterus blacodes**	Ling
Beloniformes	8. Hemiramphidae	*15. Hyporhamphus melanochir**	Southern sea garfish
		*16. Hyporhamphus sp.**	
	9. Scomberesocidae	*17. Scomberesox saurus*	Saury
Atheriniformes	10. Atherinidae	*18. Atherinosoma elongata*	Swan River hardyhead
		19. Atherinosoma macrostoma	Silverfish
		20. Craterocephalus honoriae	Hardyhead
		21. Leptatherina presbyteroides	
		22. Leptatherina wallacei	
		23. Atherinomorus ogilbyi	Ogilbyi's hardyhead
		24. Pseududomugil signifer	
	11. Isonidae	*25. Iso rhothophilus*	Surf sardine
Beryciformes	12. Berycidae	*26. Centroberyx affinis**	Nannygai
	13. Trachichthyidae	*27. Aulotrachichthys sp.**	Roughy
		28. Optivus sp.	
		29. Paratrachichthys sp.	
Gasterosteiformes	14. Macrorhamphosidae	*30. Macrohamphosus sp.*	Bellowfish
	15. Syngnathidae	*31. Hippocampus angustus*	Hairy pipefish
		32. Urocampus carinirostris	Spotted pipefish
		33. Stigmatopora argus	Black spotted pipefish
		34. Stigmatopora nigra	

Table 1. continued

ORDER	FAMILY	SPECIES	COMMON NAME
	16. Pegasidae	*35. Parapegasus natans*	Slender seamoth
		36. Acanthopegasus lancifer	
		37. Eurypegasus draconis	
Scorpaeniformes	17. Scorpaenidae	*38. Gymnapistes marmoratus**	Australian devilfish
		39. Centropogon australis	Fortesque
		*40. Helicolenus sp.**	Ocean perch
		41. Neosebastes sp.	
	18. Platycephalidae	*42. Platycephalus fuscus**	Dusky flathead
		*43. Platycephalus speculator**	Blue-spotted flathead
		*44. Platycephalus sp**	
Perciformes	19. Percichthyidae	*45. Apogonops sp.*	
	20. Callianthidae	*46. Callianthus australis*	
	21. Acanthuridae	*47. Prionurus sp.*	Surgeon fish
	22. Ambassidae	*48. Velambassis jacksoniensis*	Port Jackson perchlet
		49. Priopidichthys marianus	Yellow perchlet
	23. Terapontidae	*50. Pelates quadrilineatus*	Trumpeter
		51. Pelates sexlineatus	Six-lined trumpeter
		*52. Amniataba caudavittatus**	Yellowtail trumpeter
	24. Apogonidae	*53. Apogon rueppellii*	Gobbleguts
		54. Siphamia cephalotes	
	25. Arripidae	*55. Arripis georgianus**	
		*56. Arripis trutta**	
	26. Sillaginidae	*57. Sillago ciliata**	Sand whiting
		*58. Sillago maculata**	Trumpeter whiting
		*59. Sillago bassensis**	Southern school whiting
		*60. Sillago robusta**	Stout whiting
		*61. Sillaginoides punctata**	King George whiting
		*62. Sillago schomburgkii**	
	27. Pomatomidae	*63. Pomatomus saltator**	Tailor
	28. Carangidae	*64. Pseudocaranx dentex**	Skipjack trevally
		*65. Trachurus sp.**	Yellowtail scad
		*66. Seriola sp.**	Kingfish
	29. Coryphaenidae	*67. Coryphaena hippurus**	Common dolphinfish
	30. Sparidae	*68. Acanthopagrus australis**	Yellowfin bream
		*69. Rhabdosargus sarba**	Tarwhine
		*70. Pagrus auratus**	Snapper
	31. Gerreidae	*71. Gerres ovatus**	Silver biddy
		*72. Parequula melbournensis**	Roach

Table 1. continued

ORDER	FAMILY	SPECIES	COMMON NAME
	32. Sciaenidae	*73. Argyrosomus hololepidotus**	Mulloway
	33. Monodactylidae	*74. Monodactylus argenteus*	Diamond fish
		75. Schuetta scalaripinnis	
	34. Pempheridae	*76. Pempheris multiradiata*	Common bullseye
	35. Girellidae	*77. Girella tricuspidata**	Blackfish
		*78. Girella sp.**	
	36. Kyphosidae	*79. Kyphosus sydneyanus*	Silver drummer
		80. Kyphosus sp.	
	37. Enoplosidae	*81. Enoplosus armatus*	Old wife
	8. Mugilidae	*82. Liza argentea**	Flat-tail mullet
		*83. Aldrichetta forsteri**	Yellow-eye mullet
	39. Mullidae	*84. Upeneichthys sp.*	Goatfish
	40. Nemipteridae	*85. Pentapodus vitta*	
	41. Percophidae	*86. Enigmapercus sp.*	
	42. Pinguipedidae	*87. Parapercis haackei*	
	43. Pomacentridae	*88. Abudefduf saxatilis*	Damselfish
	44. Schindleriidae	*89. Schindleria praematura*	
	45. Sphyraenidae	*90. Sphyraena sp.**	Barracuda
	46. Labridae	*91. Achoerodus viridis**	Eastern blue groper
		92. Pseudolabrus spp.	Wrasse
	47. Latrididae	*93. Latris lineata**	Trumpeter
	48. Lutjanidae	*94. Paracaesio chrysozon*	
	49. Microcanthidae	*95. Atypicthys strigatus*	Stripey
	50. Odacidae	*96. Neoodax balteatus*	Little weed whiting
		97. Haletta semifasciata	Blue weed whiting
		98. Odax acroptilus	Rainbow cale
	51. Blenniidae	*99. Omobranchus anolius*	Oyster blenny
		100. Omobranchus rotundiceps	Rotund blenny
		101. Petroscirtes lupus	Brown sabretooth blenny
		102. Parablennius tasmanianus	Tasmanian blenny
	52. Bovichthyidae	103. Bovichthys variegatusa	
		104. Pseudaphritis urvillii	
	53. Tripterygiidae	*105. Lepidoblennius marmoratus.*	Western jumping blenny
	54. Clinidae	*106. Cristiceps australis*	Southern crested weedfish
		107. Ophiclinus gracilis	Black-backed snake blenny
		108. Heteroclinus perspicilliatus	

Table 1. continued

ORDER	FAMILY	SPECIES	COMMON NAME
	55. Creedidae	*109. Creedia sp.*	
		110. Limnichthys fasciata	
	56. Cheilodactylidae	*111. Cheilodactylus sp.1**	Morwong
		*112. Cheilodactylus sp.2**	
		*113. Nemadactylus sp.**	
	57. Gobiidae	*114. Pseudogobius olorum*	Swan River goby
		115. Favonigobius lateralis	Long-finned goby
		116. Favonigobius suppositus	Long-headed goby
		117. Arenigobius bifrenatus	Bridled goby
		118. Redigobius macrostoma	
		119. Gobiopterus semivestita	
	58. Gempylidae	*120. Rexea solandri**	Gemfish
		*121. Thyrsites atun**	Barracouta
	59. Trichiuridae	*122. Lepidotus caudatus**	Southern frostfish
	60. Scombridae	*123. Scomber australasicus**	Slimy mackerel
	61. Leptoscopidae	*124. Lesueurina sp.*	Sandfish
Gobiesociformes	62. Callyionimidae	*125. Callionymus goodladi*	Goodlad's stinkfish
		126. Foetorepus calauropomus	
	63. Gobiesocidae	*127. Gobiesocid spp.*	Clingfish
Pleuronectiformes	64. Paralichthyidae	*128. Pseudorhombus jenynsii**	Small-toothed flounder
		129. Pseudorhombus spp.	Flounder
	65. Pleuronectidae	*130. Ammotretis rostrata**	
		*131. Rhombosolea tapirina**	
	66. Cynoglossidae	*132. Cynoglossus broadhursti**	Southern tongue sole
Tetraodontiformes	67. Monacanthidae	*133. Scobinichthys granulatus**	Rough leatherjacket
		134. Brachaluteres jacksonianus	Pygmy leatherjacket
		*135. Meushenia hippocrepis**	Horseshoe leatherjacket
		*136. Acanthaluteres spilomelanurus**	Bridled leatherjacket
		*137. Acanthaluteres vittager**	Toothbrush leatherjacket
		*138. Monacanthus chinensis**	Chinaman leatherjacket

Table 2. Summary of larval fish studies carried out and underway in temperate Australian waters

(Table partially derived from Steffe (1991)).

Location:	Moreton Bay, Qld
Investigators and references:	Helbig (1969)
Brief description of study:	Distributional trends in total numbers of fish larvae at 3 sites over a 15 month period. Samples were not quantitative. Taxonomic problems with most only identified to Family or type. Number of taxa = 115
Location:	Moreton Bay, Qld
Investigators and references:	Pollock *et al.* (1983)
Brief description of study:	Survey to determine timing of entry of bream *Acanthopagrus australis* into Moreton Bay. Most larvae were caught entering at the post flexion stage, at night, during the full moon.
Location:	Fraser Island, Qld
Investigators and references:	Halliday (1990)
Brief description of study:	Plankton survey to confirm the timing and location of spawning of tailor *Pomatomus saltator*. Samples collected on the full moon in September and October 1988 and June and July 1989. *Pomatomus saltator* eggs were only caught in samples collected during September and October 1988.
Location:	Lake Macquarie, NSW
Investigators and references:	Miskiewicz (1986; 1987)
Brief description of study:	Three year survey to determine species composition, seasonal variation in abundance and size at entry of larvae into the estuary - surface tows only. Tidal and diel variations in species composition and abundances of larvae moving in and out of the estuary were also investigated. Number of taxa = 106
Location:	Tuggerah Lakes, NSW
Investigators and references:	Marsden (1986)
Brief description of study:	One year survey to determine seasonal and diel variations in abundances of larval fishes entering the lake system. Surface tows. Number of taxa = 64

Table 2. continued

Location:	Botany Bay, NSW
Investigators and references:	Steffe (1982)
Brief description of study:	Intensive sampling at two sites over a 24 hour period to examine the effects of tidal and diel factors on larval abundance. Surface tows. Number of taxa = 30
Location:	Botany Bay, NSW
Investigators and references:	SPCC (1981); Steffe and Pease (1988)
Brief description of study:	Seasonality and distribution of the larval fish assemblage at 9 sites over two years. Surface tows during day. Larval avoidance of small nets used was probably very high.
Location:	Botany Bay, NSW
Investigators and references:	Steffe (1982; 1989; 1990; 1991)
Brief description of study:	Larval fish distributions in relation to tidal currents - surface and epibenthic samples. Aimed at determining mechanisms by which larvae maintain themselves within the estuary. Number of taxa = 158
Location:	Central NSW estuaries
Investigators and references:	Suthers *et al.* (in progress)
Brief description of study:	Seasonal survey of larval fish assemblages and abundances in 9 estuaries along the NSW coast: three with riverine input, three without riverine input and three "polluted" estuaries.
Location:	Port Hacking, NSW
Investigators and references:	Bruce (1982)
Brief description of study:	One year survey of fish larvae at the CSIRO Port Hacking 50 and 100m oceanographic stations. Surface tows and vertical hauls. Study limited due to taxonomic problems and low numbers of larvae caught. Number of taxa = 16

Table 2. continued

Location:	Sydney coastal waters, NSW
Investigators and references:	Gibbs (1987)
Brief description of study:	Pilot study for Sydney Deepwater Outfalls Environmental Monitoring Programme. Multiple sampling for cost benefit analysis and design of full scale sampling programme. Oblique tows in March only. Number of taxa = 197
Location:	Sydney coastal waters, NSW
Investigators and references:	FRI (1991); Gray *et al.* (in press)
Brief description of study:	Quarterly sampling of fish larvae in sewage plumes and at reference site. Programme conducted as a component of the five year Sydney Deepwater Outfalls Environmental Monitoring Programme. Study aimed at assessing impact of sewage outfalls on the species composition, abundances and distribution. Surface and oblique tows. Number of taxa = 131
Location:	Sydney coastal waters, NSW
Investigators and references:	C. Gray (in progress)
Brief description of study:	Assessment of larval fish assemblages and abundance within, at the edge and outside of cliff-face sewage plumes - surface samples. Assessment of species composition and vertical distribution (6 depths) of fish larvae around the deepwater sewage outfalls
Location:	Sydney coastal waters, NSW
Investigators and references:	Kingsford (1990); Kingsford (in press); Kingsford and Suthers (in prep.)
Brief description of study:	Investigating variations in spatial distribution and abundances of fish larvae with regard to fronts from estuarine plumes and sewage outfalls - plankton purse seine and neuston tows.
Location:	Sydney coastal waters, NSW
Investigators and references:	Druce (1990); Druce and Kingsford (in progress); Kingsford (in progress)
Brief description of study:	An experimental and descriptive study of the fish communities associated with drift algae and other floating objects -plankton purse seine.

Table 2. continued

Location:	Sydney coastal waters, NSW
Investigators and references:	Kingsford and Suthers (1990); Kingsford *et al.* (1991)
Brief description of study:	Sampling fish larvae within surface sewage effluent plumes (Malabar and North Head) and at reference sites to assess incidences of deformities - neuston tows.
Location:	Sydney surf zones, NSW
Investigators and references:	Leis and Reader (in progress)
Brief description of study:	Sampling of larval fish at two ocean beaches (Manly) and two beaches inside Sydney Harbour. Samples collected monthly over two years. Number of taxa = 70
Location:	Central and Northern NSW coast
Investigators and references:	Miskiewicz (1987)
Brief description of study:	Three cruises on R.V. Sprightly. January, March and May, 1983. Seven transects between Sydney and Brisbane. Distribution of selected species described in Miskiewicz (1987). Work ongoing to identify other species in samples.
Location:	Central/northern NSW coastal waters.
Investigators and references:	Gorman and Graham (1985); Gorman *et al.* (1987)
Brief description of study:	Surveys aimed at collecting and identifying gemfish *R. solandri* larvae to determine spawning localities and times. Plankton surveys in coastal waters between Newcastle and the Queensland border. Surface and oblique tows down to 200m. Samples collected in August and September in 1985 and 1986. Work ongoing to identify other species in the samples.
Location:	Central/northern NSW coastal waters.
Investigators and references:	Dixon and Miskiewicz (in progress)
Brief description of study:	Study aimed at collecting whiting larvae *Sillago* spp. for electrophoresis analysis as part of stock discrimination study. Surface tows between Coffs Harbour and Newcastle in April 1989. Work ongoing to identify other species in the samples.

Table 2. continued

Location:	Gippsland Lakes, Vic.
Investigators and references:	Ramm (1986)
Brief description of study:	Distribution of eggs and larvae of the anchovy *E. australis* and the black bream *A. butcheri* in the Gippsland lakes in relation to hydrology.
Location:	Port Phillip Bay, Vic.
Investigators and references:	Jenkins (1986)
Brief description of study:	One-year survey to determine seasonal abundance and distribution of the larval fish assemblage in the Bay. Oblique tows. Number of taxa = 26.
Location:	Port Phillip Bay, Vic.
Investigators and references:	Jenkins (1987a; b)
Brief description of study:	Ages, diets and growth rates of two larval flounder species, *Rhombosolea tapirina* and *Ammotretis rostratus*.
Location:	Swan Bay and Port Phillip Bay, Vic.
Investigators and references:	Jenkins (in progress)
Brief description of study:	Distribution and seasonality of pre-settlement fish larvae in seagrass beds in the two bays.
Location:	Hopkins River estuary, Vic.
Investigators and references:	Willis (1991)
Brief description of study:	Feeding ecology of larval and juvenile black bream *A. butcheri* collected in the estuary between October 1982 and February 1983.
Location:	Hopkins River estuary, Vic.
Investigators and references:	Newton (in prep.)
Brief description of study:	One year plankton survey, at monthly intervals, between February 1984-February 1985. Investigating the seasonal and spatial distribution of fish larvae in the estuary in relation to the hydrology and the distribution of zooplankton.

Table 2. continued

Location:	Bass Strait
Investigators and references:	Holdway and Lanzing (in progress).
Brief description of study:	Programme investigating the distribution of neustonic Pontellid copepods and fish larvae. Sampling conducted between 1985-1987. Neuston tows. Work ongoing to identify the fish larvae in the samples
Location:	Tasmanian coastal waters
Investigators and references:	Thresher *et al.* (1988a; b); Gunn *et al.* (1989); Bruce (1988); Furlani *et al.* (in prep.); Furlani (in prep.).
Brief description of study:	Two year programme sampling nine transects around Tasmania - surface and oblique tows. Aimed at determining spawning times, localities, distribution and movements of blue grenadier *M. novaezelandiae* larvae in Tasmanian waters. Work ongoing to identify other species in the samples.
Location:	Eastern Tasmanian waters
Investigators and references:	Jordan and Marshall (in progress); Young and Davis (in press).
Brief description of study:	Surveys undertaken as part of a resource assessment survey for jack mackerel (*T. declivis*). Samples collected between December and April 1989, 1990 and 1991. Oblique bongo tows at inshore, mid-shelf and shelf-break stations at 8 transects along Tasmania's east coast. Work ongoing to identify other species in the samples.
Location:	Storm Bay, Tas.
Investigators and references:	Thresher *et al.* (1989)
Brief description of study:	Weekly sampling in rock pools of newly settled weedfish *Heteroclinus* sp. Settlement pulses of larvae occurred 7-9 weeks after brief irregular peaks of phytoplankton production.

Table 2. continued

Location:	South Australia/Western Australia - Great Australian Bight coastal waters.
Investigators and references:	Stevens *et al.* (1984)
Brief description of study:	Nine cruises in the Great Australian Bight between January 1979 and December 1980. Plankton samples were collected using a bongo net along a transect in the western, central and eastern Bight. Only larvae of the pilchard *S. neopilchardus*, which were caught in April and May, were identified from the samples.
Location:	South Australia - Spencer Gulf and Gulf Saint Vincent and coastal waters.
Investigators and references:	Bruce (1989c)
Brief description of study:	Focus of study is to determine the spawning localities and times, patterns of movements and age and growth of King George whiting, *S. punctata*, larvae. Data are also being collected on species composition, seasonality and distribution patterns of larvae of other commercial species such as snapper, *P. auratus*.
Location:	Blackwood River estuary, Western Australia
Investigators and references:	Lenanton (1977)
Brief description of study:	Distribution and relative abundances of larval fish within the estuary. Larval identifications restricted to familial level. Number of taxa = 6
Location:	Swan River estuary, Western Australia
Investigators and references:	Neira (1988)
Brief description of study:	Seasonality and distribution of the larval fish assemblage at 13 sites over a 1 year period. Surface tows. Number of taxa = 70
Location:	Lower Swan estuary, Western Australia
Investigators and references:	Gaughan *et al.* (1990)
Brief description of study:	Seasonality and distribution of the larval fish assemblage at 3 sites over a 1 year period. Stepped- oblique tows. Number of taxa = 60

Table 2. continued

Location:	Albany coastal waters, Western Australia
Investigators and references:	Fletcher (in progress)
Brief description of study:	Plankton surveys in coastal waters off Albany. The aim of the surveys is to collect *S. neopilchardus* eggs and larvae and determine the times and location of spawning.
Location:	Wilson Inlet, Western Australia
Investigators and references:	Neira and Potter (submitted)
Brief description of study:	Investigated the seasonal changes in the abundance and species composition of fish larvae at 7 sites throughout Wilson Inlet for a period of 20 months. The aim of the study was to determine any changes in these variables when the estuary was open to the sea. Surface tows. Number of taxa = 25
Location:	Wilson Inlet, Western Australia
Investigators and references:	Neira and Potter (in press)
Brief description of study:	Investigated the movement of larval fish into the seasonally closed Wilson inlet after the breaking of the sand bar. Number of taxa = 59.

Table 3. Species of fish cultivated at the Brackish Water Fish Culture Research Station (Battaglene and Talbot pers. comm.)

✓ = successful, X = unsuccessful

Common name	Scientific name	Broodstock	Successful hormone induction	Stages of development achieved		
				Yolk sac larvae	Larvae	Juveniles
Australian bass	*Macquaria novemaculeata*	✓	✓	✓	✓	✓
Estuarine perch	*Macquaria colonorum*	X	✓	✓	✓	✓
Snapper (red sea bream)	*Pagrus auratus*	✓	✓	✓	✓	✓
Sand whiting	*Sillago ciliata*	X	✓	✓	X	X
Trumpeter whiting	*Sillago maculata*	✓	✓	✓	✓	✓
Yellowfin bream	*Acanthopagrus australis*	X	✓	✓	X	X
Mulloway	*Argyrosomus hololepidotus*	✓	✓	✓	✓	✓

SPECIALIST SESSION

LARVAL FISH DRAWING TECHNIQUES WORKSHOP

Convenors: I. M. Suthers
J. M. Leis

SPECIALIST SESSION
LARVAL FISH DRAWING TECHNIQUES WORKSHOP

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J.M. Leis

Many budding larval fish taxonomists have difficulty in accurately drawing larvae for publication, requiring not only camera lucida techniques, but also myomere and fin ray counts. The purpose of this informal workshop of enthusiastic specialists, was to go over these techniques in a hands-on session with microscopes and specimens.

No formal record was kept of the discussion but the following background document has been provided by Tom Trnski and Jeff Leis.

A BEGINNER'S GUIDE TO ILLUSTRATING FISH LARVAE

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Clear, accurate and good-quality illustrations are perhaps the single most important feature of a larval description. The illustrations will also be the most frequently-consulted component of the description.

The aim of an illustration is to allow other workers to identify the taxon described. It should show all diagnostic characters accurately and in their correct relative position and be as unambiguous as possible. Assume the following: if something can be misconstrued, it will.

Most people will not attempt to illustrate larvae for fear they can't draw. However this excuse is invalid as the technique described below is never more than careful observation, accurate tracing, a steady hand and patience. Besides, you are denying others the opportunity to share your knowledge.

The techniques described below are by no means the only ones available. However they will function as a general introduction to production of line drawings suitable for publication.

Photographs

Colour, or black and white photographs are used in some descriptions. However, they are not generally suitable alternatives to line drawings. The main problems are depth of field, magnification and resolution, and difficulty in portraying all important characters in one frame. They also do not allow for emphasis of inconspicuous but important characters. However photographs may be traced to provide a correctly-proportioned base-sketch.

Equipment

Well-maintained, good quality equipment is essential for good quality drawings.

A high resolution stereo microscope with a maximum magnification of about 50X is best; brands like Wild and Zeiss are readily available in Australia. They may seem expensive at first, but the good optics mean less fatigue for the user, lower maintenance and less chance of misinterpretation of the image.

A camera lucida, or drawing tube, attached to the microscope is the preferred means of transferring the microscope image onto paper. This ensures correct proportion and accurate relative position of all structures. It takes practice to perfect the technique of using a camera lucida, but it is essentially just a matter of tracing the image. If you have trouble seeing a clear image of the larva or the paper, vary the light intensity over each until you can see both satisfactorily. The best magnification to use is one in which you can see the entire specimen under one field of view (this reduces distortion at the edge of the field) while important detail is still discernible. Larger specimens, or specimens with

complex characters which must be shown, can be drawn in several parts with the parts then joined by matching landmarks.

Various light source combinations are available. At the very least use a combination of transmitted and reflected (sub-stage) light. If available, a fibre-optic cold-light source allows you to cast shadows on the specimen, by varying the incident-light angle, without moving the specimen. This means there is no need to keep matching the larvae to your sketch, which is sometimes difficult if the larva is bent and will "fit" your illustration in only one position.

A clutch pencil with a 0.5mm lead means a sharp, accurate point. Lead hardness depends on personal choice, but HB is most popular because it gives a definite line which is easy to erase.

Drawing film (or polyester drafting film) is the most versatile material for the final version of your illustration. It allows you to scrape-away errors with a scalpel without totally ruining the drawing surface. Tracing paper does not accept ink very well and it is difficult to erase errors on it.

Pens with a constant line thickness are required for the final illustration. There are numerous brands of rapidograph-style drafting pens now available. If you often draw on drawing film, it is worth investing in a jewel-tipped pen (such as sapphire), as normal tips wear out quickly on this hard fill, thereafter giving you variable line width. A range of pen sizes is useful to portray different features and to give degrees of prominence. As a guide, 0.25, 0.35 and 0.5 mm nib widths are most commonly used, with occasional use of 0.18 and 0.7 mm nib widths.

However, when it comes to photo- or bromide reproductions of the original, you should restrict your ink-width range to a factor of two: for example, if your thickest line in a figure is 0.5 mm wide, a line less than 0.25 mm wide may not reproduce as clearly as you expect once it has been reduced. This is not to say you can't bend this rule, but you should be aware your thinnest lines may "drop-out" upon reduction.

Black ink varies in quality. For the highest contrast (and best results) use a very black ink. The most easily available, good quality ink is made by Rotring.

A scalpel, pencil-eraser and white paint are required to correct errors. A no. 23 (fits handle no. 4) scalpel blade is popular, but any similar profile works as well. Use the scalpel to scrape away small ink overruns.

For larger errors, an opaque white acrylic paint (available in art shops) with good masking properties will suffice. Liquid paper can be used instead but is more difficult to use because it dries so quickly.

If you do use either eraser, scalpel or paint, remember the surface texture of the drawing film will alter and will thus affect the behaviour of the ink (it will run thinner or thicker than over the drawing film) over these modified surfaces.

Style

The most important rule is to maintain consistency. A good idea is to peruse the literature and consider which illustrations you find clearest and most attractive. This a good starting point to then develop you own individual style. But avoid radical departure from convention for it may be misinterpreted. Your style must also be flexible enough to allow portrayal of the full range of variation found in fish larvae.

Do not use shading to indicate three-dimensional depth of the larva. The potential for confusion, particularly with pigment, is too great.

Wash technique to show depth and shape can be very effective, but requires a fair degree of skill, much more than pen and ink line drawings. They also often don't reproduce well in published form.

Choice of specimens

In an ideal world, the larva(e) you want to illustrate will be straight, undistorted, with all organs and meristic components intact, and melanophores that poke you in the eye. However, you may have to get missing information (such as broken fin elements or head spines) from another specimen at the same stage of development and of similar size, or perhaps from the opposite side of the damaged specimen.

A bent specimen can be flattened using a cover slip (but be wary of any distortion you may introduce) or drawn in two parts: firstly lay the anterior of the larva in a horizontal plane by resting the posterior of the larva against a paper clip or a wad of cotton gauze - draw the anterior half; then rest the anterior of the larva against the paper clip or gauze and draw the posterior half. Be sure to have some reference point (such as melanophores or myomeres) with which you can match the two halves.

In extreme cases, draw a composite of two specimens which together have the full complement of characters, but be sure to indicate this in your caption. Try to show fins in an erect position. If the fins of your specimen are not erect, use dividers with the *Camera lucida* image to bring the fin elements up into an erect position.

How many specimens should be illustrated? This varies with specimens available and how much morphology changes through development. A minimum would include the smallest and largest specimen, plus one at flexion, one at completion of fin development, and (if not already represented in one of the other illustrated specimens) one at maximum development of larval characters such as spines on the head.

Sequence of events

1. Select the specimen.
2. Onto paper do a camera lucida sketch in pencil. To eliminate uncertain lines and to confirm completion of a particular area or structure, go over the pencil marks in ink. This also allows easy and clear reproduction later (see 4). You may wish to show pigment in another colour to avoid later confusion. It is good practice to write all specimen information (name, size, collection data, catalogue number) onto your pencil sketch. If you want to include a scale bar, do it now.
3. Constantly check your illustration against the specimen and ensure all characters are the correct relative size, in their correct relative position and there is the correct number of them.
4. Reduce or enlarge your sketch using a photocopier with a zoom facility to an appropriate size. See "Before you start" below. All illustrations in your series should be the same size.
5. In ink, trace onto drawing film directly from your reduced/enlarged sketch which resulted from (4). It is necessary to have the specimen nearby to finally incorporate any additional detail (like relative intensity of pigment) and to check the accuracy of the sketch against the specimen. If possible, have a different person do this step than the person who did steps (2) and (3); in this way a further check for accuracy is introduced.
6. Photograph or bromide the original and send this copy to the publisher in camera-ready size. The fewer reduction processes, the better the final copy. Do not send original illustrations unless the publisher gives no other option, and even then only after the paper is accepted following review.

Before you start

Be sure of your identification. Be familiar with the adult fauna in your region and consider the possibility of undescribed and undetected taxa.

Consider the publication in which the illustration will appear. As a rule of thumb, draw your final illustration larger than it will appear in the publication, up to twice the published size (but check instructions to authors).

Always ensure your hands are clean. Dirty hands leave dirty marks on your illustration which are a pain to remove. In addition, fingertips become greasy, particularly on a hot day. These greasy fingerprints are invisible on drawing film but disperse the ink which then makes it difficult to maintain a uniform line width.

Show what?

Convention dictates larvae are illustrated in lateral view from the left-hand side (ie head pointing to the left). The only exception is in dextral taxa such as Bothidae and Pleuronectidae where the larvae are illustrated from the right side. If you are forced to illustrate a damaged specimen from the right, reverse the image before final inking to maintain the convention. This can be easily done on the back of the camera lucida sketch with the aid of a light table.

In some cases, it may also be useful to include a dorsal or ventral view, or perhaps a magnified view of certain diagnostic characters, such as pigmentation or head spination. However, don't overdo additional perspectives unless they are truly required to clarify characters which may be unclear or ambiguous in standard lateral view.

A good, complete illustration (Figure 1) should show all of the following:

- Accurate relative position of all structures.
- Head spination.
- Pigmentation generally refers to melanophore distribution. If you have access to fresh specimens, you may consider showing chromatophore distribution. However, this either requires an additional illustration to show only chromatophores, or can be included on the same illustration if colour printing is available. Also, it is usually necessary to distinguish between internal and external pigment; develop a style which distinguishes between these.
- Accurate number and position of myomeres. In most taxa, the number of myomeres equals the number of vertebrae +/-1.
- Gut and gas bladder outline.
- Accurate number and position of all meristic components. It is useful to distinguish an ossifying fin ray from a fully-formed fin ray and the latter from a spine by slight variations in style. If you want to show the trailing edge of fin rays, make sure it is clearly distinguishable from the leading edge.
- The cleithrum is often a useful landmark but is not essential. However, at the very least the position of the cleithral symphysis should be shown.

If you can't illustrate something accurately, say myomeres due to the poor condition of the specimen or to heavy pigment, state this in the caption. Do no omit any essential character without explanation.

If you are illustrating a developmental series it is imperative that similar structures are shown consistently throughout this series.

Do not cram too much detail into the final illustration. Any lines drawn too close together will merge or bleed upon reduction with resultant loss of detail.

Finished?

The illustration must match the descriptive text in all characters. But this is not a licence to bend the truth while illustrating. Production of an illustration is often a useful check on the accuracy of the text. Meristic components, once completely developed, must also match adult counts (but beware reared specimens frequently don't match published meristics).

It is important to deposit any specimens used in a description, particularly if illustrated, into a collection with a commitment to proper long-term maintenance of larval fishes. Catalogue numbers should be included in the publication for future reference.

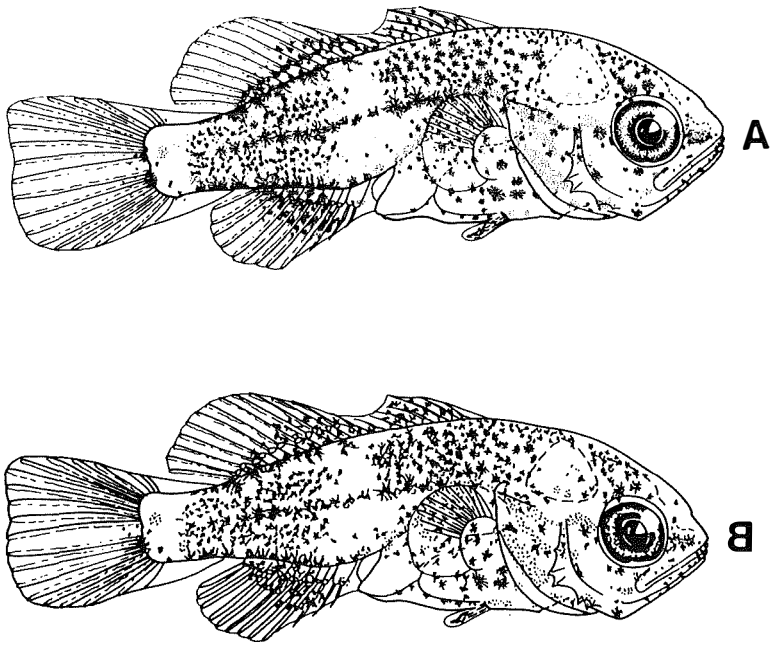

Figure 1. Two versions of a 5.7 mm SL *Lates calcarifer*. A: Publication-quality illustration clearly showing important morphological characters (from Leis and Trnski, 1989, page 145). B: An adaptation of A with some common errors including myomeres not shown; gap between iris and pupil merges; stellate melanophores overemphasized due to use of inappropriate pen size; trailing edge of anal-fin rays indistinguishable from leading edge; trailing edge of three upper-most ventral caudal-fin rays dropping-out (caused by drawing over Liquid Paper).

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WORKSHOP PROGRAM

LARVAL BIOLOGY WORKSHOP

(Tuesday 20 August 1991)

(Convener: Dr Iain Suthers, University of NSW)

0900-0915 Introduction - Dr John Glaister, President, ASFB

0915-1000 Keynote Address - Dr Rob Murdoch, N.Z. Oceanographic Institute "A review of the ecology of hoki, *Macruronus novaezelandiae* (Hector) larvae in New Zealand waters'

1000-1030 "Ichthyoplankton studies for fisheries research" - Dr John Zeldis, MAFFish, Welling ton, New Zealand (presented by Dr Don Robertson).

1030-1100 Morning Tea

1100-1230 **SESSION 1 FEEDING ECOLOGY AND CONDITION OF LARVAE**

Chairperson: Greg Jenkins, University of Melbourne and VIMS, VIC

Rapporteurs: Helen May, Bryce Stewart

Panel Speakers:

Jock Young, CSIRO Fisheries, TAS "Feeding ecology of marine fish larvae: an Australian perspective".

Daniel Gaughan, Murdoch University WA "Feeding by estuarine and marine fish larvae".

Nigel Preston, CSIRO Fisheries, QLD "*In situ* rearing of prawn larvae - testing the starvation hypothesis".

Greg Jenkins, University of Melbourne & VIMS, VIC "What can growth trajectory tell us about the nutritional state of fish larvae?"

Iain Suthers, University of NSW "The use of condition indices in larval fish".

Maria Milicich, Australian Institute of Marine Science, QLD "Do fish otoliths really record change in somatic growth rate?"

1230-1330 Lunch

1330-1500 **SESSION 2 EXTENSIVE LARVAL REARING**

Chairperson: Stephen Battaglene, NSW Ag. & Fish.

Rapporteurs: Cathy Hair, Charles Gray

Panel Speakers:

Stephen Thurstan, NSW Ag. & Fish. "Commercial extensive larval rearing of Australian freshwater native fish" (presented by Paul Brown).

John Burke, Fisheries Division, QLD "The effect of salinity in the extensive rearing of Australian bass *Macquaria novemaculeata*".

Bill Talbot & Stephen Battaglene, NSW Ag. & Fish. "The effect of temperature in the extensive rearing of Australian bass, *Macquaria novemaculeata*" (Steindachner).

Peter Gehrke, Inland Fisheries Research, NSW "Implications of water quality for larval fish metabolism, activity and growth in extensive rearing conditions."

Martin Daintith, University of Tasmania, TAS "Comparison of intensive and extensive culture of the Tasmanian whitebait *Lovettia sealii*" (Johnston).

Frances Ruwald, Sea Fisheries, TAS. "Larval feeding trials with the striped trumpeter *Latris lineata*".

1500-1525 Afternoon Tea

1525-1645 **SESSION 3 BIOLOGICAL EFFECTS OF OCEANOGRAPHIC PROCESSES**

Chairperson: Iain Suthers, University of NSW

Rapporteurs: Frances Laurenson, Linda Worland

Panel Speakers:

Simon Thorrold and David McKinnon, Australian Institute of Marine Science, QLD "Biological significance of the coastal boundary layer off Townsville, North Queensland."

Aldo Steffe and Mark Westoby, Ecology Lab. Pty Ltd and Macquarie University, NSW "Tidal currents, eddies and orientated behaviours by larval fishes."

Alan Jordan, Sea Fisheries, TAS "Interannual variability in the oceanography of the east coast of Tasmania and its effects on jack mackerel (*Trachurus declivis*) larvae."

Barry Bruce and David Short, SA Fisheries "Observations on the distribution of larval fish in relation to a frontal zone at the mouth of Spencer Gulf, South Australia."

John Booth and Robert Stewart, MAF, NZ "Distribution of phyllosoma larvae of the red rock lobster *Jasus edwardsii* off the east coast of New Zealand in relation to the oceanography."

1645-1715 **GENERAL DISCUSSION AND SUMMING UP**

Chairperson: John Gunn, CSIRO, Hobart

Rapporteurs: Frances Laurenson, Linda Worland

Panellists: Keynote Speakers and Session Chairpersons

1715-1745 Summing Up:.Dr Jeff Leis, Australian Museum, NSW

1930 **EVENING SESSION: TAXONOMY OF TEMPERATE AUSTRALASIAN FISH LARVAE**

Chairpersons: Tony Miskiewicz, Water Board and Pancho Niero, Murdoch University

Rapporteur: Tony Miskiewicz

Contributors: Barry Bruce, Tom Trnski, Aldo Steffe, Greg Jenkins, Dianne Furlani, Frances Laurenson, Alan Jordon, Charles Gray

(Evening workshop for larval fish taxonomists to generate a preliminary guide to families of temperate larvae, a list of names of relevant Australasian workers, and some figures/descriptions of larvae from workers prepared to publish in the Workshop Proceedings. This will continue into a hands-on session with microscopes and specimens on Friday. Chairpersons will present a paper at the ASFB conference summarising their findings.)

Friday, 23 August 1991 - is a lay-day to recharge the batteries for the Annual Conference. For the enthusiasts, there will be a Larval Fish Drawing Techniques Workshop, convened by Iain Suthers and Jeff Leis, 1400 - 1700.

(Many budding larval fish taxonomists have difficulty in accurately drawing larvae for publication, requiring not only camera lucida techniques, but also requires myomere and fin ray counts. This informal workshop will go over these techniques, but with only 3-6 microscopes, group size may have to be limited.)