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# Meso-scale patterns in the distribution of larval fishes across the central Great Barrier Reef lagoon and relationships with environmental variability

Thesis submitted by Simon Robert Thorrold (BSc) (Auckland) in November 1993

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## Abstract

Events occurring during the larval phase of marine fishes have important ramifications for the demographic structure of marine fish populations. Differential larval survival may drive recruitment variability and ultimately determine stock biomass. While considerable scientific attention has been devoted to larval fishes in temperate regions, studies of fish larvae in tropical environments have been rare and of uneven quality. This dissertation aimed to present detailed descriptions of the distribution patterns of small fishes, along with concurrent measurements of environmental variability, in the central Great Barrier Reef lagoon.

Larval fish were collected using both conventional plankton nets and light traps during the spring-summer periods of 1988-89, 1989-90 and 1990-91. Light traps have not been used to sample fish in open water before this study; they collected numerous fishes at sizes larger than those routinely captured in plankton nets. Data from both techniques were analysed to examine spatio-temporal variability in the distribution patterns of small fishes. Plankton nets revealed relatively stable cross-shelf patterns, with a distinctive nearshore component characterised by gobiids, callionymids, leiognathids and teraponids; a cross-shelf group including nemipterids, carangids, platycephalids and scorpaenids; and an offshore group dominated by clupeids, lutjanids, scombrids, and pomacentrids. Significant temporal coherence, across spatial scales up to 50 km, in abundance of a number of taxa with cross-shelf and offshore affinities was also found. This coherence could be generated by synchronous spawning, or by a hydrographic event acting over synoptic scales of at least 50 km in both cross-shelf and long shore directions. Light trap catches in both years were dominated by a catches at a single station in one month. In 1988, a multi-specific 'patch' of larvae were found 24 km off the coast on the CB transect, while in 1989 a similar 'patch' was located 16 km off the coast on the LR transect.

Remote sensing, utilising NOAA's AVHRR polar-orbiting satellite, was used to synoptically assess sea-surface temperatures and visible reflectance of water masses across the central Great Barrier Reef lagoon. While there was little evidence of significant thermal structure across the sampling transects, more structure was noted in false-water colour images. Turbid, coastal water was found along the coast, although the the offshore extent of this water mass varied through time. This appeared to be related to wind strength acting to determine the depth at which wave action led to resuspension of bottom sediments. The offshore extent of this nearshore water mass also appeared to delineate the approximate boundary between nearshore and offshore ichthyoplankton groupings from the net samples.

Zooplankton distributions across the inner shelf did not coincide with that of the larval fish community. Given that zooplankton are more accurate tracers of water movement than larval fish, hydrography alone could not explain the maintenance of larval fish assemblages through time. It is suggested that larval fish may be actively maintaining their positions within water masses. An alternative hypothesis that differential survival between masses was responsible for the patterns could not, however, be rejected.

Both zooplankton abundance and egg production rates of *Acrocalanus gibber*, a common copepod species, were significantly higher within a low-salinity plume derived from terrestrial runoff associated with cyclonic rains. Larval fish with cross-shelf affinities were also concentrated in the plume during the initial two days of a total of five sampling occasions. Offshore larvae became abundant at the plume front on the final two days of sampling. This accumulation may have been caused by the swathe effect of the plume front as it moved progressively offshore.

Episodic events such as cyclonic rainfall and resuspension of nutrients resulting from strong winds may be of critical importance to planktonic communities, and hence larval fish survival, in this region. Such events are impossible to predict, and therefore will only be elucidated by long-term, meso-scale monitoring of larval abundance within the pelagic environment and concurrent measurements of biological oceanography at similar scales. This study demonstrates that new developments in both biological sampling methods and satellite technology make programs eminently feasible. The renewed presence in space of a satellite (SeaWiFS) capable of determining ocean colour will further enhance the prospects of considerable advancements in determining the causes of variable survival and subsequent recruitment of tropical fish larvae.

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# Declaration

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

S R Thorrold 8 November 1993

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### General Introduction

#### 1.1 BACKGROUND

Determination of the processes structuring marine fish populations remains the focus of considerable scientific research and debate. Indeed the lack of understanding concerning the regulation of population abundance has largely precluded the primary goals of fisheries science (Rothschild 1986, Sissenwine et al. 1988). The ability to accurately predict sustainable fishing yields has yet to be achieved for most fished populations, and fisheries managers are necessarily forced into reactive management policies (Rothschild 1986, Walters and Collie 1988). Attempts to apply terrestrialbased models to marine populations have been largely unsuccessful (Roughgarden et al. 1991a, Sale 1991). Steele (1985) argues cogently that terrestrial models will never be useful analogs of marine systems due to the inherent differences in the variance structure of marine systems (where variance is dominated by long-term oscillations or "red noise") compared to terrestrial environments (where variance is dominated by short-term "white noise"). The collapse (and in some cases subsequent recovery) of both unexploited fish stocks and fisheries under active management underscores our lack of knowledge of the processes that act to control fish populations and the critical need for such information (Sissenwine et al. 1988).

Despite the concerted effort of a century of research, a general theory on the regulation of fish populations remains elusive (Jones 1989). Most long term data sets available to fish ecologists come from commercial catch records. While useful, these data unavoidably confound natural influences with the anthropogenic effects of fishing operations. Unexploited populations are rare, and once discovered do not remain unexploited for long. One consistent theme has emerged, however, from these endeavours. Abundance levels appear to be characterised by large fluctuations through time, often in the absence of any fishing effort (e.g. Soutar and Isaacs 1969, 1974, Kondo 1980, Lasker 1985, Fossum 1992). A recent publication has tracked the abundance of Pacific sardine and anchovies over the last two

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millennia (Baumgartner *et al.* 1992). These time series clearly show that collapses and subsequent recoveries have been an integral component of the population dynamics of these species throughout the last 1,700 years. Indeed the collapse of the sardine fishery that began in the 1940's, and which now appears to be in a recovery phase, does not appear to be qualitatively different to similar fluctuations in unexploited populations during earlier centuries.

Variations in year-class strength have considerable potential to influence the dynamics of adult fish populations (Rothschild 1986). Temperate fisheries ecologists as early as the beginning of the century described the effect that varying recruitment levels had on the size of subsequent year classes within the commercial herring fishery (Hjort 1914). There are a number of examples in which the rare occurrence of strong year-classes has sustained commercial catches throughout the life of the cohorts (Daan *et al.* 1990). Recently, Doherty and Fowler (in press) presented results of a study that showed convincingly that recruiment levels of a small pomacentrid in the Great Barrier Reef explained almost all the variability in the age structures of adult populations over a 10 yr period.

Recruitment variability also appears to be shared by a number of marine invertebrate taxa (e.g. Milliken and Williams 1984, Botsford et al. 1989). The red king crab, Paralithodes camtschatica, supported a large commercial fishery for 33 consecutive years before a precipitious decline resulted in the complete closure of ths fishery in 1983 (Otto 1986). Recruitment strength of year-classes to the king crab fishery varied by as much as 60 fold (Incze et al. 1986, Stevens 1990). High recruitment during two to three years in the 1960's accounted for the extremely high populations levels in the late 1970's. Subsequent year-class failures, along with high total mortality, led to the rapid decline in the abundance of legal-sized king crab that has continued throughout the last decade (Stevens 1990). While anthropogenic influences cannot be assessed independently of natural fluctuations in the heavily fished red king crab stocks, studies on unexploited invertebrates suggests that erratic year-class strength may occur in the absence of significant fishing mortality (Gaines and Roughgarden 1985, Keough 1988, Raimondi 1990).

Hjort (1914, 1926) hypothesised that recruitment may in be determined by the survival of very early larval stages. Larvae were thought to be extremely susceptible to starvation immediately after yolk sac absorption and to adverse advection that may transport larvae to an inappropriate geographical locality. Lasker (1975, 1981) proposed that wind-driven turbulent mixing of coastal and oceanic waters could break down patches of larval food, and hence lead to high incidence of starvation among first feeding larvae. Conversely, periodic physical disturbances such as storms have been shown to enhance primary and secondary productivity (Kiorboe et al. 1987, Checkley et al. 1988), and increase the encounter rates between predators and prey (MacKenzie and Leggett 1991). While these studies suggest how the physical environment may act to regulate recruitment through larval survival, direct verification of the critical period hypothesis has proved difficult. Peterman et al. (1988) reviewed available literature and concluded that recruitment levels did not appear to be set during early larval life. Recruitment was more closely correlated to abundance estimates of age one juveniles of northern anchovy than 19 day old larvae. Despite these contradictions, the 'critical period' concept remains the focus of much research in the field to this day (eg. Lasker 1975, 1981, Koslow et al. 1985, Fossum 1992).

The appeal of Hjort's hypothesis lies in the shape of a generalised larval mortality curve (Lasker 1985). This curve is assumed to be an asymptotic function of age (or size), with extremely low survivorship during the egg and early larval stages. Survivorship increases rapidly, however, with the development of locomotory and sensory capabilities. One of the consequences of this function is that small changes in mortality rates during the initial phase may lead to extreme variability in subsequent recruitment levels. Using a mathematical approach to this problem, Houde (1987, 1989) showed that small changes in mortality rates, and remarkably small changes in growth rates, can have enormous effects on the recruitment of fishes. This realisation was important, as it emphasised that comparatively small changes in the larval environment, as well as large-scale climatic phenomena (e.g. Sinclair et al. 1985, Lluch-Belda et al. 1989, 1992, McFarlane and Beamish 1992, Turrell 1992) or mass transport events (Polacheck et al. 1992), could generate both year class 'busts' and year-class 'booms'.

#### **1.2 PROBLEM AND APPROACH**

Coastal waters adjacent to the Great Barrier Reef (hereafter GBR) support commercial fisheries of at least 3,000 tonnes wet weight (worth >Aus\$15 million), and an increasing recreational catch that may take at least 7,000 tonnes annually (Hundloe 1985). Despite the importance of this resource, the major fisheries of the GBR have not been, at least until very recently, actively monitored or managed. One of the biggest obstacles to pro-active management of GBR fisheries is that remarkably little is known about the early life histories of most of these fishes. An understanding of the processes controlling the survival of these stages is critical in any attempt to predict population abundance and sustainable yields of fish stocks. Tropical fish stocks appear to be as prone to environmental forcing of stock sizes through through survival of larval and early juvenile stages (Doherty and Williams 1988) as more familiar and well-studied temperate examples (Sissenwine 1984, Rothschild 1986).

There are suprisingly few published studies on fish larvae in tropical Australia, and indeed in the tropics generally (reviewed by Leis 1991a). Larval fish programs in the GBR region have largely been confined to broadscale surveys across the continental shelf (Milward and Hartwick 1987, Leis and Goldman 1987, Williams *et al.* 1988). These programs have provided invaluable data on habitat requirements of a number of larval fish taxa, but have been conducted with limited spatial or temporal resolution. The few studies that have been conducted on smaller spatial scales have addressed specific questions regarding vertical distributions (Leis 1986, Leis *et al.* 1989, Leis 1991b) or near-reef distribution patterns (Leis 1991a, Williams and English 1992). There are few data with which to assess variability over 'meso' spatial and temporal scales (days to weeks, and 1-10's of kilometers). Variability in physical and biological processes over these scales may well be critical to larval survival and recruitment (e.g. Peterman and Bradford 1987, Davis *et al.* 1991, Maillet and Checkley 1991).

It is significant that the studies listed above also used samples collected from towed plankton nets. Several studies have suggested that conventional plankton nets may return very biased estimates of ichthyoplankton numbers, species composition and size frequency (Kingsford and Choat 1985, Choat *et al.* 1993). Small larvae (<6 mm) appear to be relatively well sampled by towed nets, while larger larvae and juveniles are only rarely

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captured. Several designs of light traps have recently been trialed which rely upon photopositive behaviour of larvae to attract specimens to collection chambers (Faber 1981, Gregory and Powles 1985, Doherty 1987a). In the GBR region, light traps have been used to monitor the return of settlement-stage larvae to reefs around Lizard Island (Doherty 1987a, Milicich 1988, 1992). Small catches of pelagic families including carangids, clupeoids and scombrids suggested that the traps may have general utility for sampling the larger larvae and pelagic juveniles in open waters (Milicich 1992). While extremely large numbers of settlement-stage reef fish have been collected in the traps, smaller larvae appear to be undersampled (Choat et al. 1993). The overwhelming conclusion of a number of studies investigating the biases of sampling techniques is that one technique in isolation is unlikely to give a representative sample of species or size composition (Kingsford and Choat 1985, Gregory and Powles 1988, Brander and Thompson 1989, Suthers and Frank 1989, Choat et al. 1993). Despite petitions from several authors (Omori and Hamner 1982, Kingsford 1990) multi-gear studies with both active and passive collection methods have only rarely been attempted (Gregory and Powles 1988, Choat et al. 1993).

Once the focus of research moves into the planktonic environment, a number of sampling difficulties arise. Ecologists are used to defining habitats in terrestrial or benthic marine environments, and allocating sampling effort accordingly (McCormick and Choat 1988, Weins 1989). Indeed, the stratification of sampling effort according to habitat type almost invariably leads to significant decreases in variance levels and concomitant increases in the power of statistical tests (Andrew and Mapstone 1987). Coastal and oceanic waters appear much more homogeneous. It is difficult, albiet not impossible, to distinguish structure in the pelagic environment with the naked eye (Kingsford 1990). This lack of stratification may be one reason for the high variances typically associated with plankton studies (Leis 1991a).

The lack of obvious structure does not mean that discontinuities are not present in oceanic waters. On the contrary, recent advances in remote sensing techniques have shown that these water masses are highly structured over spatial scales ranging from 1's to thousands of kilometres (Legeckis 1978, Kelly 1985). It is not premature to state that the development of satellite imagery has changed our conception of the dynamics of these systems (Hood et al. 1990). This change has resulted from the ability of satellites to synoptically survey large areas of ocean with a level of temporal intensity that had been impossible to achieve previously from ship-based studies alone. Images have revealed the spatial extent of large-scale features such as the Gulf Stream, California Current and Benguela Current systems (Kelly 1985, Robinson 1985, Meeuwis and Lutjeharms 1990). Perhaps more impressive has been the ability to detect meso-scale anomolies such as eddies and jets in these currents that have limited temporal persistence. Meso-scale filaments and jets (Hood et al. 1990) and sub-mesoscale 'minifilaments' (Dewey et al. 1993), as revealed in sea-surface temperature maps derived from advanced very high resolution radiometers on polarorbiting NOAA satellites, appear common features during spring and early summer off the coast of California. These features have important implications for cross-shelf sediment flux (Washburn et al. 1993) and plankton community structure and productivity (Hood et al. 1990, Mackas et al. 1991, Smith and Lane 1991) in the transition zone between coastal and oceanic water masses in this area. Meanders in the Gulf Stream, as revealed by remote sensing, have also been shown to significantly modify nutrient flux and phytoplankton distributions and productivity across the shelf of the east coast of the United States (Lohrenz et al. 1993).

A greater understanding of the influence of hydrodynamics on plankton distributions has developed along with the ability to synoptically map physical variables in coastal and oceanic waters over a wide range of spatiotemporal scales. Indeed plankton biologists have recently conceptualized a model ('dynamic biological oceanography') whereby physical processes are seen as the driving force of marine ecosystems (Legendre and Demers 1984). This model was developed from observations that the time and space scales of biological variables are essentially those of important physical processes (Denman and Powell 1984). Examples of coupling between physical and biological variables include the influence of micro-scale turbulent mixing on phytoplankton growth (Denman and Powell 1984), the response of both phytoplankton and zooplankton to internal waves (Denman and Herman 1978, Zeldis and Jillett 1982, Kingsford and Choat 1986), and the enhanced biological activity focused at physical features such as coastal fronts and jets (reviewed by LeFevre 1986). Dynamic biological oceanography has significant implications for ecologists studying the population dynamics of organisms with aquatic dispersive The most obvious message is that answers to the 'recruitment stages. problem' are unlikely to be found without collecting data simultaneously on both physical and biological variables. Studies that have combined the technological benefit of remote sensing with ecological data on similar scales have shown considerable promise in recruitment studies. One example of this approach is a series of papers on settlement patterns of barnacles to rocky, inter-tidal reefs in central California (Gaines et al. 1985, Farrell et al. 1991, Roughgarden et al. 1991a,b). A correlation between years of low upwelling intensity and larval settlement suggested that oceanography had some influence on the return of competent larvae to inter-tidal reefs (Roughgarden et al. 1991a). Further investigation showed that recruitment pulses appeared to be generated by the movement of clear oceanic water into coastal areas, driven by a reduction in upwelling strength observed in sea-surface temperatures images of the region (Farrell et al. 1991). Barnacle larvae were believed to be concentrated at the front between coastal and offshore water masses due to convergent flow at the frontal boundary. These hypotheses explained both the episodic and highly pulsed nature of settlement events to barnacle populations in central California.

#### **1.3 OBJECTIVES**

In a recent review, Doherty and Williams (1988) suggested that the dynamics of tropical reef fish populations were not qualitatively different to those of temperate counterparts. Within this framework, environmental variability is seen as the dominant source of short-term fluctuations in recruitment, due to differential survival of larvae (Doherty and Williams 1988, Rothschild *et al.* 1987, Fogarty *et al.* 1991). This convergence of thought on the processes driving the abundance of fish populations focuses attention on the larval phase of the life cycle, and the physical factors that may influence the survival and ultimate recruitment of larvae to adult populations (Roughgarden *et al.* 1991a). The present dissertation aims to present information relevant to this theme.

The approach followed in this study utilises a multi-gear sampling strategy; plankton nets are necessary to collect small larvae, light traps are an effective method to collect larger stages. Satellite imagery is used to characterise the pelagic environment during the sampling periods, and to identify oceanographic features that may impact on recruitment of coastal fishes. The biological oceanography of the zone between coastal and lagoon water masses identified from satellite imagery of the area is then examined. Finally, the influence of a readily observed riverine plume and associated front on the distribution patterns of larval fish is investigated.

This dissertation is divided as follows:

Chapter 2: The performance of light traps for sampling nektonic organisms in open waters is evaluated, with emphasis on the species and sizespecificity of the gear compared to conventional plankton nets.

Chapter 3: Distribution and abundance patterns of fishes collected in both plankton nets and light traps are described. Multivariate analyses of results from both techniques are used to identify the critical spatio-temporal scales over which these communities are varying.

Chapter 4: NOAA/AVHRR imagery employing sea-surface temperatures and visible reflectance values are used to characterize the physical environment across the GBR lagoon. The synoptic data possible from the satellite imagery are combined with the quasi-synoptic biological sampling design to examine the coupling of physical and biological processes in this region.

Chapter 5: In this chapter, the biological oceanography of the zone separating coastal and lagoon water masses in the central GBR lagoon is outlined. This zone was implicated in the preceding chapters as influencing the distributions of fishes captured in both plankton nets and light traps.

Chapter 6: The effects of a large riverine plume, generated by cyclonic rains in January 1990, on larval fish community structure are described, and the possible influence of this event on larval survivorship is discussed.

Chapter 7: In the general discussion, the major findings of this study are reiterated. Finally, areas where future research resources may be profitably spent are explored, and the potential of this approach to further studies of recruitment processes in tropical waters is discussed.

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## Evaluating the performance of light traps for sampling small fish and squid in open waters of the central Great Barrier Reef

#### 2.1 INTRODUCTION

Ichthyoplankton surveys have traditionally targeted the early larval stages of marine fishes. This emphasis has been due, at least in part, to a predilection with the 'critical period' paradigm, attributed originally to Hjort's hypotheses generated a number of studies that Hjort (1914). attempted to associate survival during some 'critical period' in early larval life with interannual variability in recruitment (eg. Lasker 1975, 1981b, Sinclair et al. 1985). Increasingly, however, attention has been focussed on the larger larval and pelagic juvenile stages (eg Munk 1988, Suthers and Frank 1989, Potter et al. 1990). This has been due largely to the failure of larval abundance estimates from ichthyoplankton surveys to correlate with subsequent year-class strength (Peterman et al. 1988). Fisheries managers have also suggested that direct monitoring of pre-recruits may be a more cost-effective management tool than conventional surveys of eggs and larvae (Walters and Collie 1988).

This shift in focus has revealed the inability of conventional plankton nets to adequately sample large, nektonic individuals. Active avoidance of nets by larvae and juveniles is now well documented (e.g. Murphy and Clutter 1972, Smith and Richardson 1977, Clarke 1983, Brander and Thompson 1989, Heath and Dunn 1990, and others). Avoidance problems are compounded by a tendency for individuals to become rarer, and more patchily distributed, with increasing size (Hewitt and Methot 1982). Greater volumes of water must therefore be sampled to provide abundance estimates with adequate precision to test relevant hypotheses. The response to both avoidance and rarity of numbers has been to build (increasingly) larger nets, designed to be towed at greater speed. Such a strategy is not, however, without difficulties. Increasing the mouth size and towing speed of a net increases the distance at which the net will be detected by both visual and pressure cues (Smith and Richardson 1977). Clarke (1983) suggested that very soon after anchovies

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reached sizes capable of avoiding slow, small plankton nets, they were able to avoid any conventional plankton sampler. Despite these caveats, the search for equipment to adequately sample juvenile stages continues to concentrate on towed net designs (Methot 1986, Munk 1988, Potter *et al.* 1990).

Research on coral reef fishes has recently devoted considerable attention to the sampling of late-larval and pelagic juvenile stages (Doherty 1987a, Milicich 1988, Thorrold and Milicich 1990). Conventional plankton tows have provided broad-scale descriptions of larval abundances (Milward and Hartwick 1986, Leis and Goldman 1987, Williams et al. 1988). Taxonomic and logistic constraints have meant, however, that these studies have revealed little about the recruitment dynamics of coral reef fish populations. Surveys of recently settled fishes have emphasised the extremely episodic nature of replenishment events (reviewed by Doherty and Williams 1988), and have led to speculation that the larvae of some coral reef fishes may be distributed in large, multi-specific 'patches' (Victor 1984, Williams 1986, Doherty 1987b). Direct verification of such patches has, however, yet to be achieved (Williams and English 1992). This has been due to both the ephemeral nature of the hypothesised patches, and difficulties sampling the pelagic juvenile stages of many reef species (Choat et al. 1993).

Consideration of these problems led Doherty (1987a) to develop an automated light trap to collect reef fish larvae immediately before they settled onto the reef. A number of coral reef fish species have been collected around lights at night, at sizes rarely captured in plankton tows (Doherty 1987a, Victor 1991). Night-lighting has also been a useful method for collecting larval and juvenile scombrids for taxonomic and experimental purposes (Wollem 1970, Graves *et al.* 1988). Indeed, while larval tunas and mackerels have been the subject of extensive sampling programs (Matsumoto 1958, Yukinawa and Koida 1985, Collins and Stender 1987), numbers of larvae collected have been disappointingly small (Miller 1979). This scarcity may reflect reduced susceptibility of these larvae to plankton nets; if scombrid larvae are growing rapidly the window during which larvae are vulnerable to towed nets may be small (Brothers *et al.* 1983, Jenkins and Davis 1990). Preliminary results (Doherty 1987a, Milicich 1988) have suggested that the traps may have general utility for sampling larvae and juveniles from a wide range of taxa. Before light traps can be used quantitatively, however, several potential biases need to be determined. The aim of this chapter is, then, to consider the biases and limitations of light traps, and to develop an optimal sampling configuration for using the traps to sample larval and juvenile fishes in open waters. The following specific questions are addressed in this chapter:

1. What species, and what sizes, will be sampled by the traps?

2. What systematic biases may be introduced due to behavioural changes during a night?

3. What is the optimum method of deployment?

4. What level of precision can be achieved with realistic replicability?

#### 2.2 METHODS AND MATERIALS

#### 2.2.1 Study area

Field work was conducted in coastal waters of the central Great Barrier Reef (hereafter GBR), over three years (1988-1990). Systematic sampling across two cross-shelf transects was conducted in October-December 1988 and October 1989-January 1990. This coincided with peak spawning activities of most of the fishes species in the area (Milward and Hartwick 1986). During the first summer four stations, each approximately eight km apart, were occupied on each transect (Figure 2.1). In the second summer the distance between stations was increased to 16 km, to allow the transects to span the width of the GBR lagoon. Six light traps were deployed at each station, 200-300 meters apart and approximately one meter below the sea surface. The traps were allowed to fish for one hour before being emptied and redeployed at the next locality. Fishing period was determined by the use of a electronic timer, which operated each trap for one hour before automatically switching off the lights in the trap. One transect could be completed in a single night of sampling and each transect was sampled at least once, and up to three times, in any given month, depending upon sea conditions; sampling dates are provided in Table 2.1. Varying levels of ambient light may affect the efficiency of the traps. Therefore, to avoid confounding differences between months with ambient light levels, and to maximise trap efficiency, all sampling was conducted within a 10 day period around the new moon.

19	88	1989			
Date	Transect	Date	Transect		
October		October			
05 October	LR	27 September	LR		
06October	CB	28 September	CB		
19 October	LR	03 October	LR		
20 October	CB	04 October	CB		
November		05 October	LR		
10 November	CB	06 October	CB		
11 November	LR	November			
December		25 October	LR		
06 December	LR	30 October	LR		
07 December	CB	31 October	CB		
08 December	LR	01 November	LR		
10 December	СВ	02 November	CB		
l		03 November	CB		
		December			
		07 December	LR		
		08 December	CB		

 Table 2.1.
 Sampling dates and transect occupancy during October to December 1988 and 1989.

#### 2.2.2 Data collection

The light traps used were similar in operation to those described by Doherty (1987a), although more compact in design (Figure 2.2). All fish taken during these collections were immediately preserved in 80-90% ethanol for subsequent identification. The traps were always collected within half an hour of the lights being switched off, to minimise both predation in the trap by piscivorous fishes and escapement. Identification of fish was taken to the lowest possible taxon, following Leis and Rennis (1983) and Leis and Trnski (1989). Identification was always to possible to family level, often to generic level, and occasionally individual species were able to be recognised. All fish were also measured under a stereo dissecting microscope with an ocular micrometer. Measurement was made to the nearest micrometer unit (0.135 mm at 10x magnification).

Specific attention was paid to the scombrid component of the catch. While identification of larval scombrids up to 8-9 mm SL is reasonably well established, distinguishing larger larvae and juveniles is problematical

(Nishikawa and Rimmer 1987). Identification of larvae and juveniles was achieved by arrangement of size series of the taxa collected, with reference to published descriptions of smaller larvae (Jenkins *et al.* 1984, Nishikawa and Rimmer 1987). Vertebral counts were used to confirm identifications. A selection of juveniles were x-rayed in order to accurately count vertebral numbers.

#### 2.2.3 Trap performance

Efficiencies of drifting traps were compared with those of anchored traps on several occasions during the sampling program. On each occasion, six traps were set in a line perpendicular to the prevailing current direction. Alternating traps were either anchored to the bottom, or allowed to drift with the water mass, and fished for one hour. Total number of fish captured by the different deployment methods were then compared.

The effect of time of night on catch rate was examined over four nights at the 16 km station on the LR transect, during October and November 1990. Four traps were fished within the same general vicinity for one hour at three times during the night, corresponding to the beginning, middle and end of a normal night's sampling (1930-2030; 2330-0030; 0330-0430). A grand mean for each time period, across all nights, was calculated, and 95% confidence intervals were then bootstrapped (with 1000 iterations: Efron and Gong 1983) to compare differences in catch rates with time of night.

Replicability and precision of the traps was considered by examining data from the LR transect in October 1989. This subset was chosen as it had maximum sampling effort (a total of 48 samples over three nights), and accounted for most (>90%) of the larvae and juveniles captured during the 1989/90 summer. To determine the optimum number of replicate traps, the procedure outlined by Bros and Cowell (1987) was followed. Data from the 16 km station on the LR transect over the three sampling nights were pooled to produce a total of 18 'replicates'. By subtracting the nightly mean from each sample within that night, a single dataset was generated with mean 0 and a common variance. Pooling across treatments is justified if the sample variances are not heterogeneous; this was tested using Cochran's test (Winer 1971). A Monte Carlo procedure was then used to generate a range of samples for each level of replication. Repeated estimates of the

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standard error were made by randomly drawing samples, without replacement, from the combined dataset, for sample sizes ranging from two to 17. The number of draws made by the Monte Carlo procedure was equal to 10% of the number of all possible combinations, with a minimum of three draws (Bros and Cowell 1987). These data were then used to construct a graph of standard error versus sample size for the total number of fish collected in the light traps per hour, and for a single species group, *Pomacentrus* spp., that was abundant over all three nights. Coefficients of variation (standard deviation/mean) for different sample sizes were also calculated for the four most abundant taxa within a station on a single night. In this case, as there were only six replicate traps, all possible combinations of each sample size were used to generate estimates of the coefficient of variation associated with each taxa.

#### 2.3 RESULTS

A total of 7969 fish were captured in two years of systematic sampling, from a fishing effort of 194 light-trap-hours in 1988, and 419 light-trap-hours in 1989. Although some 37 families were collected (Table 2.2), the catch in both years was dominated by the family Pomacentridae (Figure 2.3). Significant inter-annual variability in the numbers of each taxa collected was also apparent. Lethrinids and mullids were proportionally more abundant in 1989 than 1988. Conversely, loliginid squids were caught in higher numbers in 1988, despite less fishing effort. A number of families were caught infrequently; 11 families were represented by fewer than five individuals (Table 2.1). The largest catch of a single taxa taken by a trap in one hour was 246 *Lethrinus* spp., followed by 136 *Pomacentrus* spp., 99 clupeids and 78 loliginid squids (Table 2.2).

A total of 200 scombrid larvae and juveniles were captured in the two years of sampling. Individuals referable to each of the four scombrid tribes, i.e. Thunnini, Sardini, Scomberomorini and Scombrini, were collected. The tribe Thunnini were represented by *Euthynnus affinis* and larvae and juveniles identifiable as belonging to the genus *Thunnus*. Two taxa were collected from the genus *Scomberomorus; S. semifasciatus* and a species group containing the morphologically similar *S. commerson* and *S. queenslandicus*. Three specimens from the tribe Sardini were captured; vertebral counts of 47-48 indicated that they were *Cybiosarda elegans*.

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Finally, seven *Grammatorcynus* juveniles were collected, along with a single juvenile from the genus *Rastrelliger*.

#### 2.3.2 Size frequency distributions

Size-frequency distributions of the catch indicated that small larvae were not taken in the light traps (Table 2.2); indeed no preflexion larvae were captured during this study. Size-frequency distributions of the dominant reef-associated taxa suggested size-selection for late-stage larvae and presettlement juveniles (Figure 2.4). Sizes from the family Pomacentridae ranged from 4.8 mm SL to 24.6 mm SL, with 90% of the fish falling between 10 and 16 mm SL. *Pomacentrus* spp. dominated the numbers collected, and showed a reasonably restricted size distribution (from 7.9-18.0 mm SL; Table 2.2).

*Neopomacentrus* spp. were collected over a wider size range, from 6.4 mm SL to 24.6 mm SL (Table 2.2). Lethrinids ranged in size from 10.3 to 28.3 mm SL (Figure 2.4). Again, over 80% were concentrated in a narrow size range between 16 and 20 mm SL. Mullids were collected at sizes from 14.6 mm SL to 34.4 mm SL (Figure 2.4). Significant numbers of pelagic juveniles greater than 20 mm SL were captured, resulting in a size frquency distribution with less kurtosis than either the pomacentrid or lethrinid distributions. Interestingly, the lower size limit in these families appeared to move up as the mean size increased. Pomacentrids were caught at smaller sizes than either lethrinids or mullids, and also had a smaller average size.

Pelagic taxa were captured over much wider size ranges (Figure 2.5). Postlarval and juvenile scombrids were taken at sizes ranging from 8.4 to 44.4 mm SL (Table 2.2). Loliginid squid were captured over an even greater size range, from 5.5 to 63.4 mm Dorsal Mantle Length. Clupeids were also captured over a large size range, but a high proportion were between 24 and 30 mm SL (Figure 2.5). **Table 2.2.** Total number, maximum catch (number light-trap-hr<sup>1</sup>), and size ranges of larval and juvenile fishes collected in the light traps from waters of the central Great Barrier Reef lagoon in 1988 and 1989.

Taxon	Total	Max.	Range	Taxon	Total	Max	Range
	catch	catch	(mm SL)		catch	catch	(mm SL)
Apogonidae	61	7	6.4-13.6	Pomacentridae (cont.)			
Atherinidae	41	4	17.2-38.1	Chrysiptera spp.	17	5	8.8-11.3
Blennidae	52	6	6.8-20.2	Dascyllus aruanus	3	1	7.0-9.3
Bregmacerotidae	2	1	14.4	Dischistodus spp.	114	41	6.9-10.7
Carangidae	31	3	8.7-30.5	Neopomacentrus spp.	433	20	6.4-24.6
Chaetodontidae	19	3	6.0-22.6	Plectroglyphidodon spp.	2	1	7.0-9.6
Clupeidae				P. lacrymatus	78	3	4.8-11.3
Clupeinae	451	99	9. <b>3-5</b> 5.5	Pomacentrus spp.	3236	136	7. <del>9</del> -18.0
Dussumieriinae	26	6	29.5-40.5	P. coelestis	197	41	7.8-17.4
Dactylopteridae	80	20	5.7-15.5	Pristotis jerdoni	15	3	8.4-12.2
Diodontidae	4	1	11 <b>.6</b> -15.0	Small pomacentrids	3	1	6.0-11.3
Engraulidae	73	9	15.2-39.4	Plesiopidae	3	1	10.5-10.7
Fistulariidae	1	1	41.9	Priacanthidae	21	2	6.2-14.3
Gerreidae	11	2	11. <b>6</b> -17.5	Pseudochromidae	1	1	11.9
Gobiidae	25	2	6.8-9.6	Scombridae			
Hemiramphidae	2	1	26.4-27.2	Cybiosarda elegans	2	1	15.4-16.8
Holocentridae	7	1	9.0-27.6	Euthynnus affinis	48	10	8.4-44.4
Labridae	9	2	6.2-9.6	Grammatorcynus spp.	7	2	10.4-19.7
Leiognathidae	3	1	10.3-19.2	Rastrelliger spp.	1	1	34.7
Lethrinidae				Scomberomorus spp.	74	10	12.0-25.4
<i>Lethrinus</i> spp.	1080	246	10.3-22.1	S. semifasciatus	31	4	12.0-41.1
Lologinid squid	706	78	4.3-63.4	Thunnus spp.	31	4	10.5-23.8
Lutjanidae				Scorpaenidae	24	4	7.6-10.2
Lutjanus sp	1	1	16.9	Serranidae			
Monacanthidae	20	3	14.6-35.7	Epinephelus spp.	27	8	14.3-18.8
Mullidae	274	27	14.6-34.4	Siganidae			
Myctophidae	1	1	10.7	Siganus spp.	57	19	14.0-24.0
Nemipteridae	1	1	12.5	Sphyraenidae	5	1	23.1-23.9
Ostraciidae	2	1	5.9-10.4	Syngnathidae	14	2	49.9-55.2
Pomacentridae				Synodontidae	8	1	22.9-33.6
Abudefduf spp.	60	10	10.7-23.1	Teraponidae	27	8	10.1-42.8
Chromis weberi	302	62	7.8-13.5	Tetraodontidae	20	3	12.2-33.8
C. atripectoralis/viridis	72	5	6.9-10.9	Triptervojidae	12	4	9.9-12.4

Individual scombrid taxa were also captured over a wide size range (Figure 2.6). *Scomberomorus* individuals varied in size from 12.0 to 41.1 mm SL, with a modal size of 16.8 mm SL. *Euthynnus affinis* were captured at slightly smaller sizes (minimum 8.4 mm SL, maximum 44.4 mm SL), with a correspondingly smaller modal length of 14.1 mm SL. Individuals from the genus *Thunnus* were captured over a smaller size range than the other three taxa, from 10.5 mm SL to 29.6 mm SL, with a modal size of 15.9 mm SL. Comparison between the size-selectivity of towed nets and light traps for the genus *Scomberomorus* was made by consideration of earlier data collected in the same area by Jenkins (1981), using a 2 m<sup>2</sup> Tucker trawl. Jenkins collected specimens of *S. commerson*, *S. queenslandicus* and *S.* 

*semifasciatus* from 3.6 to 10.5 mm SL, with a modal size of 5.5 mm Sl. The smallest specimen captured in the light traps was thus slightly larger than the largest specimen captured in the Tucker trawl (Figure 2.7).

#### 2.3.3 Trap performance

The effect of time of night on catchability was investigated over four nights. The mean abundance of fish light-trap-hour<sup>-1</sup> at each of the three sampling times varied from a low of 22 fish light-trap-hour<sup>-1</sup> during the third and last hour of sampling to a high of 27 fish light-trap-hour<sup>-1</sup> during the second hour (Figure 2.8). While there is a suggestion of a peak in catchability around mid-night, the 95% confidence intervals of all three means over-lapped. The null hypothesis of no difference in catchability with time of night was, therefore, unable to be rejected.

Three comparisons of anchored and drifting traps were made. Although several more were attempted, the numbers of fish at these times were too low (< 50 fish captured in all traps) to make any meaningful comparisons. On all occasions, drifting traps out-performed anchored traps, often by large margins (Figure 2.9). This result appeared to be independent of taxa. The first comparison was dominated by clupeids and engraulids, the second by pomacentrids, and the third by pomacentrids and lethrinids.

To estimate the optimum number of replicates, functions of standard error against sample size were generated for both total number of fish captured, and the single most abundant taxa (Pomacentrus spp.) over all three nights. Total fish numbers were log-transformed to provide homogeneous variances between nights (Cochran's C 0.648 after transformation). This was not necessary for the data on Pomacentrus spp (Cochran's C 0.53). Both data sets showed similar relationships between standard error and sample size most conservative standard error estimate is (Figure 2.10). If the considered, that is the largest standard error generated by the Monte Carlo procedure for each sample size, the point of inflexion of the function curve occurred between five and six replicates. Alternatively if the average standard error measure is used, a rapid increase in precision occurs between two and three replicates. Similar conclusions are reached by considering plots of coefficients of variation versus against sample size for individual taxa on each night (Figure 2.11). Coefficients of variation ranged from 0.9

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(clupeids) to 0.2 (*Pomacentrus* spp.) for two replicates, through to 0.4 (clupeids) and 0.14 (*Pomacentrus* spp.). Both pomacentrid taxa, *Pomacentrus* spp. and *Chromis weberi*, had lower coefficients of variations than either the lethrinids or clupeids.

#### 2.4 **DISCUSSION**

The light traps in the present study captured a total of 37 familes. This was considerably more diversity than found around Lizard Island (northern GBR), the only other place the traps have been deployed to date, where Milicich (1988) recorded a total of 24 families. This is not surprising given the greater range of pelagic habitats sampled in this study; traps at Lizard Island were confined to waters immediately adjacent to the reef edge (Doherty 1987a, Milicich 1988). A number of taxa were conspicuously rare or absent from both collections, including pleuronectiform flatfish, platycephalids, apogonids, carangids, gobiids and lutjanids. The larvae of these families represented six of the seven most adundant families caught with a 2 m<sup>2</sup> Tucker trawl by Williams *et al.* (1988), in the only quantitative study of larval fish community structure in this area. Interestingly Milicich (1992) did report large numbers of apogonids, gobiids and carangids in light trap catches from Lizard Island- the reasons for the low catches of these taxa in the present study remain unknown.

The most striking feature is the taxonomic similarities of catches between locations. Pomacentrids and lethrinids have dominated three years of sampling at Lizard Island (Milicich 1992), and were also the most abundant taxa in this study. Both families appear particularly susceptible to light traps. This may be due to the vertical distributions of these taxa as the larvae of both families are concentrated in the upper water column at night (Leis 1991b). However, mullids are also very abundant in the neuston, and, although captured in light traps, they were not nearly as common as pomacentrids and lethrinids. This implies that there may be taxon-specific behaviours determining vulnerability to capture, or alternatively that pomacentrids and lethrinids may be distributed on spatial scales that increase the chance of large, albeit infrequent, catches in light traps. More site-intensive studies will be required to resolve these alternatives. The light traps captured numerous larval and juvenile scombrids, and provided specimens of several species that have yet to be described. Absolute numbers from this program were not high; less than 0.5 light-traphr<sup>-1</sup>. However, the numbers captured compare favourably with other collections, and the size distributions of the specimens made the collection unique. Jenkins et al. (1985) captured a total of 356 Scomberomorus larvae in a three year study in the same area, but did not collect any specimens larger than 10.5 mm SL. Collins and Stender (1987), in summarizing data from the MARMAP larval fish program involving some 1,163 collections from the South Atlantic Bight, reported a total of 459 S. cavalla larvae, ranging in size from 2-14 mm, and 96 S. maculatus larvae ranging in size from 2-9 mm. Similarly Grimes et al. (1990) captured a total of only 27 Scomberomorus cavalla larvae > 10 mm SL in over 700 neuston, bongo and meter net samples. Studies of larval and juvenile tunas have also lacked individuals of sizes captured in light traps (eg Davis et al. 1989, McGowan and Richards 1989). Such sizes may be critical to correct determination of age and growth parameters; at least one study has suggested that tuna larvae achieve rapid, exponential growth rates at sizes greater than those captured in towed nets (Jenkins and Davis 1990).

The differences in size-frequencies between *Scomberomorus* spp. captured in the light traps and 2 m<sup>2</sup> Tucker trawl were notable, given that the Tucker trawl was designed specifically to capture large larvae and juvenile fishes (Aron 1962). Other studies have also documented the inability of such trawl nets to catch larvae at greater sizes than smaller nets (Weibe *et al.* 1982, Choat *et al.* 1993). Indeed the rationale behind the use of larger nets to catch more larvae must be questioned: Davis *et al.* (1989) found that a 70 cm ring net consistently caught more larvae than a 2 m ring net. Whatever the optimal net size for capturing larval scombrids may be, a multi-gear sampling strategy combining towed nets and light traps will provide a more complete description of distribution and abundance patterns than either technique in isolation.

Size-frequencies confirmed data obtained from other studies (Choat *et al.* 1993) that small larvae of a number of taxa are undersampled by the light traps. The light traps do, however, catch large numbers of larvae and pelagic juveniles that are captured only rarely in plankton tows. These results may be explained by the large volume of water sampled by the light

traps. Choat *et al.* (1993) calculated that stationary light traps might be exposed to between 20,000-200,000 m<sup>-3</sup> of water in an hour at moderate current speeds. On this basis, they argued that the greater catch by light traps compared to bongo and Tucker trawl estimates could be reconciled simply by the greater volume of water sampled by the aggregation device. However, this was assuming a current speed of between 0.15- 0.35 msec<sup>-1</sup>. In the present study with drifting light traps, this explanation cannot be advanced. While there is some evidence (M.J. Milicich and S.R. Thorrold, Australian Institue of Marine Science, unpublished data) that fish may be seeing the light traps from greater distances than those used by Choat *et al.* (1993) when estimating the volume of water sampled, the most parsimonious explanation is that many of the fish captured by light traps are capable of avoiding conventional plankton nets.

The absence of any detectable effect of time of night on catchability suggests that records may be compared from traps fished at different times during the night. Further, in this study, unlike previous ones (Doherty 1987a, Milicich 1988), the light traps were allowed to drift with the water mass, rather than being anchored to the bottom. Although this had the potential disadvantage of lowering the effective volume of water sampled, it reduced the possibility of differential water flow confounding differences in abundances between traps. The result that drifting traps actually outperformed anchored traps was unexpected and indeed counter-intuitive. Anchored traps are presumably exposed to more water than drifting traps. It is possible that at higher currents speeds, fish find it harder to swim to, and enter, the traps. During the comparisons, the drifting traps moved between 0.8 and 1.25 km in the hour of fishing, which suggested that a relatively strong current was flowing at the time. Clearly more detailed work is required to determine the relationship between current speed and trap efficiency. By using drifting traps, these problems were avoided, and the traps appeared to give precise 'point-source' estimates of fish abundance.

Methot (1986) listed four desirable attributes of a juvenile fish sampler. It should filter a large volume of water, be unobtrusive to reduce avoidance by larger organisms, retain little plankton and be easy to handle. By using light attraction, the traps may be fishing large volumes of water, even when drifting with the water. According to the estimates used by Choat *et al.* (1993), one would have to tow an 85 cm bongo net 200 km to sample the

same volume as a light trap fishes in a single hour. The light traps have another major advantage in that they are easily replicated. When combined with the large volume of water sampled, this means the light traps can produce precise abundance estimates, which in this study ranged from 0.9-This compares favourably with trawl nets. Methot (1986) 0.14 (CV). reported coefficients of variation of 0.6 and 0.75, for Engraulis mordax larvae of 10 mm SL and 15 mm SL respectively, from his mid-water trawl. Light traps also appear to satisfy the second criterion, and the locomotory abilities of the fish may actually enhance capture rather than retard it. They also collect relatively small amounts of plankton (mainly large, motile mysids, euphausids and amphipods) which present few problems when sorting samples, and they do not suffer from clogging problems when fished in waters with large numbers of gelatinous zooplankton. Finally, the traps are easily deployed from a small vessel without booms or hydraulic winches, which means that multi-ship programs are much more feasible.

A major problem with the light traps is the perception that such techniques are necessarily qualitative- i.e. it is not possible to convert light trap catches to standardized densities. It must be stressed, however, that all techniques are biased, and that these biases will become more pronounced as larvae grow and become more adept at avoiding towed nets. While it is possible to calculate correction factors for plankton nets (Somerton and Kobayashi 1989), these factors become increasingly unreliable with size. Leak and Houde (1987), for instance, used data from Murphy and Clutter (1972) to calculate size-specific avoidance rates for the Bay anchovy. They suggested that at 9 mm SL, 94% of larvae were able to avoid the plankton net used in their study. The fact that avoidance levels were so high meant that a change in the size-specific avoidance rate from 90% to 99% would have altered abundance estimates by an order of magnitude without any change in the actual density of fish. This is entirely possible, given that avoidance is related to physical parameters such as light levels and water clarity (Brander and Thompson 1989), and biological factors such as the amount of biolumenscence present in the water column (Weibe et al. 1982). Munk (1988) concluded that it was impossible to standardize the IKMT net because of these problems. This implies that despite the increasing sophistication of techniques for correcting catches of fish larvae for size-selection (Somerton and Kobayashi 1989), these are unlikely to be realistic for large larvae and juveniles.

Light traps will, by their very nature, yield biased estimates of the planktonic community. Clearly if a larval or juvenile fish is not photopositive, light traps will not collect them. However, given that the species of interest is collected in the light trap, it may be possible to calculate the volume of water from which a light trap is drawing fish from a knowledge of the light sensitivity of the fish, the light output of the trap, and the optical quality of the water in which the trap is being used. These calculations have been made for Pomacentrus wardi collected in the study area. Milicich and Thorrold (Australian Institute of Marine Science, unpublished data) found that P. wardi could theoretically see, and respond to, a light trap up to 80m away in a Jerlov type 3 oceanic water mass. More importantly in the context of this study, the distance varied only by approximately 5 m from the more turbid water found near the coast (characterised as Jerlov coastal type 1), and the clearer water found offshore in the vicinty of the midshelf reefs (characterised as Jerlov oceanic type 3). This suggests that the light trap samples may be confidently compared at localities across the transects sampled in this study; this will be the focus of the following chapter.






Figure 2.2. Schematic diagram of a light trap used in this study. Diagram to scale, dimensions of light trap box 1200mm x 300mm x 300mm.



Figure 2.3 Total numbers of the six most abundant taxa captured in light traps during 1988 (solid bars) and 1989 (hatched bars).



**Figure 2.4.** Size-frequency distributions of three families of coral reef fish, Pomacentridae (n = 4532), Lethrinidae (n = 1080) and Mullidae (n = 274), captured in light traps during 1988 and 1989.



**Figure 2.5.** Size-frequency distributions of two pelagic fish families, the Scombridae (n = 200) and the Clupeidae (n = 477), and loliginid squids (n = 706), captured in light traps during 1988 and 1989.



Figure 2.6. Size-frequency distributions of *Scomberomorus* spp. (n = 74), *S. semifasciatus* (n = 31), *Euthynnus affinis* (n = 48) and *Thunnus* sp. (n = 34) captured in light traps.



**Figure 2.7.** Comparison of size-frequency distributions between *Scomberomorus* spp. captured in a Tucker trawl (solid bars; n = 356; from Jenkins 1981) and light traps (hatched bars; n = 105; this study).







**Figure 2.9.** Comparison of light trap catches (mean number of fish light-trap-hr<sup>1</sup>; +/- standard error) from anchored (solid bars) and drifting (hatched bars) traps fished in the same body of water. A: 26.9.89, 0 km station on LR transect. B: 26.9.89,16 km station on LR transect. C: 22.10.90, 16 km station on LR transect.



**Figure 2.10.** Relationship between standard error and sample size for light trap samples comprising total number of fish light-trap-hr (top) and numbers of *Pomacentrus* spp. light-trap-hr (bottom). Standard errors for replicates beyond 9 (n/2) are not reliable (Bros and Colwell 1987).





# Chapter 3

# Meso-scale distribution patterns of larval and juvenile fishes in the central Great Barrier Reef lagoon

## **3.1 INTRODUCTION**

Fisheries biologists have recognised since the beginning of the century that the population dynamics of many marine fish species may be driven by events occurring during the larval phase of the life cycle (Hjort 1914, Houde 1987). While the larval phase is restricted temporally to a period of weeks or months, extremely high mortality rates and considerable dispersive abilities suggest that this stage may have a disproportionate influence on the local abundance of adult populations (Roughgarden *et al.* 1988). Despite the potential for larval dynamics to influence population structure, the early life history of tropical marine fishes has only recently attracted attention (Leis 1991a). This lack of information stems from the reticence of reef fish biologists to sample the pelagic stages directly (Victor in press), due largely to the difficulties and cost associated with larval fish programs.

Almost all studies of larval fish distributions within tropical environments have focused on broadscale surveys (e.g. Miller 1974, Richards 1984, Shaw et al. 1985a, Young et al. 1986, Leis and Goldman 1987, Milward and Hartwick 1986, Williams et al. 1988, Soeweto and Schalk 1990, Clarke 1991). These studies have provided valuable information on the larval habitat requirements of a number of tropical fish taxa, but with limited spatial or temporal resolution. The few studies that have been conducted on smaller spatial scales have addressed specific questions regarding vertical distributions (Leis 1991b), or near-reef distribution patterns (Kobayashi 1989, Lyczkowski-Shultz et al. 1990, Boehlert et al. 1992, Williams and English 1992), with limited temporal coverage. While such studies are a necessary prerequisite to any understanding of larval biology, little remains known of the processes influencing larvae over 'meso' spatial and temporal scales (days-weeks and 1-10's of km). Paradoxically, it is over these scales that the physical and biological factors determining larval survival are probably acting (Denman and Powell 1984, Davis et al. 1991).

The reliance on towed-net technology to sample small fishes has also restricted the size range of larvae collected by larval surveys. While plankton nets sample small larval fish effectively, the activity associated with towing nets through the water column apparently leads to detection and avoidance of nets by agile nekton (Barkley 1964, Choat *et al.* 1993). Larger nets devised to counter active avoidance have met with only limited success (Clarke 1983, Munk 1988). This presents real problems in the tropics. Many coral reef fish have a pelagic juvenile stage that has considerable sensory and locomotory abilities (Leis and Rennis 1983, McCormick and Shand in press). These stages do not appear to be adequately sampled by plankton nets or mid-water trawls (Choat *et al.* 1993).

Our ability to effectively sample the motile component of planktonic communities has recently improved, due to the development of an alternative methodology that targets the pelagic juvenile stages of coral reef fishes (Doherty 1987a). Initially applied to monitor larval supply to reefal habitats (Milicich 1988, Milicich *et al.* 1992), light traps have also proved useful for collecting small fishes in open waters (Chapter 2). While the traps are effective collectors of large planktonic individuals, they appear to under-sample the smaller stages that are collected in plankton nets (Choat *et al.* 1993). This suggests that a sampling strategy combining both plankton nets and light traps would result in a more complete description of the distribution and abundance patterns of pre-settlement fishes than either technique in isolation. Despite petitions for multi-gear sampling strategies from several authors (e.g. Omori and Hamner 1982, Kingsford 1990), such programs have rarely been undertaken (Gregory and Powles 1988).

While technological advances such as light traps have improved our ability to effectively sample nektonic communities including larval and juvenile fishes, the processes generating observed distributional patterns remain obscure (Leis 1991a). Plankton biologists have recently developed a conceptual model whereby hydrodynamics are viewed as the driving force of aquatic ecosystems (Legendre and Demers 1984). Such an approach rests on the assumption that the space and time scales of variation in the physical environment correspond approximately to those of populations of marine organisms, and that the spatial scales of ecological importance are essentially the spatial scales of the important physical processes (Denman and Powell 1984). By identifying the critical spatio-temporal scales over which larval

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and juvenile fish distributions are varying, insight may be gained into the nature and scales of physical processes generating this variability (Legendre and Demers 1984). While it may be argued that larval and juvenile fishes will be buffered from the physical environment by a degree of locomotory ability, several studies have demonstrated that larval fish distributions are inextricably linked to hydrographic regimes (e.g. Fortier and Leggett 1983, Fortier *et al.* 1992), and that biological processes such as growth and mortality rates may also be mediated by environmental forcing (Peterman and Bradford 1987, Checkley *et al.* 1988, Maillet and Checkley 1991).

The objectives of this chapter are to examine variability in larval and juvenile fish distributions over a range of spatial and temporal scales. By utilising a multigear sampling strategy, incorporating both towed nets and light traps, a more complete description of distribution patterns of larval and juvenile fishes could be obtained and ontogentic shifts in distribution patterns quantified.

The specific aims are to:

1. Describe spatial and temporal variability in the distribution and abundance of larval and juvenile fishes using both towed nets and light traps.

2. Identify critical spatio-temporal scales over which the physical processes that may be generating the observed biological patterns are operating by sampling over temporal scales ranging from days to months, and across spatial scales ranging from 10's of meters to 10's of kilometers.

3. Compare and contrast the abundance patterns revealed by the two techniques.

## **3.2 METHODS AND MATERIALS**

### 3.2.1 Sample collection

Field work was conducted in coastal waters of the central Great Barrier Reef, at each of four stations along two cross-shelf transects (Figure 2.1), during October-December 1988 and 1989. One transect could be completed in a

single night of sampling, and each transect was sampled at least once, and up to three times, in each of the three months depending on weather conditions. Sampling dates are provided in Table 2.1; all sampling was conducted within a 10 day window around the new moon. Sampling equipment consisted of a 0.5 m, 505  $\mu$ m plankton net fitted with a General Oceanics digital flowmeter, and light traps as described in Chapter 2. At each station six light traps were deployed, 200-300 meters apart and approximately one meter below the sea surface, and fished for one hour. The traps were allowed to drift with the prevailing currents rather than anchoring the traps to the bottom. While this reduced the amount of water the trap sampled, it also minimised the possibility of differential water flow confounding differences between stations. During the period that the light traps were fishing three 10 min plankton tows were made in the immediate vicinity of the traps with the 0.5 m net. The net was rigged so as to fish between one and two meters below the surface.

All samples were immediately preserved in 80-90 % ethanol for subsequent identification and enumeration. In 1988, larvae from the net tows were not identified, and analyses from the first year of sampling considered only total numbers of larvae. In 1989, larvae from the net tows were identified to family level, following Leis and Rennis (1983) and Leis and Trnski (1989). All fish collected in the light traps were identified to the lowest possible taxon. However, for all statistical analyses identification of the light trap samples was truncated at the same level as that obtained for the net tows. Therefore in 1988, total numbers only were used, while in 1989, fishes were considered at the family level. Numbers of larvae collected in net samples were converted to concentrations (numbers 1000 m<sup>-3</sup>) using the volumes of water sampled during each tow calculated from the flowmeter data, while abundance of fish from light traps samples were expressed as numbers of fish light-trap-hr<sup>-1</sup>.

#### 3.2.2 Data analysis

Patterns in the distribution of larval and juvenile fishes during 1988 were compared by first generating a dissimilarity matrix between the total number of fish collected in a single sample  $(t_1)$  and each other sample  $(t_2-t_n)$ .

The dissimilarity value (s) was calculated according to the following formula:

$$s = \frac{|(t_1 - t_n)|}{(t_1 + t_n)}$$

This gave a symmetrical matrix which could be compared to model matrices of interest using Mantel's test of matrix correspondence (Mantel 1967; see section 3.2.2.1 below).

In 1989, larvae from the plankton tows were identified to family level. This allowed multivariate analysis of the distribution patterns of fish collected from both plankton nets and light traps. A standard Bray-Curtis dissimilarity matrix was generated from the family/sample data set. The dissimilarity matrix was then used as the basis for a flexible unweighted (UPGMA) clustering strategy. The family/sample matrix was then transposed and families clustered again using a flexible UPGMA. In this case, the dissimilarity matrix was generated using the Bray-Curtis algorithm after the data had firstly been standardised by expressing each value as a proportion of the maximum value recorded for that family. This standardisation is commonly used when attributes (in this case families) rather than objects (i.e. the individual samples) are clustered (Belbin 1988).

Bubble plots were used to display the associations of samples between transects, and among months and stations. Plots were generated by calculating the percentage of samples from a given month, transect and station within the sample group under consideration. For instance, if sample group 1 consisted of an equal number of samples from October and November, but none from December, two bubbles of area 0.5 units would be plotted next to October and November under sample group 1 on the UPGMA dendrogram. Results of clustering by samples and families were plotted using two-way table summaries (Smith et al. 1989). These tables are calculated by firstly determining the mean value of each family within the sample groups. Mean values across the sample groups are then summed for each taxa, and the individual family means are converted into the proportion that each family contributes to the sample groups. Finally, these proportions are averaged across the members of the family groups, to give a mean proportion that each of the family groups contributes to each of the

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sample groups. The 'bubbles' in the resulting two-way summary plots represent the percentages of the species groups upon summing the mean proportions of each family group across columns or down rows. The direction that these summations were calculated are shown by arrows on the appropriate plots.

#### 3.2.2.1 Permutation tests for matrix association

The above techniques are powerful methods for displaying patterns in multivariate datasets. However they are unable to test specific hypotheses concerning spatial and temporal variability in taxonomic composition or abundance. In 1989, for instance, both plankton net and light trap data consisted of a multivariate family/sample matrix with cruises nested within transects, and transect, month and station as main factors in a three-way, mixed model ANOVA design. A number of difficulties arise, however, if multivariate ANOVA is used to analyse the data sets. The large number of species compared to samples means that in order to get sufficient degrees of freedom, a number of taxa must be dropped from the analysis. Problems are compounded by the non-normality typical of plankton data (Mackas et al. 1985), as assumptions underlying parametric MANOVA include normal distributions of individual taxa and equal variance-covariance matrices. To overcome these problems, Mantel (Mantel 1967) and partial Mantel tests (Smouse et al. 1986) were used instead. These tests use a non-parametric, permutation method to determine statistical significance and therefore are not invalidated by any lack of dependence, non-normality or spatial autocorrelations that may be present in the data (Legendre 1993).

The Bray-Curtis dissimilarity matrices used in the preceding analyses formed the data matrix for Mantel and partial Mantel tests, with each alternative hypothesis of the ANOVA (i.e. no effect of station and no effect of time on ichthyoplankton samples) cast into a model matrix (Hudon and Lamarche 1989, Legendre and Fortin 1989). The model matrix expressing the alternative hypothesis that there were differences among stations contained 1's in the within station regions of the matrix, and 0's elsewhere. Similarly, the model matrix that represented differences among times contained 1's in the cells comparing the same times, and 0's in the amongtime cells. A test of matrix correspondence was calculated between the data (Y) and model (X) matrix using the formula;

$$r = \Sigma_{ij} (\Sigma X_{ij} Y_{ij})$$

where  $\Sigma_{ij}$  symbolises summation over all ij pairs other than i=j - i.e. either the top or bottom diagonals of the two matrices, and *r* is the observed test statistic. Then using an empirical null distribution derived from randomly permuting one of the matrices a number of times (in this case 500), the probability of obtaining a value of *r* at least as extreme as the observed *r* by chance alone was computed. All tests were two-tailed, with an  $\alpha$  value of 0.01. The test for interactions between main effects followed that described by Smouse *et al.* (1986), and is computed by determining how much extra information is provided by the addition of each of the model matrices, after firstly calculating how well the individual model matrices predict the data matrix. A comprehensive review of "approximate" ANOVA using Mantel's test of matrix association is provided by Legendre (1993).

While these tests provide a distribution free significance test analagous to MANOVA, in this instance I was less interested in documenting 'statistically significant' changes in community structure than in identifying the critical spatial and temporal scales over which ichthyoplankton were varying. A non-significant term at any level of the analysis implies that samples within any group (for instance from the same day, or from the same station) are no more similar to those from among groups (days or stations) than would be expected by chance. Alternatively, a significant result implies that samples within any group (days or stations) are more similar to each other than samples among groups. Therefore a significant result implies that this level, or scale, in the analysis contributes a statistically significant amount to the total variance within the data set. Given that it is likely that a number of significant results will be obtained, it is also perhaps more useful to estimate what proportion of the total variance resides within each level. If this was a univariate hierarchicallynested ANOVA design it would be easy to apportion variance contributions to each of the levels (Underwood 1981). While it is not possible to do this in a formal manner using the analyses outlined above, the Mantel statistic r, the measure of association between model and data matrices, does provide a means for qualitatively assessing the variance contributions of different spatial and temporal effects. A high value of matrix correspondence implies that the model term in question contributed a high amount of variance compared to a term with a lower r value.

Given that the 1988 data set consisted of total numbers only, interactive effects were not considered. I considered that this would be over-analysing the limited data available, and interpretation of these results are necessarily more conservative. Mantel and partial Mantel tests were run using "the R package for multivariate data analysis" of Legendre and Vaudor, referred to in Legendre and Fortin (1989) and Legendre (1993).

## 3.2.2.2 Univariate analyses

Further univariate analyses were conducted on the families indentified as contributing most to the station-time groups in cluster analyses of the 1989 data set. These families were identified by examining Cramer values (Belbin 1988) derived from the cluster analysis. Six taxa from both light traps and net tows were chosen. A further two families, the pomacentrids and mullids, were also examined from the net tow data. These families, along with the Clupeidae, were captured in significant numbers by both techniques, and direct comparisons of spatial and temporal variability of fish captured in light traps and plankton nets could be made.

ANOVA was used to examine variability at each of the spatial and temporal scales sampled. While the design was for each main effect (i.e. cruise, month, transect and station) to be balanced, bad weather in December meant that only one cruise could be completed on each transect. Therefore, cruises were pooled within months. After pooling, a three-factor, orthogonal ANOVA was used to test for differences between months, transects and stations. As there was uneven replication (three cruises from October and November for a total of 9 replicates, one cruise for a total of 3 replicates from December), type III sums of squares were used for all ANOVA analyses. All variables were tested for heterogeneity of variances and normality of residuals using residual analysis (Winer 1971).

In 1988, a total of 11,218 larvae from 110 plankton tows, and 3,482 larvae and juveniles from 194 light-trap-hrs, were collected over the three months of sampling. During the same months in 1989, 13,988 larvae were captured in 168 plankton tows, while the light traps collected 3,781 fish from a total of 419 light-trap-hrs. Catches from plankton nets and light traps showed distinctive taxonomic compositions. A total of 75 families were collected in the net tows (Table 3.1), while the light traps captured 36 families (Table 3.2).

**Table 3.1.** Frequency and percent frequency by family of fish larvae collected in plankton nets from October to December, 1989.

Family	Freq	% freq	Family	Freq	%freq
Gobiidae	5681	40.6	Diodontidae	16	0.1
Apogonidae	1117	7.9	Acanthuridae	13	0.1
Clupeidae	1048	7.5	Exocoetidae	12	0.1
Lutjanidae	983	7.0	Haemulidae	11	0.1
Carangidae	672	4.8	Mugiloididae	10	0.1
Nemipteridae		4.0	Belonidae	9	0.1
Teraponidae	<b>351</b>	2.5	Lophiiformes	9	0.1
Pomacentridae	290	2.1	Gerreidae	8	0.1
Monacanthidae	288	2.1	Trichonotidae	8	0.1
Bregmacerotidae	282	2.0	Leptocephali	7	0.1
Leiognathidae	256	1.8	Triacanthidae	7	0.1
Scombridae	251	1.8	Chaetodontidae	5	-
Callionymidae	230	1.6	Dactylopteridae	5	-
Platycephalidae	182	1.3	Paralicthyidae	5	-
Bothidae	134	1.0	Balistidae	4	-
Mullidae	131	0.9	Leptobramidae	4	-
Priacanthidae	124	0.9	Pomacanthidae	4	-
Scorpaenidae	102	0.7	Psettodidae	4	-
Labridae	80	0.6	Sillaginidae	4	-
Schindleriidae	73	0.5	Trichiuridae	4	-
Lethrinidae	73	0.5	Ammodytidae	3	-
Tetraodontidae	72	0.5	Fistulariidae	3	-
Synodontidae	63	0.4	Pleuronectidae	3	-
Microdesmidae	55	0.4	Pseudochromidae	3	-
Sciaenidae	54	0.4	Scatophagidae	3	-
Blenniidae	53	0.4	Carapidae	2	-
Mugilidae	49	0.4	Hemiramphidae	2	-
Sphyraenidae	48	0.3	Istiophoridae	2	-
Polynemidae	36	0.3	Kyphosidae	2	-
Serranidae	33	0.2	Ostraciidae	2	-
Syngnathidae	33	0.2	Soleidae	2	-
Myctophidae	30	0.2	Tripterygiidae	2	-
Engraulidae	28	0.2	Cepolidae	1	-
Cynoglossidae	24	0.2	Gemphylidae	1	-
Holocentridae	23	0.2	Nomeidae	1	-
Scaridae	23	0.2	Siganidae	1	-
Opistognathidae	20	0.1	Unidentified	242	1.7
			Total	13998	100

Plankton net samples were dominated numerically by gobiids, with apogonids, clupeids, lutjanids and carangids making up the five most abundant taxa. Numerically, these five taxa accounted for 68% of the total number of larvae collected. Light trap catches were dominated by pomacentrids in 1988, with only scombrids, clupeids and lethrinids contributing more than 3% of the total number of fish captured. Pomacentrids were again the most abundant taxa in 1989. Lethrinids were also abundant, along with clupeids and mullids.

	19	88	1989			19	88	1989	
Family	Freq	%freq	Freq	%freq	Family	Freq	%freq	Freq	%freq
Pomacentridae	2718	78.1	1814	48.0	Priacanthidae	11	0.3	10	0.3
Lethrinidae	118	3.4	962	25.4	Tripterygiidae	2	0.1	10	0.3
Clupeidae	131	3.8	346	9.8	Gerreidae	3	0.1	8	0.2
Mullidae	56	1.6	218	5.8	Labridae	2	0.1	7	0.2
Scombridae	173	5.0	21	0.6	Synodontidae	2	0.1	6	0.2
Dactylopteridae	10	0.3	70	1.9	Holocentridae	2	0.1	5	0.1
Blenniidae	23	0.7	69	1.9	Diodontidae	0	-	4	0.1
Engraulidae	29	0.8	44	12	Sphyraenidae	. 4	0.1	1	-
Siganidae	41	12	16	0.4	Leiognathidae	3	0.1	0	-
Atherinidae	6	0.2	35	0.9	Plesiopidae	0	-	3	0.1
Apogonidae	31	0.9	30	0.8	Bregmacerotidae	0	-	2	0.1
Serranidae	26	0.7	1	-	Hemiramphidae	2	0.1	0	-
Teraponidae	26	0.7	1	-	Fistulariidae	0	-	1	-
Tetraodontidae	1	-	19	0.5	Lutjanidae	0	-	1	-
Scorpaenidae	6	0.2	18	0.5	Myctophidae	0	-	1	-
Gobiidae	17	0.5	8	0.2	Nemipteridae	0	-	1	-
Carangidae	15	0.4	16	0.4	Ostraciidae	1	-	1	-
Chaetodontidae	14	0.4	5	0.1	Pseudocromidae	1	-	0	-
Syngnathidae	1	-	13	0.3	Scaridae	0	-	1	-
Monacanthidae	7	0.2	13	0.3	Total	3482	100	3781	100

**Table 3.2.** Frequency and percent frequency by family of small fish captured in light traps from October to December in 1988 and 1989.

### 3.3.1 Plankton tows from 1988

Analysis of net tow data from 1988 utilizing Mantel's test of matrix association suggested that there were no significant effects of cruise or month (Table 3.3). There were, similarly, no evidence of any of the spatial scales contributing significant variance to the data. This implied that on a given sampling occasion, high numbers may have been encountered at any station and on either transect. This can be seen in three-dimensional graphs of the data plotted across months and stations for both transects (Figure 3.1). High abundances were recorded in all months, on both transects, and across all stations. **Table 3.3.** Results of Mantel tests against temporal and spatial models of variability in the numbers of larvae captured in plankton nets, where r = Mantel's test statistic of matrix correspondence, ST is number of times that the recalculated test statistic after the model matrix is randomly permuted is smaller than original r value, EQ is the number of times this value is equal to r, and GT is the number of times that this value is greater than r. Prob(t) is the probability of the null hypothesis being true, obtained from the direct test of Hope (1968). \* indicates significant associations at  $\alpha = 0.01$ , ns = not significant.

Source	r	ST	EQ	GT	Prob(f)
Temporal models					
Cruise	0.02812	487	1	13	0.028 <sup>ns</sup>
Month	0.01502	436	1	64	0.130 <sup>ns</sup>
Spatial models					
Station	0.01519	438	1	62	0.124 <sup>ns</sup>
Transect	0.01065	397	1	103	0.206 <sup>ns</sup>

### 3.3.2 Light traps from 1988

Light trap results showed more consistent patterns of variability than net samples. Significant effects were found for cruises in the same month, and across cruises within months (Table 3.4). Spatial associations were also apparent across stations, although not between transects (Table 3.4). These data indicate, therefore, that there were comparatively few differences in light trap catches between transects (i.e. in the longshore direction), but that there were significant variance among stations in the cross-shelf direction.

**Table 3.4.** Results of Mantel tests against temporal and spatial models of variability in the numbers of fish captured by light traps in1988. Legend as for Table 3.4.

Source	r	ST	EQ	GT	Prob(f)
Temporal models					
Cruise	0.71206	500	1	0	0.002*
Month	2.13935	500	1	0	0.002*
Spatial models					
Station	2.06750	500	1	0	0.002*
Transect	1.80654	483	1	17	0.036 <sup>ns</sup>

The 24 km station recorded highest abundance of fish on both transects (Figure 3.2), although this was much more apparent on the CB transect than the LR transect. Much of this pattern was the result of large numbers of fish being captured at both 24 km stations in December. Samples at these stations were dominated by coral reef fishes (Table 3.5). Pomacentrids of the genus *Pomacentrus* were the most abundant taxa on all four nights (Figure 3.3). *Dischistodus* sp. were captured in higher numbers on the LR transect on the first night's sampling, but were almost absent by the second night. By contrast, *Dischistodus* was only present on the CB transect in the second

night of sampling. Other taxa, including *Epinephelus* spp. and *Lethrinus* spp. were captured in lower numbers on at least one occasion over the four nights. While the high numbers captured at both stations were largely due to a few abundant taxa, these samples also contained a numbers of taxa that were collected in very low numbers throughout the study. This is reflected by the large total number of taxa present in these samples. For instance, the 24 km station on the CB transect collected a total of 24 taxa, from some 14 families, in two nights of sampling.

Taxon	Total	Taxon	Total
Apogonidae	5	Pomacentridae (cont.)	
Blenniidae	4	Dischistodus sp.	81
Carangidae	2	Neopomacentrus spp.	63
Chaetodontidae	5	Pomacentrus spp.	936
Dactyliopteridae	2	P. coelestis	114
Gobiidae	1	Scombridae	
Labridae	1	Grammatorcynus sp.	2
Lethrinidae	55	Scomberomorus spp.	7
Mullidae	1	Thunnus sp.	9
Pomacentridae		Serranidae	14
Abudefduf sp.	11	Siganidae	31
Chromis sp.	19	Sphyraenidae	2
Chrysiptera sp.	3	Total	1368

**Table 3.5.** Total number of fish captured at the 24 km station of the CB transect on December 7 and December 10, 1988.

#### 3.3.3 Plankton nets from 1989

Cluster analysis of the 1989 plankton net data using a Bray-Curtis dissimilarity matrix and an UPGMA clustering strategy detected four main sample groups (Figure 3.4). The first split identified samples collected principally from October and November, on both transects, and almost exclusively from the 0 km station. Cluster two showed similar temporal affinities to cluster one, but was spread almost evenly across the three offshore stations, again on both transects. Cluster three was collected almost exclusively in November, from the 16 km and 32 km stations on both transects. Finally, samples from cluster four came from December, and largely from the three offshore stations.

Clustering by families revealed three major taxonomic groupings (Figure 3.5). The first grouping included apogonids, callionymids, gobiids, leiognathids and teraponids. This species group showed highest affinity with cluster one from the station-time cluster, which was in turn restricted

to inshore stations. Cluster two consisted of bothids, bregmacerotids, monacanthids, nemipterids, platycephalids, priacanthids and scorpaenids. This group was associated with sample clusters one and four, and from stations spanning the entire lagoon. Cluster three included carangids, clupeids, lutjanids, mullids, pomacentrids and scombrids. This species group was largely restricted to sample cluster four, from stations 16 -48 km from the coast.

Mantel's and partial Mantel's tests were used to more rigorously assess variability in the data over the range of spatio-temporal scales considered. These results indicate that there was significant variability over almost all spatio-temporal scales considered (Table 3.6). All main factors, except transect, were significant. The matrix containing station effects showed the highest correlation with the data matrix (r = 0.25133). Cruise and month showed similar correlations (r = 0.103 and r = 0.094 respectively), with transects not significantly correlated (r = 0.02281). Not surprisingly most first order interactions were also significant. The only non-significant interaction was the transect\*month term. Again the interaction terms emphasised the affinities of the data with station, and then month, effects.

	r	ST	EQ	GT	Prob(t)
Temporal					
Cruise	0.10343	500	1	0	0.002*
Month	0.09422	500	1	0	0.002*
Spatial	`				
Transect	0.02281	493	1	7	0.016 <sup>ns</sup>
Station	0.25133	500	1	0	0.002*
Interactions					
Month*station	0.1005	500	1	0	0.002*
Station*month	0.25365	500	1	0	0.002*
Month*transect	0.0944	500	1	0	0.002*
Transect*month	0.02368	494	1	6	0.014 <sup>ns</sup>
Transect*station	0.02641	498	1	2	0.006*
Station*transect	0.25186	500	1	0	0.002*

**Table 3.6.** Results of Mantel and partial Mantel tests against temporal and spatial models of variability in the numbers of fish captured in plankton nets in 1989. Legend as for Table 3.3.

Examination of Cramer values suggested that 6 taxa contributed most to sample groupings found in the UPGMA clustering. These taxa were, in descending order of Cramer values, gobiids, lutjanids, apogonids, clupeids, nemipterids and platycephalids. After residual analysis revealed that variances of these taxa could be considered homogeneous, a three factor ANOVA, with month, station and transect as main effects, was used to identify spatio-temporal scales over which these individual taxa were varying.

The family Gobiidae were distributed significantly differently among months and stations, although significant first order interations of month and station and transect and station suggested that the distribution patterns were complex (Table 3.7). These differences can be seen by examination of 3dimensional graphs of mean gobiid concentrations (i.e. 'cell means') plotted against station and month. The CB transect showed a consistent pattern in all three months of sampling (Figure 3.6). Gobiid larvae were found in high numbers at the inshore station, and in typically low numbers at all stations further offshore. Gobiid distributions on the LR transect were, however, more variable. In October, numbers were highest at the inshore station, very low at the 16 km station, and intermediate at the 32 and 48 km stations. In November, gobiid larvae were concentrated at the inshore station while in December maximum numbers were recorded at the 16 km station.

Lutjanids also exhibited significant effects of month and station, with the transect main effect non-significant (Table 3.7). In this case, however, all first order, and the single second order, interactions were also highly significant. Lutjanid larvae were taken in extremely high numbers in December (Figure 3.7). During this month, they were captured across the lagoon, although were more prevalent at the offshore stations on both transects. In October and November, numbers were much lower, and restricted almost entirely to the 32 km and 48 km stations.

Results of the ANOVA for apogonid larvae found that month was the only significant main effect (Table 3.7). The presence of 2 significant first order interactions (month\*station and transect\*station) and a significant second order interaction meant, however, that this effect could not be interpreted in isolation. Apogonid larvae were, in fact, distributed relatively homogeneously across months, stations and transects (Figure 3.8). A single peak in abundance at the 0 km station in November on the CB transect appeared to account for a considerable amount of the variance.

**Table 3.7.** Summary table of three factor ANOVA for six families of larval fishes collected in plankton tows from the central Great Barrier Reef lagoon. \* = significant, ns = not significant with  $\alpha$  = 0.05.

Source	MS	F value	Prob
Gobiidae			
Month	682610	7.69	0.0007*
Transect	29445.9	0.33	0.5656 <sup>ns</sup>
Station	264853	29.8	0.001*
Month*transect	58618	0.66	0.5184 <sup>ns</sup>
Month*station	400074	4.51	0.0003*
Transect*station	259602	2.92	0.0363*
Month*transect*station	115221	1.3	0.2625 <sup>ns</sup>
Lutianidae			
Month	374548	239	0.0001*
Transect	376	0.24	0.6243 <sup>ns</sup>
Station	55724	35.7	0.0001*
Month*transect	731	0.47	0.6273 <sup>ns</sup>
Month*station	22755	14.6	0.0001*
Transect*station	128752	82.4	0.0001*
Month*transect*station	65777	42.1	0.0001*
Apogonidae			
Month	38581	20.2	0.0001*
Transect	3148.1	1.64	0.2019 <sup>ns</sup>
Station	3451.3	1.8	0 149705
Month*transect	1547.6	0.81	0.1407
Month*station	6813.2	3.56	0.0027*
Transect*station	21719	11 4	0.0001*
Month*transect*station	8324.8	4.35	0.0001
Clupeidae	0024.0	4.00	0.0000
Month	174034	68.5	0.0001*
Transect	32587	12.8	0.0005*
Station	14505	5.71	0.001*
Month*transect	46300	18.2	0.0001*
Month*station	14908	5.87	0.0001*
Transect*station	48154	19	0.0001*
Month*transect*station	19258	7.58	0.0001*
Nemipteridae			
Month	50380	115	0.0001*
Transect	121.5	0.28	0.5988 <sup>ns</sup>
Station	12083	27.67	0.0001*
Month*transect	1758.3	4.03	0.0201*
Month*station	5040	11.5	0.0001*
Transect*station	20104	46	0.0001*
Month*transect*station	13387	30.7	0.0001*
Platycephalidae			
Month	6490.9	58.1	0.0001*
Transect	9.92	0.09	0.7661 <sup>ns</sup>
Station	1610	14.4	0.0001*
Month*transect	40.7	0.37	0.6949 <sup>ns</sup>
Month*station	1188	10.6	0.0001*
Transect*station	963	8.6	0.0001*
Month*transect*station	974	8.7	0.0001*

Concentrations of clupeid larvae were, in contrast to the apogonids, extremely patchy. This is reflected by the fact that all main effect and interaction terms in the ANOVA were highly significant (Table 3.7). Larvae were particularly abundant in December on the CB transect but, unlike the lutjanids, this trend was not apparent on the LR transect in this month (Figure 3.9). The 16km station showed the lowest numbers in all months on the LR transect. Again, however, this pattern was not seen on the CB transect.

All main effects and interaction terms were significant for nemipterid larvae, with the exception of the effect of transect (Table 3.7). High concentrations were present across several stations in December, on both transects. On the CB transect, numbers were highest inshore, while on the LR transect numbers peaked at the 16 and 32 km stations (Fig. 3.10). Concentrations were reasonably even across all stations in October and November, although they were slightly higher at the 2 inshore stations on the CB transect.

The transect main effect, and the month\*transect interaction, were the only non-significant results from ANOVA of larval platycephalid concentrations (Table 3.7). Platycephalids were captured in high numbers in December (Figure 3.11). There was some coherence between transects during this month with maximum concentrations at inshore stations. The LR transect recorded peak numbers at the 16km station, with high numbers at both 0 km and 32 km stations. Numbers on the CB transect were highest at the 0 km station, with a gradient out to the 48 km station. Concentrations in October and November showed little recognisable patterns, either across stations or transects.

#### 3.3.4 Light traps from 1989

Light trap data were subjected to the same mulivariate analyses as those outlined above for the net tow samples. Cluster analysis of the Bray-Curtis dissimilarity matrix generated from the family/sample data matrix revealed 4 distinct groupings (Figure 3.12). Clusters one and two were made up mostly from samples taken during October and November respectively, almost equally on both transects, and spread relatively evenly across all stations. Cluster three represented samples from the 16 km station on the

LR transect in October, along with three samples from the same station in November. Finally, samples from cluster four were taken in December, on both transects, and from the three offshore stations.

Clustering by families also revealed four major groupings (Figure 3.13). The first family grouping consisted of apogonids, clupeids, engraulids and scombrids. This group was largely confined to clusters one and two of the sample dendrogram, which was distributed ubiquitously across stations and transects. The second family group consisted of a single family, the Blenniidae, and contributed mainly to sample cluster one. Sample cluster three was also a single family grouping of the family Dactylopteridae, and was restricted to the 16, 32 and 48 km stations in December. Finally, family cluster four was made up of atherinids, lethrinids, pomacentrids and mullids. This group was found almost exclusively within sample cluster three, from the 16 km station on the LR transect in October.

Mantel's and partial Mantels tests were used to examine spatio-temporal variability in light traps catches in more detail (Table 3.8). Models incorporating the four main effects were all significant, although correlations were higher with the temporal models (r= 0.12983 for the cruise effect, and r = 0.19587 for the month effect) than spatial models (r = 0.06657 effect of transect, and r = 0.09998 for effects of station). All first order interactions were also significant. Again, however, models including the month effect were more highly correlated than models with only spatial components of transect and station.

Cramer values from the UPGMA clustering was examined to identify the six individual families contributing most variance to the data matrix. These families were, in order of decreasing Cramer values, Pomacentridae, Lethrinidae, Mullidae, Dactylopteridae, Clupeidae and Engraulidae. Variances of all families were intractably heterogeneous after a number of possible transformations, and hence the three factor ANOVAs used for the coincident net tow samples could not be employed. Interpretation of these results were based instead on three-dimensional 'cell mean' graphs plotting light trap numbers versus month and station, for each transect. These plots were identical to those produced for the net tow data in the proceeding section.

	r	ST	EQ	GT	Prob(t)
Temporal					
Cruise	0.12983	500	1	0	0.002*
Month	0.19587	500	1	0	0.002*
Spatial					
Transect	0.06657	500	1	0	0.002*
Station	0.09998	500	1	0	0.002*
Interactions					
Month*station	0.19631	500	1	0	0.002*
Station*month	0.10085	500	1	0	0.002*
Month*transect	0.19582	500	1	0	0.002*
Transect*month	0.06640	500	1	0	0.002*
Transect*station	0.05677	500	1	0	0.002*
Station*transect	0.10070	500	1	0	0.002*

**Table 3.8.** Results of Mantel and partial Mantel tests against temporal and spatial models of variability in the patterns of juvenile fish distributions as measured by the light traps in 1989. Legend as for Table 3.3.

Pomacentrids were numerically dominant in the light trap catch. They were, however, only captured in high numbers in October on the LR transect, at the 16km station (Figure 3.14). Pomacentrids were virtually absent from the CB transect throughout the sampling period. Lethrinids showed an almost identical pattern, with extremely high numbers at the 16 km station on the LR transect in October (Figure 3.15). Very few were captured on any other sampling occasion. Mullid abundance also peaked at this same place in time, although smaller numbers were captured over all three months, and across most stations (Figure 3.16). Dactylopterids were restricted temporally to samples from December (Figure 3.17). Unlike the preceeding taxa, however, they were not concentrated at any particular station. Numbers were relatively high across the three offshore stations on the LR transect, and across all stations on the CB transect. Clupeids and engraulids were captured predominantly at inshore stations (Figure 3.18).

High abundance of a number of taxa were recorded at the 16 km station on the LR transect in October. Indeed the total of 2277 fish from this single station represented 60% of the total catch in 1989; in the case of the family Lethrinidae, this figure was greater than 90%. Numbers of the principal taxa were variable, however, on each of the three cruises within October. *Pomacentrus* spp. were the most numerous taxa, and were captured in high numbers on all three cruises (Figure 3.20). Lethrinids were extrememly abundant on the second cruise, with much lower numbers collected on cruises one and three. *Chromis* sp. showed a similar pattern to the lethrinids, with highest abundance on cruise two. Mullids, however, were captured in progressively higher numbers throughout the sampling period. While these four taxa dominated numbers numerically, a number of rare taxa were also taken at the 16 km station during October (Table 3.9). Chaetodontids, gerreids and monacanthids were all represented in samples from this time.

Taxon	Total	Taxon	Total
Apogonidae	4	Pomacentridae (cont.)	
Atherinidae	9	Dischistodus	1
Blenniidae	1	Neopomacentrus	4
Bregmacerotidae	2	Plectroglyphidodon	9
Carangidae	10	Pomacentrus	940
Chaetodontidae	3	Pristotis jerdoni	11
Clupeidae	5	Scombridae	
Engraulidae	2	Scomberomorus	1
Gerreidae	5	Scorpaenidae	14
Lethrinidae		Siganidae	4
Lethrinus	838	Syngnathidae	9
Monacanthidae	6	Synodontidae	4
Mullidae	134	Syphraenidae	1
Pomacentridae		Tetraodontidae	7
Chromis	253	Total	2277

 Table 3.9.
 Total number of fish by taxon collected at the 16 km station on the LR transect in

 October, 1989.

## 3.3.5 Comparison of towed net and light trap distributions

Comparison of distribution patterns of larval and juvenile fishes collected by towed nets and light traps was hampered by two factors. Firstly, taxonomic differences in catches between the two techniques meant that only three taxa, clupeids, pomacentrids and mullids, were captured in sufficient numbers by both techniques for any meaningful comparison to be made. Secondly, heterogeneous variances from the light trap data were such that ANOVA could not be used to quantify spatio-temporal variability from the light trap catches. Therefore, comparisons were necessarily qualitative, based on the three-dimensional plots of cell means.

Larval clupeids captured in plankton tows were taken at offshore stations on the LR transect; reasonable numbers at the inshore station were only seen in December (Figure 3.9). Clupeids collected in light traps on this transect were dominated by collections at the inshore station in October, with low numbers across all stations in November and December (Figure 3.18). On the CB transect, net collections showed considerable variability among months and across stations. Numbers were low at the inshore station in October and November, but were high across the 0, 16 and 32 km stations in December. Light trap catches on this transect were lower than on the LR transect, and were spatially restricted to the 0 km and 16 km stations.

Pomacentrid larvae captured in plankton nets were relatively uniformly distributed among months, and across the three offshore stations, on the LR transect (Fig. 3.21). Pomacentrids captured in the light traps on this transect were, however, restricted almost entirely to the 16 km station in October (Figure 3.14). Distributions of larvae collected in plankton nets were more heterogeneous on the CB transect among months. In October, numbers were low, and uniform, across stations. In November, larvae were restricted to the 2 offshore stations. Finally, numbers were relatively high across all stations in December, with maximum abundance at the 32 km station. Very few pomacentrids were taken in the light traps on this transect throughout the sampling period.

Larval mullids from the net tows on the LR transect were distributed remarkably similarly to the pomacentrids (Figure 3.22). Larvae were distributed reasonably evenly across the three offshore stations, but were virtually absent from the inshore station. Mullids captured in the light traps were largely restricted to the 16 km station in October, although small numbers were taken at the inshore station in all three months (Figure 3.16). Distribution patterns were different on the CB transect. Larval abundance was more uniform, with no obvious effect of station. Highest numbers were taken in December, at the 0 and 16 km stations. Mullids taken in the light traps were taken in low, but again reasonably uniform, numbers among months and across stations.

## 3.4 DISCUSSION

This study was designed to examine variability in the distribution patterns of larval fishes across a range of spatial and temporal scales. Plankton distributions are inherently patchy (Mackas *et al.* 1985), and the number of significant main effects and interaction terms in both multivariate and univariate tests demonstrated that ichthyoplankton distributions in the central GBR lagoon are characterised by variability over the entire range of spatio-temporal scales sampled in the present study. While these results emphasised the complexity of larval distribution patterns, the analyses did serve to highlight the spatio-temporal scales at which most of the variance in the data sets resided. This in turn suggested the scales over which physical and biological processes generating the observed distribution patterns were likely to be operating over (Legendre and Demers 1984).

Net tows from 1989 revealed a relatively stable spatial pattern, with a distinctive inshore ichthyoplankton community captured at the inshore station, a lagoonal community found across all stations, and an offshore community taken from all stations except the inshore locality. Milward and Hartwick (1986) noted the presence of three distinct family groupings across the central GBR lagoon, corresponding to nearshore, cross-lagoon and While that study was based solely on outer-lagoon communities. presence/absence data, the present study largely confirms their results. While the nearshore larval fish community was restricted to the 0 km station in 1989, the distribution patterns of total fish larvae from 1988 suggests that this community may have been present at the 8 km station also. This trend is shown most clearly on the CB transect, where numbers at the 0 and 8 km stations show reasonable coherence, while the 16 and 24 km stations appear to be varying independently of the 2 inshore stations. Milward and Hartwick (1986) also suggested that the demarcation between inshore and offshore family groups occurred at approximately 10 km from the coast.

Several studies in tropical Australian waters have found strong cross-shelf gradients in distribution patterns of larval fishes using classification analyses similar to the one employed in the present study. Young *et al.* (1986) found some degree of separation between inner-shelf and mid-shelf samples from transects across the continental shelf off northwestern Australia, although in several months inner and mid-shelf stations clustered together. They did note a major discontinuity in ichthyoplankton composition just inshore of the shelf break. Leis and Goldman (1987) could find no consistent pattern on a cross-shelf transect that spanned the mid to outer shelf near Lizard Island, in the northern GBR. Finally Williams *et al.* (1988) also failed to find clear cross-shelf trends in larval distributions on a transect that also included mid to outer shelf stations in the central GBR. One may conclude from these studies that the major demarcation in larval fish community structure in the GBR region is between inshore and mid-and outer-shelf waters. There may be, however, differences between mid

and outer shelf communities that have yet to be detected. Taxonomic grouping at the family level means that more subtle, intra-family differences have necessarily been obscured. Williams *et al.* (1988) also noted that reef fish families that did show clear patterns in adult distributions across the shelf were rare to absent in their collections. Clearly more information on species-specific distribution patterns are needed.

Longshore differences in larval fish distributions between transects were generally not as strong as the cross-shelf gradients among stations. However, a number of taxa did show similar patterns that indicated there were differences in larval distributions on the two transects. Gobiids larvae were concentrated at the 0 km station on the CB transect, with very few larvae captured at any of the other stations. On the LR transect this pattern was not nearly as strong with considerably more variability among months. Net tow data from 1988 confirms this impression as there was stronger cross-shelf gradient, with high larval concentrations inshore, along the 24 km of the CB transect than on the LR transect. Lutjanids, clupeids, nemipterids, and platycephalids were all characterised as offshore larvae in the cluster analysis of 1989 net tow data. All these taxa were, however, picked up in reasonable numbers at the 0 km station on the CB transect but not on the LR transect. Pomacentrid and mullid larvae showed a similar pattern. This suggests that coastal water was restricted closer to the coast on the CB transect, and conversely that offshore water may channeled closer to Cape Bowling Green than Cape Clevelend.

While the spatial component of variation in the net tow data from 1989 was dominant, there was also a significant temporal signal. In December, for instance, a number of taxa showed large increases at offshore stations on both transects, including lutjanids, nemipterids, pomacentrids and mullids. The coherence of taxa argues that this was the result of an event acting over synoptic scales at least 50 km in both cross-shelf and alongshore directions. It is possible that events in the planktonic environment affected a number of different taxa in a similar way. Increased primary productivity over these scales have been documented due to an intrusion of cold, nutrient-rich water from the Coral Sea (Furnas and Mitchell 1987). Enhanced primary production may also lead to increased zooplankton abundances and hence higher larval survival rates. The other major source of nutrient-rich water in the central GBR lagoon comes from occasional large freshwater discharge events (Wolanski and Jones 1981). Flow records from the Burdekin River, which is the largest source of freshwater into the central GBR lagoon (Sammarco and Crenshaw 1984), showed no significant freshwater discharge at this time. It is perhaps more likely that that this effect may have been the result of spawning activities over these spatial scales, although there is surprisingly little known about the spawning habits of shorefishes in this region.

Distribution patterns of small fishes captured in the light traps were much more transitory than those of the plankton nets. Catches in both years were dominated by samples from a single station, in December 1988 and October 1989. Studies of settlement patterns of coral reef fishes have led to the speculation that larvae may be distributed in large, meso-scale patches (Victor 1984, Williams 1986, Doherty 1987b). The fact that only one patch was found in each year suggests such patches are a relatively rare occurrence, albeit numerically extremely important. Pomacentrid larvae were the main component of the catch in both years. A number of rare taxa, including epinephiline serranids, siganids and chaetodontids were also captured along with the abundant taxa. This is reflected in the large number of taxa from these samples. In 1988, the 24 km station on the CB transect collected a total of 24 taxa, from some 14 families, in 2 nights of sampling. Similarly in 1989 the 16 km station on the LR transect also collected 24 taxa, from 20 families. Given that these family lists include both pelagic and demersal spawners (Thresher 1984), it seems unlikely that the patches were the result of a single, multi-specific spawning event. Rather, the patches appear to be formed by either active aggregation of larvae (i.e. a behavioural response), or passive accumulation in some oceanographic feature.

Unfortunately logistic constraints meant that the spatial dimensions of the patches determined from the light trap data could not be mapped quasisynoptically (eg Incze *et al.* 1989). Patch sizes of reef fish larvae have been estimated to be of the vicinity of 30-50 km from inferences from settlement studies (Victor 1984, Williams 1986, Doherty 1987b). Only one study has provided a direct measurement of the patch dimensions of reef fish larvae from ichthyoplankton tows. Williams and English (1992) concluded that a patch of larvae off Myrmidon Reef, Townsville was at least 7 km wide. In 1988, there was some evidence that the long-shore dimension of the patch was at least of the order of 50 km, given that numbers were elevated at the 24 km stations on both the LR and CB transects. This estimate is, however, unavoidably confounded by advective processes. In the central GBR lagoon long-shore currents may run at up to 0.4 m.sec<sup>-1</sup>, which means that neutrally bouyant particles may travel up to 50 km in a single 24 h period (Wolanski and Bennett 1983). There was some indication that the patch was moving progressively southeast, as Dischistodus larvae were captured on the LR transect on December 6 1988, and then in high numbers on the CB transect on December 10. Winds were light to moderate from the north quadrant during this time (Australian Institute of Marine Science unpublished data from Cape Bowling Green weather station from 1988), and currents in the middle of the lagoon were therefore almost certainly dominated by longshore drift to the southeast (King and Wolanski 1992). In 1989, the patch was confined to a single station, so we can only say with confidence that patch dimensions were less than 32 km in the cross-shelf direction. It was perhaps surprising that the patch was not detected subsequently on the CB transect, given that winds were favourable for transport in this direction (Australian Institute of Marine Science unpublished data from Cape Bowling Green weather station from 1989). This suggested that the cross-shelf dimension of such patches may be relatively small, and indeed Parslow and Gabric (1989) found in a modelling study that parcels of neutrally-buoyant particles in this region tended to form streaks that aligned parallel to prevailing longshore currents. Synoptic mapping of patch dimensions using light trap arrays would appear to be the only way to determine patch size in a definitive manner.

Any comparison of the distribution patterns of net tows and light traps at a community level is unavoidably confounded by the different taxonomic composition of the catch from the two techniques (Choat *et al.* 1993, chapter 2). Three taxa were, however, collected in large enough numbers for a direct comparison to be made. Distribution patterns of larval clupeids, pomacentrids and mullids from net collections were similar. Larvae were associated with the offshore planktonic assemblage, and were most abundant at these stations in December. Data from the light traps suggested that, at the size ranges captured by this technique, pomacentrids and mullids were also distributed similarly. Both families were caught in high numbers at the 16 km station on the LR transect in October. The differences in distribution patterns between techniques suggests that the physical or biological processes generating these patterns are size, or stage, dependent.

Within size (or stage) groupings, small pomacentrids and mullids appear to be influenced by similar physical processes, or at least processes acting over similar spatio-temporal scales (Denman and Powell 1984).

Clupeids in the light traps were captured almost exclusively in nearshore waters, while smaller larvae in plankton nets were taken at offshore stations. Mixed-species schools of juvenile clupeids, includingAmblygaster sirm and Sardinella gibbosa, are locally abundant in nearshore waters along the coast of Townsville (Williams and Cappo 1990), although spawning in A. sirm and S. gibbosa occurs in offshore waters (M. Cappo and D.McB. Williams, Australian Institute of Marine Science, unpublished data). This indicates that larvae are migrating from mid and outer lagoon stations to juvenile inshore nursery grounds at approximately the size at which they become vulnerable to capture in the light traps at around 14-15 mm SL. A pattern of offshore spawning coupled with migration of larvae to inshore nursery grounds has been documented for the Atlantic menhaden, Brevortia tyrannus, along the east coast of the United States and for the gulf menhaden, Brevortia patronus, in the Gulf of Mexico. Atlantic menhaden enter nearshore waters ages at sizes ranging from 18-22 mm in length (Nelson et al. 1977), while gulf menhaden larvae enter estuaries when they are 12 to 25 mm in length (Sogard et al. 1989). Shaw et al. (1985b) suggested a passive mechanism for this inshore migration that included longshore advection, entrainment into the coastal boundary layer, and finally transport into nearshore waters by the seasonal rise of sea level in spring. There is no evidence that a similar mechanism may be operating in central GBR lagoon, as modelling studies suggest that cross-shelf transport in this area is minimal (King and Wolanski 1992). Directed swimming by postlarvae would seem to be a more plausible mechanism for the inshore migration.

Recent advances in our understanding of the current flows inside the central GBR lagoon may give some insight into the processes generating distribution patterns of small fishes in the central GBR lagoon. King and Wolanski (1992) argued that a strong velocity shear existed across the lagoon under all wind conditions. This shear zone acts to inhibit water exchange from nearshore areas to the mid and outer lagoon as inshore water remains coastally trapped. This lack of significant cross-shelf mixing across the inner half of the lagoon would seem the most parsimonious explanation for the
consistent differences in larval fish community structure between the 0 km station and all other lagoon stations. Interestingly the model does suggest that offshore water moves closer to the coast on the CB transect than on the LR transect, which is consistent with the inshore station on the CB transect having higher numbers of larvae with offshore affinities as determined from the cluster analyses.

Fish captured in the light traps showed very different spatio-temporal variability to the net collections, and these distribution patterns are presumably generated by physical oceanographic phenomena acting over different spatial and temporal scales. King and Wolanski (1992) noted the presence in model simulations of a linear front between coastal and lagoon water masses, at approximately 12-15 km from the coast, under light southeasterly winds. This coincides approximately with the 16 km station where the patch of larvae collected in light traps was found in 1989. It is unlikely, however, that the same feature generated the patch in 1988, which was located some 24 km from the coast. If indeed catches were related to this front, fish may have concentrated there due to passive accumulation as the frontal zone is characterized by low current velocities. The observation, however, that smaller larvae captured in the plankton nets were not aggregated in this vicinity argues that some active orientation by the larger fish captured by the light traps may have been occurring.

The possible presence of a frontal zone between coastal and offshore water masses provided a convenient explanation for the light trap catches in 1989. Without simultaneous measurements of the physical environment, however, such arguments remain speculative. The following chapter examines these questions, utilizing oceanographic data collected simultaneously, and over the same spatial scales, as the distribution patterns of small fish were monitored here.







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**Figure 3.2.** Mean catches (+/- standard errors) of small fish from light traps at stations across the central GBR lagoon on LR transect (top) and CB transect (bottom), October to December 1988. Note different z axis scales between transects.



Figure 3.3. Mean numbers (+/- standard errors) of abundant taxa captured by light traps at the 24 km stations in December 1988, along with mean number of taxa captured (last bar). Top: LR transect, 6 December (solid bars) and 8 December (hatched bars). Bottom: CB transect, 7 December (solid bars) and December 10 (hatched bars).



**Figure 3.4.** Summary of UPGMA cluster analysis for net tow data from 1989, showing relationship of temporal and spatial factors to cluster groupings. The symbols represent the percentage of a sample group which occur in each month, on each transect, and among stations. Percentages within each of these factors add to 100%. The arrow indicates direction in which these percentages were summed.







Figure 3.6. Gobiidae. Mean concentrations of larvae (+/- standard errors) from net tows at stations across the central GBR lagoon on the LR transect (top) and CB transect (bottom), October to December 1989.



Figure 3.7. Lutjanidae. Mean concentrations of larvae (+/- standard errors) from net tows at stations across the central GBR lagoon on the LR transect (top) and CB transect (bottom), October to December 1989.







Figure 3.9. Clupeidae. Mean concentrations of larvae (+/- standard errors) from net tows at stations across the central GBR lagoon on the LR transect (top) and CB transect (bottom), October to December 1989.







Figure 3.11. Platycephalidae. Mean concentrations of larvae (+/- standard errors) from net tows at stations across the central GBR lagoon on the LR transect (top) and CB transect (bottom), October to December 1989.



**Figure 3.12.** Summary of UPGMA cluster analysis for light trap data from 1989, showing relationship of temporal and spatial factors to cluster groupings. The symbols represent the percentage of a sample group which occur in each month, on each transect, and among stations. Percentages within each of these factors add to 100%. The arrow indicates direction in which these percentages were summed.







































**Figure 3.22.** Mullidae. Mean concentrations of larvae (+/- standard errors) from net tows at stations across the central GBR lagoon on the LR transect (top) and CB transect (bottom), October to December 1989.

## Chapter 4

# Relationships between remotely-sensed ocean water properties and the distribution patterns of small fish in the central Great Barrier Reef lagoon

## 4.1 INTRODUCTION

Distribution patterns of planktonic organisms are characteristically heterogeneous over a wide range of spatio-temporal scales (Legendre and Demers 1984, Mackas *et al.* 1985). Much of this inherent patchiness appears to driven by the response of plankters to the physical environment (Denman and Powell 1984). Numerous studies have documented the influence of oceanographic processes on the distribution and abundance of organisms that inhabit neritic and oceanic waters (Le Fevre 1986). These studies have encompassed an impressive range of scales, from 1' and 10's of meters associated with features such as tidal fronts (Dustan and Pickney 1989) and internal waves (Shanks 1983, Kingsford and Choat 1986), to 'meso' spatio-temporal scales associated with coastal fronts, eddies and jets (eg Thomas and Emery 1988, Thomas 1992, Thomson *et al.* 1992), through to basin-wide phenomena indicative of large-scale movements of water masses (Klimley and Butler 1988).

Our ability to examine the coupling of biological and physical processes on meso and small scales has recently increased dramatically, due to the development of satellite imagery (Hood *et al.* 1990). Indeed, the ability to collect truly synoptic information on oceanographic features from satellites has fundamentally changed the way we view the ocean environment (Legeckis 1978). Ship-based studies had only been able to document oceanographic features at a quasi-synoptic level, with spatial coverage that was necessarily limited by the relatively slow speeds at which research vessels can travel. Such approaches could never have revealed the temporal complexity of features such as the Gulf Stream and the California Current that have been so graphically displayed by sea-surface temperature images derived from satellites (Kelly 1985, Hood *et al.* 1990). An array of satellites have been used to derive sea-surface temperature and water 'colour' maps of the ocean. The most frequently used technique has taken advantage of the infrared sensor on NOAA's VHRR and AVHRR polar orbitting satellite. Maps of sea-surface temperatures can be derived with a pixel size ('resolution') of 1.1 km<sup>2</sup>. Coverage is available approximately every 12 hours. While this temporal coverage is not as complete as available with the geo-stationary GEOS satellite (Maul et al. 1984), the increased resolution and spatial coverage of the NOAA/AVHRR satellite has led to this tool been widely used in oceanographic and fisheries applications (Njoku et al. 1985). The coastal zone color scanner (CZCS) on the Nimbus 7 satellite provided information on water colour in the visible range. The narrow band widths (20 nm for the 443 centre wavelength of channel 1) of each of the sensors enabled algorithms to be developed that related the ratio of channels 1 and 3 to the amount of chlorophyll a in the surface waters (Robinson 1985). Unfortunately the Nimbus 7 satellite is no longer operational, and similar information will not be available until the SeaWiFS satellite comes on line in mid 1993 (Wickland 1991). Finally, the multi-spectral scanner (MSS) and thematic mapper (TM) sensors on the LANDSAT satellites also have considerable potential for oceanographic studies. Features include increased spatial resolution over both AVHRR and CZCS, and an impressive array of channels in visible wavelengths. However, the relatively long periods between overpasses (approximately 14 days) has limited the utility of this scanner for marine applications that require higher temporal resolution (but see Carpenter and Thomson 1984).

While satellite imagery has proved extremely useful in temperate regions, applications in tropical waters have been less frequent. There are several reasons for this lack of attention. Firstly, tropical areas often have more moisture in the atmosphere than temperate regions (Maul *et al.* 1984). All satellites require reasonably clear skies for useful imaging. A second reason is the isothermal nature of many tropical waters (e.g. Muller-Karger *et al.* 1991). The sea-surface maps that have proven so useful in characterizing the Gulf Stream (Robinson 1985), California current (Mooers and Robinson 1984) and Angola-Benguela current systems (Meeuwis and Lutjeharms 1990) have provided comparatively little information on flows in tropical regions. Finally, financial wealth, and research institutions, are distributed disproportionately away from the tropics, and consequently interest in tropical waters has lagged some way behind that in higher latitudes.

The objective of this chapter is to examine relationships between remotelysensed measurements of sea-surface temperature and water colour and the distribution patterns of larval and juvenile fishes within the central GBR lagoon. A number of studies have combined biological sampling (e.g. Shannon et al. 1984, Thomas and Emery 1988, Galat and Verdin 1989, McGowan and Richards 1989, Murdoch et al. 1990, Thomas 1992) or fisheries statistics (e.g. Laurs et al. 1984, Fiedler and Bernard 1987, Herron et al. 1989, Healey et al. 1990, Power and May 1991, Thomson et al. 1992) with real-time satellite imagery to gain insight into the coupling of biological and physical processes. I hoped to be able to relate larval and juvenile fish catches with specific hydrographic features detectable in processed images from the NOAA/AVHRR satellite. Water circulation within the central GBR lagoon has also been modelled extensively (Dight et al. 1988, Wolanski and Ridd 1990, King and Wolanski 1992). These studies may provide verification for the existence and persistence of features detected in the satellite imagery. The following specific questions were asked:

1. Are there discernable features in NOAA/AVHRR sea-surface temperature and water colour images of the central GBR lagoon?

2. If so, are these features predicted by models of water circulation patterns in this area?

3. Finally, do these features appear to be varying over similar spatiotemporal scales as the larval and juvenile fish distribution patterns outlined in the previous chapter?

## 4.2 METHODS AND MATERIALS

#### 4.2.1 Data acquisition

A series of NOAA/AVHRR images were archived during the sampling periods from October to December 1989. Scenes were geometrically and radiometrically corrected using an ARLUNYA workstation. Channel 4 (10.5 to 11.3  $\mu$ m) and Channel 5 (11.5 to 12.5  $\mu$ m) radiances were converted to sea-surface temperatures (hereafter SST) using a radiometric algorithm based on the procedure of Lauritson *et al.* (1979). Channel 1 (580-680 $\mu$ m),

corresponding to blue-green light, was also examined. There was no way to correct the AVHRR channel 1 band for Rayleigh and aerosol scattering as can be done for CZCS and LANDSAT images (Robinson 1985). It was assumed, therefore, that these parameters did not change significantly across the area of interest in each individual image. Given that this area was reasonably small (a linear transect approximately 50 km long), this seemed reasonable.

Subsequent enhancement was carried out using IDRISI (1991). Land and areas of high cloud cover were initially masked black. Lighter areas of potential cloud cover were not masked, as this process is necessarily subjective. Both SST and visible channels were then false-colour enhanced. The scaling factor was, however, kept constant so that images could be usefully compared through time.

A number of workers have noted the influence of meteorological forcing on current patterns in the GBR region (e.g. Wolanski and Bennett 1983, Wolanski and Ridd 1990, King and Wolanski 1992). Wind data are available through weather stations maintained by the Australian Institute of Marine Science. Wind speed and direction were recorded at a station on Cape Bowling Green throughout the sampling period, and these data were accessed to help interpret features observed in the satellite imagery.

## 4.2.2. Effects of bathymetry

The penetration of electromagnetic radiation in water is a function of wavelength, as light of high wavelengths is able to penetrate to greater depths that those of low wavelegths. This has important ramifications for remotely-sensed data. Channel 4 and 5 are both low frequency channels, and penetrate less than a millimeter into ocean waters (Robinson 1985). Bathymetry therefore has no significant effect on the measurement of sea surface temperatures. Visible radiance registered by channel 1 does, however, have significant penetrance in ocean waters. Signals from this channel could not be unambiguously attributed to changes in water colour without first accounting for bathymetric effects. It was not practicable to remove bathymetry from the entire image. Instead, depth-free values were calculated across the same transects at which larval and juvenile fish distributions were sampled in the preceding two chapters (Figure 2.1).

Depth was removed from the channel 1 signal using the following technique. The radiance signal measured by the satellite sensor,  $(R_i)$ , consists of the signal due to the ocean colour  $(R_c)$  plus the bottom reflectance  $(R_b)$ , i.e.

$$R_i = R_c + R_b$$

If we assume that bottom reflectance is even across the transect then we can model this reflectance based upon water depth (Z) and the water attentuation coefficient using an exponential decay function (Jupp and Mayo 1984)

$$R_b \alpha exp(-2k_d * Z)$$

It follows that bottom reflectance  $(R_b)$  is given by

$$R_{b} = R_{i} * exp(-2k_{d} * Z)$$

and that the amount of visible radiance corrected for bottom reflectance (Rc) is given by

$$R_{c} = R_{i} - (R_{i} * exp(-2k_{d} * Z))$$

The water attenuation coefficient can be determined by examinating the attentuaton of the signal with depth (Figure 4.1). The depth at which the bottom is no longer 'seen' by the satellite is equivalent to a secchi disk reading  $(Z_{sd})$ . The water attenuation coefficient  $(k_d)$  is related to  $Z_{sd}$  according to the following equation (Megard and Berman 1989);

$$k_d = 1.5/\mathbf{Z}_{sd}$$

Water depth was estimated by firstly determining mean low water values across the transect from the surveyed chart of the area. The water depth was then calculated by using tide tables to determine the height above mean low water at the exact time of the satellite overpass.

Once a 'depth-free' signal was obtained, values were standardized to maximize gradients in water colour across the scenes.

This was achieved by standardizing depth-free values using the following formula:

$$R_{s} = (R_{i} - R_{min} / R_{max} - R_{min}) * 100$$

where  $R_s =$ standardized 'depth-free' value

$$R_i$$
 = 'depth-free' water colour value

 $R_{max}$  = maximum 'depth-free' value across transect

Finally, these values were then plotted across each of the transects that were sampled for larval and juvenile fish in the proceeding chapter. Sampling methodology used to collect the small fish is as described in Chapter 3.

## 4.3 RESULTS

#### 4.3.1 Sea-surface temperatures

A total of five usable images were collected during October through December, 1989. While 15 images were archived, excessive cloud-cover on 10 of these images prevented their use. Usable scenes were captured on 27 September, 29 September, 3 October, 30 October and 10 December. Seasurface temperatures were initially examined for gradients across the lagoon. These images suggested that the central GBR lagoon was reasonably isothermal throughout the sampling period. Three representative images are presented here.

On 27 September a broad tongue of warm water was visible through the northern part of the central GBR, ending at the Whitsunday Islands (Figure 4.2a). A close up view of the sampling area showed a band of warmer water trapped within Cleveland Bay and Bowling Green Bay (Figure 4.2b), but no differentiation in SST across either LR or CB transects. By 3 October, the tongue of warmer water appeared to have moved slightly south, and had become more obtuse (Figure 4.3a). Warm water was no longer visible within the bays, and again there was no variation in SST across the lagoon

(Figure 4.3b). On 30 October, two small parcels of warm water were evident, one off Cape Bowling Green, and a second slightly further to the south (Figure 4.4a). The LR transect was essentially isothemal, while the outer half of the CB transect came into contact with the northern edge of warm water parcel (Figure 4.4b).

#### 4.3.2 Channel 1 - visible

Maps of false-water colour were produced for each of the five overpasses used in the SST analyses. A strong gradient in turbidity was found across both transects in all images (Figures 4.5 to 4.9). In order to compare and contrast the position of turbid, coastal waters and clear lagoon waters among images the latter water mass was defined arbitrarily as the last two colours on the false colour scale. Depth-corrected data also showed that turbid water was distributed along the coast, with clearer water varying distances from the coast. In these plots the distance from shore at which false water colour first reached the lowest value along each transect was taken to be the edge of the coastal water mass.

While the image from 27 September had considerable cloud cover, the inner lagoon was cloud-free across both transects (Figure 4.5a,b). Turbid water was located close to the coast, within Cleveland Bay and Bowling Green Bay. There was a rapid increase in water clarity across the inner shelf, and indeed lagoon water appeared to be little more than a few kilometers offshore along either LR or CB transects. Cloud cover was also high in the image from 29 September (Figure 4.6a). While only the inner lagoon was visible coastal water appeared to extend slighly further seaward than in the image on 27 September (Figure 4.6b). The final image from October was the clearest from this month (Figure 4.7a). In this scene coastal water was again trapped along the coast (Figure 4.7b). However, coastal waters appeared to extend further offshore, at distances between eight and 11 km along the transects, than in either of the two previous images. In November, the single usable image from this time was exceptionally clear (Figure 4.8a). Turbid water was again found along the coast. In this image the edge of the coastal water mass appeared to be approximately six to eight km from the coast. Finally, the December image was clear only on the LR transect. On this occasion, the coastal water mass appeared to have been pushed against the coast, and into Bowling Green Bay (Figure 4.9a,b).

#### 4.3.3 Wind conditions

In late September, winds were predominately northeasterly in direction, and generally less than six m.sec<sup>-1</sup> (Figure 4.10). In early October, wind direction swung to the southeast, with a small increase in wind speed, for a period of several days. On 4 October wind patterns reverted to light northeasterlies. During late October and early November, winds were consistently out of the north to northeast. Indeed there was little southeast trade wind activity throughout October. Sampling in December was restricted by a period of sustained, strong southeasterly winds during late November and early December. Sampling could only be conducted after winds had lessened and swung to the north east around 7 December.

## 4.3.4 Physical/biological interactions

Larval distributions of three families from the net tow collections in 1989 were plotted along with 'depth-free' water colour acoss both LR and CB transects. These families were the most numerically abundant taxa in each of the three family groupings identified by cluster analysis in Chapter 3 (see section 3.3.3). The light trap catch in 1989 was dominated almost entirely by catches on the LR transect in October. Therefore only data from this month and transect were used when examining relationships between light trap catches and false-water colour.

#### 4.3.3.1 October

On 27 September false-water colour on the LR transect showed high turbidity inshore, with a strong gradient across the inner shelf to lagoon water located approximately 10 km from the coast (Figure 4.11). In the image from 3 October this gradient was again clearly visible. The false water colour profile suggested the presence of a front between coastal and lagoon waters at this time as there was a sharp drop in turbidity approximately 10 to 11 km along the transect. Larval gobiids collected in net tows were captured in high numbers at the inshore station on the LR transect on all three cruises, and associated with turbid coastal waters. High values were also recorded on the the first cruise at the 32 and 48 km stations. The fact, however, that larval abundance was low at the 16 km station on all three cruises suggests that these gobiids were probably mid-shelf taxa rather than those of the coastal assemblage. Nemipterids were spatio-temporally patchy,

and were collected at all stations on at least one of the three cruises. Lutjanids were restricted to the two outer-most stations throughout the sampling period.

Light trap catches were dominated by large numbers of fish at the 16 km station on the LR transect (Figure 4.12). Pomacentrids were captured in high numbers on all three cruises, although numbers declined noticably on the last cruise. Lethrinids were captured in low numbers on the first cruise, were abundant on the 3 October cruise, and then had declined again by 5 October. Mullids became progressively more abundant throughout the sampling period, reaching maximum densities on 5 October.

Net tow data for pomacentrids and mullids during this time were also examined to determine if small larvae of these taxa were distributed similarly to the larger individuals taken in the light traps (Figure 4.13). Distribution patterns of both taxa varied between techniques. Pomacentrid larvae taken in the plankton nets were captured in highest numbers at the 32 and 48 km stations. Larvae were almost absent from the 16 km station, where high numbers of larger individuals were captured in the light traps, and rare within coastal water at the inshore station. Mullids were captured evenly across the 16, 32 and 48 km stations, and were rare at the 0 km station within the coastal water mass.

Water colour on the CB transect showed a similar pattern to the LR transect, with a sharp gradient from turbid coastal water to clearer lagoon water across the inner shelf (Figure 4.14). Interestingly this gradient was sharper than on the LR transect, with lagoonal water found only six km along the CB transect in both scenes. Larval gobiids showed a strong tendancy to be concentrated within the narrow band of turbid coastal water. There was no indication of the presumed mid-shelf gobiid taxa at offshore stations on this transect. Nemipterids were again encountered at all stations across the transect, with highest numbers taken at the 16 km station and low numbers found at the 48 km station. Lutjanids were most abundant at the 32 km station, although they were captured in small numbers at the 16 and 48 km stations; a few specimens were also collected at the inshore station.

#### 4.3.3.2 November

Water colour values from November on the LR transect again showed turbid, inshore waters along the coast with lagoonal water located 12 km along the transect (Figure 4.15). No colour front was discernable across the transect. Larval gobiids were captured at all stations along the transect, with highest abundance recorded on at the 0 km station on the first cruise. However significant numbers were also collected at the 16 km station on cruises one and two. Nemipterids showed a similar pattern to October with high, variable, distributions across the transect and among cruises. Lutjanids were again confined to the outer two stations of the transect.

The CB transect again showed a gradient from turbid inshore water to clearer offshore water, although there appeared to be a less sharp decline in water colour across the inner shelf than in the October image (Figure 4.16). The transition zone between coastal and lagoon waters was visible at approximately 10-12 km along the transect. Larval gobiids, which in October were captured almost entirely at the inshore station, were also captured in moderate numbers at the 16 km station on the first cruise. This cruise coincided with the satellite overpass which showed coastal water extending further into the lagoon than in the previous month. Nemipterids were confined to the two inshore stations during this month. Lutjanids were again found only almost exclusively at the outer two stations.

#### 4.3.3.3 December

Turbibity in December on the LR transect declined progressively along the transect, levelling off approximately 16 km from the coast (Figure 4. 17). While the image from December suggested that the offshore water was located close to the coast at the time, the 'depth-free' values from along the LR transect do not show this pattern. Different atmospheric conditions among months, and the use of a consistent scaling factor, may have led to this impression. The 'depth-free' values were scaled from data in the December image, and likely to be at least internally consistent. They are, therefore, probably a more accurate potrayal of the relative positions of coastal and lagoon waters in this month. Only one ichthyoplankton cruise was made across the LR transect during this month. Gobiids were captured in highest numbers at the 16 km station, although overall concentrations

were considerably lower than in October or December. Numbers for both nemipterids and lutjanids were, however, very high. Nemipterids were concentrated in the middle of the lagoon, at the 16 and 32 km station. Lutjanids were captured in high numbers at the 48 km station, and to a lesser degree at the 16 km station. A small number were also captured at the inshore station, where they had been extremely rare in the first two months of sampling.

## 4.4 **DISCUSSION**

Two problems often encountered when analysing remotely sensed data from tropical waters were experienced in this study. Firstly, high water vapour levels meant that the number of usable images during the sampling period was low. October was the only month that more than one image Secondly, several studies have noted that could be analysed in detail. tropical and sub-tropical waters tend to be relatively isothermal, especially in summer months (Muller-Karger et al. 1991, Power and May 1991). This also appeared to be the case in the central GBR. The SST maps derived from AVHRR sensors showed very little temporal structure, at least on the scales considered in this chapter. Such images may well be useful for determining the influence of large-scale events related to global phenomena such as El Nino on water mass circulation on scales of 100's to 1 000's of kilometers. The lack of a strong thermal gradient across the GBR lagoon meant, however, that SST's were not useful for defining boundaries between coastal and lagoonal water masses in this area.

While the SST images revealed comparatively little information, visible reflectance measured by channel 1 of the AVHRR sensor showed considerably more promise. Scenes from this channel showed a repeatable pattern of turbid coastal water inshore, clearing to lagoonal water between six and 16 km from the coast. While some of these similarities may be due to bathymetry, there was sufficient temporal dynamism among images, after firstly removing a depth component, to suggest that at least some of the influence of bathymetry had been removed.

A strong turbidity gradient across the inner shelf of the cental GBR lagoon was evident in all maps of false-water colour derived from the NOAA/AVHRR images. The exact position of this feature did, however, change both between transects and among months. Studies on the physical oceanography of the central GBR lagoon are relevant to these observations. Wolanski and Ridd (1990) presented evidence that a 'coastal boundary layer' (CBL) formed in nearshore waters in tropical Australia. In the central GBR region, and in the absence of significant freshwater input, the CBL forms between estuarine and coastal waters at depths no greater than five meters. Thus while the edge of the CBL may be visible as a turbidity front, it is found much closer to the coast than the turbidity feature detected by satellite imagery in this study. Wolanski and Ridd (1990) also used the visible bands from the AVHRR sensor to display the presence of turbid, barotrophic, coastal boundary layer in the Gulf of Carpentaria. Wolanski and Ridd found no evidence for a similar CBL from salinity data or current profiles in the central GBR region. Scenes from channel 1 AVHRR in the present study appeared, however, very similar to the image of the Gulf of Carpentaria, which suggests that this feature may also be present in the central GBR region.

King and Wolanski (1992) developed a larger scale numerical model of water circulation in the central GBR lagoon. They suggested that under certain wind conditions a velocity shear occurred across the lagoon, caused primarily by the interaction of the East Australian Current (EAC), south east winds and friction due to the slope of the bottom. The location and strength of the shear zone was dependent on both the strength of the EAC and of winds. Under a no-wind situation, currents flowed long-shore to the southeast. The shear zone was located approximately 22 km along the LR transect, but only 15 km along the CB transect. Under a light southeastly wind (2-6 m.sec<sup>-1</sup>), a flow reversal occurred with coastal waters moving northeast with the wind while lagoonal waters continued to move southeast under the influence of the EAC. A zone of low current flow formed 11 to 12 km along both LR and CB transects. Finally, under strong southeast wind conditions current direction reversed across the entire lagoon and moving flowed to the northeast. The shear zone was located at approximately the same distance offshore as in the no-wind simulations, and again the shear was closer to the coast on the CB transect (14 km along the transect) than on the LR transect (22 km along the transect). While the effects of winds from directions other than southeast was not considered, winds from the northern sector would presumably act in a similar manner to an increase in the strength of the EAC, forcing the shear zone further offshore (B. King, Australian Institute of Marine Science, personal communication).

King and Wolanski's model may give some insight into the mechanisms determining the variations in the outer extent of coastal water detected in the satellite imagery of the area. On 27 September, for instance, the boundary between coastal and lagoonal water was approximately 10 km along the LR transect, and six km along the CB transect. Winds at this time were light and from the north sector. Under these conditions, the shear zone in King and Wolanski would be 22 km along the LR transect and 15 km along the CB transect. On 3 October, winds were light to moderate south easterly, and under these conditions the model predicted a separation zone between coastal and lagoonal water at 11 to 12 km along both transects. Satellite imagery from the LR transect did indeed suggest a front between water masses at approximately 11 to 12 km. There was, however, no evidence for this feature from data collected on the CB transect. Satellite imagery from October 31 showed the boundary between coastal and lagoonal waters around 12 km, although wind patterns through October were light to moderate north to northeasterly. This implies that the shear zone was considerably further offshore than the boundary between coastal and lagoon waters visible in the satellite imagery. In December winds were light to moderate from the north quandrant, although the over-pass was preceded by strong south easterlies. Under both wind conditions the shear zone on the LR transect would be at least 20 km along the transect, whereas the imagery suggested that the boundary between coastal and lagoon water masses was approximately 16 km along the transect.

It seems unlikely, therefore, that the shear zone depicted in King and Wolanski's (1992) model simulations is determining the outer extent of turbid, coastal waters in the GBR lagoon. Belperio (1978) proposed that prevailing wind conditions, or more specifically wave height, controlled the offshore extent of the coastal waters due to resuspension of bottom sediments. He suggested that wind strength determined wave height which in turn regulated the critical depth at which wave-induced shear stresses on the sea bed were insufficient for the entrainment of sediment. An ultimate limit to this coastal zone is set by the maximum wave height, which in central GBR is approximately at 22 m water depth (Belperio 1978). This hypothesis also predicted that the outer extent of the coastal zone will be
closer to the coast on the CB transect, as depths drop off much quicker on the CB transect than on the LR transect. The 22m contour is found 15 to 16 km along the LR transect, but only six km along the CB transect.

How does Belperio's model compare with the remotely-sensed data? The model predicted that under the light wind conditions present during late September to early November the coastal zone would be approximately six to eight km from the coast. This is in general agreement with results from the satellite imagery. Resuspension probably occurred out to the critical depth of 22 m during the strong wind event of late November and early December, and indeed the December image showed that coastal water was located approximately 16 km from the coast, in 22 m of water, on the LR transect. There is, then, some evidence from satellite imagery that the extent of coastal water in the central GBR is dependent upon wind strength, and hence probably resuspension of bottom sediments. Belperio's model did not, however, predict the strong colour front detected on 3 October on the LR transect. This front may only form under the light south easterly wind conditions necessary to generate a reverse flow to the north west along the coast as suggested by King and Wolanski (1992).

Two studies have utilised CZCS imagery to synoptically map surface chlorophyll in the central GBR. Huau (1987) found that a front between (relatively) high chlorophyll coastal water and low chlorophyll lagoon water in the vicinity of Cape Bowling Green did not extend more than five to six km from the Cape in any of the scenes that she analysed. These images also suggested that the coastal zone did not extend beyond 10 km from the coast in the vicinity of Cape Clevelend. Gabric et al. (1990) used CZCS imagery to examine seasonality in chlorophyll a concentrations in the central Great Barrier Reef region. In a particularly clear scene from October 1980, a stong chlorophyll front was located 15 to 16 km along the LR transect, and five to six km along the CB transect. In the other two interpretable images this front appeared closer to the coast (five to six km) on both LR and CB transects. The similarity of inshore patterns in chlorophyll a distributions to those derived in the present study from channel 1 AVHRR suggest that the scenes analysed by both Huau and Gabric and co-workers may contain considerable signal due to bathymetry. This problem is complicated in the coastal areas of the central GBR, where water depth, turbity and chlorophyll are often highly correlated (S. Bainbridge and S. Gay, Australian Institute of Marine Science, unpublished data). Gabric *et al.* (1990) note this problem, and suggest that given optical penetration depths of less than five meters even in mid-lagoonal waters during this time, bathymetric effects would only apply to inshore waters. However, penetration of wavelengths of 580-680  $\mu$ m was considerably more than five meters in lagoonal waters during this study. Clearly some caution is required when interpreting images that have not been depth-corrected, especially in the shallow waters of the inner shelf.

Larval distribution patterns from net tow collections showed similar spatial structure to the patterns in false-water colour. The inshore grouping determined in the previous chapter, typified here by the gobiids, were consistently associated with the coastal water mass. Coastal water was detected out as far as the 16 km station on the LR transect in December. This was the only time that maximum catches of gobiids were found at the 16 km station rather than inshore station. Nemipterids were typical of families captured across the lagoon. No preferences for either coastal or lagoonal water masses were evident, although this does not preclude the presence of species-specific differences than went undetected here. Lutjanids were only rarely captured in inshore waters; the majority were collected at two offshore stations on the LR transect and the 16, 32 and 48 km stations on the CB transect. This infers that lutjanids are associated only with clear, lagoon water masses. Milward and Hartwick (1986) also found that lutjanids were restricted to outer lagoonal waters from samples collected eight years previously to the present study, suggesting that this pattern has a high degree of temporal stability.

The processes determining the extent of the coastal zone (either a velocity shear across the lagoon or by resuspension of sediments) will have very different implications for the maintenance of larval fish assemblages noted by Milward and Hartwick (1986) and in Chapter 3. The shear zone will act to passively restrict cross-shelf movement of larvae across the zone, although considerable mixing is presumably occurring across the inner lagoon within the coastal water (Wolanski and Ridd 1990). If spawning is also spatially restricted (i.e. fish with nearshore larvae are spawned in coastal waters; Milward unpublished data cited in Milward and Hartwick 1986), hydrological constraints would lead to little mixing of larvae across the shear zone. However the larval fish community at the 16 km station on the LR transect was clearly lagoonal in composition, despite being on the coastal side of the shear zone (Chapter 3). This suggests that hydrography may not be primary mechanism maintaining larval assemblages across the lagoon. If resuspension of bottom sediments is determining the offshore extent of coastal water, there will be little hydrographic separation of water masses. This, in turn, implies that the larvae may be actively choosing the water mass in which they reside, or alternatively that differential mortality of larvae within the two water masses may be generating the observed cross-shelf patterns in larval fish communities (Williams 1986, Roberts 1991).

Evidence for the influence of larval behaviour on subsequent distribution patterns comes mainly from studies of estuarine and coastal systems, where vertical migrations into counter-current systems may allow larvae to maintain positions within estuaries (Weinstein et al. 1980, Fortier and Leggett 1983, Norcross and Shaw 1984) or larval retention zones (Iles and Sinclair 1982, Sinclair 1988, Munk and Christensen 1990, Bradford and Iles 1993). While some data suggest that there may be vertical shear in current velocities within the GBR (Wolanski and Hamner 1988, Wolanksi et al. 1989), these have been generated by the combination of tidal currents and topographic irregularities in the vicinity of reefs. There is no evidence of strong vertical shear within the central GBR lagoon (Wolanski and Ridd 1990), although some larvae may utilise the epibenthic layer to avoid horizontal advection (Leis et al. 1989). The ability of larvae to make horizontal migrations has yet to be considered in detail (Leis 1991a). Given recent evidence that the swimming abilities of tropical reef fish larvae may have been underestimated by models developed from temperate larvae (McCormick and Milicich in press), this possibility needs to be considered.

There is no direct evidence with which to evaluate the potential for differential mortality rates of larvae between water masses. Estimating realistic mortality rates for larval fishes is notoriously difficult (Houde 1987, Davis *et al.* 1991). In GBR waters these problems are compounded by taxomomic difficulties whereby few larvae can be reliably identified to species (Leis 1991a). It is possible that the turbidity regimes within the two water masses may lead to differential feeding success and hence survival. Feeding rates of of larvae have been shown to both increase and decrease with increasing levels of turbidity (Boehlert and Morgan 1985, Breitburg 1988). Zooplankton abundance (Sammarco and Crenshaw 1984) and species composition may also vary across water masses, which may also affect feeding success and survival. Such ideas will remain speculatory until advances in larval taxonomy enable these hypotheses to be tested directly.

Light trap catches were significantly more ephemeral than net tows, with catches at a single station in a single month contributing over 90% of the total catch in 1989 (Chapter 3). This made interpreting distribution patterns of fish captured in light traps difficult, as any correlation was based on a single point. It was, nevertheless, noteworthy that the patch of presettlement reef fish collected at the 16 km station on the the LR transect coincided with a colour front detectable at that approximate position in the satellite imagery on 3 October. It must be noted that this front was not present in the scene from 27 September even though numbers of pomacentrids were high at the 16 km station on that night. Lethrinids were only collected in high numbers on 3 October, and it may have been that the front concentrated these fish for the time that the front persisted. This remains speculative, however, and the most parsimonious explanation for the high catches of lethrinids on 3 October remains that it simply reflected small-scale variability of larvae within the larger 'patch'.

While a number of authors have speculated that reef fish larvae may be distributed in meso-scale 'patches' (Victor 1984, Williams 1986, Doherty 1987b), there have been few direct measurements of such patches or possible hydrographic features that may generate them. Victor (1984) hypothesized that a coastal front may be responsible for aggregating larval bluehead wrasse, Thalassoma bifasciatum, which in turn led to coherent patterns of settlement across the reefs that he surveyed. No data on the oceanography of the area, or indeed distribution patterns of larval bluehead wrasse, were presented with which to evaluate this hypothesis. Williams and English (1992) noted that abundance of several reef fish taxa increased across stations separated by as much as six km in the vicinity of Myrmidon Reef, on the outer shelf of the central GBR on a single sampling occasion. They also detected water temperature anomalies that may have indicated the presence of a cold meso-scale eddy associated with the patch of larval fish (Wolanski 1986). Meso-scale eddies have been shown to aggregate pelagic (Thomson et al. 1990) and mesopelagic fishes (Olson and Backus 1985), and the convergence associated with such structures may also act to entrain or aggregate fish larvae (Kingsford 1990). While this hypothesis is intriguing,

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the influence of these eddy structures on larval distributions, and subsequent recruitment, remain to be determined.

While the processes determining the cross-shelf extent of the coastal water mass in the central GBR lagoon have yet to be unambiguously identified, there is some evidence that it is related to resuspension of bottom sediments. If correct, the 22 m contour would mark the outer extent of the coastal zone, although wind conditions would determine how far coastal water was found offshore at any time. A composite map of the positions of both the boundary between coastal and lagoon water, was derived from the satellite imagery, and the shear zone predicted by King and Wolanski's (1992) model (Figure 4.18). The graphic shows that the boundary between coastal and lagoon water is often a considerable distance inshore of the shear zone, at least when long-shore current velocities are high. Results from this study and that of Milward and Hartwick (1986) emphasised the affinity of the inshore ichthyoplankton assemblage with the turbid coastal waters. Sammarco and Crenshaw (1984) found, however, a different pattern when examining zooplankton distributions along the LR transect. Their midlagoon station, 24 km along the transect, showed inshore associations on approximately 50% of sampling dates, and offshore affinities on all other occasions. This suggests, therefore, that zooplankton may be influenced by different hydrographic features within the central GBR lagoon than larval fishes. In the next chapter, I examine zooplankton dynamics, along with physico-chemical variability, at stations across the transition zone between coastal and lagoon water masses in this location.







Figure 4.2a. Colour-enhanced map of sea-surface temperature in the central GBR region on 27 September, 1989.



Figure 4.2b. Colour-enhanced map of sea-surface temperature across the central GBR lagoon adjacent to Townsville on 27 September, 1989. Lines show LR and CB transects.



Figure 4.3a. Colour-enhanced map of sea-surface temperature in the central GBR region on 3 October, 1989.



Figure 4.3b. Colour-enhanced map of sea-surface temperature across the central GBR lagoon adjacent to Townsville on 3 October, 1989. Lines show LR and CB transects.



Figure 4.4a. Colour-enhanced map of sea-surface temperature in the central GBR region on 30 October, 1989.



Figure 4.4b. Colour-enhanced map of sea-surface temperature across the central GBR lagoon adjacent to Townsville on 30 October, 1989. Lines show LR and CB transects.



**Figure 4.5a.** Colour-enhanced map of visible band (channel 1) from the NOAA/AVHRR satellite in the central GBR region on 27 September, 1989.



**Figure 4.5b.** Colour-enhanced map of visible band (channel 1) from the NOAA/AVHRR satellite across the central GBR lagoon adjacent to Townsville on 27 September, 1989. Lines show LR and CB transects.



Figure 4.6a. Colour-enhanced map of visible band (channel 1) from the NOAA/AVHRR satellite in the central GBR region on 29 September, 1989.



**Figure 4.6b.** Colour-enhanced map of visible band (channel 1) from the NOAA/AVHRR satellite across the central GBR lagoon adjacent to Townsville on 29 September, 1989. Lines show LR and CB transects.



Figure 4.7a. Colour-enhanced map of visible band (channel 1) from the NOAA/AVHRR satellite in the central GBR region on 3 October, 1989.



**Figure 4.7b.** Colour-enhanced map of visible band (channel 1) from the NOAA/AVHRR satellite across the central GBR lagoon adjacent to Townsville on 3 October, 1989. Lines show LR and CB transects.



**Figure 4.8a.** Colour-enhanced map of visible band (channel 1) from the NOAA/AVHRR satellite in the central GBR region on 30 October, 1989.



**Figure 4.8b.** Colour-enhanced map of visible band (channel 1) from the NOAA/AVHRR satellite across the central GBR lagoon adjacent to Townsville on 30 October, 1989. Lines show LR and CB transects.



Figure 4.9a. Colour-enhanced map of visible band (channel 1) from the NOAA/AVHRR satellite in the central GBR region on 10 December, 1989.



**Figure 4.9b.** Colour-enhanced map of visible band (channel 1) from the NOAA/AVHRR satellite across the central GBR lagoon adjacent to Townsville on 10 December, 1989. Lines show LR and CB transects.



Figure 4.10. Wind speed and direction at 12 hr intervals from Cape Bowling Green during September to December, 1989. Vectors point towards source of wind. Lines above x axis show sampling periods during each month.



Figure 4.11. Depth-corrected false water colour (27 September, dashed line; 3 October solid line), and distributions of 3 families of larval fish from net tows along the LR transect on 27 September open bars), 3 October (hatched bars) and 5 October (solid bars).



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**Figure 4.12.** Depth-corrected false water colour (27 September, dashed line; 3 October solid line), and distributions of 3 families of small fishes from light traps on the LR transect on 27 September (open bars), 3 October (hatched bars) and 5 October (solid bars).



**Figure 4.13.** Distributions of larval pomacentrids and mullids from net tows along the LR transect on 27 September (open bars), 3 October (hatched bars) and 5 October (solid bars).



**Figure 4.14.** Depth-corrected false water colour (27 September, dashed line; 3 October solid line), and distributions of 3 families of larval fish from net tows along the CB transect on 28 September (open bars), 4 October (hatched bars) and 6 October (solid bars).



**Figure 4.15.** Depth-corrected false water colour on 30 October, and distributions of 3 families of larval fish from net lows along the LR transect on 25 October (open bars), 30 October (hatched bars) and 1 November (solid bars).



**Figure 4.16.** Depth-corrected false water colour on 30 October, and distributions of 3 families of larval fish from net tows along the CB transect on 31 October (open bars), 2 November (hatched bars) and 3 November (solid bars). \* indicates station not sampled on that day.



Figure 4.17. Depth-corrected false water colour on 10 December, and distributions of 3 families of larval fish from net tows along the LR transect on 7 December.





# Chapter 5

# Biological oceanography across the boundary between coastal and lagoon waters in the central Great Barrier Reef

## 5.1 INTRODUCTION

The influence of boundary zones between different water masses on the distribution patterns of pelagic fish and plankton has been recognised for centuries (Uda and Ishino 1958). Frontal processes may operate over a wide range of spatial and temporal scales; from hundreds of metres over a tidal cycle for headland fronts, to planetary scales of the major currents along continental margins such as the Gulf Stream, Kuroshio, Benguela and East Australian Current systems (reviewed by LeFevre 1986). While the biological oceanography of these large-scale systems is comparatively well documented, little is known about the biological dynamics of coastal fronts (Wolanski and Hamner 1988).

Coastal fronts can be generated in a number of ways. Plume or riverine fronts represent the leading edge of a low salinity lens discharging from a river or estuary onto the continental shelf (Bowman 1988). Riverine fronts are often characterised by sharp horizontal discontinuities in both temperature and salinity (e.g. Wolanski and Jones 1981, Govoni et al. 1989). Tidal mixing fronts form between stratified (typically shelf) water and tidally well-mixed (typically coastal) water masses. Density and chemical signatures of these two water masses are more subtle than those of riverine fronts, but still exhibit vertical and horizontal discontinuities (Richardson 1985, Le Fevre 1986, Richardson et al. 1986, Taggart et al. 1989). Coastal fronts can also separate topographically-trapped coastal water from faster-flowing offshore water (Sakamoto and Tanaka 1986, Nakata et al. 1989, King and Wolanski 1992). Such fronts may be distinguished by salinity (Wolanski and Ridd 1990) or temperature (Nakata et al. 1989) differences, and in tropical waters of eastern Australia can be observed from ocean color and temperature maps derived from satellite imagery (Wolanski and Ridd 1990, Chapter 4).

Larval fish biologists have recently focused considerable attention on coastal fronts. Indeed meso-scale hydrographic phenomena have been implicated in the survival and subsequent recruitment of larval fishes (Iles and Sinclair 1982, 1985, Richardson *et al.* 1986, Heath and MacLachlan 1987, Kiorboe *et al.* 1988, Govoni *et al.* 1989). The spatio-temporal scales over which processes affecting larval fish mortality are likely to operate (1-10's of kilometers, 1-10's days) are consistent with the dynamic scales of coastal fronts (Legendre and Demers 1984). Increased primary (Pingree *et al.* 1975, Raine *et al.* 1990, Lohrenz *et al.* 1990) and secondary (Kiorboe and Johansen 1986) production has been documented at frontal boundaries. Further studies have noted enhanced abundance of zooplankton and small fishes at these interfaces compared to stations inside and outside the frontal zone (Govoni *et al.* 1989, Nakata 1989, Raid 1989, Grimes and Finucane 1991, Govoni and Grimes 1992, Kingsford and Suthers in press).

In the previous two chapters, larval fish assemblages were shown to change significantly across the central GBR lagoon. This change coincided with a strong turbidity gradient across the inner shelf, which in turn may have been related to water depth and wind conditions via resuspension of bottom An ultimate limit to bottom resuspension occurs at water sediments. depths of approximately 22 m (Belperio 1983), which coincides with both the outer extent of mud sediments and faunal dicontinuities in both benthic invertebrate community structure (Arnold 1980, Birtles and Arnold 1988, Arnold et al. ms) and larval fish assemblages (Milward and Hartwick 1986, Chapter 3 and 4 this study). Little remains known, however, of the biological oceanography of these water masses. Sammarco and Crenshaw (1984) found that an 'inner lagoon' community, consisting of higher abundances of most taxa, "wove back and forth across the lagoon through time", and that this movement was linked to the level of river discharge into coastal waters. This contrasts with the relatively static boundary delineating larval fish communities (Milward and Hartwick 1986, Chapters 3 and 4 this study), which may indicate that the mechanism(s) determining the distribution patterns of zooplankton are qualitatively different to those influencing larval fish.

The aim of the present chapter is to determine the effects of the interaction between coastal and lagoon waters on zooplankton distributions and productivity. Boundary zones between water masses are often sites of enhanced biological activity (Le Fevre 1986), and may act to focus zooplankton secondary production spatially (Kiorboe *et al.* 1988, Smith and Lane 1991). This will, in turn, influence the feeding conditions encountered by larval fishes in such areas. Zooplankton may also be useful tracers of water mass movements (Mackas and Sefton 1982, Thomas 1992). While a number of zooplankton taxa have a degree of control over vertical distribution, they are by definition incapable of significant horizontal migrations (Harding *et al.* 1986, Power 1989 and others). Contrasting distribution patterns of zooplankton with those of larval fishes may, then, give some indication of the relative importance of hydrography and behaviour in the maintenance of larval fish assemblages in the central GBR lagoon. The specific aims of this chapter are to;

1. Describe physical (temperature, salinity) and biological (chlorophyll a) parameters at 3 stations across the inner GBR lagoon over a seven month period.

2. Describe zooplankton distributions and estimate spatial and temporal variability in egg production rates of a coastal copepod species as a measure of fluxes in copepod secondary production.

3. Determine if there is coherency in the distribution patterns of zooplankton and larval fish communities across the inner shelf of the central GBR lagoon.

## 5.2 METHODS AND MATERIALS

#### 5.2.1 Study area

Sampling was conducted in the central GBR lagoon, off the coast of Townsville. Fixed stations eight km (station 1), 16 km (station 2) and 24 km (station 3) along the LR transect (Figure 2.1) were visited approximately once a month from October 1990 to May 1991, on the following days: October 25, November 3, November 17, December 16, January 19, January 23, March 9 and May 7. The 16 km site (station 2) corresponded to the critical depth that delineates the ultimate extent of bottom resuspension across the transect (Belperio 1983). Given the relationship between zooplankton community structure and freshwater input documented by Sammarco and Crenshaw (1984), watershed discharge during the sampling period was estimated from discharge of the Burdekin River, obtained from the Queensland Water Resources Commission. The Burdekin is the largest source of river discharge in the central Great Barrier Reef region (Wolanski and Jones 1981).

#### 5.2.2 Physical oceanography and chlorophyll determinations

At each station, three water samples were collected at each of three depths, at the surface, mid-water, and in the bottom depth strata, 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. Temperature and salinity data were then used to calculate  $\sigma_t$  values according to the international one-atmosphere equation of Millero and Poisson (1981). In the laboratory, water samples were filtered through a 10 µm sieve to provide total and > 10 µm chlorophyll *a* values. A single total surface chlorophyll *a* sample was also taken from each station. Samples were then filtered onto Whatman filters and extracted in 90% acetone. Chlorophyll *a* determination with correction for phaeopigments was made spectrophometrically using a Turner fluorometer and the methods described by Strickland and Parsons (1972).

#### 5.2.3 Zooplankton collections

At each station, three vertical plankton hauls using a 150  $\mu$ m plankton net (diameter 0.5m) were made, and samples preserved in 5% formalin/seawater. Zooplankton samples were subsequently enumerated and abundance converted to numbers.m<sup>-3</sup> in the laboratory. A gentle subsurface horizontal tow was made to collect live copepods for egg production experiments. Several species of copepod were initially trialled- *Acrocalanus gibber* was chosen as it was abundant and easy to recognise and handle. Nine 250 ml pyrex bottles were filled with water collected from each station, which had been passed through a 100  $\mu$ m filter to remove most juvenile copepods. The 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 number of eggs and nauplii in each bottle were counted to determine the egg production rate of each female. Since no acclimation period was allowed, egg production in

the laboratory reflected the feeding conditions encountered in the field by the copepods prior to capture.

## 5.2.5 Data analysis

Differences in chlorophyll values between stations and through time were compared using an orthogonal two-way ANOVA model, with cruise and station as main effects. A similar model was also used to test for differences in zooplankton abundance among stations and over time. Total plankton, total copepod numbers and abundances of each of the four most numerous taxa (small calanoids, larvaceans, *Parvocalanus crassirostris* and *Acrocalanus gibber*) were examined in this manner. Assumptions of homogeneity of variances and normality of residuals in all ANOVA's were tested using residual analysis (Winer 1971). Daily egg production rates of *Acrocalanus gibber* could not be compared in this way, as the inability to collect *A. gibber* at all stations in all months made the design irrepairably unbalanced. Results are therefore presented graphically.

# 5.3 RESULTS

## 5.3.1 Physical data

Salinity profiles over the sampling period were dominated by the input of low-salinity water during January 1991 (Figure 5.1). The low salinity water reached Station 1 on January 18, but was not detected until January 23 at stations 2 and 3. This water was restricted to the surface layers, although small drops in salinity were also measured at the mid and bottom depths. There were also indications of the formation of a halocline on two other occasions (November 3 and December 16). The haloclines were not, however, as pronounced as in January. Higher salinity water was found at the surface, which suggests that the stratification was probably due to surface evaporation.

Water temperatures were characteristed by consistent thermal structure with depth across stations, and by a steady upward trend in temperature during summer, peaking in January before cooling off through March and May (Figure 5.2). Thermal stratification was evident at all three stations except during May, although the depth of the thermocline varied between stratification events. All three stations showed coherency in thermal signals throughout the sampling period, with stratification at the three stations occurring simultaneously and in the same depth stata.

Density ( $\sigma_t$ ) was plotted so as to maximise contrast between stations at each of the three depths (Figure 5.3). All three depths show a similar trend. From October to December, no differences in density were apparent among the three stations. However, after the input of low density water in January, station 3 was characterised by denser water than the two inshore stations, although this was only convincing for the surface waters. Flow rates from the Burdekin River throughout the sampling period indicated that significant fresh water was introduced to the GBR lagoon throughout January and February (Figure 5.4). Continued freshwater input may, then, have led to this density difference.

Chlorophyll a concentrations showed remarkably few deviations throughout the sampling period, varying between 0.2 and 0.7  $\mu$ g.l<sup>-1</sup> (Figure 5.5). Station 1 had consistently higher total chlorophyll values than either station 2 or 3, which were similar. The > 10  $\mu$ m chlorophyll *a* component was also consistently higher at station 1 than the two offshore stations. Analysis of variance of both total and > 10  $\mu$ m chlorophyll *a* detected significant station and cruise effects, along with a significant cruise\*station interaction (Table 5.1). The interaction between cruise and station appeared largely due to the effect of plume water on chlorophyll *a* distributions. Although total chlorophyll values at station 1 actually dropped during this period, a sharp increase in chlorophyll a at both stations 2 and 3 was apparent as the plume water moved offshore. These values represented the largest total chlorophyll measured during the study at station 2, although higher values were recorded at Station 3 in May. Movement of low-salinity water offshore was also associated with an increase in > 10  $\mu$ m chlorophyll *a* at stations 2 and 3. However maximum values of the > 10  $\mu$ m chlorophyll component were attained in December at station 1, and in May at stations 2 and 3.

Source	MS	F value	Prob.
Total chlorophyll			
Cruise	0.109	28.92	0.0001
Station	0.245	64.82	0.0001
Cruise*station	0.021	5.74	0.0001
> 10 µm			
Cruise	0.082	30.37	0.0001
Station	0.033	12.37	0.0001
Cruise*station	0.011	4.14	0.0001

**Table 5.1** Results of two-way ANOVA procedure, with cruise and station as main effects, for total chlorophyll *a* and > 10  $\mu$ m chlorophyll *a*.

# 5.3.2 Zooplankton

Abundance of all six zooplankton taxa were analysed for effects of cruise and station using an orthogonal two-way ANOVA. Results of the tests were similar for all taxa; both main effects were significant, along with significant interactions (Table 5.2). Interpretation of the interaction terms from the abundance plots suggested that the freshwater plume may have been a significant cause of the interaction effects. Interactions were also generated by occasional high numbers of a number of taxa including total plankton and total copepods at station 2, despite a general trend for higher numbers at the inshore station.

Total plankton abundance showed considerable variability through time, and no consistent trends among stations (Figure 5.6). Generally, station 1 had higher plankton numbers than the two offshore stations. On two occasions, however, station 2 had higher abundances than station 1. This variability is reflected in significant cruise, station effects in the two-way ANOVA, as well as a significant cruise\*station interaction (Table 5.2). Total copepods showed a similar pattern, and again all factors in the ANOVA were significant (Table 5.2). Station 1 had consistently higher numbers than the offshore stations on six of the eight sampling occasions; on the 17 November cruise, and in March and May, station 2 recorded the highest numbers of copepods.

Source	MS	F value	Prob.		
Total plankton					
Cruise	80207437	161.01	0.0001		
Station	21207300	42.57	0.0001		
Cruise*station	6976694	14.01	0.0001		
Total copepods					
Cruise	9759053	131	0.0001		
Station	8042793	108	0.0001		
Cruise*station	1266506	17	0.0001		
Small calanoids					
Cruise	6052195	189.6	0.0001		
Station	257275	8.06	0.001		
Cruise*station	244956	7.67	0.0001		
Larvaceans					
Cruise	1159606	50.25	0.0001		
Station	407484	17.66	0.0001		
Cruise*station	214065	9.28	0.0001		
P. crassirostris					
Cruise	639103	55.82	0.0001		
Station	473355	41.34	0.0001		
Cruise*station	130208	11.37	0.0001		
A. gibber					
Cruise	552340	129.61	0.0001		
Station	246528	57.85	0.0001		
Cruise*station	108740	25.52	0.0001		

Table 5.2 Results of two-way ANOVA procedure, with cruise and station as main effects, for six zooplankton taxa.

Both total plankton and total copepod abundances showed moderate increases as a lens of low-salinity water moved offshore through the sampling stations during January (Figure 5.6). Distribution patterns of the four most numerous taxa showed much greater affinities with this freshwater plume. Small calanoids, predominantly Paracalanus juveniles, showed a large peak in abundance in March, at all three stations (Figure 5.7). Interestingly, Station 2 had higher numbers than either of the other two stations in both March and May. Larvaceans reacted extremely rapidly to the hydrographic conditions associated with the low-salinity water. The degree to which larvacean abundance tracked the plume water can be seen by examining data from January (Figure 5.7). Numbers increased by almost an order of magnitude over four days as the plume moved offshore from station 1 on January 18 through the two offshore stations on January 23. High numbers were also recorded at the offshore station in March, before dropping off in May, while station 2 recorded the highest abundance on January 23, in March and in May.

Parvocalanus crassirostris appeared to have predominately inshore affinities, exhibiting a gradient of abundance from station 1 to station 3 (Figure 5.8). This species was, however, also abundant at Stations 2 and 3 in January and March. Again the freshwater plume appeared instrumental in either transporting the individuals offshore, or providing conditions suitable for growth and reproduction. Acrocalanus gibber abundance appeared to be correlated remarkably well with the initial input of fresh water into the central GBR lagoon (Figure 5.8). High numbers, initially at station 1, and then across all three stations, were recorded during January. Numbers had dropped again by March, and individuals were rare in May.

#### 5.3.3 Copepod egg production

Daily egg production rates for *Acrocalanus gibber* were obtained from at least one station in October, November, January, March, and May. Female *A. gibber* were not captured in sufficient numbers to conduct experiments in December. Daily egg production varied from a low of three eggs.female<sup>-1</sup> day<sup>-1</sup> at station 2 in March to a high of 40 eggs female<sup>-1</sup> day<sup>-1</sup> at station 3 on January 23 (Figure 5.9). Egg production rates showed no significant relationship with either total chlorophyll *a* or > 10 µm chlorophyll (Figure 5.10, Table 5.3).

**Table 5.3** Results of regression analysis, with daily egg production of *Acrocalanus gibber* as the dependent variable, and total chlorophyll *a* and > 10  $\mu$ m chlorophyll *a* as independent variables.

Source	MS	F value	Prob.	r <sup>2</sup>
Total chlorophyll				
Model	13.8	0.121	0.735	0.011
> 10 µm chlorophyll				
Model	40.5	0.362	0.559	0.032

The low-salinity plume that occurred in January was associated with little change in surface chlorophyll *a* at stations 1 and 2, and extremely high values at station 3, along with high adult *A. gibber* abundance and high egg production rates (Figure 5.11). Highest chlorophyll values were not associated with the main body of the plume- as noted above, chlorophyll values were not enhanced at station 1 during this time. Rather, surface chlorophyll appeared to be highest near the front between plume and lagoon water- at station 1 on January 18, and then at station 3 on January 23 as the plume moved offshore (as indicated by density values in Figure 5.11).

Egg production rates were enhanced at all plume stations, although the exact nature of this increase could not be determined due to the lack of adult *A. gibber* in plankton samples from lagoon waters outside the plume on these occasions.

## 5.4 DISCUSSION

Zooplankton distributions in the present study were characterised by large temporal and spatial variability over all scales considered. This variability was exemplified by significant first-order interactions between cruise and station for every zooplankton taxa considered. Much of the variability appear to be driven by hydrography, and in particular the presence of a large freshwater intrusion in January 1991. A number of zooplankton taxa showed affinity with the low-salinity plume. Sammarco and Crenshaw (1984) also noted the influence of runoff on zooplankton community structure in the central GBR lagoon. They suggested that inshore and offshore plankton 'assemblages' were present. The inshore association being characterised by higher abundance of almost all net zooplankton taxa. The coarse taxonomic resolution of their data (usually no further than class) meant, however, that they had no way of assessing whether these associations were caused by faunal differences, or simply differences in total abundance.

A number of zooplankton taxa showed a rapid increase in concentrations within plume waters. Larvaceans and *Acrocalanus gibber* were both taken in highest numbers during January, and associated with the plume. *Parvocalanus crassirostris* was generally more abundant at inshore stations; passage of the plume across the inner shelf led to high numbers at the 24 km station. Interestingly, several taxa responded at different rates to this influx. Larvaceans, *A. gibber* and *P. crassirostris* increased as soon as the plume crossed each station. Small calanoids did not peak until March, perhaps due to a lagged response to the January plume or in response to the continued input of freshwater during January and February. Total plankton numbers therefore appeared to remain high throughout January and February, although the species composition of the community changed between the January and March sampling occasions.

Egg production rates of Acrocalanus gibber ranged from mean values of four eggs.female<sup>-1</sup>day<sup>-1</sup> to 40 eggs.female<sup>-1</sup>day<sup>-1</sup>. These values span the range reported for other tropical copoepd species; Bestiola similis produced five to 17 eggs.female-1day-1 (Kimmerer 1984), Acartia tonsa laid approximately 53 eggs.female-1day-1 (Ambler 1985) and Acartia erythraea produced 12.9 eggs.female<sup>-1</sup>day<sup>-1</sup>. While there was no consistent pattern across stations in this study, highest egg production rates were recorded from within the lowsalinity plume water during January. McKinnon and Thorrold (in press) also found high rates of egg production of A. gibber the following year associated with a cold upwelling event. While the present study did not find a significant relationship between either total chlorophyll *a* or >10  $\mu$ m chlorophyll a, McKinnon and Thorrold did find such a relationship over a total of 2 years of sampling. This implies that food may be limiting during most of the year, and that A. gibber may be capable of dramatic increases in productivity when hydrographic events produce a favourable food environment.

Food quality may play a major role in determining egg productions (Kleppel 1992). There is some evidence that large-celled diatoms, the preferred food of many herbivorous copepods, respond quickly to rapid increases in nutrient levels. 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. Furnas suggested that this was largely due to storm wave activity resuspending nutrients from sediments. Interestingly dinoflagellates, which are a major component of the phytoplankton community, did not show the same increases in growth rate. Measurements of total chlorophyll may, then, be of limited value when examining the potential for variability in food supply to influence zooplankton biomass and productivity.

Distribution patterns of zooplankton may give some insight into the position and movement of water masses within across the inner lagoon. There was a lack of any distinctive cross-shelf patterns in abundance of the taxa considered here. This suggests that there is substantial mixing of water across the inner shelf, presumably driven by tidal excursions and diffusive processes (Dight *et al.* 1988, King and Wolanski 1992). In a longer study at

the same stations, McKinnon and Thorrold (in press) found some evidence of an 'inshore' zooplankton community, although the association was characterised by high abundance of a number of taxa rather than faunal differences. Interestingly, they found that stations were classified into inshore and offshore groupings under strong southeast winds, and winds from the northern quadrant. Under light southeast winds, however, all stations showed offshore affinities. This suggests that when a strong shear zone is present, there is comparatively little water exchange between the mid and inner lagoon. Significant intrusions of lagoon water may occur under light southeast winds when longshore velocities are sluggish.

In the previous chapter, it was argued that the extent of turbid coastal waters was not delineated by the shear zone predicted by King and Wolanski (1992), but rather appeared to be the result of suspension of bottom sediments by wind-generated waves (Belperio 1978). The presence of turbid coastal water, as determined from satellite imagery, correlated reasonably well with larval fish associations across the inner lagoon (Chapter 4). Zooplankton assemblages appeared, however, to be more tightly coupled to the position and strength of the shear zone (McKinnon and Thorrold in press). Α schematic diagram of the hypothesized position of the boundary between inshore and offshore zooplankton assemblages shows the dynamic nature of the transition zone (Figure 5.13). This contrasts with a similar graphic of the position of the offshore extent of coastal waters, and by inference the inshore larval fish community, detailed in chapter 4 (Figure 4.17). Given that zooplankton are more likely to be passive tracers of water movement than larval fish, hydrography alone does not appear to generate the observed larval fish assemblages. Rather, turbidity levels could set the inshore or offshore limits of coastal and lagoon assemblages. This may be due to active selection on the part of larvae, or could act through differential mortality rates in turbid versus clear lagoon water (Chapter 4).

While there was no consistent trend across stations through time, zooplankton abundance was often higher at the 8 km station than at the 16 and 24 km stations. Robertson *et al.* (1988) found that zooplankton abundance was generally an order of magnitude higher at stations immediately adjacent to the coast in this area than the values recorded in the present study. Given the sensitivity of young larvae to starvation (Lasker 1981), it seems paradoxical that some cluepid species, for instance,

utilise nearshore nursery habitats as juveniles (Williams and Cappo 1990), yet spawn in offshore waters. One possible explanation is that nearshore waters also harbour considerably more invertebrate predators of eggs and larvae than more oligotrophic lagoonal waters (Suthers and Frank 1990).

Spawning in water masses relatively free from predation ('safe sites') has been discussed by Alvarino (1980) for northern anchovy and by Frank and Leggett (1986) and Leggett (1986) for capelin. A series of studies (Moller 1980, 1984, Purcell 1981, 1984, 1989, Purcell et al. 1987, de Lafontaine and Leggett 1988, Purcell and Grover 1990, Cowan and Houde 1993) have shown that siphonophores may be major predators of fish larvae. Brewer et al. (1984) reported that crustacean zooplankton may be voracious predators of small larval fish. Purcell (1985) suggested that ctenophores and pelagic cnidarians may also remove significant numbers of young larvae from the water column. Movement of juvenile clupeids into nearshore habitats may, therefore, be related not only to the development of sufficient locomotory ability to make the migration to inshore waters (Chapter 3), but may also correspond to the size at which predation from invertebrates has been minimized (Pepin et al. 1992). Interestingly a number of lutjanid species also appear to spawn in offshore waters, while juveniles utilise nearshore nursery areas. Mesocosms may be a potentially useful way of testing this hypothesis by examining survivorship of larvae in different water masses under various predator regimes (reviewed by de Lafontaine and Leggett 1987).

Zooplankton dynamics at stations across the central GBR lagoon appear to be sensitive to a number of hydrographic processes including the input of freshwater and wind-forced current flows. The rapid response of zooplankton taxa, both in terms of abundance and secondary productivity, to the low-salinity plume generated by Cyclone Joy emphasises the potential importance of episodic, but rare, meterological events on coastal plankton dynamics (Thresher *et al.* 1992). McKinnon and Thorrold (in press) found that egg production rates of *Acrocalanus gibber* were high after an intrusion of upwelled water in December 1991. It is hypothesized that plankton dynamics in the central GBR lagoon appear, therefore, to be driven by episodic hydrographic phenomena causing large increases in the abundance of suitable food items for the reproductive success of herbivorous copepods. This appears to be a powerful mechanism for producing differential

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survival of shorefish larvae that are present in the water column at the time of these events, which may be in turn generate the recruitment variability characteristic of reef fishes in this region (Williams 1986). There appears little doubt, for instance, that the low-salinity plume waters in January provided an extremely rich food environment for larval fishes. In the next chapter, I examine the distribution patterns of larval fishes in relation to this plume and associated plume front.







Figure 5.2. Temperature profiles in bottom, mid and surface waters at 3 stations across the central GBR lagoon, November 1990 to May 1991.



**Figure 5.3.** Sigma  $_t$  profiles at 3 stations in surface, mid and surface waters across the central GBR lagoon, November 1990 to May 1991.



Figure 5.4. Daily streamflow of the Burdekin River at Clair, October 1990 to May 1991.











Figure 5.7. Mean concentration of small calanoids and larvaceans (+/- standard errors) at 3 stations\_across the central GBR lagoon, October 1990 to May 1991.















**Figure 5.11.** Relationship between seawater density ( $\sigma_t$ ), surface chlorophyll *a*, mean concentration of *Acrocalanus gibber* (+/- standard errors), and daily egg production (eggs.female <sup>-1</sup> day <sup>-1</sup>: +/- standard errors), at 3 stations across the central GBR lagoon, December 1990 to May 1991.



**Figure 5.12.** Schematic representation of the offshore extent of nearshore zooplankton communities under strong long-shore currents in either NW or SE directions (top) and sluggish long-shore currents (bottom). Arrows indicate direction and relative strengths of long-shore current components. Circles indicate ichthyoplankton stations, squares mark zooplankton stations.

# Chapter 6

## Ichthyoplankton distributions in the vicinity of a riverine plume

### 6.1 INTRODUCTION

Spatio-temporal variability in watershed discharge is a critical determinant of nutrient flux in nearshore waters (Harrison *et al.* 1991). Freshwater input is usually manifested in coastal regions as riverine plumes. These plumes are shallow (typically less than five meters), buoyant lenses of low salinity water overlaying denser, more saline water (Garvine 1986). Phytoplankton biomass and primary productivity can respond rapidly to freshwater discharge (Rudek *et al.* 1991). Zooplankton communities in coastal waters also appear to react quickly to discharge events, with abundance (Sammarco and Crenshaw 1984) and copepod egg production rates (McKinnon and Thorrold in press, Chapter 5) being positively correlated with freshwater input.

Riverine plumes may also have considerable implications for the survival and recruitment of larval fishes. Riverine plumes are highly stratified and biologically-active water masses (Bowman 1988). Most attention has concentrated on the accumulation of planktonic organisms at plume fronts (Govoni *et al.* 1989, Grimes and Finucane 1991, Govoni and Grimes 1992), although the plume and associated front may also serve to aggregate both suitable prey organisms and potential predators (Bailey and Houde 1989). Food concentrations may affect larval mortality directly due to starvation. Perhaps more commonly, low food levels may lead to reduced growth rates, and hence increase the rate of predation during longer larval durations (Houde 1987). The unique physio-chemical signature of plume waters may also be important cues for post-larval and juvenile fishes migrating to estuarine nursery areas (Shaw *et al.* 1985a).

Despite the potential significance of riverine plumes to recruitment processes, the influence of these hydrographic structures on ichthyoplankton dynamics are far from clear. Govoni *et al.* (1989) described enhanced abundances of larval fish at the Mississippi River plume front.

Grimes and Finucane (1991) also suggested that neustonic ichthyoplankton were concentrated within a 6-8 km 'frontal zone' that separated water of the Mississippi River plume from adjacent shelf water. They proposed a working hypthesis whereby accumulated biomass in frontal waters leads to enhanced feeding conditions, and hence larval survival and subsequent recruitment. While the causal mechanisms for these aggregations are not fully understood, hydrodynamic convergence at the plume front appears to play a considerable role (Govoni and Grimes 1992). Convergent zones, usually manifested as slicks between adjacent rippled areas, are indeed common hydrographic phenomena in coastal waters (Kingsford 1990). A number of studies have documented increased plankton abundances within these features (Zeldis and Jillett 1982, Shanks 1983, Kingsford and Choat 1986, Kingsford et al. 1991), although it has yet to be established that larvae associated within these convergent zones experience enhanced growth or survival (Powell et al. 1990).

The relatively high, and constant, discharge rates from large river systems such as the Mississippi and Columbia generate plumes with a high degree of temporal persistence (Bowman 1988, Dagg et al. 1987). Plumes are transient features usually associated with cyclonic rains in coastal waters of northeast Australia (Wolanski and Jones 1981). The inherent unpredicability of plume formation in this area has meant that very little is known of the influence of such events on planktonic assemblages. The presence of Cyclone Joy in January 1991 brought Townsville City its wettest January on record. Freshwater runoff led to the formation of a large riverine plume, both off the coast of Townsville (Chapter 5), and around major rivers such as the Fitzroy River (Brodie and Mitchell 1992). While there is some information on nutrient and chlorophyll distributions associated with these events (M. Furnas and A. Mitchell, Australian Institute of Marine Science, unpublished data), little is known concerning the effect of large amounts of freshwater on ichthyoplankton communities within the Great Barrier Reef lagoon. The objective of this chapter is to examine the effect of this plume on the distribution and abundance of ichthyoplankton in the central GBR lagoon. I asked the following specific questions:

1. Are distinct ichthyoplankton assemblages present inside and outside of the plume?

2. Do larval fishes aggregate at the riverine plume front?

3. Finally, can the observed distribution patterns of the larval fishes be related to the phytoplankton and zooplankton dynamics within the water masses determined in Chapter 5?

### 6.2 METHODS AND MATERIALS

#### 6.2.1 Sample collection

The low-salinity plume and associated front were observed from 19 January to 25 January, 1991 (Figure 5.1 Chapter 5). The plume front was located visually, by a distinct colour change between turbid plume water and clearer lagoon water. *Oscillatoria*, flotsam and foam were also concentrated at the frontal boundary, which aided in identifying the feature. Physical oceanographic data from Chapter 5 were used to determine convergent water velocities associated with the interface between the two water masses. The following equation was used to scale the upper bounds of the potential convergent velocity (pv) at the plume front (Govoni *et al.* 1989).

$$pv = (g \cdot \Delta \sigma_t)^{1/2} \cdot h$$

where  $g = \text{acceleration due to gravity (9.8 ms^{-2})}$ 

 $\Delta \sigma_t$  = difference in density between the two water masses

h =height of plume

*p* = average density of the two water masses

The height of the plume was not determined; Wolanski and Jones (1981) measured a plume height of three meters in an earlier study in the area, and this value was used in all calculations. Ichthyoplankton was collected using a 75 cm ring net fitted with 505  $\mu$ m mesh and a calibrated General Oceanics

digital flowmeter. Sampling was conducted on the following dates: 19 to 22 January, and 25 January. As it was necessary to locate the front visually, all sampling was conducted during daylight between 1000 and 1500 hrs. The net was towed between 0.5 and 1 m below the surface for 10 minutes, at approximately 1 m.sec<sup>-1</sup>. Three replicate tows were made at each of three stations; on, and parallel to, the plume front, and at stations three km inside (i.e. in plume water) and outside (i.e. lagoon water) of the front. The order in which stations were sampled was randomised to minimise the influence of time of day and tidal state on larval fish abundance. All samples were immediately fixed in 90% EtOH, which was replaced 24-36 hrs after collection. Fish larvae were removed from the samples under a dissecting microscope and identified to family level (Leis and Rennis 1983; Leis and Trnski 1989). The one exception was for the family Carangidae, where the tribe Carangini (type A carangids) was separated from all other carangids (type B carangids). Numbers were then converted to larval concentrations, i.e. numbers of larvae 1000<sup>-3</sup>.

### 6.2.2 Statistical analyses

The total ichthyoplankton data set, consisting of 45 samples by 50 taxa, was initially subjected to multivariate pattern analysis. A Bray-Curtis dissimilarity matrix was generated from the family/sample data set; this was then used as a basis for UPGMA clustering and non-metric multidimensional scaling (MDS) ordination techniques. In order to verify the reality of clusters determined by the UPGMA analysis, the cluster groups were mapped onto the MDS plot of the first and second vectors. A scree plot of Cramer values (Belbin 1988) from the cluster analysis identified the families that contributed most weight to each of the clusters. Bubble plots were then used to display the abundances of these species in each sample on the MDS plot. Analyses used the PATN statistical package (Belbin 1987).

"Approximate" analysis of variance was used to test for the influences of spatial and temporal variability on ichthyoplankton distributions (Legendre *et al.* 1990, Legendre 1993; see section 3.2.2.1). Briefly, each null hypothesis (i.e. no effect of position or time on larval distributions) was cast into a model matrix, which contained 1's in the within-effect positions and 0's elsewhere. A test of matrix correspondence (Mantel 1967) was then calculated between the data matrix (in this case the same Bray-Curtis

dissimilarity matrix from above) and various model matrices. This was compared to a null distribution of matrix correspondence values derived from randomly permuting one of the matrices 500 times. All tests were two-tailed, with  $\alpha$  value of 0.05. Tests for interactions between main effects utilised the partial Mantel's tests described by Smouse *et al.* (1986).

Further univariate analyses were conducted on the larval fish taxa identified by the multivariate techniques as contributing most of the variance to the data. ANOVA was initially used to examine the influences of cruise date and position on abundance of individual families. To give a more powerful test of spatial effects, we pooled samples through time and bootstrapped 95% confidence intervals on the overall mean abundance at each station. One thousand bootstrap estimates were calculated using the 15 samples from each of the three positions relative to the frontal boundary (inside the front, on the plume front, and outside the front). Ninety-five percent confidence intervals (CI) on the sample means were simply the 2.5 and 97.5 percentiles of the frequency distributions of the bootstrap estimates (Efron and Gong 1983).

### 6.3 RESULTS

#### 6.3.1 Hydrography

Physical oceanographic data presented in Chapter 5 showed the offshore movement of a shallow lens of low salinity water (approximately 20 ppt) off the coast of Townsville during the study period. A strong turbidity front was formed between turbid, plume water and clearer coastal water; flotsam and the blue-green algae Oscillatoria were also aggregated at the plume front. On the first day of sampling (January 19) the plume front was located 16 km from the coast. By the next day, the front had moved a further three km offshore. Several days later, the plume had reached a maximum distance offshore (30 km), and the turbidity front was reduced to a gradual change between green plume water and blue coastal water. Density characteristics of the two water masses suggested potential convergent velocities were initially high (up to 0.96 m.sec<sup>-1</sup>) on 18 January as warm, low-saline plume water moved out over cold, high-saline coastal water. Potential velocities dropped as the front moved further offshore (approximately 0.6 m.sec<sup>-1</sup> on January 23), as density differences between the water masses were reduced.

Table 6.1	Frequency and percent frequency of fish larvae collected at positions in coasta
water, alor	g the frontal boundary, and in low-salinity plume water, on 5 days in January 1991.

Coastal	Freq	%	Front (cont.)	Freq	%
Holocentridae	204	21.7	Bothidae	11	0.7
Mullidae	113	12	Tetraodontidae	9	0.6
Pomacentridae	100	11	Labridae	8	0.5
Carangid A	91	9.7	Platycephalidae	8	0.5
Gobiidae	56	6.0	Balistidae	6	0.4
Dactylopteridae	54	5.8	Priacanthidae	4	0.3
Apogonidae	46	4.9	Trichonotidae	3	02
Callionymidae	43	4.6	Nemipteridae	2	0.1
Diodontidae	43	4.6	Serranidae	2	0.1
Carangid B	38	4.1	Leptobramidae	1	-
Monacanthidae	18	1.9	Unidentified	60	4.1
Tetraodontidae	14	1.5	Total	1469	
Synodontidae	11	12			
Syphraenidae	11	12	Plume		
Bothidae	10	1.1	Carangid A	772	46
Lutjanidae	9	1	Gobiidae	102	6.1
Platycephalidae	8	0.9	Mullidae	89	5.3
Blenniidae	6	0.6	Apogonidae	57	3.4
Balistidae	5	0.5	Platycephalidae	55	3.3
Scorpaenidae	5	0.5	Lutjanidae	45	27
Microdesmidae	4	0.4	Scorpaenidae	40	2.4
Teraponidae	4	0.4	Scombridae	39	23
Scombridae	3	0.3	Carangid B	35	21
Clupeidae	2	02	Clupeidae	34	20
Mugilidae	2	02	Holocentridae	33	20
Nemipteridae	2	02	Teraponidae	27	1.6
Acropomidae	1	0.1	Bothidae	24	1.4
Cynoglossidae	1	0.1	Pomacentridae	24	1.4
Labridae	1	0.1	Monacanthidae	22	1.3
Ostraciidae	1	0.1	Mugilidae	22	1.3
Pseudochromidae	1	0.1	Syphraenidae	18	1.1
Siganidae	1	0.1	Dactylopteridae	16	1.0
Soleidae	1	0.1	Callionymidae	15	0.9
Trichonotidae	1	0.1	Diodontidae	11	0.7
Unidentified	28	3.0	Microdesmidae	10	0.6
Total	938	•	Priacanthidae	10	0.6
			Nemipteridae	7	0.4
Front			Lethrinidae	4	0.2
Mullidae	258	18	Tetraodontidae	4	0.2
Pomacentridae	171	12	Cynoglossidae	3	0.2
Holocentridae	136	9.3	Leiognathidae	3	02
Gobiidae	132	9.0	Leptobramidae	3	02
Carangid A	125	8.5	Opistognathidae	3	02
Dactyloptendae	98	6.7	Synodontidae	3	0.2
Apogonidae	/9	5.4	Carapidae	2	0.1
Carangid B	61	42	Gerreidae	2	0.1
Lutjanidae	45 .	31	Labridae	2	0.1
Callionymidae	30	25	Siliginidae	2	0.1
Scompridae	35	24	Ballstidae	1	-
Monacantnidae	33	22	Bienniidae	1	-
	18	1.2			•
Diadantidaa	16	1.1		1	-
Lothrinidae	10	1.1	Loptoconboli		•
Nierodoomidoo	10	1.0	Depudeebramidee		-
Supportidae	15	1.0	Signaidee	1	-
Syndoniidae	10	0.0	Solidaa	1	-
Sebeenidee	12	0.9	Trichopotidoo	1	-
Tompopidoo	10	0.9	Linidoptified	116	- 70
Biopplideo	10	0.0	Total	100	7.0
bienniidae	12	0.7	Total		_

This was presumably due to mixing processes along the frontal boundary. Indeed a degree of mixing must have been occurring, as salinity values of coastal water beneath the plume also dropped appreciably from measured values before the plume had moved across the stations (Figure 5.1).

#### 6.3.2 Ichthyoplankton

A total of 4,072 fish larvae, representing some 49 families, were collected from 45 plankton tows. The taxomomic composition of the samples showed substantial differences between water masses (Table 6.1). Type A carangids were the most abundant taxa, but were only dominant inside the plume, where they accounted for almost 50% of the larvae captured (compared to 8.5 % at the front and 9.7 % outside the front). Mullids were caught at all positions, although they were most abundant at frontal stations, representing 18% of the larvae captured at the front, 12 % outside the front and 5.3 % inside. Holocentrids were taken in high numbers outside and on the plume front (21% and 9.3% repectively), but were rarely captured inside the plume (2%). The pomacentrids showed a similar distribution, comprising 11% of larvae occurring outside the plume, 12% at the frontal boundary, and 1.4 % inside the plume. A number of additional taxa, although caught in lower numbers, also showed highly structured distributions. Scombrids and lutjanids were captured at a number of stations inside and on the plume front, but were rarely found in samples outside the plume. Platycephalid and scorpaenid larvae were captured almost exclusively within the plume.

Multivariate pattern analysis confirmed the differences in the distribution and abundance patterns of fish larvae among water masses. Cluster analysis suggested that four groupings may usefully be discerned from the data (Figure 6.1). The most distinct cluster (cluster D) contained plume samples from the first two days of sampling. Cluster C consisted of the remainder of the plume stations, along with three samples from each of frontal and lagoonal water masses, collected on the last three days. The final two groupings contained a mixture of both frontal and lagoon samples- cluster B contained samples largely from the final three days of sampling, cluster A samples from the initial two days. Multi-dimensional scaling largely confirmed the groupings obtained from the cluster analysis (Figure 6.2). Considerable separation was apparent between plume samples (cluster D) and front and coastal samples (cluster A) during the first two days of sampling. This pattern became less distinct during the final three days (clusters B and C).

A scree plot of Cramer values from the UPGMA clustering showed that type A carangids contributed the most weight to the identification of clusters (Cramer value 0.91; Figure 6.3). The families Mulllidae, Holocentridae, Scorpaenidae and Platycephalidae also had high Cramer values. Bubble plots of these five taxa showed that high numbers of type A carangids, platycephalids and scorpaenids were associated with cluster D- i.e. plume samples from the first two days (Figure 6.4). This pattern was most pronounced for the carangids as both platycephalids and scorpaenids were also abundant in several isolated samples from clusters B and C respectively. Mullids from days one and two were largely restricted to cluster A, which were predominately frontal samples, with several coastal samples, from days one and two. Holocentrid larvae were most abundant in cluster B, which included coastal and front samples from days three and four.

Mantel's and partial Mantel's tests were used to more rigorously assess spatio-temporal variability in ichthyoplankton numbers. These tests showed that there were significant effects of both station and date, as well as a significant station\*date interaction (Table 6.2). The similarity matrix did, however, show more affinity to the spatial model (r=0.326; partial r=0.334) than the temporal one (r=0.1; partial r=0.128), although both factors were clearly influencing larval fish distributions patterns.

**Table 6.2** Results of Mantel and partial Mantel tests against spatial and temporal models of variability. Prob(t) is the probability of the null hypothesis being true, obtained from Mantel's approximate test. In partial Mantel's tests, the matrix held constant is named after the brackets.

Source	٢	t	Prob(t)
(Larvae, station)	0.326	10.3	0
(Larvae, date)	0.1	3.0	0.001
(Larvae, station)date	0.334	10.5	0
(Larvae, date)station	0.128	3.9	0

Plots of the distribution patterns of total fish larvae, and of the five most abundant taxa, illustrate the variability both across the plume front and through the sampling period. Total numbers of larvae were initially high inside the plume front. In the latter half of the sampling program, greater numbers of larvae were captured at the frontal boundary (Figure 6.5). These data were reflected in significant station, date, and station\*date interaction effects in the ANOVA (Table 6.3). Mean abundances over all sampling dates were highest within the plume, although 95% CI's overlapped with those at

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the plume front (Figure 6.6). Frequency distributions of mean abundances from the bootstrap routine confirmed that abundance differed inside and outside of the plume front, with the magnitude of the frontal station intermediate between the two.

Type A carangids were abundant during the initial two days of sampling within the plume, but were largely absent during the rest of the sampling period (Figure 6.7). ANOVA detected a significant station effect, as well as a significant station\*date interaction (Table 6.3). Bootstrapped CI's at each of the sampling stations show that the carangids were significantly more abundant inside the plume than in frontal or coastal waters (Figure 6.8). Mean abundances inside the plume were almost an order of magnitude higher than on the front or outside it.

Mullid larvae were relatively abundant throughout the sampling period (Figure 6.9), with significant effects of both station and date (Table 6.3). Bootstrapped 95% CI's showed that larvae were significantly more abundant at the plume front than either inside or outside the front (Figure 6.10), which were not significantly different.

Holocentrid larvae were captured in low numbers during the first two days of sampling, and then only in coastal water (Figure 6.11). Abundances were higher during the final days of sampling, both on and outside the front. The ANOVA reflected this pattern, with significant station and cruise effects, along with a significant station\*date interaction. Mean abundances were highest in coastal waters, although numbers were not significantly different to those at the plume front (Figure 6.12). Abundances outside and on the front were significantly different to those inside the frontal boundary.

Pomacentrid larvae were captured in low numbers outside and on the plume front during the first two days of sampling (Figure 6.13). On 22 January, pomacentrid larvae were abundant at the plume front. The ANOVA detected significant differences between stations, but not between dates. There was, however, a significant station\*date interaction (Table 6.3). The plume front station had the highest numbers across stations, although 95% CI's from outside and on the plume front overlapped (Figure 6.14). Frequency distributions of the bootstrapped means showed clear distinctions between all three stations, although high variability at the front station precluded a significant difference between the frontal and coastal stations.

Finally, gobiids showed no clear association with either date or station (Table 6.3, Figure 6.15). ANOVA detected a significant effect of station, along with a significant station\*date interaction. Confidence intervals on the mean abundance at all stations overlapped (Figure 6.16), and the frequency distributions of means from the bootstrap analysis also indicated that gobiids did not appear to be influenced by the plume structure.

Source	MS	F value	Prob
Total larvae			
Station	0.34	23.72	0.0001
Date	0.06	4.4	0.0061
Station*cruise	0.33	22.57	0.0001
Carangids type A			
Station	0.62	13.55	0.0001
Date	3.90	2.16	ns
Station*date	1.50	5.21	0.0004
Mullids			
Station	0.64	3.47	0.044
Date	1.00	5.31	0.002
Station*date	0.40	2.17	ns
Holocentrids			
Station	2.67	19.87	0.0001
Date	0.84	6.27	0.0009
Station*date	0.34	2.56	0.0296
Pomacentrids			· · · · · · · · · · · · · · · · · · ·
Station	3.47	27.6	0.001
Date	0.27	2.1	ns
Station*date	0.57	4.55	0.001
Gobiids			
Station	0.92	5.30	0.01
Date	0.38	2.18	ns
Station*date	0.74	4.31	0.002

**Table 6.3** Results of a two-way ANOVA procedure, with position relative to the plume front (station) and sampling date (date) as main effects, for total larvae and the five families contributing most to cluster discrimination in the multivariate analysis.

## 6.4 **DISCUSSION**

Convergence zones are formed by a number of hydrographic phenomena in coastal waters (Kingsford 1990). Riverine plumes generate particularly strong convergent velocities, driven by density differences between lighter (in this case warmer and less saline) plume water and heavier (colder and more saline) coastal water (Garvine 1986). Studies documenting enhanced densities of larval fishes at plume fronts have emphasised the passive accumulation of positively buoyant or surface-seeking organisms (Govoni *et al.* 1989, Powell *et al.* 1990, Grimes and Finucane 1991, Govoni and Grimes 1992). Convergent zones undoubtedly act to concentrate zooplankton and larval fishes over small spatial scales of 10's-100's of meters (Kingsford and Suthers in press). In the present study, however, only a single family, the Mullidae, were significantly more abundant at the front than either inside or outside the plume. Vertical distributions will also have a marked effect on the degree to which such surface features will influence abundance patterns (Sabates 1990), and it is perhaps not surprising that mullids are among the most surface-oriented shorefish larvae in the study area (Leis 1991b).

The absence of consistently high numbers of larvae at the plume front in the present study may have been related to the strength of convergent flows at the frontal boundary. Potential convergent velocities were therefore calculated using the same numerical procedures as Govoni *et al.* (1989) used in their study of the Mississippi River plume and associated front. The results indicated convergent velocities of between 0.5 and 1 m.sec<sup>-1</sup>, which were higher than those from the Mississippi River plume front (0.1-0.3 m.sec<sup>-1</sup>) reported by Govoni *et al.* (1989) and similar to empirical data from the same area reported in a later study (Govoni and Grimes 1992). This suggests that that the failure to document consistently high ichthyoplankton abundance at the plume front was not due to differences in the strength of convergence between the Mississippi River plume front and the plume front sampled here.

There is little doubt that the low-salinity plume and associated front did have a profound effect on ichthyoplankton distribution patterns over larger spatial scales. A number of taxa were associated with either the plume or lagoon water masses. Carangids, platycephalids and scorpaenids were all found almost exclusively in the plume water, while other families were only rarely captured in plume water (holocentrids and pomacentrids). A previous study of the Mississippi River plume front found little evidence of faunal differences between water masses (Grimes and Finucane 1991). Kingsford and Suthers (in press) found that a number of larval fish taxa, including the families Gobiidae, Sillaginidae, Gerreidae and Sparidae, were found in highest numbers in plume waters off the coast of Sydney, Australia. They also noted a distinct ichthyoplankton assemblage associated with plume fronts. There was considerable day-to-day variability between larval fish distributions and hydrography. This variability may have been due to the pulsing of both physical factors such as tidal state and freshwater input, as well biological influences such as primary and secondary productivity rates.

Significant interactions between sampling date and position for all larval fish families in the present study also emphasised the dynamic nature of the plume and aassociated front in the present study. While sampling positions remained constant with respect to the plume front, the geographic position of these stations changed daily as the front moved offshore. Riverine plumes in the study area are directed offshore by source momentum, and are also deflected northward by a combination of the buoyancy differential between water masses and Coriolis forces (Wolanski and Jones 1981). In this study, the plume front moved progressively offshore during the sampling period. Initially the plume front was located eight km from the coast, and by the end of the study was approximately 20 km off the coast before lateral and vertical mixing along the interface presumably broke down plume integrity (Wolanski and Jones 1981). Several families, including the Holocentridae and Pomacentridae, were initially present in lagoon water but became more abundant at the front in the latter half of the sampling period. Aggregation at the plume front may have been due to the 'swathe' effect of the front as it progressed further offshore. Further support for this mechanism comes from the observation that frontal samples were far more similar to collections from lagoon waters than within the plume. Finally, both holocentrids and pomacentrids were found predominately in lagoon waters of the mid to outer GBR lagoon in earlier chapters, and were only rarely encountered in turbid coastal waters. These fish may, then, have accumulated at the front either by active avoidance of the turbid, lowsalinity plume, or alternatively may have been passively entrained at the plume front by convergent flows.

Vertical distributions were not considered in this study. The shallow nature of the plume (probably < four meters; Wolanski and Jones 1981) dictated that any comparisons between water masses be confined to surface collections. While this is unlikely to have confounded differences detected between water masses, it will almost certainly have restricted the number of families collected. Leis (1991b) found that most reef fish larvae in the northern GBR lagoon had highest concentrations deep in the water column during the day. Not surprisingly, the families that had peaks in density in surface waters (Pomacentridae, Holocentridae, Mullidae), were among the most abundant families captured in this study.

Planktonic characteristics of the water masses discussed in Chapter 5 may bear some relationship to the high abundance of several taxa within the plume. Total plankton abundance, densities of a number of copepod species and egg production of a common coastal copepod (*Acrocalanus gibber*) were all dramatically higher in plume waters than the lagoon water mass (chapter 5, McKinnon and Thorrold in press). Copepod nauplii form the basis of most larval fish diets (Leis 1991a), and growth and subsequent survival of young fish may be increased within riverine plumes. Dagg and Whitledge (1991) found exceptionally high densities of copepod nauplii within the Mississippi River plume, and suggested that the plume may provide enhanced feeding conditions for larval fishes. Fortier *et al.* (1992) also showed increased nauplii abundance within the Gaspe current, a bouyancy-driven coastal jet that advects estuarine waters into the Gulf of St. Lawrence. Taken together, these studies indicate that plume environments may be an important habitat for larval fishes in a number of coastal systems.

Ichthyoplankton studies on the Mississippi River plume have emphasised the influence of the plume front on larval fish abundances (Govoni *et al.* 1989, Grimes and Finucane 1991). Grimes and Finucane (1991) stated categorically that "ichthyoplankton were concentrated in frontal waters". The unbalanced nature of the sampling design (three plume stations compared to 21 front and 20 coastal stations), coupled with questionable statistical analyses, suggests that such a conclusion was not justified on the basis of the data they presented. Govoni *et al.* (1989) documented enhanced densities of fish larvae at the Mississippi River plume front, although variability at both coarse (between stations) and fine (between replicates) spatial scales meant that these differences were not statistically significant. The more intensive sampling program used in the present study may well have minimised between-replicate variability, and improved the power of the significance tests, as four of the most common taxa showed significant differences between stations. Differences between stations emphasised the taxon-specific effect of the plume on ichthyoplankton distributions. The plume front aggregated families with predominantly offshore larval distributions, although the narrow linear nature of the frontal structure necessarily limited the spatial scale over which it operated. Alternatively, the low-salinity plume probably constituted a rich food resource for those larvae able to take advantage of the enhanced plankton abundances within it. Given that plume waters may cover 1,000's of km<sup>2</sup> in this region (Belperio 1978), the low-salinity plume may have affected larval fish survival and recruitment far more than the associated plume front. A similar argument can be made for the temporal dynamics of the plume structure. Although the plume front broke down after a week, zooplankton abundances remained enhanced in the study area for at least 6 weeks (Chapter 5).

Attention placed on linear structures such as the Mississippi River plume front may have under-emphasized the potential of plume waters to provide enhanced conditions for growth and survival of fish larvae (Richardson 1981). Powell et al. (1990) found that, contrary to expectations, larval fish captured at the plume front were in worse condition than those inside and outside the front. As they noted, convergence associated with the front may have served to aggregate larval fish with weak locomotory abilities that perhaps were unlikely to survive. If this is the case then the high numbers of larvae at the plume front found by Govoni et al. (1989) and Grimes and Finucane (1991) may be of little significance to subsequent recruitment patterns, but may instead simply act to concentrate fish larvae with little prospect of survival. Plume waters in the present study apparently offered enhanced feeding conditions for larvae over a much broader area than the plume front. Given that plume waters can cover 1,000's of km<sup>2</sup> in this region (Wolanski and Jones 1981), the low-salinity plume may have affected larval fish survival and recruitment far more than the associated plume front. Although difficult to predict, and therefore sample, stochastic or chaotic meteorological events leading to pulsed availability of nitrogen (e.g. Jordan et al. 1991) or carbon (Thresher et al. 1992) in coastal waters may well be of considerable importance to survival and recruitment of fishes whose larvae inhabit coastal waters.



**Figure 6.1.** Dendrogram from UPGMA cluster analysis of family/sample marix. Positions with respect to front (outside front, on front and inside front) are labelled, along with cruise number (1 to 5).  $\beta$ = -0.1.



**Figure 6.2.** MDS ordination plot of vectors 1 and 2 from famiy/sample matrix, derived from a Bray-Curtis measure of dissimilarity. Groupings from UPGMA cluster analysis are super-imposed on MDS plot (see Figure 6.1). Stress = 0.15.



Figure 6.3. Scree plot of families against Cramer vaues from UPGMA clustering strategy. Five taxa with highest values were (in descending order) type A-carangids, mullids, holocentrids, platycephalids and scorpaenids.



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Figure 6.4b. (cont.).







**Figure 6.6.** Total larvae. Mean concentrations (+/- bootstrapped 95% confidence interval: top), and frequency distributions of bootstrapped means (bottom) generated by randomly selecting 15 samples from each of the positions relative to the front, with replacement (see section 6.2.2 in text).



**Figure 6.7.** Type A carangid larvae. Mean concentrations of total larvae (numbers 1000m <sup>-3</sup>, +/- standard errors)collected inside, on and outside of the plume front on five cruises in January 1991.



**Figure 6.8.** Type A carangid larvae. Mean concentrations (+/- bootstrapped 95% confidence interval: top), and frequency distributions of bootstrapped means (bottom) generated by randomly selecting 15 samples from each of the positions relative to the front, with replacement (see section 6.2.2 in text).






**Figure 6.10.** Mullidae. Mean concentration of larvae (+/- bootstrapped 95% confidence interval: top), and frequency distributions of bootstrapped means (bottom) generated by randomly selecting 15 samples from each of the positions relative to the front, with replacement (see section 6.2.2 in text).



**Figure 6.11.** Holocentridae: Mean concentration of larvae (numbers 1000m<sup>-3</sup>, +/- standard errors) collected inside, on and outside of the plume front on five cruises in January 1991.



**Figure 6.12.** Holocentridae. Mean concentration of larvae (+/- bootstrapped 95% confidence interval: top), and frequency distributions of bootstrapped means (bottom) generated by randomly selecting 15 samples from each of the positions relative to the front, with replacement (see section 6.2.2 in text).







**Figure 6.14.** Pomacentridae. Mean concentration of larvae +/- bootstrapped 95% confidence interval: top), and frequency distributions of bootstrapped means (bottom) generated by randomly selecting 15 samples from each of the positions relative to the front, with replacement (see section 6.2.2 in text).



Figure 6.15. Gobiidae. Mean concentration of larvae (numbers 1000m<sup>-3</sup>, +/- standard errors) collected inside, on and outside of the plume front on five cruises in January 1991.



**Figure 6.16.** Gobiidae. Mean concentration of larvae (+/- bootstrapped 95% confidence interval: top), and frequency distributions of bootstrapped means (bottom) generated by randomly selecting 15 samples from each of the positions relative to the front, with replacement (see section 6.2.2 in text).

## Chapter 7

# **General Discussion**

### 7.1 INTRODUCTION

Shorefishes support important commercial, artisanal and recreational fisheries throughout tropical oceans. While the actual yield from these fisheries may not be overly impressive (0.48 million metric tons in 1983, Longhurst and Pauly 1987), they provide an invaluable resource for fishermen with low incomes and few other food sources (Russ 1991). Understanding the population dynamics of these fishes is necessary both to develop effective management strategies for tropical fish stocks and more generally in the development of ecological theory capable of predicting abundance levels in marine populations. Much of the work on tropical marine fishes has been conducted on coral reef fishes. Reef fish biologists traditionally assumed that demersal resources, and not larval supply, were the major regulating factors in the control of community structure (Richards and Lindeman 1987). This view has now undergone major revision (Williams 1980, Doherty 1983, Victor 1986). The realisation that larval supply may be driving the demographics of adult populations (Doherty and Fowler in press) necessarily focuses attention on events occurring during the larval phase in the life cycle of coral reef fishes.

Research on temperate fish stocks have long recognised the potential for survival and transport during the larval stages to influence the abundance of fish stocks (Hjort 1914, 1926). While larval fish biologists working in temperate waters have generated a vast amount of literature on the early life history of marine fishes, temperate larvae are not necessarily good analogues for the larvae of tropical shorefishes. Developmental times are often much faster in the tropical waters, and tropical larvae may develop sensory and locomotory abilities at earlier ages than temperate counterparts. One can compare tropical and temperate larvae if full development of the caudal fin is used as a measure of locomotory ability (Richards and Lindeman 1987). In larval herring, *Clupea harengus*, the caudal fin is fully developed at about 20 mm (Fahay 1983), or 40-50 days (Townsend and Graham 1981, Henderson *et al.* 1984). Develoment of the caudal fin in larval gadoids such as *Gadus morhua* is complete at 15 mm SL (Fahay 1983) or 40-50 days (Bolz and Lough 1983). In contrast, percoid reef fish complete caudal fin development at 4-7 mm SL (Richards and Lindeman 1987), which we can assume to be approximately 7-10 days old (Thorrold and Milicich 1990, Victor in press). A sampling technique that can catch larvae up to the completion of caudal fin development will, then, be able to collect larval herring or cod up to 50 days old but will be able to catch reef fish larvae for only the initial stages of the larval phase (Clarke 1983). Choice of gear is a critical component of any planktonic study (Kingsford 1990). In the study of the larvae of tropical marine fishes it may assume even greater importance than studies of clupeioform and gadiform fishes in temperate environs have indicated (Methot 1986, Munk 1988, Potter *et al.* 1990).

#### 7.2 MAJOR FINDINGS

The development of light traps (Doherty 1987a) gives an added dimension to planktonic studies of fish larvae. Light traps appear to sample the pelagic juvenile stages of a number of reef fishes that are captured rarely in either plankton nets or midwater trawls (Choat et al. 1993). In the case of extremely active fishes such as scombrids, the light traps have enabled unique collections of these specimens to be obtained (Chapter 2). Size distribution comparisons between mid-water trawls and light traps strongly suggest that larger larvae and juveniles are simply not sampled effectively by the nets. There remains some debate as to whether this is due to active avoidance of nets, or the ability of the light traps to same large volumes of water (Choat et al. 1993). The result is, however, that light traps collect sufficient numbers of these fishes to allow distributions to be quantified and examined in a statistically rigorous manner. Conversely, however, light traps do not sample individuals smaller than approximately 10 mm SL. While the need for multi-gear sampling strategies to target different stages of the early life history of these fishes is obvious (Kingsford 1988), such programs have rarely been instigated (Gregory and Powles 1988).

A source of concern with the light traps is the perception that such techniques are necessarily qualitative, as it is not possible to convert light trap catches to standardized densities. It must be remembered, however, that all techniques are biased to some degree (Munk 1988, Chapter 2). Light traps differ from plankton nets in that environmental conditions such as ambient light levels and turbidity may effect efficiency of the trap. In this

study, the influence of ambient light levels was minimised by only sampling through a 10 day window around the new moon. Turbity presents a greater problem, especially given the differences noted in Chapter 5 across the transects. Two factors, however, argue against any significant effect of turbidity on light trap catches. No relationship was found between water clarity and catch rate. That is, numbers did not increase consistently as one went further offshore. Light trap data in both years were also dominated by catches at a single station in a single month. It seems highly unlikely that this was the result of an encounter with an exceptionally clear body of water at this station. The second piece of evidence relates to the response of fish to light in the differing water masses. Milicich and Thorrold (Austalian Institute of Marine Science, unpublished data) calculated that Pomacentrus wardi would respond to light from up to 80 m in Jerlov type 3 oceanic water that characterise the outer half of the central Great Barrier Reef lagoon. More importantly, this distance only changed by 5 m in the Jerlov coastal type 1 water found nearer to the coast. Assuming that the light traps are drawing fish from the surface waters only (a reasonable assumption for pomacentrids- P.J. Doherty, Australian Institute of Marine Science, unpublished data), this represents little more than a 10% increase in the volume of water sampled at the offshore stations. Clearly this is not enough to account for the differences in catches encountered during this study.

Plankton nets revealed relatively stable cross-shelf patterns, with a distinctive nearshore component characterised by gobiids, callionymids, leiognathids and teraponids; a cross-shelf group including nemipterids, carangids, platycephalids and scorpaenids; and an offshore group comprising lutjanids, scombrids, pomacentrids. These taxonomic affiliations were generally in agreement with a study conducted eight years earlier (Milward and Hartwick 1986), which suggests a high degree of temporal stability in these patterns. While multivariate analysis clearly identified that this cross-shelf trend contributed most of the variance within the data set, a significant temporal component was also identified. This was largely caused by samples from December 1989, when large numbers of lutjanids, nempiterids and carangids were captured on both transects, and all stations except the inshore station on both transects.

It is interesting to note that the December samples were collected after a prolonged period of strong south east winds (Chapter 3). Walker and O'Donnell (1981) suggested that nutrient levels and primary productivity were coupled to benthic processes by intermittent, wind-driven resuspension of bottom sediments. Gabric et al. (1990) documented a large chlorophyll a bloom after such a wind event from CZCS imagery of this area which they linked to resuspension of nutrients from sediments. While necessarily speculatory, it is possible that the large numbers of larvae may have been related to this wind event. Increased chlorophyll a levels could have led to increased planktonic abundances, and therefore enhanced feeding conditions and survival for larval fishes. There is some evidence that algal levels are related to copepod egg production rates in coastal waters of the Great Barrier Reef lagoon. Acrocalanus gibber, a common coastal copepod, appears capable of more than doubling egg production rates when hydrographic events produce a favourable food environment (McKinnon and Thorrold in press). Copepods appear to be the major food source for tropical reef fish larvae (Leis 1991a). Links between planktonic productivity and larval fish abundance and condition will be a profitable area for further study (Kiorboe et al. 1988).

Very different spatio-temporal patterns in the distribution and abundance of small fish in the central Great Barrier Reef lagoon were revealed by plankton nets and light traps. Unfortunately taxonomic differences largely confounded attempts to directly compare distribution patterns of individual taxa. Lutjanids, apogonids and carangids were common components of the plankton nets, but were only rarely captured in the light traps. Similarly lethrinids were very abundant in the light traps in the second year of sampling, but were an infrequent component of the plankton net catch. The families Clupeidae, Pomacentridae and Mullidae were, however, collected in reasonable numbers by the two techniques. Larval clupeids showed evidence of an inshore migration from mid and outer lagoon waters to nearshore areas. Larvae collected in plankton nets were largely restricted to mid-lagoon stations, while larvae were captured in high numbers by the light traps at inshore stations. Interestingly there is some evidence to suggest that the mackerel tuna, Euthynnus affinis, may migrate offshore from the central GBR lagoon to waters surround reefs in more offshore waters. Post-larvae of E. affinis were collected in high numbers at mid-lagoon stations in a later study using light traps across the LR transect,

while larger juveniles were collected two months later around mid and outer-shelf reefs (S. Thorrold and P. Doherty, Australian Institute of Marine Science, unpublished data). Given that post-larvae and juveniles of the different species moved in opposite cross-shelf directions, a strong behavioural component must be present in at least one of these migration patterns. Comparisons of the families Pomacentridae and Muliidae supported the inference drawn above that ontogenetic stages of the planktonic phase of reef fish were distributed in a qualitatively different manner. Both families were grouped with the offshore ichthyoplankton assemblage from plankton tow collections, while light trap samples were dominated by catches at the 16 km station on the LR transect in October. Interestingly, the mullids and pomacentrids showed cognate patterns within techniques, suggesting that the biotic and abiotic processes influencing the distributions of these larvae were acting in very similar ways between these two families.

Light trap catches in both years were dominated by a catches at a single station in one month. In 1988, a multi-specific patch of larvae were found 24 km off the coast on the CB transect, while in 1989 a similar patch was located 16 km off the coast on the LR transect. These data provide convincing demonstration of the presence of multi-specific patches of presettlement reef fish larvae in open waters, although the dimensions of these patches could not be accurately assessed. Several authors had speculated that such patches may exist, based on settlement patterns of reef fishes (Victor 1984, Williams 1986, Doherty 1987b). Indeed, the light trap data in this study appears to be qualitatively similar in some respects to those from moored light traps around Lizard Island (Milicich 1992). Milicich noted an extremely large pulse in the first year of sampling that was not repeated in 3 subsequent years of monitoring (Milicich 1992, Meekan 1992). Taken together, these data appear consistent with the hypothesis that major settlement events occur when occasional dense patches of larvae collide with reef habitats (Victor 1984, Williams 1986, Doherty 1987b). An alternative hypothesis, however, that the large pulse at Lizard Island may have been due to increased survivorship of locally-retained larvae cannot be discounted. While the degree to which Lizard Island is self-recruiting is unknown, Leis (1986) proposed that some retention may be occurring on the windward side where Milicich's (1992) light traps were moored.

Given that reef fish larvae may be distributed in meso-scale, multi-specific patches in the central Great Barrier Reef lagoon, what mechanism generates patch formation? Victor (1984) argued than since the labrids he examined had variable planktonic durations, the patch was unlikely to be the result of a synchronous spawning event (Canino *et al.* 1991, Davis *et al.* 1991). Rather, he hypothesised that some oceanographic front may act to aggregate, and then deliver, larvae to reefs in the San Blas islands. No oceanographic data were available, however, to assess this idea. Williams and English (1992) suggested that the presence of a meso-scale eddy may have led to anomolously high larval fish concentrations around Myrmidon Reef, in the central Great Barrier Reef. Again a lack of concurrent physical data linking oceanographic phenomena to larval fish abundance means that such relationships are of a speculatory nature only.

In this study, NOAA/AVHRR satellite imagery was used to examine temperature and turbidity across the sampling transects. While there appeared to be few gradients in SST across the region of interest, visible reflectance as measured by channel 1 on the AVHRR sensor showed considerably more structure (chapter 4). A gradient was observed in most images across the inner lagoon, with the outer limit of turbid, coastal water apparently set by resuspension of bottom sediments. A strong turbidity front between coastal and lagoon water on the LR transect was evident in a single image from October. Winds at this time were the light southeasterlies which, according to King and Wolanski's (1992) model, may generate a reverse current flow to the northeast along the coast. The presence of this front coincided approximately with a patch of reef fish larvae detected in light trap samples. It is possible that the front led to patch formation, either due to passive accumulation in the low current zone (Thomson et al. 1992), or alternatively to active aggregation at the frontal boundary (reviewed by LeFevre 1986). A similar mechanism cannot, however, be advanced for the patch located in 1988, which was located 24 km from the coast and therefore beyond the influence of coastal waters. The significance of the boundary between coastal and lagoon waters to larval reef fishes remains to be established definitively.

The offshore extent of the turbid coastal water mass appeared to influence the distribution patterns of smaller larvae from the plankon net samples (Chapter 4). The boundary between coastal and lagoon waters delineated ichthyoplankton with nearshore affinities from those clustered in an offshore grouping. This offshore group was found across the lagoon except at the inshore station of both transects. Interestingly, this group contained several reef fish taxa, including pomacentrids and lutjanids. These data are relevant to the distribution of adult reef fish across the central GBR, which also show strong cross-shelf trends. Williams and Hatcher (1983) were the first to suggest that these differences were not driven by adult ecology, but rather by the availability of suitable larval habitat. Roberts (1991) also suggested that larval habitat may influence large-scale distribution patterns of coral reef fishes in the Red Sea. Some anecdotal information lends weight to this hypothesis. Satellite imagery suggests that the coastal front intersects the Palm Islands, approximately 30 km north of Townsville, along the eastern (or offshore) coast of the island group (unpubl. data). Reef fish communities on this eastern shore are characterised by mid-shelf species. However, on the western side of the islands, reef fish communities are predominantly near-shore in affinity (D.McB. Williams, pers. comm).

Several potential mechanisms may act to determine associations of larvae within these different water masses. The simplest explanation is that there is insufficient cross-shelf water exchange to mix the larvae spawned in either water mass. Zooplankton distributions provide a test for this hypothesis as they are often closely linked to current regimes (Mackas and Sefton 1982), and as such may be useful as langrarian tracers of water movement (Thomas 1992). Results presented here and in a later study (McKinnon and Thorrold in press) also suggest that hydrography has considerable influence on zooplankton community structure across the inner GBR lagoon. Zooplankton assemblages appear to be coupled with the position and strength of a shear zone across the lagoon caused by interactions between the East Australian Current, prevailing wind conditions and a frictional effect due to bathymetry (King and Wolanski 1992). Offshore plankton communities move close to the coast when lonshore current velocities are sluggish, but are located further offshore when longshore velocties are high in either direction (McKinnon and Thorrold in press). Larval fish assemblages do not, however, show the same pattern. Both inshore and offshore assemblages were more tightly linked to turbidity gradients, apparently driven by bottom resuspension, than by the position of the shear zone. Assuming that the zooplankton communities are better tracers of water mass movements than larval fish, it wouild appear that hydrographic separation cannot explain maintence of distinct larval fish assemblages across the inner GBR lagoon. A caveat is necessary when interpreting these data, as the ichthyoplankton and zooplankton sampling were not conducted concurrently. However, larval fish community structure was similar to that documented eight years earlier by Milward and Hartwick (1987), suggesting considerable temporal stability. Similarly McKinnon and Thorrold's study spanned 20 months including two summers, which indicates that the conclusions drawn here were not affected by temporal confounding.

While hydrographic separation does not appear to account for larval fish assemblages across the inner shelf, two biological processes may be maintaining these patterns. Differential mortality, due to either high turbidity (in the coastal water mass) or food levels (low in offshore water mass) may act to selectively remove fish larvae from either water mass type. Alternatively, larvae may be actively avoiding moving between different water masses. While both hypotheses are plausible, we are unlikely to be able to test either without a much greater understanding of larval taxonomy than is presently known. As Roberts (1991) points out, survival rates in each of the water masses will need to be measured to test between the differential mortality and differential distributions hypotheses outlined above. Mortality rates of larval fish are notoriously difficult to quantify under optimal conditions, and indeed there are no estimates available for larval mortality for any coral reef fish larvae (Leis 1991a). It may prove to be more plausible to examine early-life-history scans of otoliths using electron microprobe or inductively-coupled plasma mass spectrophotometry (ICPMS) technology to determine if larvae are indeed making significant cross-shelf excusions (Radtke 1988, Townsend et al. 1991).

Coastal waters in the central GBR lagoon are characterised by consistently higher phyto- and zooplankton biomass than found in mid and outer lagoon waters (McKinnon and Thorrold in press, Chapter 4). Given that one might expect better conditions for early larval survival within coastal waters it seems paradoxical that a number of taxa appear to spawn in offshore waters, including members of the families Clupeidae and Lutjanidae. Larvae of at least some of these taxa appear to make inshore migrations to nearshore juvenile nursery grounds. One reason for this life history strategy might be that the oligotrophic lagoon waters may be

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relatively free from invertebrate predation pressures (Johannes 1978, Bailey and Houde 1989). While there are insufficient data avaliable to test this hypothesis, several factors sugggest potential predators may be aggregated in nearshore waters. Cuboid medusae such as the box jellyfish, Chironex *fleckii*, have a polyp phase found in coastal estuaries, and adults appear to be restricted to coastal areas (Baker and Williamson 1986). Gelatinous zooplankton were also occasionally extremely abundant in larval fish tows at the inshore stations of both the LR and CB transects, yet were rare or absent from offshore samples taken at the same time (personal observations). Oscillations in predator abundance have the potential to dramtically influence larval survival (Hewitt et al. 1985, Leak and Houde 1987), and hence subsequent recruitment strength. A far better understanding of the dynamics of predator populations within the central GBR lagoon is required before these ideas can be subjected to rigorous testing.

Riverine plume have considerable potential to influence recruitment dynamics of marine fishes. While most attention has focused on plume fronts (Govoni et al. 1989, Grimes and Finucane 1991, Govoni and Grimes 1992), the plume itself may be important both as a place of enhanced biological activity and as a cue for migration of coastal and estuarine species. In the present study zooplankton abundance and egg production rates of Acrocalanus gibber were significantly higher within low-salinity waters associated with terrestrial runoff. Several larval fish taxa were also largely concentrated within the plume, at least during the initial sampling Interestingly the fish larvae concentrated in the plume, occasions. including carangids, platycephalids and scorpaenids, were from the crossshelf taxonomic grouping determined in Chapter 3. These larvae appear capable of tolerating a wide range of turbidity, and may have gained significant nutritional advantage from residing in plume waters. Powell et al. (1990) could find no evidence of enhanced condition of larvae located at the front of the Mississippi River plume. While this lack of sensitivity may have been due to the dynamic nature of the front, the plume itself provided a temporally-stable environment for at least a week. Methods comparing growth and condition of larvae inside and outside of the plume show promise, however better taxonomic resolution is required for such studies.

Without adequate means of monitoring recruitment strength of many taxa, it is difficult to assess the effect of the plume on recruitment of the families whose larvae were abundant at the time of plume formation. Year-class strength of all species recruiting to shallow windward reef slopes on midshelf reefs adjacent to the plume have, however, been monitored since 1982/83 (Williams et al. in press). In 1990/91, almost all species (predominately pomacentrids and labrids) recruited in extremely low numbers. Overall, recruitment was down an order-of-magnitude on the previous eight yea mean (D.McB. Williams, Australian Institute of Marine Science, unpublished data). This has been attributed to the exceptional wet season with low-salinity waters affecting both pre-settlement fish and newly-settled individuals (D.McB. Williams, personal communication). Reef fish larvae were generally absent from plume waters, although mullids were concentrated at the plume front and both holocentrids and pomacentrids became more abundant at the plume front during the latter part of the study (Chapter 6). Kingsford and Suthers (in press) also found that mullids were located at the front of riverine plumes off the coast of Sydney, Australia. They did note that a number of reef fish families, including pomacentrids, were preferentially distributed in plume waters. Clearly geographic and species-specific responses to the plumes make generalisations about the impact of such structures on survival and recruitment of larval fishes difficult.

### 7.3 CONCLUSIONS

A major focus of temperate fisheries ecology is determining at what stage in the life history recruitment levels are determined. Debate continues as to whether this occurs during the early larval stages (Lasker 1981), or at latelarval early juvenile stages (Peterman *et al.* 1988, Bailey and Spring 1992). The contention that the survival of early larval stages largely controls recruitment strength has been around in various forms since Hjort (1914, 1926) first proposed the 'critical period hypothesis'. Indeed, this hypothesis has been a central paradigm in temperate fisheries ecology. There is, however, little evidence for this hypothesis in temperate regions (May 1974, Peterman *et al.* 1988). Several workers have shown that larval indices are not good predictors of subsequent recruitment to fished stocks several years later (Peterman *et al.* 1988, Bailey and Spring 1992). In tropical reef environments, a direct link between larval supply and recruitment

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(Milicich *et al.* 1992) argues that recruitment strength is determined during the larval phase (Robertson *et al.* 1988, Meekan *et al.* 1993). Many reef fish species have relatively short larval durations compared to fishes from higher latitudes, which both shortens the time frame during which mortality must act on larval populations, and may lead to higher overall mortality rates. Both considerations suggest that detecting causes of differential larval survival may well be more tractable in tropical ecosystems than in temperate regions.

Short larval durations found in many tropical fishes may also act to reduce density-dependent regulation, as predators have less time to aggregate and competitive relationships have less time to develop (Bailey and Houde 1987). Thus tropical fish populations may be less buffered from climatic variability than temperate fishes (Doherty and Williams 1988). If variability in recruitment is occuring in coral reef systems over meso-scales (Victor 1984, Doherty 1987b), then phenomena such as wind events leading to nutrient resuspension (Walker and O'Donnell 1981, Gabric et al. 1990), upwelling (Furnas and Mitchell 1987), or freshwater input (Chapters 5 and 6) may impact on recruitment by enhancing larval survivorship. Of course the above phenomena will not necessarily lead to increased larval survival. Increased primary and secondary productivity may also lead to blooms of invertebrate predators, which may impact deliteriously on larval survival and recruitment. A thorough understanding of the effects of meteorological and hydrographic events on the entire planktonic community, and of the trophic links within this community, will be necessary to answer such questions. Such events are impossible to predict, and therefore interactions between climate, plankton dynamics and recruitment will only be elucidated by long-term, multidisciplinary monitoring programs.

Proposing such multidisciplinary studies is neither novel or revolutionary (Richards 1982, Boehlert 1986). While such long-term commitments are difficult to extract from funding agencies, it would seem that anything less will have little chance of making substantial advances in our understanding of the processes regulating population dynamics of tropical fishes. Large, multi-disciplinary programs such as the US GLOBEC-funded study of the physical and biological oceanographic processes controlling fish stocks on Georges Bank (U.S. GLOBEC News No. 4, August 1993) remain perhaps the best opportunity to make significant advances in our understanding of the factors determining recruitment variability in marine fish populations. The present study demonstrates that given new developments in both biological sampling methods and satellite technology, such programs are eminently feasible on smaller, but biologically relevant, spatio-temporal scales. The renewed presence in space of a satellite (SeaWiFS) capable of determining ocean colour (Wickland 1991) will further enhance the prospects of considerable advancements in determining the causes of variable survival and subsequent recruitment of tropical fishes.

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## **APPENDIX 1**

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29 August 1994

Professor J.H. Choat Department of Marine Biology James Cook University of North Queensland Townsville Q4811 AUSTRALIA

Dear Professor Choat,

I have recently received copies of comments of the external examiners' on this thesis. I believe that most if not all of the comments represent differences of opinion rather than errors in the methodologies that I used. Appendix 1 therefore represents my detailed response to points raised by each of the external reviewers.

Yours sincerely,

Simon Thorrold

## Appendix 1

Response to comments of external examiners

Examiner 1:

1. Chapter 3, page 44. Justification of critical level for Mantel's test for 1988 data.

My rationale for applying an a value of 0.01 in the Mantel's tests from the 1988 data reflects the fact that total numbers only were used in this analysis. In the following year, all larvae were identified to family level. Interactive effects were also not considered in 1988, and interpretation of these results were necessarily more conservative (see page 41).

2. Values for keys in figures 4.1-4.9. The examiner wanted to see actual values on scales shown in figures 4.1-4.9. Unfortunately, there are no "correct" values to be presented in these figures. While it is possible to get reasonably accurate temperatures from the NOAA/AVHRR satellites in temperate regions, the algorithms to correct for atmospheric moisture levels in north eastern Australia have yet to be developed. Temperatures are therefore accurate to probably no more than  $+/-2^{\circ}$ C. Rather, the approach used here is to use *gradients* in SST and turbidity to look for oceanographic features. This does not rely on accurate measures of SST and turbidity, but rather assumes that Rayleigh and aerosol scattering did not change across the area of interest in each individual image (see page 85). However, in the false-colour enhancement procedure, the scaling factor was kept constant among images, so that as much temporal information was retained in the images as possible (again explained on page 85). Therefore the keys in the figures can be considered ranging from 0 to 1, or 0 to 100, but are relative numbers only.

3. Tables 5.1 and 5.2, pages 124 and 125. The examiner wanted to see station and cruise means. Cruise and station means (with accompanying estimates of standard error) for both chlorophyll and zooplankton data are presented in figures 5.5-5.8. There would seem to be no reason to duplicate the data by tabulating as well- the figures allow a much easier appreciation of the data than would be achieved in a table.

## Examiner 2:

1. Non-parametric equivalents not used when analysing light trap data in chapter 3. The examiner appears to be referring to the fact that light trap data for individual families were not analysed statistically. He suggests that there may have been non-parametric tests may have been appropriate. The problems with analysing the light trap data is obvious when examining the data plots. Variances are high- indeed a single catch in a single month at a single station represented more than 80% of the total number of larvae collected by this technique in both years of the study. This also has the result of leaving 0's in most of the cells. Non-parametric tests based on rank ( the tests to which I presume the examiner refers) are not a panacea for this kind of data. Indeed the examiner appears to be unaware that the non-parametric tests he is advocating do not assume normality but DO assume homogeneity of variances (see Potvin and Roff (1993) Ecology 74: 1617-1628). I would argue that it is specious to *attempt* to statistically analyse such data, and stand behind the graphical approach used here.

2. Type 2 error associated with the bootstrap test of no effect of time on night on light trap catches on page 20. There is no way of rigorously applying power analysis to bootstrapped means. The technique of bootstrapping is relatively new, and there is not the same theoretical basis for power analyses that is available for ANOVA. Indeed the distribution-free nature of the test is one of the reasons why it is being used increasingly by a number of people. However, one only needs to look at the means and CI's to come to an intuitive feeling for the power of the test. Ninety-five percent confidence intervals were between 25 and 30% of the mean for each of the 3 times of night. Given that I am comparing spatio-temporal influences whose means differ by, in some cases, over 2 orders of magnitude, I stand by the assertion that differences in the time of night are extremely unlikely to have generated this pattern.

3. Failure to apply SNK-type tests on the individual ANOVA's of plankton net data in Chapter 3. This criticism seems unwarranted, as the only time SNK-type

tests were not applied throughout the thesis was when significant interactions in the ANOVAs were detected. Of course it is not valid to use *a posteriori* multiple comparisons tests when significant interactions are present.

4. Use of a comparatively small net in Chapter 3. The choice of a small net simply reflected the gear available at AIMS- the research boat I used was not equipped with a hydrographic winch capable of towing large nets, despite my efforts to outfit it with one. Some points need to be made. Firstly, the tows were made at night, which will have led to less avoidance of the relatively small net. Secondly, sub-surface tows were made so as to fish the same water mass as the light traps were fishing. Examiner 1 notes that the traps may have been drawing larvae and pelagic juveniles from deeper waters. However the available evidence suggests that light traps fished at several depths catch very different larval assemblages, suggesting that there may be comparatively little vertical movement of larvae into the light traps. In this situation, I feel somewhat between a rock and a hard place. However, I think I adopted a conservative approach by fishing both the plankton net and the light trap within the same depth stratum. The available evidence (Leis 1991a) suggests that there is little vertical structure in ichthyoplankton distributions at night. This is not the case during daylight hours. Finally, I feel obliged to point out that there is evidence that it doesn't matter what size net you tow, you will not capture the late-stage larvae taken in the light traps in a net (Choat et al. 1993). Indeed, Clarke (1983) showed that larvae were actually uniformly susceptible to towed nets of any size until they reached a critical age at which they were no longer susceptible to any towed gear.

5. Lack of field verification of King and Wolanski's (1992) model. The examiner's criticism of the model developed by King and Wolanski seems misplaced. King and Wolanski's model was indeed parameterized by field observations from multiple deployments of current meters across the central GBR lagoon. The criticism that the model could be better validated can be levelled at any modelling study- if the model is completely field-verified there is clearly no need for a model. I realise that this chapter was more speculatory than others presented here, but as noted by one of the examiners, I made this clear in the text. I simply conclude that there is more evidence for the sediment-resuspension model than King and Wolanski's shear zone. Clearly this is the

case. King and Wolanski's model may be wrong, and the shear zone may be located in a different position, but I fail to see how that alters my conclusions based on the data presented by King and Wolanski, Belperio and in this thesis.

6. Apparent errors in Figures 6.6 and 6.8. These data have been rechecked, and found to be correct. I remain unsure of why the examiner thought these figures may have contained errors.

## Examiner 3

1. The examiner noted that it would have been beneficial to have current measurements along with the light trap data. Unfortunately, it was not practicable to measure current velocities at the station- this would have necessitated the deployment of current meters in surface waters of a major shipping channel. However, this was one of the reasons for developing the use of drifting traps in this dissertation. By allowing the traps to drift with the current, thereby reducing the possibility of differential water flow confounding differences in abundance amongst traps and deployments.