Distributions and Diets of the Larvae of Tropical Shorefishes near the Northwest Cape of Australia

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ABSTRACT

The importance of understanding the factors influencing growth and survival of larval fishes and their effect on subsequent recruitment has been recognised in temperate areas since the late 1800's. Despite this, our knowledge of these topics is severely limited for tropical larval fishes. In this study, early stage larval fishes were sampled using towed bongo plankton nets at sites on the southern North West Shelf of Australia (NWS) (21º49'S, 114º14'E), between October and February of 1997/98 and 1998/99. The first summer was characterised by El Niño - Southern Oscillation (ENSO) driven upwelling and high primary productivity, compared to the second summer when water temperatures were warmer and primary production was lower. I examined 9944 fish larvae from 76 families captured with the bongo nets. Benthic percoid shorefishes dominated surface assemblages in both summers and this pattern may be typical of tropical shelf environments. Abundance and diversity of larval fishes were lowest in October and increased from November through to February. Assemblages displayed weak cross-shelf patterns with a few taxa being more abundant at inshore sites (e.g. monacanthids), but others were more abundant offshore (e.g. scombrids). Although the composition of assemblages remained relatively consistent, many taxa (e.g. pomacentrids and carangids) showed differences in abundance between summers. Multivariate analyses found no relationships between abundance patterns of larval fishes and biophysical variables such as temperature, salinity and zooplankton biomass. Seasonal changes in abundance may thus reflect differences in the spawning activities of adult fishes and/or larval survival.

Knowledge of the diets of tropical fish larvae is limited to only a few taxa. Here, we describe the diets of 591 individuals from 50 families of tropical larval shorefishes collected off the Northwest Shelf of Australia (21º49'S, 114º14'E), effectively doubling the number of families for which have we dietary data. The diversity of prey items eaten differed significantly among families. The majority of fish larvae ate copepods but there were some interesting exceptions. Chaetodontids ate only chaetognaths, acanthurids and nemipterids ate appendicularians, and tetraodontids ate predominately non-copepod prey (44% decapod larvae, 20% bivalves and 15% protists). Within the fish families that specialised on copepod prey there were marked differences in the types of copepod prey, with a clear preference shown for calanoid copepods,

particularly small calanoids such as *Bestiolina similis* and *Temora* spp. Copepod communities in the area were food-limited and we suggest that the ability of some larval fishes to feed on components of the microbial food web may be an important determinant of their success.

Further research into the feeding ecology of tropical larvae should consider the relationship between fish condition and prey type within the overall biophysical environment of the larvae. Identification of tropical larvae to species is still problematic and the use of genetic techniques may improve taxonomic resolution. Increasing our knowledge of the behaviour of tropical fish larvae will assist in interpretation of predator-prey relationships.

STATEMENT OF THE CONTRIBUTIONS OF OTHERS

Fees for this masters were covered by an Research Training Scheme (RTS) place. I received no stipend and funded myself though part and full time work. My supervisors, Mark Meekan (AIMS), Dave McKinnon (AIMS) and Mark McCormick (JCU), read and commented on various drafts of all written work and provided funding to send me to two conferences (Australian Society of Fish Biologists in Cairns 2002 and Australian Coral Reef Society 2003 in Townsville).

The icthyoplankton samples were collected by the Australian Institute of Marine Science (AIMS) as part of a 2 year project on the biological oceanography of the North West Shelf of Australia. Samantha Duggan (AIMS) sorted and identified the zooplankton data used in the prey selectivity calculations. The environmental data used was collected by AIMS as part of their project and made available for me to use with my fish distribution data. John Carleton (AIMS) advised me on appropriate data analysis techniques and also undertook the multi-variate regression tree (MRT) analysis used in the analysis of environmental data with the fish distribution data, as this required a specialised software package.

AIMS funded a visit to the Australian Museum in order to confirm fish identifications. Assistance with fish identifications was received from Jeff Leis and Tom Trnski (Australian Museum), Vicki Bates (AIMS), and Mike Kingsford (JCU). Dave McKinnon identified the gut contents of the larval fishes.

The CSIRO data used in the distribution data was provided to me through Peter Young and CSIRO staff.

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1 General Introduction

Most marine fishes are extremely fecund. Despite this very few of the larvae that hatch from these eggs survive the planktonic stage. One of the consequences of these life history traits of high egg production and differential mortality is that small variations in larval survivorship can create large variations in the number of fish that enter juvenile and adult habitats (Fogarty *et al.* 1991, Koslow 1992). This has important implications for the management of exploited species and for this reason factors affecting the mortality of planktonic larval fishes has been a key focus of research in fisheries ecology since the late 1800's (Heath 1992).

A central topic of research in this field has been the link between physical factors, production processes, and the survival of fish larvae. This work suggests that inter-annual variation in the temporal coincidence of larval fish and their prey contributes to recruitment variation (Lasker 1981, Cushing 1990). However, research to date has centred mostly on a few commercially valuable fish species from temperate areas and from upwelling systems in tropical areas (e.g. Olivar & Shelton 1993, McLaren *et al.* 1997, Napp *et al.* 2000), where production is periodic and is driven by high levels of large celled algal species such as diatoms. These plankton blooms form the basis of food chains that support high concentrations of large copepod species, which in turn are preyed upon by larval fishes. Work within these systems has lead to the conclusion that high prey abundance is critical for the survival of first feeding larvae (*sensu* Hjort 1914). However, small copepod species are abundant in all oceans of the world (Hopcroft *et al.* 2001) and there are alternate pathways of primary production (microbial and picoplankton), which can be utilised by other fish species (Daly & Smith 1993, Mousseau *et al.* 1998). Trophic pathways in such systems might produce a dissipation of energy at levels below those of consumers such as larval fish and result in a weaker link between primary production and fish numbers (Runge 1988).

Description of distribution and abundance patterns is the first step in determining the events that may influence the survival of larval fishes in the plankton. Variation in larval assemblages is known to occur vertically, horizontally, seasonally, and because of the underlying habitat (Leis 1993). The spawning patterns of adult fishes (Doyle *et al.* 1993, Nonaka *et al.* 2000) and physical and hydrographic features such as upwellings

(e.g. Murdoch 1990a, Roy *et al.* 1992), estuarine plumes (e.g. Kingsford & Suthers 1994), tidal and coastal shelf fronts (e.g. Lochman *et al.* 1997) contribute to this variation. Larvae also have a variety of behavioural (Leis 1991) and physiological (Govoni *et al.* 1986) capabilities that alter with development (Fuiman & Higgs 1997), which may affect their distribution patterns. Interpretation of spatial and temporal patterns of distribution and abundance of larval fishes requires consideration of the diverse scales on which these factors act.

In comparison to temperate environments, relatively little is known of the distribution or ecology of fish larvae from tropical systems, particularly those adjacent to coral reefs. Indo-Pacific tropical coral reefs have the greatest diversity of fish anywhere, with over 1000 species from c. 241 families (Lowe-McConnell 1987) occurring in this region. Moreover, tropical ichthyoplankton assemblages are known to contain a mix of both meso- and epi-pelagic species as well as those from the reef itself (Ahlstrom 1971, 1972, Nonaka *et al.* 2000). This taxonomic diversity reflects a variety in reproductive strategies (viviparous, brooders, migrating and non-migrating spawners, Johannes 1978); egg types (pelagic or benthic) and sizes (from mm to cm, Thresher 1988, Thresher & Brothers 1989); larval durations (from a few days to months); growth rates (Cowen & Sponaugle 1997, Searcy & Sponaugle 2000); sizes at settlement (from mm to cm); larval morphologies and behavioural capabilities (Leis *et al.* 1996). This variation in life history traits, in addition to spawning activities of adults that are often protracted, results in tropical ichthyoplankton assemblages that have a high diversity of taxa and contain a mixture of developmental stages.

The primary causes of mortality of larval fishes in the plankton are starvation and predation (Hunter 1976). These act on morphological and physiological characteristics of the fish larvae, in particular, body size and growth rates (Miller *et al.* 1988, Houde 1989). The growth rates of fish larvae are affected by both intrinsic (e.g. egg size, genetics, maternal condition) and extrinsic (e.g. food quantity and quality, temperature) factors. However, from the perspective of an individual larval fish, its goal in life is to eat, grow and avoid being eaten, so prey availability is paramount to survival.

Consequently, the next step for examining factors that affect the survival of larval fishes is a description of the prey types utilised by different larvae. The seasonal variation in

the types and sizes of available prey, as well as physical processes affecting this production, has been suggested to affect the success of larval feeding. In temperate areas, prey availability has been a focus for research for well over a century (Heath 1992). A variety of factors have been identified and found to contribute to variation in growth and survivorship of larvae. These include the quantity and quality of prey (Anderson 1994); location and timing of plankton blooms (Cushing 1990); and interaction with physical factors (e.g. currents and circulation patterns, Iles & Sinclair 1982, temperature, Buckley *et al.* 1984, and turbulence, Dower *et al.* 1998). In contrast, in tropical waters, although the importance of planktonic processes are recognised (Robertson *et al.* 1988, McCormick & Molony 1992, 1995), very little research has occurred into factors affecting the survival of tropical fish larvae during the planktonic phase of their life.

The taxonomy of tropical larvae is still in its infancy and this is a major obstacle to answering questions about the planktonic lives of larval fishes. In temperate systems it is often possible to identify larvae to species when examining relationships between feeding, growth and survivorship. However, identifications to this level are very problematic in tropical systems due to the diversity within many genera that does not, as yet, allow individual species to be recognised. A further complicating factor is that it is often difficult to obtain sufficient material of an individual species for the desired analyses (Leis 1993). For these reasons, generalisations about the ecology of tropical larval fishes are usually made at the level of family or subfamily, which assumes that the capabilities and development of larval fishes within these groupings are similar.

Relatively little research has been conducted on ichthyoplankton in tropical waters and this is particularly so off the western coast of Australia. The west coast of Australia, unlike the west coasts of other Southern Hemisphere continents, is unusual in the lack of strong persistent upwelling (c.f. the Humboldt current system off South America and the Benguela off Africa). Instead the presence of the southwards flowing, warm water Leeuwin current, counteracts the tendency for the system to upwell (Pearce 1991). The North West Shelf of Australia (NWS) is a broad shallow part of the continental shelf that receives very little terrestrial run-off from the adjacent arid landscape. Nutrients may be supplied by weak summer upwelling events, tropical cyclones and through tidal motion (Holloway *et al.* 1985), which is predominately along-shelf near the coast and

cross shelf at the shelf break (Holloway 1983). Pelagic secondary production in the area appears to be food limited (McKinnon & Duggan 2001). Close to North West Cape (NWC), the shelf narrows, reducing the transition between the inshore waters of Exmouth Gulf and the oceanic waters of the Indian Ocean. Just south of the Cape, Australia's second largest coral reef, Ningaloo, extends southward parallel to the coast. The southward flowing Leeuwin Current forms off the NWS, bringing warm tropical water along the coast, and counteracts upwelling by the West Australian Current. The Leeuwin Current, although present all year, is weakest between November to April and it is during these months that the wind driven, predominately northward flowing Ningaloo Current forms (Taylor & Pearce 1999). Inter-annual variations in the strength of these currents are affected by ENSO events (Pearce 1991).

1.1 Aims

In this thesis, I aim to:

1) review the effect of prey selectivity on the growth and development of marine larval fishes with a particular focus on the relevance of this to tropical larval fishes;
2) describe the family composition, distribution and abundance patterns of larval fish assemblages on the southern Northwest Shelf of Australia over two summers;
3) identify potential biophysical factors that may determine temporal patterns in ichthyoplankton communities;
4) describe the diets of larvae in 50 families of tropical shorefishes;
5) explore whether the prey types eaten differed among taxa; and
6) examine prey selectivity for a subset of co-occurring larvae.

2 Literature Review

2.1 INTRODUCTION

2.1.1 Background

Recruitment variation is regarded as the main influence on adult population abundance; thus, an understanding of events affecting this is of great interest (Heath 1992). Feeding has been connected to the survival of larval fishes and hence recruitment. The seasonal variation in the types and sizes of available prey, as well as physical processes affecting this production, has been suggested to affect the success of larval feeding (Hjort, 1914, Cushing 1975, Lasker 1981, Cushing 1990).

Several hypotheses link survival to the temporal coincidence of larvae and their prey, whether through local productivity or a variety of physical processes ("critical period" *sensu* Hjort 1914, "stable ocean" Lasker 1981, "match mismatch" Cushing 1990). These assume that prey abundance is important to larval survival. Alternate hypotheses relate recruitment variation to physical processes affecting the retention of larvae in nursery grounds regardless of the feeding conditions (Hjort 1914, Iles & Sinclair 1982). However, the differences in scale between examining physical processes and predator-prey interactions have problems that require consideration (Taggart & Frank 1990).

Body size and growth rates have been linked to survival (Miller *et al.* 1988, Houde 1989). Larger, faster growing larvae may be less susceptible to predation and starvation by virtue of their size alone, and by reducing the time spent in the vulnerable planktonic stage, resulting in increased survival compared to smaller larvae. Growth rate is affected by both intrinsic (e.g. egg size, genetics, maternal condition), and extrinsic (e.g. food, temperature) factors. The feeding conditions alone experienced by the larvae may ensure faster growth, although within a population larvae that are able to grow fast may have increased probabilities of survival compared with others experiencing the same conditions, even in poor feeding environments (Meekan & Fortier 1996). In addition, fish experiencing higher temperatures develop faster; thus this may be an important influence on growth rate. It has been suggested that tropical larvae are likely to experience faster growth rates than temperate fish as they are living at higher temperatures, however, if food limitation were a problem their faster physiological rates would result in increased mortality due to increased energetic demands (Houde 1989).

This review is only concerned with the feeding processes of pelagic larval fish. The importance of prey availability, its interaction with, and effect on, growth and development, as identified from temperate studies will be examined to see how applicable it may be to tropical marine fish larvae. The intrinsic factors that affect the growth and development of marine larval fish are outside the scope of this review; however, some extrinsic factors will be discussed.

2.1.2 Terminology

The larval period relates to the first few weeks of life, from hatching through to metamorphosis, during which dramatic changes occur in morphological, physiological and behavioural traits. Newly hatched larvae will have quite different abilities from larvae a few days later. Although definitions vary as to what constitutes the larval period (Heath 1992, Leis & Carson-Ewart 2000), this review will consider it to cover the time from first feeding to when the larvae leave the pelagic environment. Where applicable, specific reference will be made to certain life history stages; "First feeding" larvae generally refers to larvae that are switching from obtaining energy from their yolk sac (endogenous) to planktonic (exogenous) feeding (Heath 1992). "Flexion" occurs when the notochord turns upwards and the caudal fin forms and in many taxa, this may coincide with fin development (Leis & Carson-Ewart 2000). "Growth" is considered to have occurred when biomass increases with time, whereas "development" refers the maturation of characters.

2.2 LARVAL FEEDING

2.2.1 Physiological and Behavioural Capabilities

To obtain energy for growth a larval fish needs to successfully encounter, capture and digest prey. Developmental changes will influence the types and sizes of prey that larvae are able to utilise. Temperate feeding studies have predominantly been on Clupeiform or Pleuronectiform species, whereas Perciform larvae dominate tropical waters, particularly those near coral reefs (Leis & Carson-Ewart 2000). The

physiological (Govoni *et al.* 1986) and behavioural (Leis 1991) capabilities of these groups will be very different.

Detection of prey will be influenced by their size, motion, smell and pigmentation (Buskey *et al.* 1993) as well as the relative motions of predator and prey (Dower *et al.* 1997). Larval fish are visual planktivores (Hunter 1981, Gerking 1994), thus the development of visual acuity will influence prey perception. Larvae of the tropical fish, *Premnas biaculeatus*, were found to have well developed visual acuity and a higher feeding success rate at a smaller size than comparable studies found for temperate clupeid species (Job & Bellwood 1996). However, this comparison was based on similar sized larvae, which do not allow direct comparison due to developmental differences of similar sized taxa (see size considerations). Development of swimming abilities will also affect how successful a larva will be in locating and capturing prey. Some tropical fish species are shown to rapidly increase swimming abilities during the larval period (Figure 1, Fisher *et al.* 2000). This is especially marked following flexion, which occurs at a smaller size for many tropical fish compared to temperate clupeids.

Feeding rates are often determined by gut content analysis. Larval fish are selective feeders, which will determine the observed prey in their guts, and differential digestion of various prey types can lead to over- or underestimates of their importance in larval diets (Govoni *et al.* 1986). Most larvae will start out with a relatively straight undifferentiated gut (Leis & Carson-Ewart 2000). This persists in clupeiforms wheras in many percoid species a convoluted and well-differentiated gut will develop (Govoni *et al.* 1986). Convolutions may increase the resident times of prey in the guts and thus assimilation efficiency. This could be over estimated however, as larvae with coiled guts will be more likely to retain food in the gut and are less likely to purge the guts upon capture than are straight-gutted larvae (Govoni *et al.* 1986).

Smaller or soft-bodied prey may be digested faster than larger or hard-bodied prey (McLaren *et al.* 1997, Sutela & Huusko 2000), suggesting that assimilation may vary with both the size and type of prey. Additionally, temperature may also affect digestion rates, as metabolic processes are faster at higher temperatures (Houde 1989). These factors need to be taken into consideration and analysis of prey selection from the gut should only consider the foregut contents to reduce these affects. Thus, interpretations

of ingestion rates from gut contents need to consider species-specific differences in gut morphology and digestive abilities.

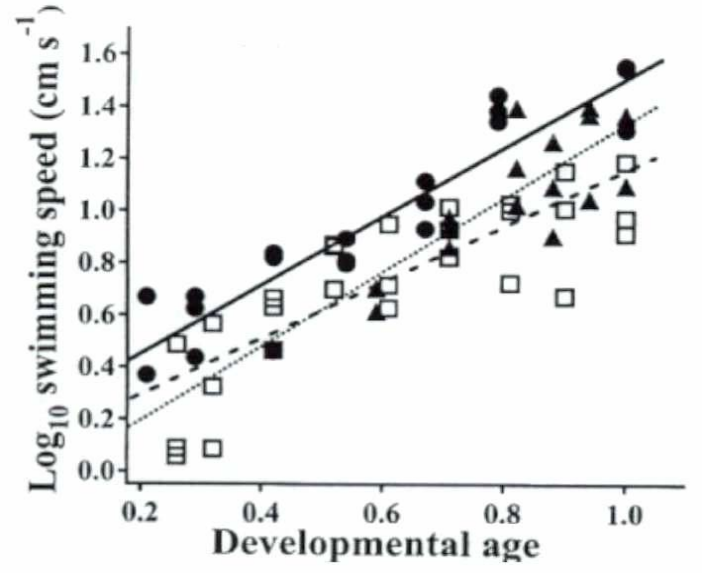

Figure 1. Development of swimming ability in tropical fish larvae.
Pomacentrus amboinensis (●), *Sphaeramia nematoptera* (□) and *Amphiprion melanopus* (▲). Developmental age = total age/ total larval duration, where total age = age of fish (days post hatch) + egg duration and total larval duration = larval duration (days post hatch) + egg duration. (Source : Fisher *et al*, 2000)

Many studies utilise a visual assessment of gut fullness as a measure of feeding success (Young & Davis 1990, McLaren *et al.* 1997, Rissik & Suthers 2000). Although this is a subjective measure, bias can be minimised if guts are separated and coded so origin is not known during assessment (Rissik & Suthers 2000). Furthermore, consideration must be given to gut morphology when using this measure to compare different species, as this will affect the results.

2.2.2 Prey Type

Studies from both tropical and temperate areas show that larval fish eat a wide range of microzooplankton prey including copepods, tintinnids, appendiculeria, mollusc veligers, chaetognaths, rotifers, dinoflagellates, fish larvae, phytoplankton and ciliates (Hunter 1981, Leis 1991). Yet, in any one species, even if only for part of their larval development, the life stages of copepods predominate in the diet. This probably reflects their abundance in the microzooplankton. In multi-specific natural assemblages, the degree of dietary overlap varies considerably (Govoni *et al.* 1983, Jenkins 1987, Fortier

& Harris 1989, Economou 1991, Gaughan & Potter 1997), which likely relates to the prey availability in their feeding environment. However, species-specific patterns of selection are always evident but alter with larval development and prey availability.

First feeding larvae tend to be euryphagous and specialisation becomes more evident with ontogeny (Hunter 1981), and is especially marked in piscivorous species (Figure 2). Scombrid larvae generally commence feeding on a range of prey including dinoflagellates, copepods and appendicularians (Young & Davis 1990). Utilisation of fish prey occurs after the development of swimming abilities and gut differentiation (Jenkins *et al.* 1984). Thus, changes in types of prey consumed will be affected by the rate of developmental change (Figure 3). This has often been generalised into size dependent considerations (see Size Considerations). However, the perceived euryphagy of first feeding larvae may be the result of very few studies identifying prey beyond broad taxonomic categories (e.g. see Figure 2), but Lasker (1975) reported selection for different species of dinoflagellate by the northern anchovy *Engraulis mordax*.

Parallels in diet specificity occur between taxonomically related species, although this is often overridden by inter-specific differences. Gadoid larvae have all been found to depend primarily on copepod life stages (Last 1978b, 1980, Economou 1991). However, in the North Sea, haddock (*Melanogrammus aeglefinus*) had a broad diet that included non-copepod prey, although other gadoids preferentially selected different copepod species (Economou 1991). Pleuronectids also consume copepod stages but include in their diet a larger proportion of appendicularians compared to other groups of fish larvae (Last 1978a, Liew 1983, Jenkins 1987, 1988). Of eleven larval flatfish species caught in shelf waters of the Great Barrier Reef, three preferred copepods; five species preferred appendicularians; two preferred a mix of chaetognaths and appendicularians; while copepods and appendicularians predominated in one species (Liew 1983). Additionally, interoceanic affinities of predator-prey relationships are also evident. *Trachurus declivis*, off Tasmania, preferentially selected the copepod *Microsetella rosea* (Young & Davis 1992), whereas *T. symmetricus*, off California, selected *M. norvegica* (Arthur 1976). This points to prey selection being related to larval morphology, behaviour and physiology as well as prey characteristics, such as behaviour, size, and shape, which aid in recognition and capture.

Larval fish may act to optimise survival by utilising high calorific foods when available. Calanoid copepods have been found to preferentially select the most nutritional food available (Kleppel & Burkart 1995). This may explain the consistently higher levels of carotenoid pigments and lipids found in highly pigmented calanoid species compared to *Oithona* spp. (Mitchell 1991). Preferential selection of calanoid copepods has been found in both temperate (Pepin & Penney 1997) and tropical fish species (Mitchell 1991) when prey was not limited.

Above all, availability may override preference. The larvae of *T. declivis*, a temperate fish, altered their diet with distribution and abundance changes of prey (Young & Davis 1992). By comparison, the larvae of the tropical fish, *Hypoatherina tropicalis*, did not increase prey specialisation with ontogeny and this was possibly related to the poor feeding conditions encountered by these larvae in One Tree Lagoon (Schmitt 1986). Therefore, the feeding conditions encountered will be reflected in the fish's guts by the prey consumed (see Feeding environments).

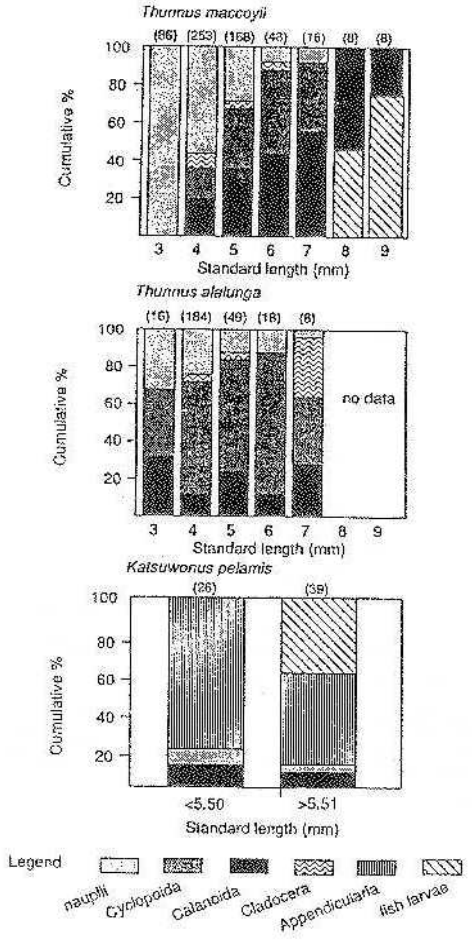

Figure 2. Frequency of occurrence of major prey taxa in relation to larval fish size class for 3 species of tropical Scombridae from the Indian Ocean.
Numbers of larvae examined are given in brackets. (Source: Young & Davis 1990).

2.2.3 Size Considerations

Most larval fish eat microzooplankton, which are considered the proportion of the plankton between 20 and 200µm (Hunter 1981). One problem associated with assessing the influence of prey availability on larval fish survival was the use of standard ichthyoplankton nets of either 500µm or 333µm to sample larval fish prey. These nets under sample microzooplankton leading to problems with the interpretation of the importance of prey abundance to larval fish survival (Frank 1988). This problem is particularly highlighted in recent work demonstrating that in tropical waters up to 80% of the available copepod biomass would not be sampled by a 600 µm net, by comparison in temperate waters nearly 75% of the available copepods would be missed using a 505µm net (Hopcroft *et al.* 2001). Thus, the availability of suitable prey for larval fish may have been severely underestimated in many studies to date.

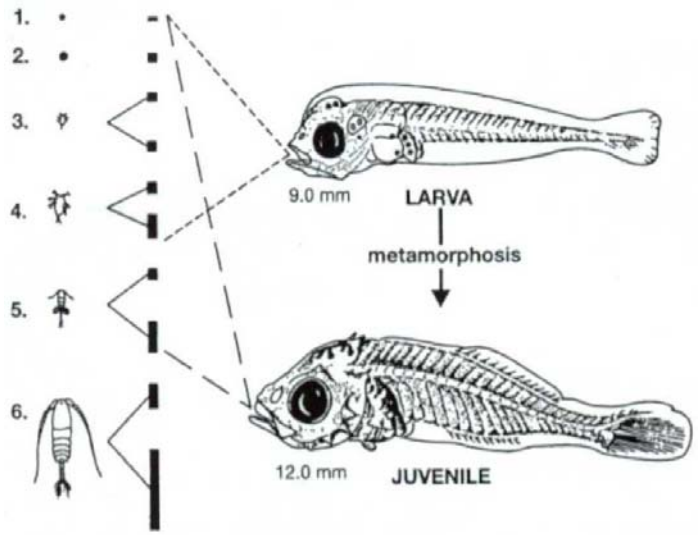

Figure 3. Schematic representation of prey preferences for a 9.0 mm larva and a 12.0 mm pelagic juvenile redfish, *Sebastes* spp.
The prey are represented as eggs, nauplii and copepodites for *Calanus finmarchicus* (Nos. 2, 4 and 6) and *Oithona similis* (Nos. 1, 3 and 5), with the bars representing their sizes, drawn to scale with respect to the redfish. The dashed lines enclose the preferred prey types. The figure emphasises that *O.similis* copepodites are not a preferred prey, even though they are very similar in size to *C.finmarchicus* nauplii. (Source: Anderson 1994).

Prey size has been related to prey selectivity. Many studies have demonstrated strong positive relationships between larval size and mouth gape, which is usually, measured as mandibular length (Shirota 1970, Pearre 1986, Munk 1997, Scharf *et al.* 2000). While minimum prey size often remains the same during ontogeny, maximum size increases with mouth size (Govoni *et al.* 1983, Sabates & Saiz 2000). The mean rate of increase of prey size and gape size varies between species (Figure 4). This relates to

larval morphology, but also points to the need to understand the behavioural scope of larval fish in view of prey availability (Schmitt 1986, Bremigan & Stein 1994, Gaughan & Potter 1997, Pepin & Penney 1997). Thus, if abundance of the preferred prey size is low then the larvae will be more likely to continue eating smaller prey sizes to obtain enough energy. However, if larger sized prey is available the larvae will be able to utilise this prey as mouth size increases.

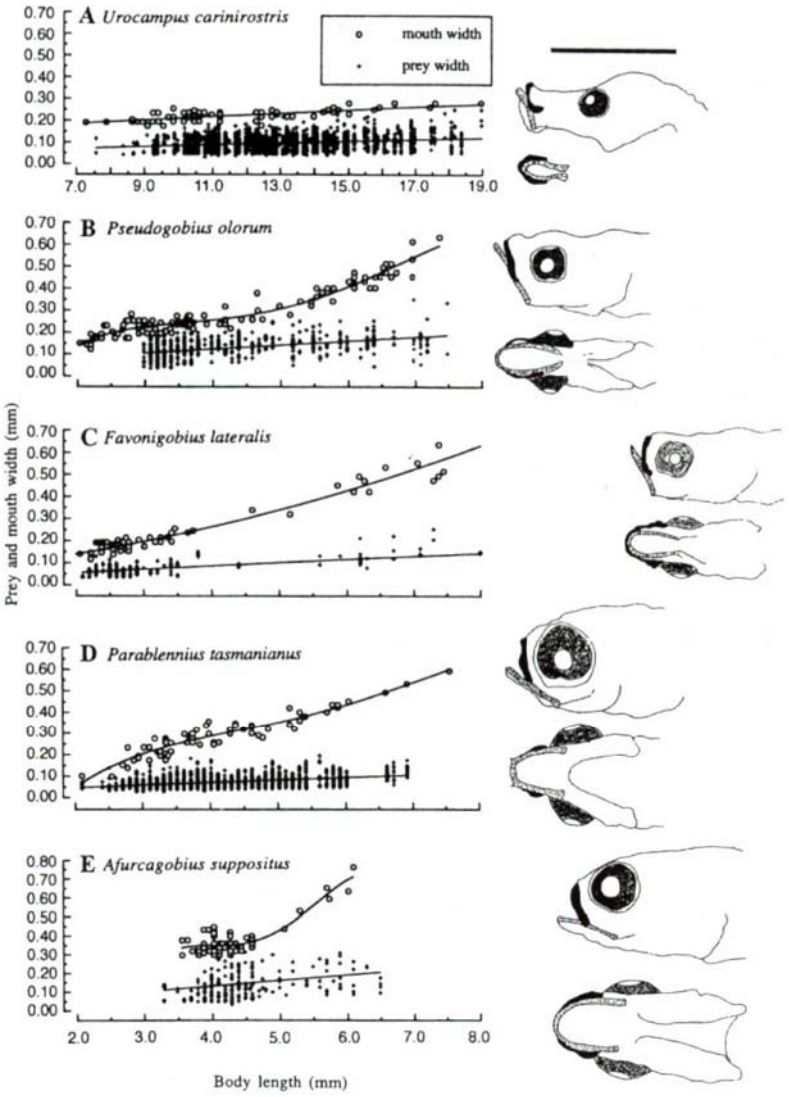

Figure 4. Prey width and larval mouth width for larvae of 5 species of fish caught in Wilson Inlet between October 1988 and April 1989.
Lateral and ventral views of the head of a representative larva of each species are also given; the upper jaw is indicated in black, the lower jaw is indicated with stippling (scale bar equals 1.0 mm). The examples were all taken from a 5.00 mm larva, except for *Urocampus carinirosstris,* which was taken from a 10.5 mm larva. (Source: Gaughan & Potter 1997).

Some studies have suggested that although the absolute prey size increases, the ratio of predator size to log transformed prey size remains constant (Pearre 1986, Munk 1992, 1997, Scharf *et al.* 2000). These represent different viewpoints. The absolute increase of size of prey relates to a change in the ability of the larvae to obtain larger sized prey due to an increase of gape, development of prey capture ability and visual acuity. Thus, consideration of this measure is useful when considering impact on the prey community. In comparison, consideration of the ratio of predator to prey length relates to energy requirement per larval size and gives an indication of energetic costs (Sabates & Saiz, 2000). So, this measure is more useful when asking questions relating to the bio-energetic cost for the larvae.

The increasing size spectrum of prey consumed by larvae as they grow could relate to improving their survival chances by maximising their use of available energy sources (Houde 1997). Thus, an optimal foraging strategy for a larva will be to maximise prey ingestion in relation to encounter rates. Smaller prey will be harder to see but easier to catch and more abundant, whereas larger prey will be easier to see but may be rarer and harder to catch. As the larvae grow the ability to catch larger prey may mean this prey is disproportionately more important for energetic requirements but maintenance can occur by utilising smaller prey. Therefore, it may be the biomass spectra of the available prey that will ultimately determine the useable food resource for the larvae (Munk 1997). Production processes will affect this and the benefits to the larvae will be developmentally and species specific.

Inter-specific comparisons based on size need to consider the physiological and behavioural capabilities of the larvae (Fuiman & Higgs 1997). Last (1980) found that herring, *Clupea harengus*, sprat, *Sprattus sprattus* and sand eels, *Ammodytes marinus* all took smaller prey at comparable lengths to other species. All these species have an elongated body form and he suggested that if comparable developmental capabilities are considered then food types between species are very similar. The developmental differences between a 5.0mm clupeiform and a 5.5 mm perciform larva (Figure 5) will result in drastically different prey capture abilities. This highlights the importance of considering larval capabilities when making inter-specific comparisons and not just size differences

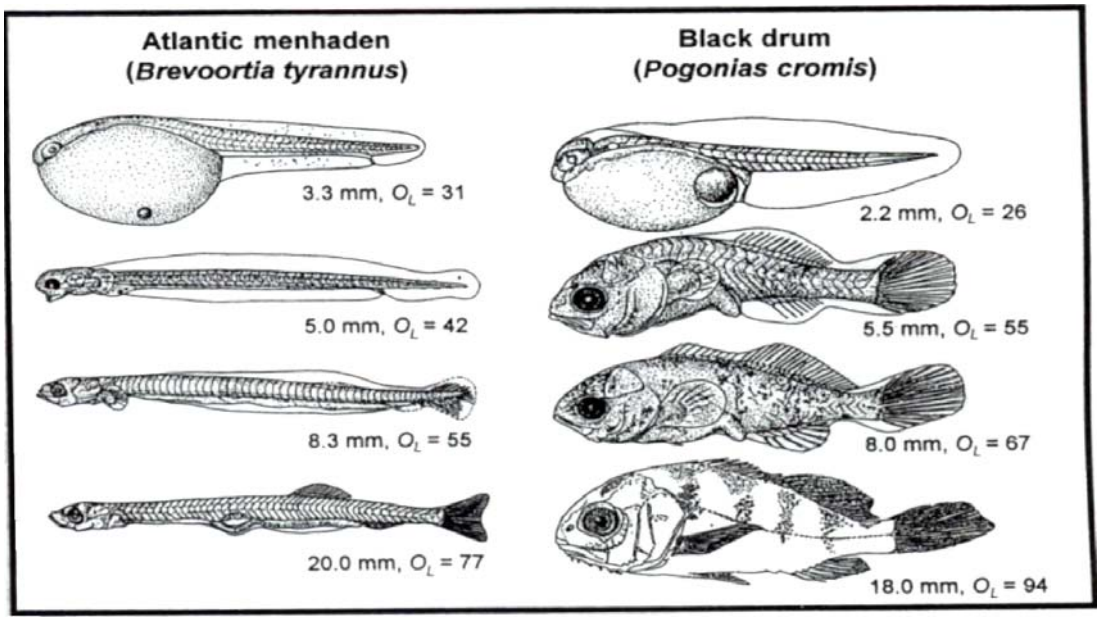

Figure 5. Comparison of clupeiform (Atlantic menhaden *Brevoortia tyrannus*) and perciform (Black drum *Pogonias cromis*) larvae.
Uppermost pair of drawings show substantial differences in morphology at similar stages of ontogeny (O_L). Remaining drawings show substantial differences in morphology at similar lengths. (Source: Fuiman & Higgs 1997).

2.2.4 Timing of Feeding

Larval fish are visual predators (Blaxter 1986b) and this is supported by both tropical and temperate studies finding that they are predominantly diurnal feeders. In field studies assessment of feeding activity has generally been interpreted from gut fullness, which usually show that feeding is lowest at night and peaks of feeding occur at dawn and dusk (Last 1980, Young & Davis 1990, McLaren & Avendano 1995, McLaren *et al.* 1997). The types and sizes of prey consumed and the digestive capabilities of the fish species for particular environmental conditions will affect this pattern (see Physiological and behavioural capabilities). Assessment of larval fish prey selection needs to take account of diel feeding variability when making statistical comparisons (MacKenzie *et al.* 1999).

2.2.5 Vertical Distribution

Both fish larvae and their prey exhibit differences in their vertical distribution often on a daily cycle. Walleye pollock (*Theragra chalcogramma*) larvae have been found to swim in the horizontal when suitable food is located but exhibit vertical swimming behaviour when no food is available (Spring 1996 in Napp *et al.* 2000). This may act to maintain their position in patches of food once located or to locate food patches when none is available (Owen 1981 in Napp *et al.* 2000). Vertical distribution of fish larvae and their prey has been related to species specific foraging behaviours acting to maximise feeding in relation to light intensity (Hillgruber *et al.* 1997) or an optimal foraging strategy in relation to food availability and predators (Fortier & Harris 1989). However, the development of visual abilities by individuals within taxa and the functional differences of these abilities between taxa will affect these strategies. Thus, it may be these differences in visual capabilities that will determine the vertical distribution of larval fish and thus the depth at which they will be able to forage effectively (Job and Bellwood, 2000).

2.3 FEEDING ENVIRONMENTS

2.3.1 Feeding locations

The availability of prey is important to larval fish and this will be determined by where they feed. Prey is not distributed evenly throughout the pelagic environment and certain hydrographic features have been found to be of particular importance. Larval fish feed in a wide range of these features such as upwellings (e.g. Murdoch 1990b, Roy *et al.* 1992), tidal and coastal shelf fronts (e.g. Lochman *et al.* 1997) and estuarine plumes (e.g. Kingsford & Suthers 1994). The significance of these features will differ. For example, the nutritional importance of an estuarine plume front was found to depend on the identity and origin of a particular larval species. The kyphosid, *Kyphosus* spp., fed more in the plume than in shelf waters compared to the mugilid, *Liza argenta*, which fed equally well in all water masses (Rissik & Suthers 1996). Although in the eastern Bering Sea different processes have been identified operating in the shelf and oceanic water masses, which have different consequences for larval feeding success (Napp *et al.* 2000). Therefore, when assessing the relevance of a physical feature to larval fish

feeding, consideration needs to be given to the particular species and the conditions they may be suited to exploit.

The types of productivity present around these features will affect the sizes and types of prey present to be exploited by the larval fish. Research has concentrated on fish species including cod (*Gadus morhua*) and herring (*Clupea harengus*) that utilise energy through classic food chains by exploiting the seasonal production of high concentrations of large copepod prey in temperate seas. This has lead to the idea that high concentrations of prey may be necessary especially for first feeding larvae. Furthermore, the prevailing view has been that tropical seas represent poor feeding environments due to the presence of smaller copepods species and lower productivity levels and therefore that food may be limited. However, early developmental stages and small copepods dominate in both tropic and temperate seas (Figure 6, Hopcroft ***et al.*** 2001). Energy can be moved through microbial and picoplankton pathways (Cushing 1990, Mousseau ***et al.*** 1998), and variation can occur on a daily, seasonal or interannual basis (Daly & Smith 1993). This challenges the traditional view. Thus, fluctuations in larval fish survival may be less tied to factors affecting prey abundance *per se*, but rather associated with variations in the resulting sizes and types of prey produced.

The presence of many of these hydrographic features and the factors influencing production occurs on a large or meso-scale, while larval fish behaviour and prey selection operates at small scales, which make reconciliation difficult (Taggart & Frank 1990). The small-scale patchiness of larvae and their prey is recognised (e.g. Jenkins 1988); however sampling this small-scale patchiness and relating it to the abilities of larvae to locate prey is problematic. It may be that an understanding of these small-scale processes is required in order to elucidate what is affecting survival of individual fish larvae. Possibly patch selection rather than prey selection may determine an optimal foraging strategy (Winkler & Orellana 1992). An understanding of these processes may lead to a better understanding of how feeding success effects recruitment success.

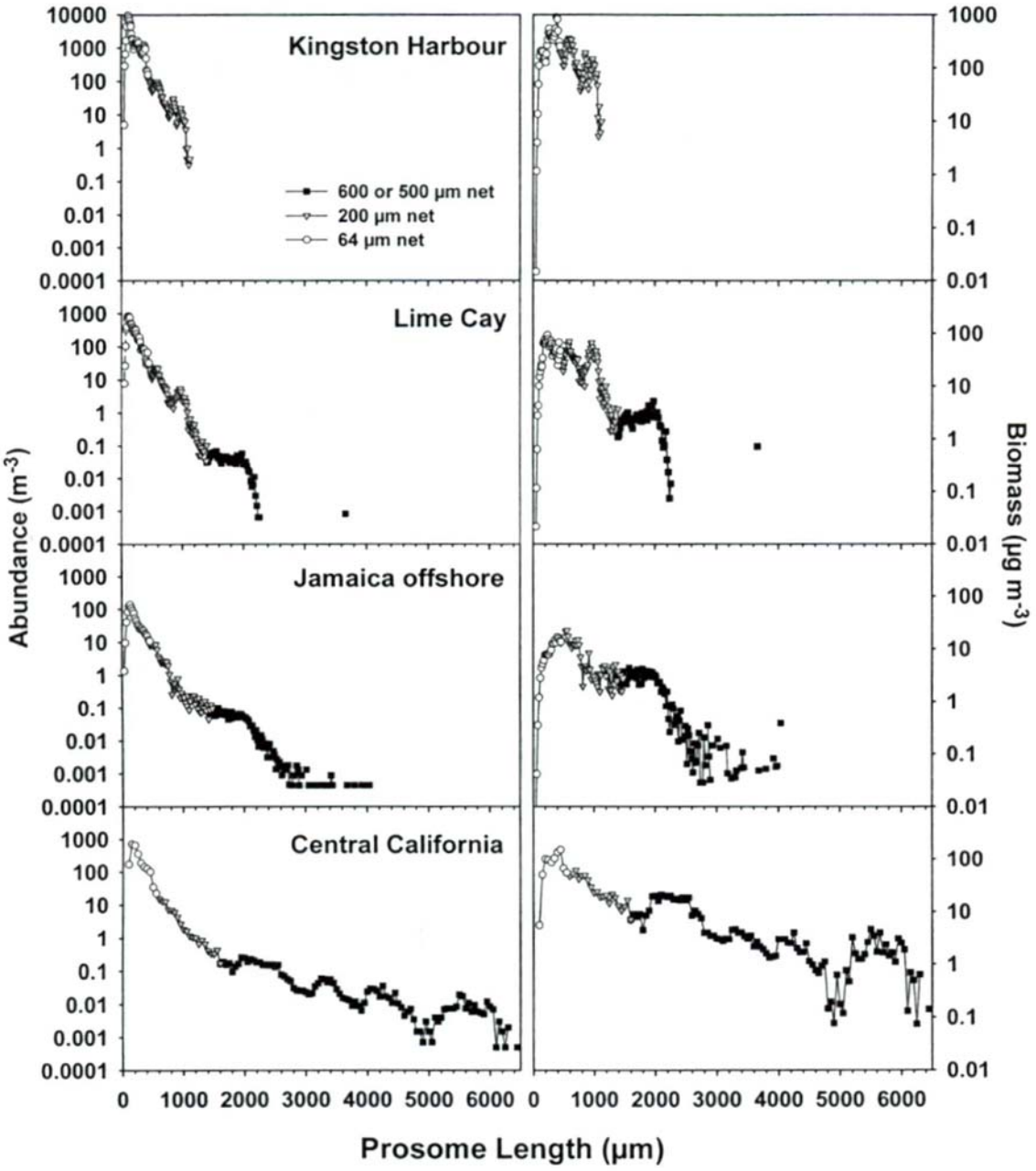

Figure 6. Composite abundance and biomass size spectra of zooplankton from 3 tropical sites in the Caribbean, Kingston Harbour, Lime Cay and Jamaica offshore, and temperate sites off Central California.
All composites based on three different mesh sizes of nets and averaged over seasons. Values are normalised to a 10 µm length interval. (Source: Hopcroft *et al.* 2001).

2.3.2 Physical factors – Temperature and Turbulence

A number of physical factors have been determined to affect the feeding success of larvae. Temperature has often been cited as an important influence on larval survival both indirectly by influencing productivity and directly by affecting prey assimilation and larval development (Ottersen & Loeng 2000). Larvae living at higher temperatures will have faster metabolic rates and thus if food is limited this may result in poor

condition and reduced survival (Houde 1989). Although production levels in the tropics may be lower than in temperate areas (but see Feeding Environments) there is little evidence for reduced feeding rates, as many larvae will display a high incidence of feeding (Houde & Lovdal 1984, Schmitt 1986). In fact, tropical larval goatfish have been shown to survive periods without food and thus demonstrate being adapted to exploit a patchy feeding environment (McCormick & Molony 1992).

When the effects of temperature are removed, the weight growth relationship shows similarities across taxa and between feeding environments in both tropic and temperate areas (Figure 7, Houde 1990, Houde & Zastrow 1993). In fact, temperature may have more effect on survival than body size (Houde, 1990). Temperature history has been demonstrated as important in determining developmental rates in tropical goatfish (McCormick & Molony 1995). To be able to elucidate the effects of temperature on the growth and development of marine larval fish temperature data are required in conjunction with prey selection and growth information. Although, separating these effects from other factors would require multi-factorial experiments.

Turbulence has received much attention recently, mostly in connection to small-scale turbulence and how it affects the encounter rates of larvae and their prey (for review see (Dower *et al.* 1997). Problems with determining the significance of small-scale turbulence are related to difficulties in separating turbulence effects from predator and prey behavioural effects and to the practice of averaging turbulence rates, which may mask the importance of instantaneous velocities. MacKenzie and Kiorboe (2000) studied instantaneous velocities and demonstrated that, at least for the pursuit of prey, increased turbulence could decrease the detection of prey by larval fish compared to those in calm conditions. Moreover, small-scale variation in turbulence has shown that the benefits on short-term growth rates are obtained at intermediate levels of turbulence (Gallego *et al.* 1996). Dower *et al.* (1998) did not find this effect but did find that increased turbulence resulted in radiated shanny (*Ulvaria subbifurcata*) larvae feeding on larger prey.

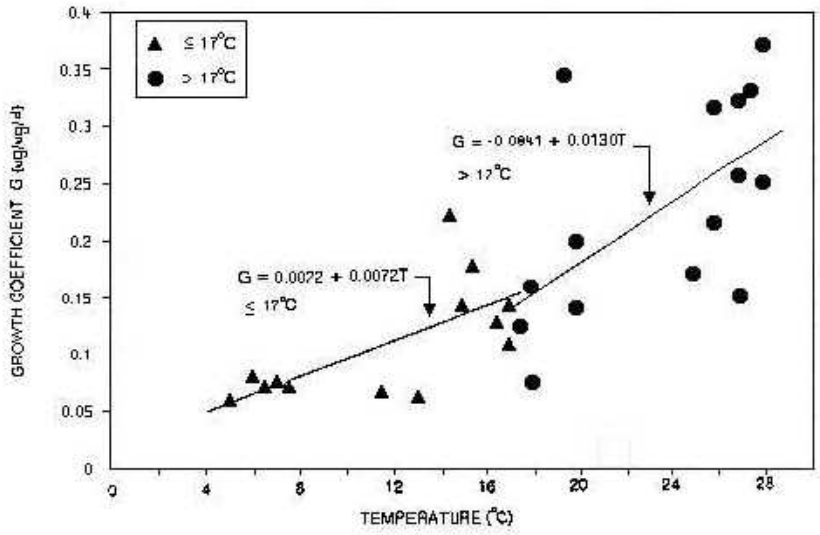

Figure 7. Regressions of instantaneous growth rates in relation to temperature for marine fish larvae from < 17ºC and >17ºC waters.
(Source: Houde 1990).

On a larger scale, turbulence has been associated with disrupting feeding conditions (Lasker 1975). Roy *et al.* (1992) suggested the idea of an optimal environmental window, associated with medium wind intensity, facilitating recruitment. Presumably, medium wind conditions may also be related to optimal feeding conditions for the larvae. Spawning of tropical fish may be timed to coincide with minimal wind to maximise the chances that larvae will return to their natal reef (Johannes 1978). As spawning location relates to the feeding environment that the larvae will encounter, turbulence may be a consideration that needs to be explored for tropical fish larvae. Multi-specific assemblages would need to be studied under similar environmental conditions to separate turbulence effects from species-specific behavioural effects (Dower *et al.* 1997).

2.4 CONSEQUENCES OF SUCCESSFUL FEEDING

The feeding environment experienced by fishes during their pelagic larval life will influence growth rates. Studies in temperate waters have demonstrated the importance of water mass associations (Jeffrey & Taggart 2000), vertical distribution (Grønkjær *et al.* 1997), availability of preferred prey (Anderson 1994), genetic factors (Purchase & Brown 2000) and parasites (Sirois & Dodson 2000a, b) on growth rates and thus recruitment success. These studies used condition measures to relate the consequences

of growth in relation to various factors and how they will influence survival. Tropical fish larvae are known to display variable larval growth rates (Cowen & Sponaugle 1997, Searcy & Sponaugle 2000), but the planktonic processes that affect these are virtually unknown. It is probable that some of the same influences that have been identified as affecting growth rates in temperate areas will also operate on tropical fish larvae. The use of condition measures in conjunction with feeding studies has not yet been studied for tropical fish larvae.

2.5 CONCLUSIONS

Despite nearly a century of research, a direct link between food availability and recruitment is still elusive. This is possibly due to studies considering the mean characteristics of a population, when successful growth to recruitment may actually be the result of the unique characteristics of an individual and the environment it encounters during development (Heath & Gallego 1997). This points to the need to consider the interactions occurring at a scale suitable to the individual larvae and their prey when determining factors that affect successful feeding and growth. Within the constraints of species-specific capabilities, larval fish appear to be highly flexible in their foraging. Prey abundance *per se* has not been found to be limiting, as larvae have demonstrated the ability to ingest food even in low prey environments (e.g. Schmitt 1986). What constitutes poor feeding conditions for one species at a particular stage of development may provide good feeding conditions for another. Thus, considering the survival consequences for an individual as it moves through a patchy and dynamic environment may provide answers on a population level.

Research on larvae from temperate waters has focussed on relatively few commercial species, thus the range of feeding strategies has possibly been underestimated and too much emphasis may have been placed on the importance of the seasonal plankton blooms to explain successful larval fish feeding and recruitment (Mousseau *et al.* 1998). Therefore, the taxonomic diversity of fish in the tropics must be considered along with the corresponding variety in spawning strategies (Johannes 1978). There is no "typical" tropical larva and larvae of different species will encounter an array of different developmental environments. It is only by undertaking studies of multiple species

experiencing the same feeding conditions and by using standardised sampling techniques that generalisations may be possible (Pepin & Penny 2000).

One of the reasons for a lack of information in tropical areas on larval feeding ecology has been a dichotomy in the reasons for studying early life history stages in tropical and temperate areas. Tropical studies, particularly those on coral reef fish larvae, have tended to concentrate on the dispersal of larvae and how they arrive at the reef (Cowen & Sponaugle 1997). This has resulted in very little research into planktonic processes as they affect larval growth and development. A further hindrance into studies of tropical larval fish has been a lack of taxonomic knowledge. This has started to be addressed (Leis & Carson-Ewart 2000) but remains an obstacle for larval feeding studies given that most of the processes that need to be considered operate at the species level, and identification beyond family is still problematic. Although within a family or subfamily, the capabilities and developmental changes of larval fish are often comparable and thus it may be possible to derive generalisations from selected taxa within these groupings (Job and Bellwood, 2000).

3 Temporal Patterns in Distributions

This chapter has been published: Sampey, A, Meekan, M.G., Carleton, J. H., McKinnon A.D., and McCormick, M.I. (2004). Temporal patterns in distributions of tropical fish larvae on the North-West Shelf of Australia. Marine and Freshwater Research 55: 473 - 487.

3.1 Introduction

Larval fish assemblages are spatially and temporally dynamic; variation in composition and abundance occurs horizontally (Leis & Miller 1976, Leis 1982, Leis *et al.* 1998) and vertically (Leis 1986) and at time scales ranging from hours (Kingsford 2001) to seasons (Leis 1991, Heath 1992). Multiple processes contribute to this variability and may include the spawning activities of adult fishes (Doyle *et al.* 1993, Nonaka *et al.* 2000), developmental changes in an individual larva's capabilities (Leis 1991, Leis & McCormick 2002), and aspects of the biophysical environment that larvae inhabit (Cowen 2002). The latter factors may interact to produce spatial and temporal pattern, for example when hydrographic features such as upwelling (Murdoch 1990b, Roy *et al.* 1992), tidal (Kingsford *et al.* 1991, Kingsford & Suthers 1996) and coastal shelf fronts (Lochman *et al.* 1997) concentrate larvae and their food resources, or when wind driven mixing results in turbulence. These factors can influence larval survival (Dower *et al.* 1997) and the formation and persistence of larval assemblages (Boehlert & Mundy 1993).

In temperate regions, the distribution and abundance patterns of larval fishes have been the subject of research for decades. In contrast, there have been relatively few studies in tropical environments. Most work in the tropics has focused on spatial patterns, either at small scales (10's of km) close to coral reefs (e.g. Leis & Goldman 1987) or at large scales (100-1000's of km) across continental shelves (e.g. Young *et al.* 1986) and oceans (e.g. Ahlstrom 1971, 1972). Very few studies have examined temporal patterns (but see Sponaugle *et al.* 2003), although sampling techniques such as light traps, crest nets and purse seines, have recently been used to describe patterns in abundance of late stage larvae of reef fishes in the waters around coral reefs. These studies have demonstrated lunar cycles in larval abundance with peaks occurring around the new moon (e.g. Meekan *et al.* 1993, McIlwain 2003). Such patterns reflect spawning cycles

of adults (Robertson *et al.* 1988), but have also been linked to environmental factors such as temperature, turbulence and zooplankton biomass (Doherty & Williams 1988, Milicich 1994, Sponaugle & Cowen 1996, Wilson & Meekan 2001, 2002). However, such sampling techniques are often highly selective for particular taxa (e.g. pomacentrids) and biased towards late stage individuals (Choat *et al.* 1993). In comparison, information on temporal patterns of abundance of the early life history stages (pre and immediately post-flexion) of larval fishes is scarce, particularly in coastal shelf regions.

Here, I describe temporal patterns in the distribution and abundance of the early life history stages of tropical fishes on the North West Shelf of Australia (NWS). Although the region is the site of several major fisheries that target both pelagic and demersal finfish and invertebrates, very little is known of the processes and food chains that support fisheries production on the NWS. To date, only one study (Young *et al.* 1986) has examined spatial and temporal patterns in ichthyoplankton in this region. Other broad scale studies recorded the greatest densities of zooplankton in Australian waters on the Shelf (Tranter 1962).

3.2 Aims

The early stages of tropical larval fishes were sampled during two summer recruitment seasons on the southern NW Shelf of Australia using towed plankton nets. El Niño-Southern Oscillation (ENSO) conditions typified the first summer (1997/98), compared to the second summer (1998/99), which was characterised by La Niña conditions.

Specifically, I aimed to:

1) document the family composition, distribution and abundance of larval fishes captured in two years that differed markedly in environmental conditions, and
2) identify potential biophysical factors that may determine temporal patterns in ichthyoplankton communities.

3.3 Methods

3.3.1 Study sites & field collections

The present study was conducted during cruises made by the *RV Lady Basten* in the vicinity of Australia's North West Cape (hereafter NWC) in the austral summers of 1997/98 and 1998/99. Ichthyoplankton sampling focused on two sites, a shallow inshore site (B, water depth ~20m, Figure 8, Table 1) located at the mouth of the Exmouth Gulf, and an offshore shelf break site (E, water depth ~100m, Figure 8, Table 1). Additionally, another inshore site (TB, water depth ~16m, Figure 8, Table 1), located further north on the shelf near Thevenard Island, was sampled on 4 occasions in 1998 (Figure 8, Table 1).

Ichthyoplankton were collected by oblique tows to ~16m depth at all sites using Bongo nets (0.8m net diameter, 500μm mesh), fitted with a General Oceanics flowmeter. Sampling periods were timed to coincide with the new moon, a peak spawning and recruitment time of some reef fishes (Thresher 1984). Additionally, tows were usually taken near dusk, in order to 1) reduce the effects of diurnal variation in larval abundance and 2) ensure full guts, as larval fishes are visual predators (Blaxter 1986a) with peaks in feeding occurring at dawn and dusk (Last 1980, Young & Davis 1990, McLaren & Avendano 1995, McLaren *et al.* 1997), and thus facilitate dietary analysis (see Chapter 3). During each sampling period, varying numbers of replicate tows were taken on different days at each site (Table 2). From each tow, one net of the bongo sampler was initially preserved into 5% formalin and the other into 70% ethanol (ETOH). All samples were later transferred to 70% ETOH.

Biophysical data was collected at the beginning and end of each bongo net tow. Temperature, salinity and chlorophyll *a* data were collected using a CTD (Seabird SBE25) fitted with a fluorometer (Chelsea Fastracka) and zooplankton was sampled using vertical net tows (0.5 m diameter ring net, 73 μm mesh) (see Meekan *et al.* 2003 for more details).

3.3.2 Sorting and identification

Larval fishes were sorted into types with the aid of a dissecting microscope and enumerated. Due to the time involved in processing samples, only one net was sorted. The flexion and post-flexion larval fish component of the samples (hereafter referred to as post-flexion larvae or larval fish) were identified to family using the available reference literature (Okiyama 1964, Moser *et al.* 1984, Smith & Heemstra 1986, Neira *et al.* 1998, Leis & Carson-Ewart 2000). Larvae were categorised as "unidentified" when they were too damaged to identify with any certainty.

3.3.3 Data analysis

The counts of larvae present in each net tow were standardised to number of larvae per m^3, on the basis of flow meter readings. The flow meter malfunctioned on three tows, and an average volume of all other stations sampled (1021.6 m^{-3}) was used to calculate volumes for these tows. All analyses used data sets of numbers of larvae per m^3. The high inter-replicate variability that typifies ichthyoplankton community data sets precluded parametric statistical analysis. Consequently, the data sets were analysed using non-metric multi-dimensional scaling (nMDS) and cluster analyses to identify patterns in space and time, followed by multivariate regression tree (MRT) analysis (De'ath 2002) to identify environmental factors influencing these patterns. "Unidentified" fishes were present in most groups and were removed from the data sets to avoid any confounding of differences among groups. A species sample matrix was generated consisting of families as rows and net tows as columns (76 families from the 44 samples containing identifiable larvae).

NMDS and cluster analyses were conducted using PRIMER (Plymouth Routines in Multivariate Environmental Research) v5.1 (Clarke & Warwick 2000). In order to allow the contribution of rare species to the patterns, data sets were transformed to 4^{th} root values as this down-weights the influence of abundant species and is invariant to scale changes (Field *et al.* 1982). The Bray-Curtis distance measure was applied to produce a dissimilarity matrix; this distance measure is insensitive to zero values while preserving the influence of abundant taxa. NMDS (minimum of 25 iterations) and hierarchical

group averaged cluster analyses were then used to produce 2-dimensional ordinations and dendrograms.

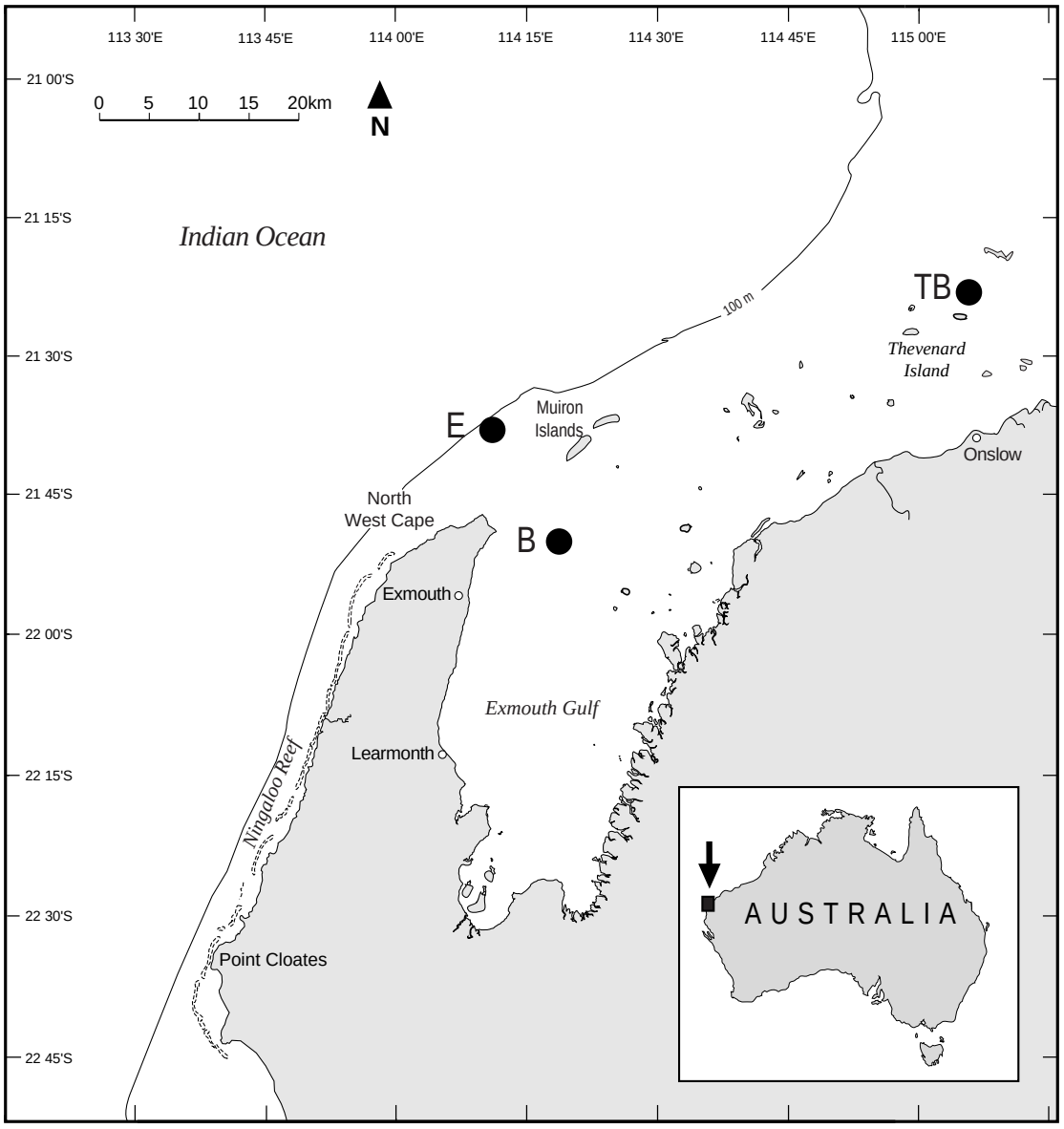

Figure 8. Location of ichthyoplankton sampling sites on the southern North West Shelf between October and February 1997/98 and 1998/99.

I used MRT analysis to determine the influence of spatial (location), temporal (year and month), and biophysical (temperature, salinity, chlorophyll *a* and zooplankton biomass) variables on the abundance of families of larval fishes. This analysis allowed the data to be partitioned in a stepwise fashion so that the relative influence of each variable was evident and provided information on the percentage contribution of each family to the groups formed by the regression tree. In order to relate the biophysical data with the fish community sampled I first examined vertical profiles from corresponding net tows for

vertical stratification, when these were well mixed at the same scale as my larval fish sampling I used an average of the values collected from the surface 16m only for each corresponding net tow. The data was transformed to 4^{th} root values to facilitate comparisons with the nMDS and cluster analyses. I used the Manhattan Distance measure, as it is suitable for gradient data. The fit of the data to the tree was defined by the cross-validated relative error (CVRE) (De'ath 2002). Families characteristic of a particular group were identified using an index value calculated from the product of the relative abundance and the relative frequency of occurrence of this family within the group (Dufrêne & Legendre 1997). I considered index values >50 to be high, values from 50-20 to be moderate and those <20 to be low, families with values in the moderate to high range were defined as characteristic of a group.

Table 1. Number of net tows taken at each site during each sampling period.

Sample Period	Inshore (B)	Offshore (E)	Inshore (TB)
25 Oct – 3 Nov 1997	3	3	-
26 Nov – 6 Dec 1997	3	2	-
26 Dec '97– 4 Jan '98	3	3	-
21 Feb – 2 Mar 1998	3	3	-
16 – 24 Oct 1998	3	3	-
16 – 23 Nov 1998	3	1	2
16 – 23 Dec 1998	1	1	2
10 – 19 Feb 1999	3	3	-

3.3.4 Comparison to Young et al (1986)

In order to expand the temporal extent of the study, I compared a subset of my data from the Exmouth sites only (B & E) with data from the study by Young *et al* (1986). The raw data from Young *et al's* (1986) study was obtained from the Commonwealth Science and Industry Research Organisation's (CSIRO) Marine Research Data Centre and is reproduced here with the permission of CSIRO. Young *et al* (1986) sampled every two months along two transects on the North West Shelf between September 1982 and October 1983. Samples were collected at night by oblique tows throughout the water column, or to 100m depth, using a Maruchi A plankton net (130 cm diameter, 2mm mesh and 0.33 mm cod end, TSK 8-mile flowmeter) in 1982 and with a modified Isaac Kidd Midwater trawl (mouth area 2.89m^2, 2mm mesh, Rigosha flowmeter Model 2536B) in 1983 (Young *et al* 1986). I selected data from the eastern transect as sampling had occurred during months (i.e. October, December and February) that

coincided with my sampling regime. Sites (the inner shelf, Site No. 1, 19º25'S, 119º30'E, 41m and outer mid shelf, Site No. 3, 18º45'S, 119º05'E, 110m) were selected to correspond to the depths and cross shelf locations of my work. For analysis, "mullid-like" larvae in the Young *et al* (1986) data sets were combined with pomacentrids. Count data was summarised from both studies and is presented for the highest ranked taxa only. Due to the problems with the temporal comparison in Young *et al*'s (1986) study, which was confounded by different net types, only abundance data from the months of October and December 1982 is presented for selected families of larval fishes.

3.3.5 Terminology

Terms used to describe developmental stages of larval fishes follow those of Leis and Carson-Ewart (2000). Flexion is defined as the time when the notochord turns upwards and the caudal fin develops, which usually coincides with fin formation. The larvae were categorised in relation to the usual habitat of the adult fishes, either pelagic or demersal. Larvae were further categorised as oceanic or coastal fishes following the criteria of Leis and Carson-Ewart (2000), where the latter are all fishes that occur as adults in less than 200m depth of water close to shore. This categorisation was not always clear-cut at the taxonomic level of family (e.g. bregmacerotids have species that are coastal and oceanic by this definition). Productivity or production refers to both primary (e.g. algal, microbial) and secondary (e.g. copepods, appendicularians) sources of energy that may be utilised by larval fishes.

3.4 Results

3.4.1 Biophysical Environment

Waters at the inner shelf sites (B and TB) were generally well mixed for temperature, salinity and chlorophyll at all sites and times (Figure 9). At the shelf break (offshore site E) the surface mixed layer extended to 20m or more. Generally, these surface waters were well mixed with a <2ºC temperature difference throughout the water column but a weak thermocline sometimes established (3, 6.5 and 4 ºC difference between surface and bottom waters in December 1997, February 1998 and 1999 respectively). Salinity was invariant (~35) within and between summers at all sites, but was slightly higher

inshore than offshore as a result of evaporation within Exmouth Gulf (Figure 9 & Figure 10). Chlorophyll *a* concentrations estimated from *in situ* fluorescence were usually <1 $\mu g\ l^{-1}$, with values in the surface mixed layer lower than in the underlying water column (e.g. 0.31 $\mu g.l^{-1}$ at the surface of site B in February 1998 to a maximum of 0.95 $\mu g.l^{-1}$ at 19m and 0.15 $\mu g.l^{-1}$ to a maximum of 0.82 $\mu g.l^{-1}$ at 45m at site E in February 1999) (Figure 9).

Temperature increased by approximately 5ºC from October to February in each summer, ranging from a mean of 22.7ºC inshore at site B in October 1997 to 27.9 ºC offshore at site E in February 1998 and from 23 ºC at site B in October 1998 to 28.9 ºC offshore at site E in February 1999 and were approximately 1ºC higher in 1998/99 than in 1997/98 for each site and time combination (Figure10). Mean temperatures at the inshore site TB were higher than either B or E in October and December 1998 (25.9 vs 24.8 and 27.7 vs 25.8 and 25.2 respectively). Mean chlorophyll *a* levels were higher in the first summer compared to the second for each site/time combination (e.g. 0.86 $\mu g.l^{-1}$ at site B, October 1997 vs 0.64 $\mu g.l^{-1}$ in October 1998; and 0.66 $\mu g.l^{-1}$ at site E in December 1997 vs 0.36 $\mu g.l^{-1}$ in 1998). There was a trend for chlorophyll *a* levels to be higher inshore than offshore except in November and December 1997 and December 1998. In general, mean zooplankton biomass was higher inshore at site B compared to site E (e.g. 38.4 vs 24.9 mg m^{-3} in December 1997) and higher, although very variable, in the first summer compared to the second (e.g. 163.4 mg m^{-3} at site B and 24.0 at site E in February 1998 vs 102.8 at site B and 10.1 at site E in February 1999).

3.4.2 Taxonomic composition of ichthyoplankton

Total catches in the bongo nets included 1269 fish eggs and 9944 fish larvae. Of these fishes, 5613 were pre-flexion and 4017 post-flexion larvae from 76 families (Figure 2). A total of 314 fishes (~8%) were too damaged to identify. Identified larvae were typically 3-5mm TL. Seventy seven per cent of the larvae were demersal and 23% pelagic as adults. Larvae of shorefishes such as gobiids, pomacentrids, and bothids constituted the majority (82%) of catches. Larvae of oceanic fishes, e.g. myctophids, gonostomatids and melanostomeids, contributed 6% of catches and the remaining 12% were of indeterminate origin e.g. carangids, bregmacerotids.

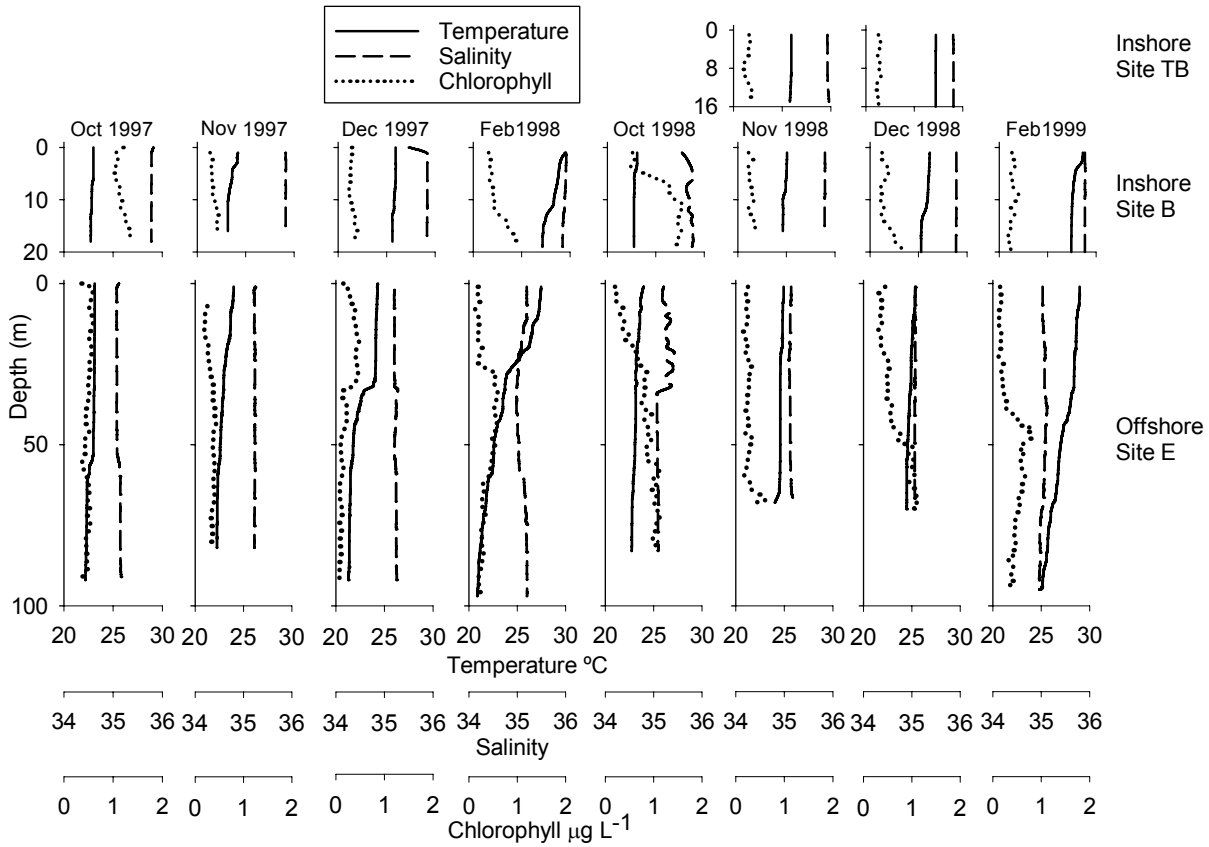

Figure 9. Representative vertical profiles of temperature, salinity and chlorophyll a for each site and time combination.

The five most abundant families (Gobiidae; 24%, Pomacentridae; 8%, Carangidae; 8%, Callionymidae; 7% and Monacanthidae; 5%) accounted for more than 50% of the total numbers of larvae collected by the study (Table 2). Fourteen families were represented by single individuals in catches. Perciform fishes dominated (66%) catches, while pleuronectiform, clupeiform, and gadiform fishes represented 6, 4 and 1% of catches respectively.

3.4.3 Total numbers of fish eggs and larvae

Fish eggs were collected in very low numbers in 1997/98 and in October 1998 and February 1999 at all sites (Figure 11a). High numbers of eggs were caught at site B in November (3500 per 10 000 m^3), and December (4500 per 10000m^3) 1998. There was a trend for pre-flexion larvae to be collected in higher numbers at site B than at either site E or TB (Figure 11b). In general, abundance of pre-flexion larvae increased during the summer from October through to February in each year. In the early summer (October

and November) of 1997 abundances of pre-flexion larvae were higher than in 1998. The reverse was true late summer (December and February), with higher abundances of pre-flexion larvae being observed in the second summer (1998/99) compared to the first (1997/98). Post-flexion larvae were only slightly less abundant than pre-flexion larvae at all times and sites, although they displayed similar trends to those of the pre-flexion larvae. Abundance of post-flexion larvae was similar at both sites (B and E) in 1997/98 and at all sites (B, E and TB) in 1998/99 (Figure 11c). The exception to this was the much higher mean abundance of post-flexion larvae recorded at site B in the late summer of 1998/99. In all cases variability in catches among replicate net tows was high, as indicated by the standard errors (SE).

3.4.4 Distribution patterns of fish assemblages

The results of the MDS and cluster analyses showed that samples clustered into 8 groups due to assemblage composition (Figure 12). In general, the samples formed a gradient from October through to February (Figure 12b) and from offshore to inshore sites (Figure 12c). There was no clear inter-annual grouping of the samples (Figure 12d). Groups 1 and 5 to 8 contained very low numbers of larvae (<5% of the total, Figure 13a) and largely consisted of samples collected in October (Figure12b). Almost 95% of the larvae (Figure13a) were grouped into just 3 cluster groups, (2, 3 and 4). These were collected in samples during November, December and February in both summers (Figure 12b).

Groups 1, 5 and 8 predominantly consisted of samples collected from the offshore site E (Figure12c) and all contained Myctophids (Figure13b, f & i). The majority of the samples in this study clustered into Group 2 (72% of total larvae, Figure12a) and included catches from all sites and both summers but only from the months of November, December and February (Figure12 a-d, Figure13a & c). Gobiids dominated (32%), followed by carangids (10%) and pomacentrids (9%) (Figure 13c). However, there was some grouping of samples within this cluster due to site (inshore vs offshore, (Figure 12a-c).

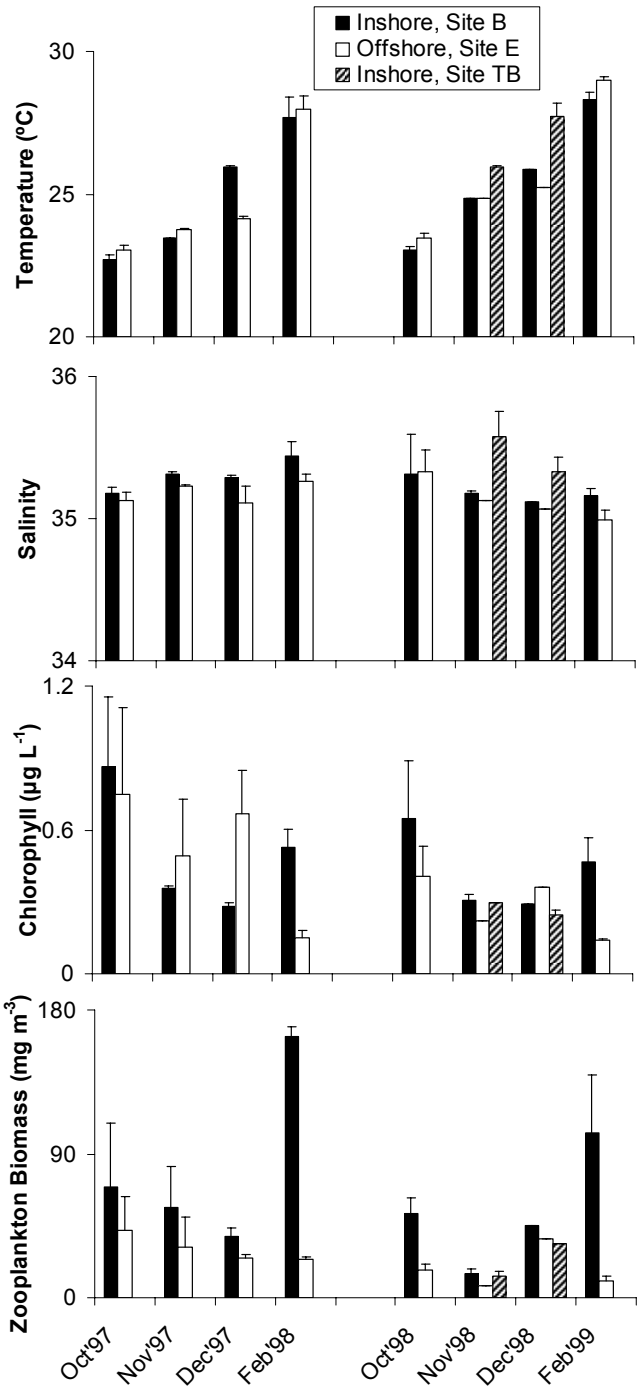

Figure 10. Mean (± SE) of temperature, salinity, chlorophyll a and zooplankton biomass near North West Cape and Thevenard Island between October and February 1997/98 and 1998/99.
Values were calculated from the average of values for the surface 16m. NB. No zooplankton biomass data were available for site TB.

Table 2. Summary of the identity, total numbers and the amount of variance (%) that each identified family contributes to the total variance in the data set (family total) from the Multivariate Regression Tree (MRT) analysis for fish larvae collected near North West Cape (21°46'S, 114° 14'E), and Thevenard Island (21°20'S, 115° 00'E), Western Australia in the summers of 1997/98 and 1998/99.

Taxa are considered to inhabit coastal waters unless otherwise indicated, Demersal^{D}, Pelagic ^{P}, Oceanic*, Oceanic/Coastal^{+}, some species are demersal$^{\sim}$. The % contribution is further partitioned by each tree split (month & site) and for the whole tree (tree total). Families are ranked in descending order of the % of their total tree variation. Values are rounded to 2 decimal places.

Family	Count	Month	Site	Tree total	Family total	Family	Count	Month	Site	Tree total	Family total
Syngnathidae^{D}	54	0.59	0.79	1.37	2.8	Exocoetidae^{P+}	2	0.01	0.04	0.05	0.41
Carangidae^{P+}	327	1.28	0.03	1.3	4.01	Tetraodontidae^{D}	15	0.05	0	0.05	1.28
Monacanthidae^{D}	219	0.83	0.42	1.26	3.6	Sparidae^{D}	7	0.02	0.03	0.04	0.71
Apogonidae^{D}	174	0.8	0.26	1.06	3.71	Centriscidae^{D}	5	0.01	0.02	0.03	0.52
Microdesmidae^{D}	151	0.41	0.56	0.97	3.09	Gempylidae^{P+}	3	0.02	0.02	0.03	0.64
Gobiidae^{D}	983	0.62	0.03	0.64	4.48	Gerreidae^{D}	5	0.02	0.02	0.03	0.68
Gonostomatidae^{P*}	53	0.01	0.62	0.64	2.78	Opistognathidae^{D}	5	0.01	0.02	0.03	0.52
Pomacentridae^{D}	335	0.4	0.2	0.6	3.26	Synodontidae^{D}	6	0.02	0.01	0.03	0.67
Scombridae^{P+}	112	0.2	0.4	0.6	3.25	Chaetodontidae^{D}	2	0.01	0.02	0.02	0.41
Clupeidae^{P}	67	0.18	0.27	0.45	2.09	Nomeidae$^{P*\sim}$	4	0.01	0.01	0.02	0.48
Nemipteridae^{D}	48	0.11	0.33	0.44	2.3	Paralichthyidae^{D}	4	0.02	0	0.02	0.64
Callionymidae^{D}	286	0.29	0.13	0.43	3.19	Siganidae^{D}	7	0.02	0	0.02	0.72
Myctophidae^{P*}	183	0.19	0.2	0.39	3.53	Trichonotidae^{D}	4	0.02	0	0.02	0.64
Bothidae^{D}	113	0.34	0.03	0.37	3.16	Triglidae^{D}	2	0.01	0.02	0.02	0.4
Lutjanidae^{D}	46	0.27	0.09	0.37	2.66	Uranoscopidae^{D}	1	0.02	0	0.02	0.22
Sphyraenidae^{D}	34	0.29	0.07	0.36	2.3	Acanthuridae^{D}	1	0	0.01	0.01	0.21
Blenniidae^{D}	69	0.15	0.18	0.33	2.81	Acropomatidae^{D}	1	0	0	0.01	0.21
Platycephalidae^{D}	18	0.18	0.12	0.3	1.87	Berycidae^{D}	1	0	0	0.01	0.21
Bregmacerotidae^{P+}	49	0.03	0.25	0.28	2.62	Champsodontidae^{D}	3	0.01	0	0.01	0.51
Lethrinidae^{D}	47	0.2	0.03	0.23	2.07	Cirrhitidae^{D}	1	0	0	0.01	0.2
Serranidae^{D}	34	0.13	0.1	0.22	1.72	Creediidae^{D}	7	0	0.01	0.01	0.33
Cynoglossidae^{D}	123	0.13	0.05	0.18	2.41	Dactylopteridae^{D}	1	0	0.01	0.01	0.21
Pegasidae^{D}	6	0.04	0.11	0.16	1.01	Eel leptocephalii^{D}	8	0	0.01	0.01	1.05
Fistulariidae^{D}	8	0.08	0.04	0.12	1.31	Gobiesocidae^{D}	2	0.01	0	0.01	0.41
Pseudochromidae^{D}	13	0.01	0.11	0.12	1.27	Haemulidae^{D}	15	0.01	0	0.01	1.34
Aploactinidae^{D}	9	0.03	0.08	0.11	0.93	Kraemeriidae^{D}	2	0	0	0.01	0.24
Soleidae^{D}	3	0.02	0.1	0.11	0.64	Melamphaidae^{P*}	1	0.01	0	0.01	0.21
Pomacanthidae^{D}	5	0.03	0.07	0.1	0.82	Melanostomiidae^{P*}	1	0	0.01	0.01	0.21
Engraulidae^{P}	98	0.03	0.07	0.09	1.04	Pempheridae^{D}	1	0	0.01	0.01	0.21
Pinguipedidae^{D}	56	0.02	0.06	0.09	1	Priacanthidae^{D}	12	0.01	0	0.01	1.32
Labridae^{D}	18	0	0.08	0.08	1.72	Psettodidae^{D}	1	0	0	0.01	0.21
Leiognathidae^{D}	32	0.02	0.06	0.08	0.92	Samaridae^{D}	1	0	0	0.01	0.24
Ophidiidae^{D}	4	0.03	0.06	0.08	0.82	Schindleriidae^{D}	10	0.01	0	0.01	0.66
Mullidae^{D}	23	0.05	0.03	0.07	1.82	Sillaginidae^{D}	1	0	0	0.01	0.22
Scorpaenidae^{D}	10	0.06	0.01	0.07	1.21	Solenostomidae^{D}	1	0	0	0.01	0.22
Terapontidae^{D}	40	0	0.07	0.07	1.23	Xenistmidae^{D}	1	0	0.01	0.01	0.21
Holocentridae^{D}	5	0.01	0.05	0.06	0.52	Scaridae^{D}	3	0	0	0	0.62
Howellidae$^{P*\sim}$	2	0.06	0	0.06	0.4	Tripterygiidae^{D}	13	0	0	0	1.45
						Split total		8.44	6.46	14.9	100
Pre-flexion	5613					Total Post Flexion	4017				
Fish Eggs	1269					Unidentified	314				

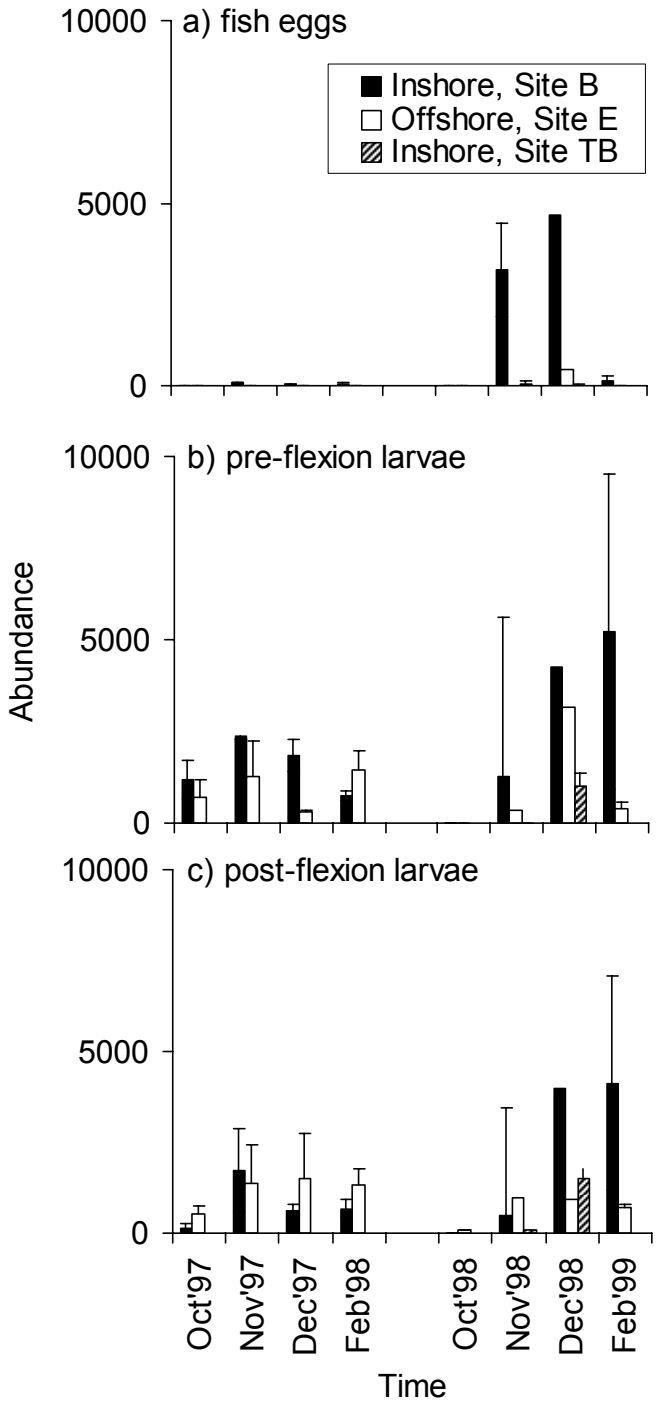

Figure 11. Abundance (No. 10000m^{-3}, mean ± SE) of fish eggs (a), pre- (b) and post-flexion (c) larvae collected near North West Cape and Thevenard Island between October and February 1997/98 and 1998/99.

Groups 3, 4, 6, and 7 only contained samples from inshore sites B and TB (Figure 12c) and all groups had different assemblage compositions. Group 3 illustrates the very patchy nature of ichthyoplankton distributions, where one sample contained 20% of the total number of taxa found in all samples (Figure13a). This sample, from site B in February 1999, included callionymids, cynoglossids, gobiids, and pinguipedids (Figure

12a-d, Figure 13d) and contributed to the high variation in total numbers of post flexion larvae seen for site B in February 1999 (Figure 11). High numbers of engraulids (Figure 12a-d, Figure 13a & e) dominated Group 4, which contained samples from the TB site only. Group 6 was defined by the presence of carangids and callionymids in one sample from site B in October 98 (Figure 12a-d, Figure13a & g). Group 7 contained samples from the inshore sites (B and TB) in October and November that had low abundance and were dominated by pomacentrids and blennids (35 and 28% of larval fishes, respectively, Figure 12a-d & Figure 13a & h).

3.4.5 Temporal and spatial influences on fish assemblages

The results from the MRT analysis supported the patterns obtained using the MDS and cluster analyses. The tree formed from this analysis had a cross-validated relative error (CVRE) of 0.976 and a standard error (SE) of 0.052 and consisted of 3 groups (R1-3). Month and site explained 15% of the total variation in the data set and none of the other factors (temperature, salinity, chlorophyll *a* or zooplankton biomass) contributed to the tree (Table 2). The primary split in the data was due to month (8.5% of the variation) with catches during October, (R1, 11 net tows), being very different to those collected in November, December and February. This separation was partly due to the abundance and diversity of taxa being much lower in October than in the other months (Figure 11, Figure 12 and Figure 13). The second split differentiated catches on the basis of site (6.5% of the variation) with inshore sites, B and TB (R2, 20 net tows), separating from the offshore site, E (R3, 13 net tows).

The partitioning of the variance in the MRT analysis showed that just five families (Gobiidae, Carangidae, Apogonidae, Monacanthidae and Myctophidae) explained almost 20% of the total family variation (Table 2). This component of the variation in the data was related to abundance and these five families dominated counts of larvae in the samples. A second set of five families (Syngnathidae, Carangidae, Monacanthidae, Apogonidae and Microdesmidae) explained about 40% of the tree variation (Table 2). This component of variation was related to distribution patterns, and all these families displayed discrete spatial or temporal distributions.

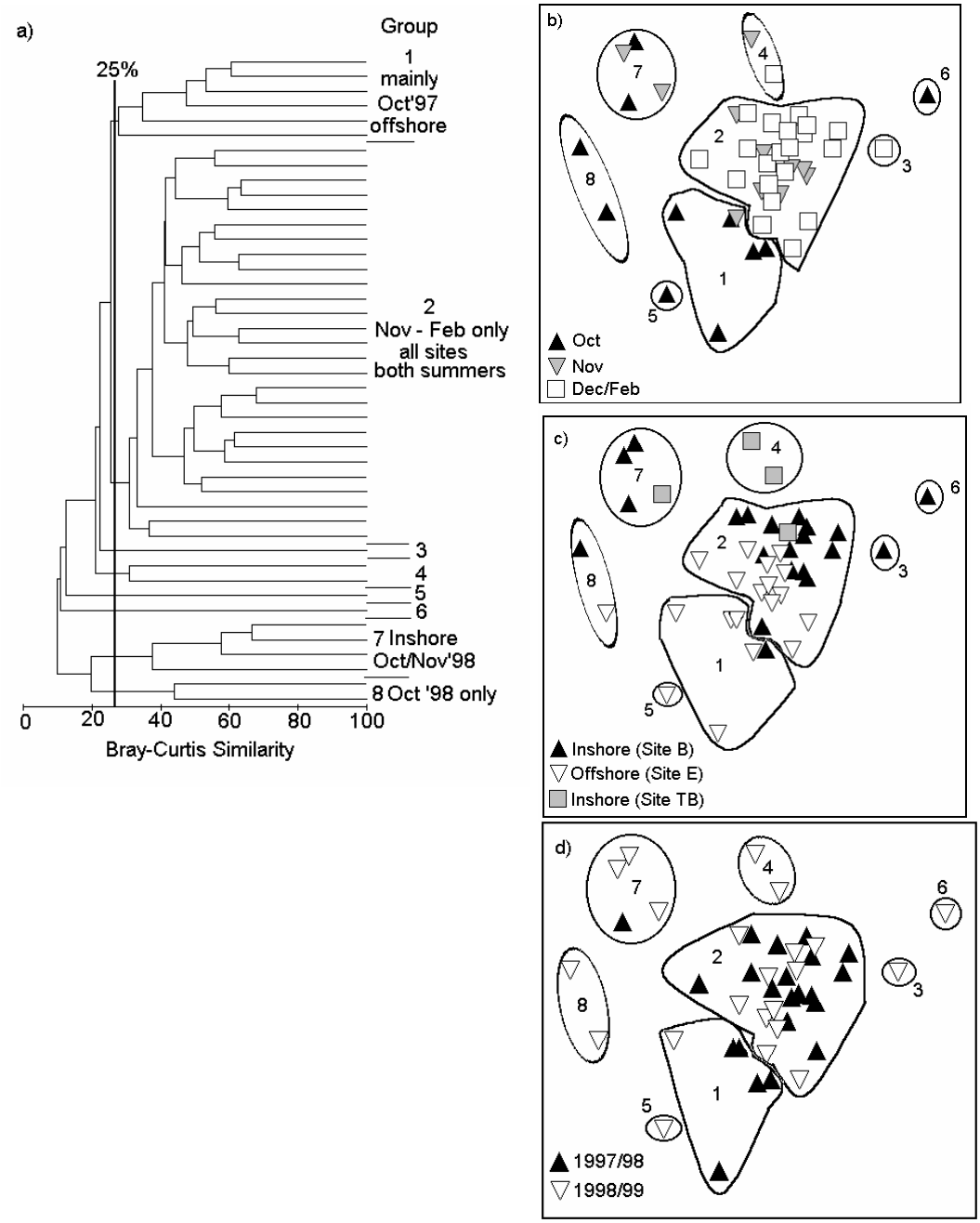

Figure 12. Dendrogram (a) and 2-dimensional ordinations (Stress 0.17) generated from a similarity matrix of 76 families from 44 samples.
The symbols represent month (b), site (c), and year (d). Symbols that are closer together are more similar in composition and abundance than those further apart. Clusters 1-8 were distinguished from the dendrogram and plotted onto the ordination as indicated by ellipses. NB there is a temporal (Oct to Feb) and spatial (Offshore to Inshore) gradient.

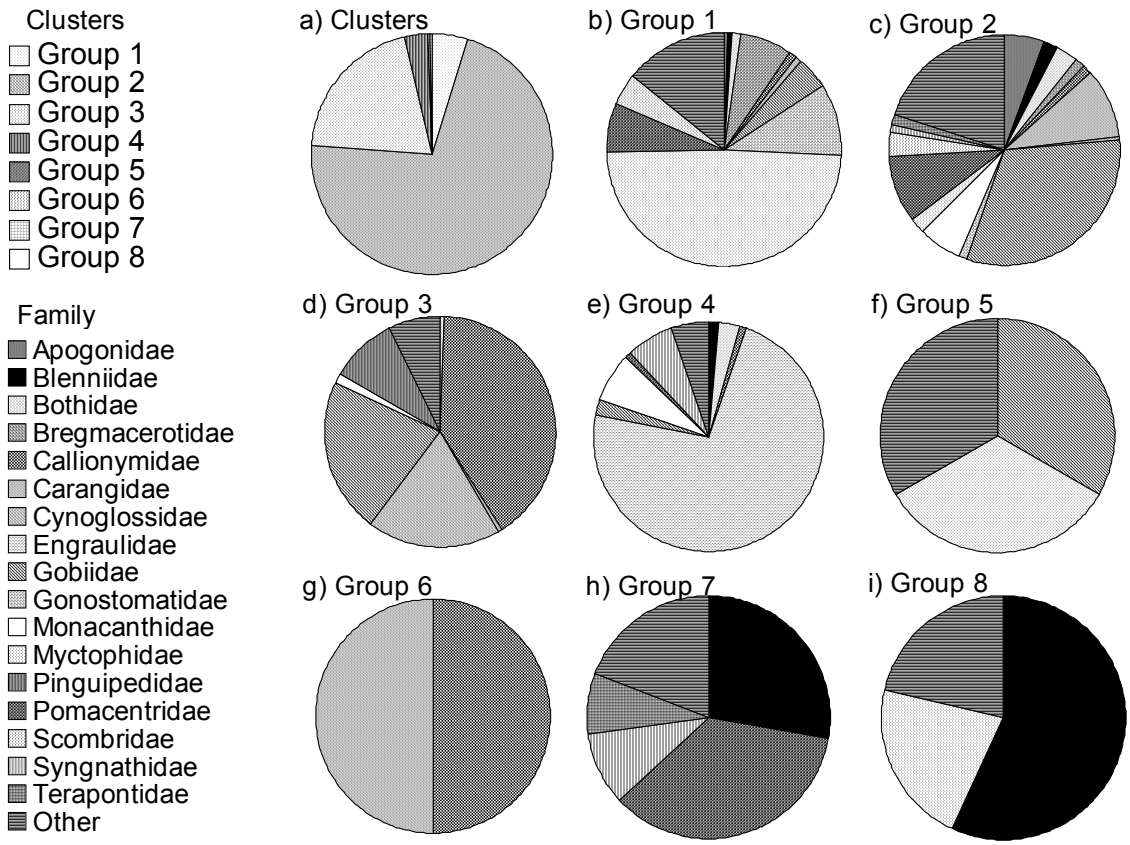

Figure 13. Pie graphs represent the percentage contribution of larval fishes to each cluster group (a) and then for each group, a breakdown of the contribution of individual families to that group (b-i).

3.4.6 Individual family distributions

Catches of the various families of larval fishes displayed trends due to site, month and year (Figure 12). For example, syngnathids and monacanthids occurred predominantly at the inshore site B and were only present in catches from November to February in each year (Figure 14). They had high indicator values (64 and 54 respectively) for the inshore summer group identified by the MRT analysis (group R2, Table 3). Both families were also present at site E with low mean abundance in December and February 1998 (Figure 14).

Myctophids were predominately collected by tows at the offshore site and were present during all sampling periods, although on two occasions they occurred at the inshore site in October 1997 and December 1998 (Figure 14). They were the only family that displayed a moderate indicator value for October (29, Table 3) and also recorded a

moderate indicator value for the offshore site (Group R3, 21, Table 3). Gonostomatids and bregmacerotids displayed a similar pattern with moderate indicator values for the offshore site (Group R3, 35 and 22 respectively, Table 3) although being present in catches at the inshore site B in October '97 and December '98 (Figure 14).

Table 3. Indicator families identified from the MRT analysis for each tree group.
Index values are the product of the relative abundance and relative frequency of occurrence of the family in each group. In this study, a family was considered indicative of a group if they recorded a moderate to high index value (i.e. index value >20). Families indicated in bold have a high indicator value.

	Tree Group		
	Oct	**Nov-Feb**	
Family	**R1**	**R2 –Inshore (B & TB)**	**R3 – Offshore (E)**
Aploactinidae		20	
Apogonidae			**53**
Blenniidae			39
Bothidae		31	21
Bregmacerotidae			22
Callionymidae		35	
Carangidae		30	41
Clupeidae		35	
Cynoglossidae		21	
Fistulariidae			21
Gobiidae		42	30
Gonostomatidae			35
Lethrinidae			22
Lutjanidae			32
Microdesmidae			**55**
Monacanthidae		**54**	
Myctophidae	29		20
Nemipteridae		34	
Pegasidae		25	
Platycephalidae		29	
Pomacanthidae		20	
Pomacentridae		29	42
Pseudochromidae			21
Scombridae			**51**
Serranidae			26
Soleidae			23
Sphyraenidae			29
Syngnathidae		**64**	

Some taxa (e.g. gobiids, pomacentrids, apogonids and bothids, (Figure 14) occurred in all sample periods but generally recorded low mean abundances in October. There was an indication of inter-annual differences in the mean abundances of some families. For example, pomacentrids were generally collected in highest abundances at site E, and had a higher mean abundance in catches in the second summer compared to the first (Figure 14). Carangids, bothids and scombrids also showed higher mean abundance in the first summer compared to the second (Figure 14). Callionymids were generally in low abundance in catches at most sites and times, although they occurred in high

numbers in catches in February 1999 at site B (231 individuals, Group 6 in Figure 12, Figure 13 & Figure 14).

3.4.7 Comparison to Young et al (1986)

In the subset of my data used for this comparison (site TB excluded), I recorded 6640 larval fish from 61 families wheras Young *et al.* (1986) collected 4204 larvae from 68 families. Rank abundances were similar, with four taxa in common ranked in the top 10 by both studies (Table 4). Some of the differences in ranking of families between studies appear to be correlated with morphology of larvae. Greater numbers of deeper bodied forms, such as pomacentrids, scombrids, monacanthids and callionymids were captured in my study, whereas Young et al. (1986) collected more slender bodied taxa, such as synodontids, clupeids and schindleriids. The high rank of callionymids and microdesmids in my study was likely due to the very high numbers of these larvae captured in single samples at site B in February 1999 ((Figure 12, Figure 13 & Figure 14 and at site E in February 1998 (Figure 14).

Table 4. Comparison of the rank abundance and % of the total for the top 10 most abundant larval fish families' (common families to both studies in bold) for families of larval fish from the current study with that from Young *et al* (1986).
Data from Young *et al* (1986) is summarised for the eastern transect only, selected sites (8 &10) and months and compared with data from the current study for comparable months only.

Current Study	Count	%	Young *et al* (1986)	Count	%
Gobiidae	658	10	Gobiidae	733	17
Callionymidae	259	4	Pleuronectiformes	503	12
Carangidae	249	4	Carangidae	333	8
Pleuronectiformes	173	3	Synodontidae	264	6
Microdesmidae	139	2	Clupeidae	214	5
Monacanthidae	134	2	Apogonidae	191	4
Myctophidae	133	2	Leptocephalidae	185	4
Pomacentridae	131	2	Bregmacerotidae	172	4
Apogonidae	94	1	Schindleriidae	152	4
Scombridae	77	1	Leiognathidae	141	3

The mean abundances of larvae I recorded were generally higher than those of Young *et al* (1986) (Figure 14 & Figure 15), however, as different nets were used by each study, only the trends in relative abundances were considered here. In both studies, apogonids, carangids, gobiids and monacanthids all displayed increases in abundance in catches from October to December (Figure 14 & Figure 15). There were also consistent spatial patterns in both studies, with monacanthids and syngnathids more abundant at inshore than offshore sites, and bregmacerotids, gonostomatids, myctophids and pleuronectiforms were more abundant at offshore sites.

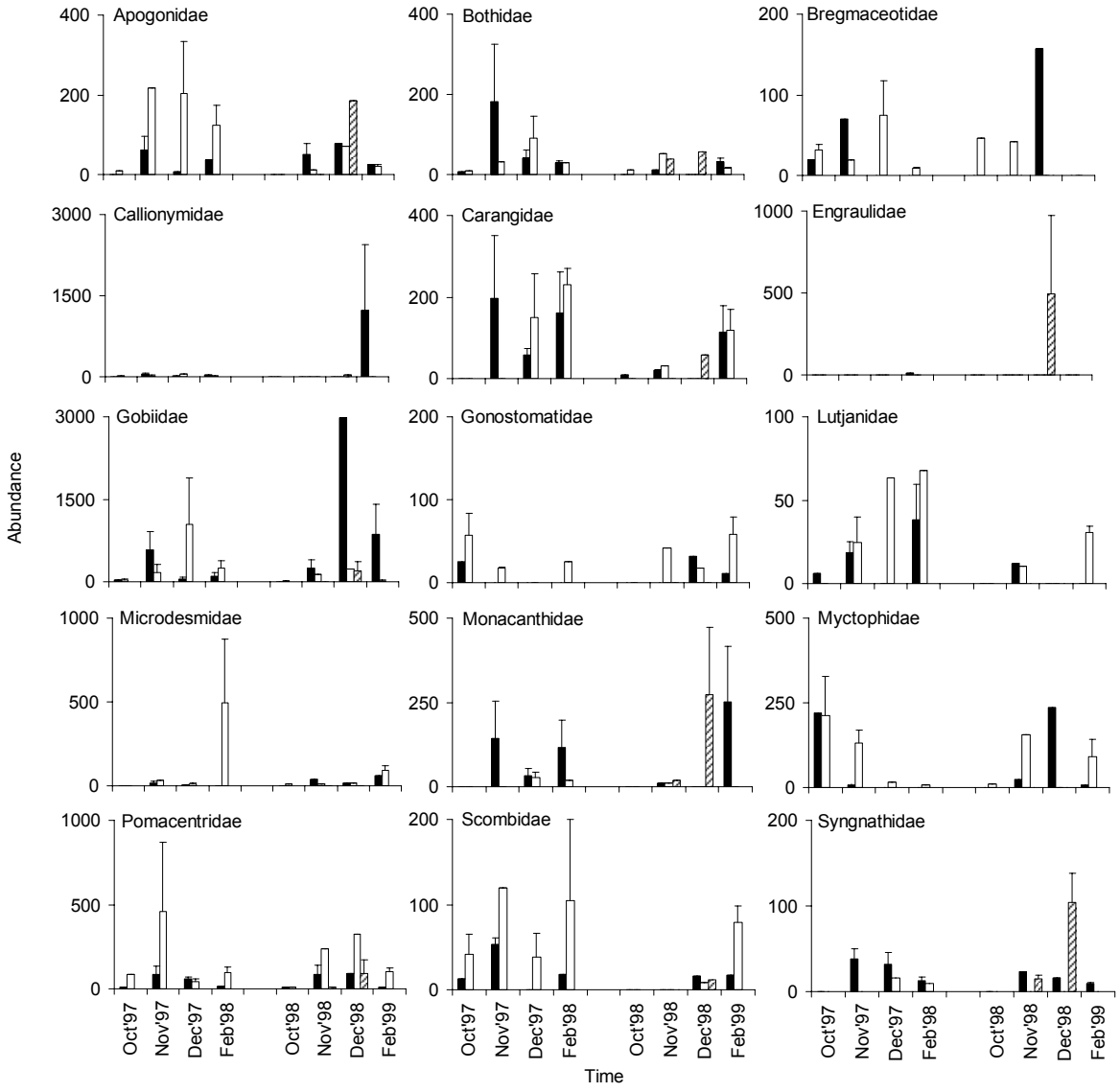

Figure 14. Abundance (No. 10000m^{-3}, mean ± SE) of selected families of post-flexion larval fish collected near North West Cape and Thevenard Island between October and February 1997/98 and 1998/99. Inshore, site B (dark), offshore, site E (light), and inshore, site TB (hatched).

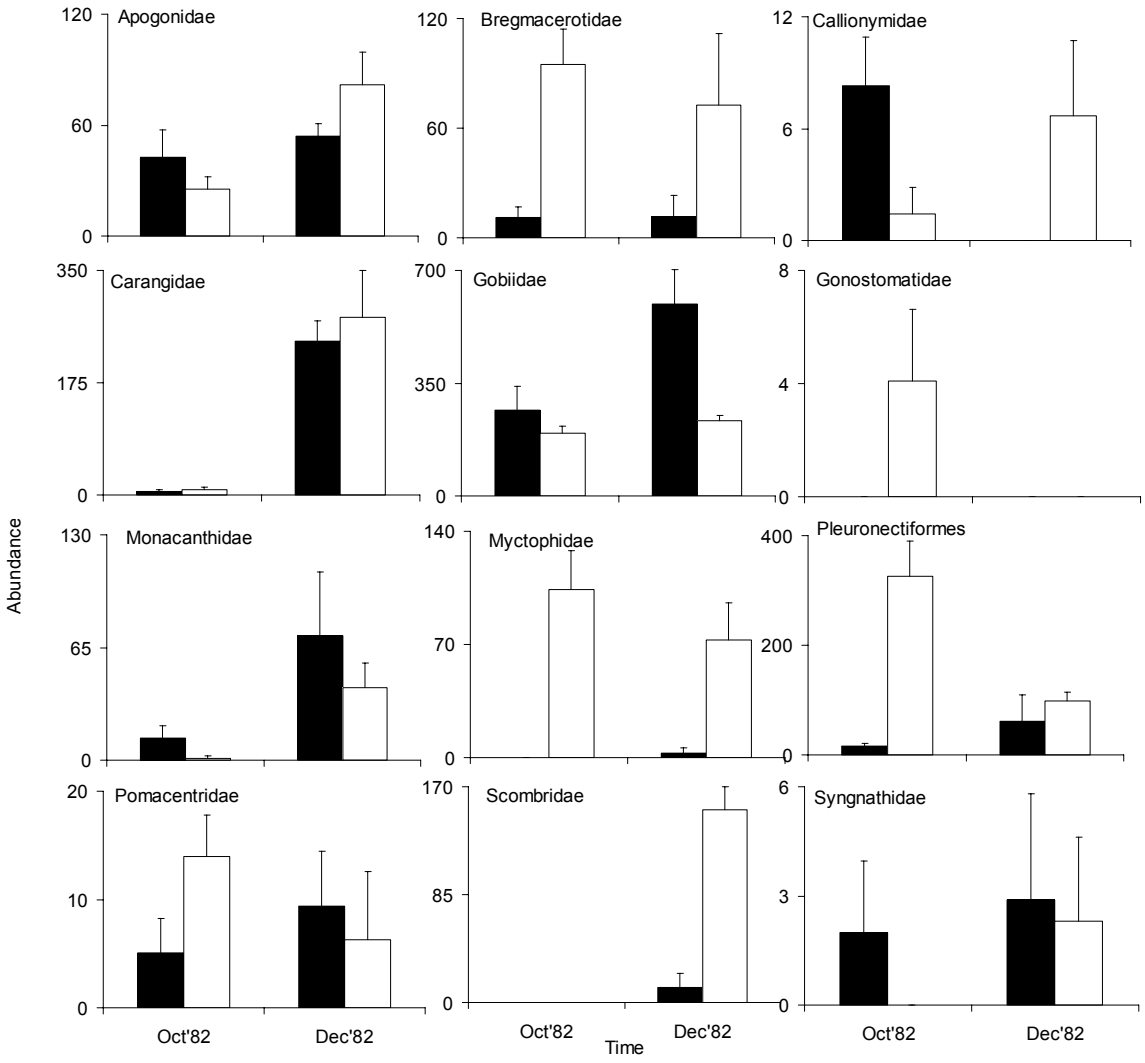

Figure 15. Abundance (No. 10000m^{-3}, mean ± SE) of selected families of larval fish collected from the eastern transect on the North West Shelf of Australia in 1982 and published in Young et al 1986. Inshore, site 8 (dark) and offshore, site 10 (light).

3.5 Discussion

3.5.1 Tropical ichthyoplankton communities

The diversity of ichthyoplankton recorded by any study tends to reflect the spatial and temporal scales of sampling. Near the NWC, 76 taxa of larval fishes were captured, which is comparable to surveys at other tropical localities in the Indo-Pacific region when sampling occurred during a summer (Table 5). For example, on the Great Barrier Reef (GBR) Williams *et al.* (1988) recorded 70 and Thorrold and Williams (1996) 75 taxa of larval fishes at stations on cross-shelf transects. Studies that recorded a higher diversity of taxa (e.g. 96, Leis and Goldman 1987; 85, Chamchang and Chayakul 2000;

80, Tzeng *et al.* 1997; 102, Young *et al.* 1986) generally sampled over broader spatial (100's of km) or temporal (yrs) scales.

The taxonomic composition of ichthyoplankton assemblages can convey information on the origin of water masses (Smith & Suthers 1999) and the underlying habitat (Leis 1993). In the vicinity of NWC, the summer ichthyoplankton community contained a mix of coastal (e.g. carangids) and oceanic (e.g. myctophids) fishes but was dominated by small demersal shorefishes (e.g. gobiids, pomacentrids, apogonids). These three taxa are dominant components of the fish fauna on Ningaloo Reef (McIlwain 2003) and it is possible that some of the larvae caught in this study were spawned at this locality, although a sampling program covering a greater area that included Ningaloo would be required to test this hypothesis.

Comparison of my results with those of previous studies of tropical ichthyoplankton (Table 5) shows that small demersal shorefishes often dominate ichthyoplankton assemblages over continental shelves (e.g. pleuronectiforms, gobiids, apogonids, Williams *et al.* 1988) or near coral reefs (e.g. gobiids, apogonids, pomacentrids, Leis & Goldman 1987, Table 5). When oceanic water masses are sampled, myctophids and gonostomatids dominate (Ahlstrom 1971, 1972, Nonaka *et al.* 2000). The work shown in Table 5 used a variety of net sampling techniques, which can have an important influence on the identity of taxa collected by the study, due to differences in net diameter and mesh size, towing speed and the problem of net avoidance (Young *et al.* 1986, Choat *et al.* 1993, Pepin & Shears 1997). Despite this issue, there was a high degree of similarity in composition of catches among studies (Table 5) suggesting that these consistent patterns represent general trends in the larval fish communities of tropical shelf environments.

Table 5. Summary of ichthyoplankton studies on tropical coasts.
Spatial scale: cross (+) and along (-) shelf. Net type: Bongo [a], Plankton [b], Conical [c], Maruchi [d], Isaac Kidd [e], Tucker trawl [f]. Not all taxa recorded *. Taxa summarised at family level or above and selected based on rank abundance. Habitat: *oceanic*, **neritic**, and coastal. Families: 1 – Apogonidae, 2 – Bothidae, 3 – Bregmacerotidae, 4 – Carangidae, 5 – Clupeidae, 6 – Cynoglossidae, 7 - Eel leptocephalii, 8 – Gobiidae, 9 – Gonostomatidae, 10 – Lutjanidae, 11 – Myctophidae, 12 – Phosichthyidae, 13 – Pleuronectiformes, 14 – Pomacentridae, 15 – Scaridae, 16 – Scianidae, 17 – Serranidae, 18 – Sternoptychidae.

Location	Scale of sampling		#	Dominant	Study
	Spatial	Temporal	Taxa	Taxa	
Atlantic					
Brazil	+—	winter summer autumn	83[a]	*11, 12, 18* **11, 15, 18, 4** **11, 15, 8**	(Nonaka *et al.* 2000)
Mexico	bay littoral inlet	summer autumn winter	81[a] 23[c] 38[c]	4, 16, 5 **6, 3, 2** *11, 9*	(Sanvicente-Añorve *et al.* 2000)
Indian					
Arabian Sea/ Persian Gulf	+—	5 months	47[b]	3, 8, 17, 4 **8, 1, 4,** *11, 9*	(Nellen 1973)
North West Shelf	+	1 year	104[de]	**13, 8, 7, 4**	(Young *et al.* 1986)
"	+	2 summers	76[a]	**8, 14, 4**	Present study
Pacific					
Central	around atoll	1 month	54[e]	*11, 9,* **8, 1**	(Boehlert *et al.* 1992)
Great Barrier Reef	near island	2 years	96[b]	1, 8, 14	(Leis & Goldman 1987)
"	+	summer	70[f]	**13, 4, 8, 1**	(Williams *et al.* 1988)
"	+	spring summer	75[b]	**8, 1, 5, 10, 4**	(Thorrold & Williams 1996)
"	+	22 months	47[f]*	**2, 4, 8**	(Milward & Hartwick 1986)
South China Sea	Ocean	2 months	85[ab]	*11, 9, 3*	(Chamchang & Chayakul 2000)
Taiwan	Bay	1 year	80[d]	14	(Tzeng *et al.* 1997)

3.5.2 Spatial and temporal patterns

I found only weak cross-shelf pattern in ichthyoplankton communities, with families such as monacanthids more abundant at my inshore sites and scombrids and myctophids more abundant at the offshore site. As a result, my analyses tended to group families into a single neritic assemblage. In contrast, cross-shelf variation in assemblages is a strong and consistent finding of other studies and has been documented from both temperate (Cowen *et al.* 1993, Gray & Miskiewiecz 2000) and tropical (Thorrold & Williams 1996) waters, with fauna typically classified into distinct coastal, neritic and offshore communities (Leis & Miller 1976, Leis 1982, Cowen *et al.* 1993, Sanvicente-

Añorve *et al.* 1998, Nonaka *et al.* 2000). My contrasting results probably reflect the fact that sampling occurred over a very limited extent and depth across the shelf, potentially missing taxa, particularly at the deeper offshore site E, thus my conclusions are limited to surface waters of the shelf.

Seasonal changes in the composition and abundance of assemblages are a common feature in tropical waters (see Leis 1993 for review). Sampling occurred from mid-spring to late summer and I recorded an increase in diversity and mean abundance through these months in both summers. This was evident as a gradient of change in assemblage composition from spring through to summer on the nMDS plots. For a number of taxa (e.g. gobiids, monacanthids, carangids and syngnathids) the biggest increase in abundance occurred between October and November, which represents a mid- to late spring transition in the ichthyoplankton communities on this part of the shelf. Similar increases in abundance during summer have been documented for taxa in different tropical locations, for example carangids in the Atlantic (Nonaka *et al.* 2000) and for many taxa, notably apogonids, on the GBR (Thorrold & Williams 1996).

3.5.3 Underlying processes

Intra-seasonal changes in abundance of larval fishes may reflect the spawning activities of adult fishes, differential larval survival or a combination of these processes (Heath 1992). Although information on spawning patterns on the NWS was not collected concurrently with the larval fish samples, it is known that many reef fishes have a distinct spawning season over summer months and that reproductive behaviour will peak at some point during this time (Thresher 1984, Lobel 1989, Robertson 1990, Cowen *et al.* 1993, Davis & West 1993, Meekan *et al.* 1993, Sadovy 1996, McIlwain 2002). This may account for the increase in diversity and abundance of assemblages during the summer. However, it is unlikely that this is the sole factor determining abundance patterns. Circulation patterns on the NW Shelf change during summer, the Leeuwin Current weakens, and the Ningaloo Current forms (Taylor & Pearce 1999). As a result, cool nutrient rich water is upwelled episodically onto the shelf resulting in increased but variable productivity during the summer (Holloway *et al.* 1985, McKinnon & Duggan 2001, Meekan *et al.* 2003). These increases in productivity may

promote better conditions for larval feeding, growth and survival, reinforcing spawning patterns.

Although there was little change in the composition of ichthyoplankton assemblages between summers, there were marked changes in abundance of some of the component taxa. For example, I found that pomacentrids were far more numerous in catches in the second summer than the first, whereas other taxa such as carangids displayed the opposite pattern. Each summer was characterised by very different environmental conditions and these changes in the biophysical environment were likely to have had a strong influence on feeding, growth and ultimately the survivorship of larvae, and may account for the inter-annual differences in abundance of taxa I recorded. A companion study provides some evidence that this was the case. Meekan *et al* (2003) used light traps to collect late stage larvae of *Pomacentrus coelestis* in the region of NWC during the same months as my study. Similar to my findings, catches of this species were much greater in the second summer (1483 individuals) than the first (197 individuals). Otolith analysis of these fishes showed that on average, larval *P. coelestis* grew more slowly in the 1997/98 summer than the 1998/99 summer (0.48mm/d vs 0.53mm/d respectively) and that water temperature explained 30% of the variation in growth, while chlorophyll *a* and zooplankton abundance explained only minor amounts (4.1 and 3.5% respectively). Since fast growth is known to promote the survival of larvae (Miller *et al.* 1988, Bailey & Houde 1989) this suggests that relatively warm water temperatures may account for the differences in abundance of pomacentrid larvae recorded by my study between summers. It is clear, however, that such physical factors do not explain differences in abundance of all taxa of larval fishes collected in my net tows. As mentioned above, families such as carangids showed the opposite pattern to that of pomacentrids and were more abundant in the first summer than the second. For these, feeding conditions may be a more important determinant of growth rate than water temperature. Although growth rate data for larval carangids on the NWS is unavailable for comparison, the diets of larval *Trachurus declivis* collected off Tasmania over three summers were affected by interannular differences in the abundance of their zooplankton prey (Young & Davis 1992). During summers when low nutrient, warmer sub-tropical waters intruded into their study area, larger zooplankton prey were absent and the carangid larvae fed on smaller prey. Smaller prey may have lower calorific content than larger prey and this may have affected growth rates of these larvae.

Unfortunately, Young and Davis (1992) did not measure growth rates and the influence of these dietary differences on larval survival is unknown.

The contrasting responses of different taxa to the same environmental conditions may account for the inability of my multivariate analyses to find strong relationships between abundance patterns of larval fishes and biophysical variables such as temperature, salinity and zooplankton biomass. This might have been exacerbated by the problem that I was able to identify only very few larval fish to species. Despite great progress in the taxonomy of tropical fish larvae (Leis and Carson-Ewart 2000), most samples could only be identified to the level of family at best. This meant that species with potentially contrasting environmental responses could not be distinguished in the analysis of data sets and were simply pooled into broad taxonomic categories. Analysis of at the level of individual species (e.g. Meekan *et al.* 2003) is likely to give a far more powerful insight into the relationship between larval fishes and their environment. However, the seasonal and site changes in biophysical variables that were recorded in the study area (this paper, McKinnon and Duggan 2001; Meekan *et al.* 2003) are reflected in the site and month differences that were identified in the MRT analysis.

3.5.4 Conclusions

During summer, surface ichthyoplankton assemblages on the NW Shelf of Australia appear to be dominated by demersal percoid shorefishes and display consistent increases in diversity and abundance from October to February. Individual taxa showed dissimilar trends of abundance between summers, either as a result of taxon specific differences in the spawning activities of adult fishes or differences in larval survival as a result of changes in environmental conditions. Despite the limited spatial replication of my study, I recorded similar patterns in abundance of larval fishes as those found by Young *et al* (1986). The consistency of my findings to those of Young *et al.*, notwithstanding the use of different net types and sampling protocols, provides a synoptic picture of the early stage larval fish assemblages present on the NWS.

4 Diets of Larvae of Tropical Shorefishes

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4.1 INTRODUCTION

The importance of an understanding of the feeding ecology of marine fishes during the larval stage has been recognised for nearly a century (Hjort 1914). Variation in food availability is thought to have major effects on larval growth and survivorship and can ultimately determine the numbers of juvenile fish recruiting to adult populations (Houde 1987). To date, dietary studies have almost exclusively originated from temperate environments and have examined commercially important species such as cod, *Gadus morhua*, haddock, *Melanogrammus aeglifinus,* and herring, *Clupea harengus* (from the orders Gadiformes and Clupeiformes). These studies show that larval fishes consume a wide range of zooplankton prey including phytoplankton, dinoflagellates, naked ciliates, tintinnids, rotifers, copepods, mollusc veligers, chaetognaths, appendicularia, and other fish larvae (Hunter 1981, Leis 1991). In contrast, relatively few studies have described the feeding ecology of larval fishes in tropical environments where perciform fishes dominate (Leis 1991). Taxonomic differences between these orders of fishes, which correspond to differences in body form (elongate vs compact) and swimming abilities (fast vs slow) for a given size of larvae (Leis *et al.* 1996, Fuiman & Higgs 1997, Leis & Carson-Ewart 1999, Fisher et al. 2000, Fisher & Bellwood 2001, Leis & McCormick 2002), as well as major differences in temperature and prey communities, may mean that generalisations from temperate studies are unlikely to apply to tropical larvae.

Net collections of ichthyoplankton from tropical waters are remarkably diverse and contain few larvae that can be identified to species (Leis 1993, Leis & Carson-Ewart 2000). When attempting to identify prey items in guts, problems of species diversity are greatly magnified. Consequently, dietary studies of tropical fish larvae have been limited to fewer than 35 species of shorefishes (Leis 1991, Østergaard *et al*. 2005),

representing only a small fraction of the over 1000 species found on Indo-Pacific coral reefs (Lowe-McConnell 1987).

4.2 Aims

To provide a broad overview of the feeding of larvae of tropical shorefishes and generate testable hypotheses for future research about the nature of dietary specialisation, prey selectivity and the role of larval fish as predators in tropical planktonic ecosystems, I aimed to:

1) describe the diets of 50 families of larvae of tropical shorefishes ;
2) explore whether diets differed among taxa for i) all taxa examined and ii) copepod specialists, by identifying the copepod prey items at an increased level of taxonomic resolution;
3) see if family level differences in the diet still occur when spatiotemporal variation is removed by examining the larvae collected in one net tow; and
4) calculate prey selectivity for some of the prey items of 7 co-occurring larval shorefishes.

4.3 METHODS

4.3.1 Sample collection and processing.

Ichthyoplankton were collected during cruises in the vicinity of the NWC (21º49'S, 114º14'E) in the austral summers of 1997/98 and 1998/99. Sampling focused on a shallow inshore site (B, ~20 m depth,) located at the mouth of the Exmouth Gulf, and an offshore shelf break site (E, ~100 m depth) (see Fig. 1 in Sampey *et al*. 2004). Oblique tows of Bongo nets (0.8 m net diameter, 500 μm mesh) to ~16 m depth were used to collect larvae at both sites. To ensure full guts, sampling occurred near dusk, as larval fish are visual predators (Blaxter 1986) with peaks in feeding occurring at dawn and dusk (Last 1980, Young & Davis 1990, McLaren & Avendano 1995, McLaren *et al.* 1997). For full details of sampling techniques see Sampey *et al*. (2004). Zooplankton was sampled using vertically towed nets (0.5 m diameter, modified WP-2 net, 73 μm mesh; see Meekan *et al.* 2003).

Larval fishes were sorted into recognisable taxa and identified to the lowest taxonomic level possible (usually family). Taxa were initially selected for gut analysis based on abundance, with up to 20 individuals of particular taxa targeted wherever possible from the same sample. Subsequently, fish were analysed based on whether they could be considered to be reef fishes (*sensu* Leis & Carson-Ewart 2000). Standard (SL) and mandible (ML) length were measured with an ocular micrometer. The guts were carefully excised from the body wall with electrolytically sharpened tungsten needles and placed onto a microscope slide into a drop of glycerin, as this assists dissection by dampening particle movement and also aids the detection of food items due to its clearing properties (Arthur 1976). A subjective measure of gut fullness (1 - empty, 2 – ¼, 3 - ½, 4 - ¾, and 5 – full) and the state of digestion of the contents (1 – intact prey, 2 – exoskeleton starting to separate from the body, and 3 – exoskeleton or bits only) was recorded (Young & Davis 1990). The guts were then teased apart and the contents were identified to the lowest taxonomic level possible and enumerated.

4.3.2 Data analysis.

Prey items were pooled into 21 categories to display broad trends. For each prey category an index of relative importance (IRI) (Sassa & Kawaguchi 2004) was calculated:

$$IRI = \%N * \%FO$$

where %N for each prey item was the number of times a particular prey item occurred as a percentage of the total number of prey items found for that fish taxon and %FO was the frequency of occurrence of a particular prey item expressed as a percentage of the total number of stomachs examined for each fish family (McKinnon et al. 2002, Sassa & Kawaguchi 2004). I considered prey categories that had an IRI > 1000 to be major dietary components for that family, those with an IRI between 100 - 1000 to be moderate components and < 100 to be minor components.

Data analysis was conducted in PRIMER v6β and Statistica 6.1 using the results from non-empty guts. I used ANOVA on the Shannon diversity index (H'), which was calculated for each fish in PRIMER, to test for differences in prey diversity among fish families. The multivariate analytical approach was to examine data at various scales of prey identification and spatio-temporal occurrence of fish larvae to elucidate

relationships among the fish families and their prey. I first removed unidentified prey as a category (~3% of total prey items) as these occurred across many families and thus did not contribute to my understanding of the dietary difference among families. An average of each prey item per family was calculated and a data matrix constructed by considering the families as samples and the pooled prey categories as variables (46 families by 20 prey categories). The numbers of prey in a larva's gut will be influenced by the size of the gut and this will differ between taxa. To compensate for this, I first standardised the data by converting the prey to a percentage composition of the total prey items for each fish family. A similarity matrix was then produced using the Bray-Curtis distance measure as it is insensitive to zero values while at the same time preserving the influence of abundant prey items. Group averaged clustering and non-metric multi-dimensional scaling (nMDS) analyses were then performed (minimum of 25 iterations) to produce dendrograms and two-dimensional ordinations. The adequacy of the nMDS was assessed using stress values. A stress of < 0.1 provides a good ordination, a stress of < 0.2 provides a useful ordination and stress values > 0.2 need to be examined at higher dimensions to avoid misinterpretation (Clarke & Warwick 2000). Generally, the three-dimensional plots of the datasets provided a better representation of relationships (i.e. lower stress values). However, these were best viewed on the computer screen where they could be manipulated and translated poorly to print and were also difficult to plot with cluster analyses. Consequently, I chose to only display the two-dimensional plots, which displayed the same trends as the three-dimensional plots. I examined the cluster and nMDS plots to see what groupings formed and then set a cut-off of 30% similarity (Clarke & Warwick 2000). SIMPER (similarity percentages) was then used to determine the prey items that had contributed to the groupings observed from the cluster and nMDS analyses.

To provide a more detailed description of the taxa of copepods being eaten, I repeated these analyses on a subset of the data for families of fish larvae that fed predominately on these prey. I removed both unidentified prey and copepod fragments and identified copepod adults to genus and juveniles to order, while non-copepod preys were lumped into one category (data matrix of 27 prey items for 38 families of larval fishes).

The previous analyses considered larvae from a variety of sampling sites and times, so the differences recorded among families could have been confounded by spatio-

temporal differences in the prey encountered. To examine if family level differences were still observed in the diets of co-occurring larvae, I repeated the analyses on a subset of larvae that were all collected in one sample from an inshore site (B, ~ 20 m depth) on 17 February 1999. For these I used similar prey categories to those in the copepod analysis, although not all of these prey categories occurred in this sample (data matrix of 11 families and 17 prey categories). Finally, prey selectivity was assessed for these same co-occurring larvae using Chesson's α index (Chesson 1978):

$$\alpha = (r_i/p_i)(\sum r_i/p_i)^{-1} \ (i = 1,\ldots, m)$$

where r_i and p_i are the proportion of prey item *i* in the diet and in the water column respectively and *m* is the number of prey items. Neutral preference occurs at 1/*m*. The proportion of prey in the water column was estimated from the average of zooplankton densities (number m^{-3}) for two vertical net tows, while the proportion of prey items in the diet was estimated using an average count of prey items that occurred in guts. The sub-sampling procedures for counting zooplankton samples meant that zooplankton that occurred in densities <6 m^{-3} in the field may not have been detected in the samples, despite being present at the sampling location. Prior to calculation of α, prey items not present in the guts (e.g. *Acrocalanus gibber*) and prey items not recorded from the water column, whether because they were potentially rare (e.g. *Clausocalanus farrani, Corycaeus asiaticus*, *Oithona rigida*, *Parvocalanus* sp., *Pseudodiaptomus* sp.), the levels of identification/groupings differed (e.g. copepod nauplii, *Oithona* spp. and poecilostome juveniles), or because they were not counted as part of the zooplankton sampling data (e.g. *Dynophysis*), were excluded. This limits my conclusions to the relative selectivity of some components of the plankton. I considered $\alpha > 4$ to indicate high selectivity for a particular prey item, $4 > \alpha > 1$ moderate selectivity and $\alpha < 1$ indicated low selectivity. To look in more detail at differences within a family the gobiids were able to be split into two groups, Gobiidae mixed spp., which were all of an elongate body form, and Gobiidae sp. 6, which was a deep bodied darkly pigmented species. Prey selectivity was assessed for 6 families of larval fish (7 taxa) (n > 5 individuals).

4.4 RESULTS

4.4.1 Fish lengths, gut fullness and digestion ratings

I examined whole gut contents of 591 individuals from 50 taxa of predominately early post-flexion larvae of ~4mm SL (Table 1). Mean SL ranged from 3 mm (callionymids, aploactinids, carangids, leiognathids, and serranids) to 25 mm (fistulariids). Mean ML ranged from 0.3 mm (synodontids) to 1.6 mm (fistulariids). Mean gut fullness ranged from empty (1 ± 0, engraulids, berycids, and scarids) to full (5 ± 0, aploactinids, opistognathids, pomacanthids, priacanthids, and samarids), i.e. all individuals in these families recorded empty (GF = 1) or full (GF = 5) guts so there is no variation around the mean result. The majority of prey items were in an advanced stage of digestion (digestion rating > 2); even in those individuals whose guts also contained intact prey items.

4.4.2 Prey composition of diets

Prey diversity, measured as the Shannon diversity index, differed among families (MS = 0.9, F = 6.1, df = 46, $p < 0.05$) and was highest for siganids and labrids (2.1 and 2 respectively, Table 1). Seven families recorded an index of relative importance (IRI) of 10000 as only 1 prey type was recorded in all of the larvae examined (Table 2). These larvae included nemipterids and acanthurids, which preyed upon appendicularians; chaetodontids, which ate chaetognaths; and cirrhitids, opistognathids and solenostomids, which ate copepodites. These findings are limited by the examination of only one larva for each of these families, except for nemipterids (13 individuals) and chaetodontids (2).

Copepods were major prey items for the majority of families. Copepod juveniles were the most important dietary component for 34 families of larvae (copepodites and nauplii, 24 and 10 families respectively, Table 2). Adult copepods were major prey items for many families (e.g. Corycaeidae (*Corycaeus* spp and *Farranula* spp.) for gobiesocids, blenniids, labrids and priacanthids). Only two families consumed non-copepod prey as a major component of their diet, tetraodontids ate molluscs (mostly gastropods) and lethrinids (*Lethrinus* sp.) ate polychaetes (IRI 4909 and 1829 respectively). The only other larvae to eat polychaetes were monacanthids and gobiids

Table 6. Families of larval fishes used for gut content analysis.
Total guts examined, TGE; number of empty guts, EG; Mean ± sd of Standard (SL) and Mandibular (ML) length; Gut Fullness (GF), 1 - empty, 2 – ¼, 3 - ½, 4 - ¾, and 5 – full; Shannon Diversity Index (loge), H′; Spatiotemporal collection details (ST), B – inshore, station B, E – offshore, station E, T – inshore, station TB, O – October, N – November, D - December, F – February, 7 – 1997, 8 – 1998, 9 – 1999 (see Sampey et al 2004 for further collection details), Stage ^{S} – Pre-flexion ^{Pe}, Flexion^{F}, Post-flexion^{Po}. * - larvae from 1 sample at Station B, February 1999, number in superscript indicates the number of individuals if different from total examined.

No.	Family	Common Name	TGE	EG	SL mm	ML mm	GF	H'	ST ^{S}
	Clupeiformes								
1	Clupeidae	herrings, sardines, sprats	20	12	11 ± 2	0.7 ± 0.1	1 ± 1	0.3	BD7^{Po}
2	Engraulidae	anchovies	20	20	7 ± 1	0.8 ± 0.2	1 ± 0	-	TD8^{Po}
	Aulopiformes								
3	Synodontidae	lizardfishes	6	5	6 ± 4	0.3 ± 0.1	1 ± 1	0.7	EF8EN7^{PeFPo}
	Ophidiiformes								
4	Ophidiidae	cusk eels	3	1	9 ± 7	1.2 ± 0.7	3 ± 2	0.8	END7BD8^{FPo}
	Gobiesociformes								
5	Callionymidae	dragonets	21*	0	3 ± 1	-	3 ± 1	1.5	BF9^{Po}
6	Gobiesocidae	clingfishes	2	0	5 ± 3	0.7 ± 0	4 ± 1	0.2	EF8BF8^{PePo}
	Beryciformes								
7	Berycidae	redfishes	1	1	5 ± 0	1 ± 0	1 ± 0	-	BN7^{Po}
8	Holocentridae	squirrelfishes	8	0	5 ± 1	0.8 ± 0.1	3 ± 1	1.2	EF9^{PeFPo}
	Gasterosteiformes								
9	Centriscidae	razorfishes	5	1	5 ± 6	0.7 ± 0.1	3 ± 1	1.1	BF9TD8^{PePo}
10	Fistulariidae	flutemouths	7	0	25 ± 22	1.6 ± 1	4 ± 1	1.5	BN7EN8F9^{PePo}
11	Solenostomidae	ghost pipefishes	1	0	4 ± 0	0.4 ± 0	4 ± 0	0	TN8^{Pe}
12	Syngnathidae	seahorses & pipefishes	24	1	22 ± 10	0.7 ± 0.2	4 ± 1	0.9	BD7TND8^{Po}

Table 6 Continued

No.	Family	Common Name	TGE	EG	SL mm	ML mm	GF	H'	ST [S]
	Scorpaeniformes								
13	Aploactinidae	velvetfishes	4*	0	3 ± 0	0.5 ± 0	5 ± 0	0.9	BF9[Po]
14	Scorpaenidae	scorpionfishes	10	0	6 ± 2	1 ± 0.6	4 ± 1	1.1	BN7F9ED7NF8TD8[PePo]
15	Platycephalidae	flatheads	17*[4]	0	5 ± 1	1 ± 0.3	4 ± 1	1.2	BND7F8F9ED7TD8[PeFPo]
	Perciformes								
16	Acanthuridae	surgeonfish	1	0	5 ± 0	0.6 ± 0	2 ± 0	0	EF8[Po]
17	Apogonidae	cardinalfishes	10	0	5 ± 1	0.9 ± 0.2	3 ± 1	1.5	ED78 [PePo]
18	Blenniidae	blennies	10	0	5 ± 1	0.9 ± 0.1	4 ± 1	1.4	ED8 [PeFPo]
19	Carangidae	jacks, trevallies	3*	0	3 ± 1	0.6 ± 0.5	5 ± 1	1.2	BF9[Po]
20	Chaetodontidae	butterflyfishes	2	0	6 ± 0	0.9 ± 0.2	4 ± 1	0	BN7TD8 [Po]
21	Cirrhitidae	hawkfishes	1	0	5 ± 0	1 ± 0	4 ± 0	0	BF9[Po]
22	Gobiidae	gobies	39*	1	5 ± 1	0.6 ± 0.2	3 ± 1	1.8	BF9[Po]
23	Haemulidae	sweetlips, grunts	12	0	4 ± 1	1 ± 0.1	4 ± 1	1.3	BON7D8TD8ED7 [FPo]
24	Labridae	wrasses	14	3	7 ± 2	1 ± 0.2	3 ± 1	2	BN7D8EOND7 [Po]
25	Leiognathidae	ponyfishes	20*	4	3 ± 0	0.5 ± 0.1	2 ± 1	1.1	BF9[FPo]
26	Lethrinidae	emperors	20	2	4 ± 3	0.6 ± 0.4	4 ± 1	1.3	BN7[Po]
27	Lutjanidae	snappers & fusiliers	20	0	5 ± 1	0.8 ± 0.2	4 ± 1	1.8	EF8BF8EF9[PePo]
28	Microdesmidae	wormfishes & dartfishes	20	3	9 ± 1	0.9 ± 0.1	2 ± 1	1.2	EF8[Po]
29	Mullidae	goatfishes	15	0	4 ± 0	0.6 ± 0.1	4 ± 1	1.5	ED7F89BN78D7[FPo]
30	Nemipteridae	threadfin & monocle breams	13	2	4 ± 1	0.7 ± 0.2	3 ± 1	0	BF9[PeFPo]
31	Opistognathidae	jawfishes	1*	0	4 ± 0	0.5 ± 0	5 ± 0	0	BF9[Po]

Table 6 Continued

No.	Family	Common Name	TGE	EG	SL mm	ML mm	GF	H'	ST [S]
32	Pinguipedidae	grubfishes & sandfishes	20*	0	4 ± 1	0.8 ± 0.1	4 ± 1	1.8	$BF9^{Po}$
33	Pomacanthidae	angelfishes	5	0	5 ± 2	1 ± 0.2	5 ± 0	1.2	$BF89TD8^{PoF}$
34	Pomacentridae	damselfishes	12	0	8 ± 1	1.4 ± 0.2	4 ± 1	1.2	$EN78^{Po}$
35	Priacanthidae	bigeyes	10	0	5 ± 2	1 ± 0.5	5 ± 0	1.7	$BN7F8EOD7F9^{PeFPo}$
36	Pseudochromidae	dottybacks & eelblennies	10	0	6 ± 2	1.1 ± 0.3	3 ± 1	0.8	$BN7END8^{PePo}$
37	Scaridae	parrotfishes	2	2	10 ± 2	0.9 ± 0.1	1 ± 0	-	$BN7EO8^{Po}$
38	Scombridae	tunas and mackerels	20	0	5 ± 1	1 ± 0.2	4 ± 8	1	$EF8^{PeFPo}$
39	Serranidae	groupers & reef basses	20	0	3 ± 0	0.5 ± 0.1	5 ± 1	1.3	$BN7^{PePo}$
40	Siganidae	rabbitfishes	6	0	9 ± 5	0.7 ± 0.1	4 ± 0	2.1	$BF9TN8^{Po}$
41	Sphyraenidae	barracudas	20	1	6 ± 1	1.1 ± 0.3	3 ± 1	1.1	$BND7N8EN7DF8TD8^{PePo}$
42	Terapontidae	grunters	20	0	4 ± 0	0.7 ± 0.1	4 ± 1	0.5	$BN8^{Po}$
43	Trichonotidae	sand divers	4	2	8 ± 4	1 ± 0.4	2 ± 1	0.7	$BF8EF8TD8^{PePo}$
44	Tripterygiidae	triplefins	10	1	7 ± 2	0.9 ± 0.2	3 ± 1	1.8	$BON7D8F9ED8^{PePo}$
45	Uranoscopidae	stargazers	1		4 ± 0	1 ± 0	3 ± 0	0	$EO7^{Po}$
	Pleuronectiformes								
46	Bothidae	left-eye flounders	22^{*2}	11^{*2}	9 ± 3	0.8 ± 0.4	2 ± 1	1.1	$BN7F9^{Po}$
47	Cynoglossidae	tongue soles	20*		5 ± 2	0.5 ± 0.2	4 ± 1	1.3	$BF9^{Po}$
48	Samaridae	crested flounders	1*		4 ± 0	0.8 ± 0	5 ± 0	0.6	$BF9^{Po}$
	Tetraodontiformes								
49	Monacanthidae	leatherjackets & filefishes	28^{*8}	6	5 ± 3	0.4 ± 0.2	3 ± 1	1.6	$BF9^{Po}$
50	Tetraodontidae	puffers	11		4 ± 1	0.6 ± 0.2	4 ± 1	1.3	$BN7D8EN8TD8^{PeFPo}$

Table 7. Prey composition of the diets of larvae of fish families collected by plankton nets near the NWC as indicated by an index of relative importance (IRI). Values are calculated from positive guts only (Engraulidae, Berycidae, and Scaridae are omitted). Family number is from Table 1.

	Family No																					
Prey item	**1**	**3**	**4**	**5**	**6**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
Copepod egg							105																
Copepod nauplii	38			152			1053	418			96				267		1786			187	267	50	1481
Copepod copepodites	3231		4762	7065	278	882	4632	3833	10000	8330	10096	6140	2442		2800	360	536		10000	3211	1400	199	2852
Acartia spp.								348		573													
Corycaeidae			476	65	14167	74						140				3520				9		1063	
Harpacticoids				478						2	3462	18								321		166	
Large calanoids								35					11										
Small calanoids		833		266		2647	105	557		408		526	2930		267	40	1429			321	133	17	19
Oithona sp.			476	49						670	96	772			67	1680	536			428	2200	648	19
Oncaeidae				49												40				20		66	
Copepod fragments		833		87		2647	105	139		4			400		267					223	33	17	19
Decapod larvae								139					11										
Euphausiid larvae																						17	
Mollusc																80						66	
Polychaetes																				2			
Protists				5																			
Appendicularia														10000								17	
Chaetognaths																		10000					
Fish eggs/larvae								35															
Other																				2			
Unidentified remains															67					2			

	Family No.																						
Prey Item	**26**	**27**	**28**	**29**	**31**	**32**	**33**	**34**	**35**	**36**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**
Copepod egg		10	15						125		43	769							341			23	
Copepod nauplii	720	2314	2294	1673			857	103	234		3319	3625		517	8196		222					1179	
Copepod copepodites	80	628	2868	145	10000	1711	8000	7250	1406	5320	11	38	2877	6060	172	1250	556			3789		1497	
Acartia spp.													91										
Corycaeidae		31				800		288	3938				753							343			45
Harpacticoids						1222	36	6					457	9						6160	3333	6	
Large calanoids																							
Small calanoids	80	408		255		1283	2750	519	63	40		240	571	138	44		222		38		6667	397	23
Oithona sp.		283	15			67	1071	462	16				1142	69		1250	667			723			
Oncaeidae						50		26		40			91							274			
Copepod fragments	80	408		255		6		519	16			240	23	34	44		56		38			23	
Decapod larvae						272							46										136
Euphausiid larvae										40													
Mollusc													137									23	4909
Polychaetes	1820																					6	
Protists																						51	364
Appendicularia				194					31		3840						222		947				
Chaetognaths		212		12									23										
Fish eggs/larvae													68				56						
Other			118						141		11												23
Unidentified remains		39		982						360		10	91				56	10000	152				91

but only as a minor part of their diet (IRI 51 and 2 respectively). Gastropods were a minor dietary component of blennids and labrids (IRI 80 and 66) and bivalves for siganids and monacanthids (IRI 137 and 23).

A generalist feeding strategy was indicated for only three families, where only moderate values (IRI >1000) were recorded for a particular type of prey. These included bothids, which preyed on appendicularia (IRI 947); synodontids preyed on small calanoids and copepod fragments (IRI 833 for both prey groups); and tripterygiids who preyed on *Oithona* spp. (IRI 667), copepod juveniles (IRI 556), copepod nauplii, small calanoids and appendicularia (all IRI's 222).

Some prey items were only ever eaten as minor components of diets. Large calanoids (*Undinula vulgaris* and *Euchaeta* spp.) were eaten by fistulariids and platycephalids (IRI 35 and 11 respectively). Fish eggs were eaten by siganids and tripterygiids and a fish larva (a goby) was eaten by the largest larva examined, a fistulariid of 65mm (IRI 68, 56, and 35 respectively). Protists (*Dynophysis* sp. and a radiolarian) were recorded from callionymids, monacanthids and tetraodontids (IRI 5, 51 and 363).

4.4.3 Dietary differences among fish families

Clustering and nMDS analyses of all families produced 6 groups at 30% similarity (Fig. 1a-c). Two groups were formed by families that ate only one prey type: chaetodontids (Family 20), which ate chaetognaths (Group 1), acanthurids (Family 16) and nemipterids (Family 30), which ate appendicularians (Group 2). Group 3 was formed by tetraodontids (Family 50), which ate a mixed diet of mainly non-copepod prey including decapod larvae (44%), bivalves (20%) and protists (15%). Group 4 was composed of gobiesocids (Family 6) that preyed on corycaeid copepods (85% of diet) and copepod juveniles (15%, mainly *Oithona* sp.). Bothids (Family 46), samarids (Family 48) and synodontids (Family 3) (Group 5) had the most diverse diets. Bothids were closer to Group 2 due to a high proportion of appendicularian prey but also near Group 6 due to the incidence of copepods in their diet. Synodontids and samarids were plotted closer together as they both ate small calanoids. The remaining families formed a large group (Group 6) that specialised on copepod prey including copepod copepodites and nauplii

(56%), calanoid copepods (13%), *Oithona* sp. (10%), harpacticoid and corycaeid copepods (each contributing 5% of total prey items).

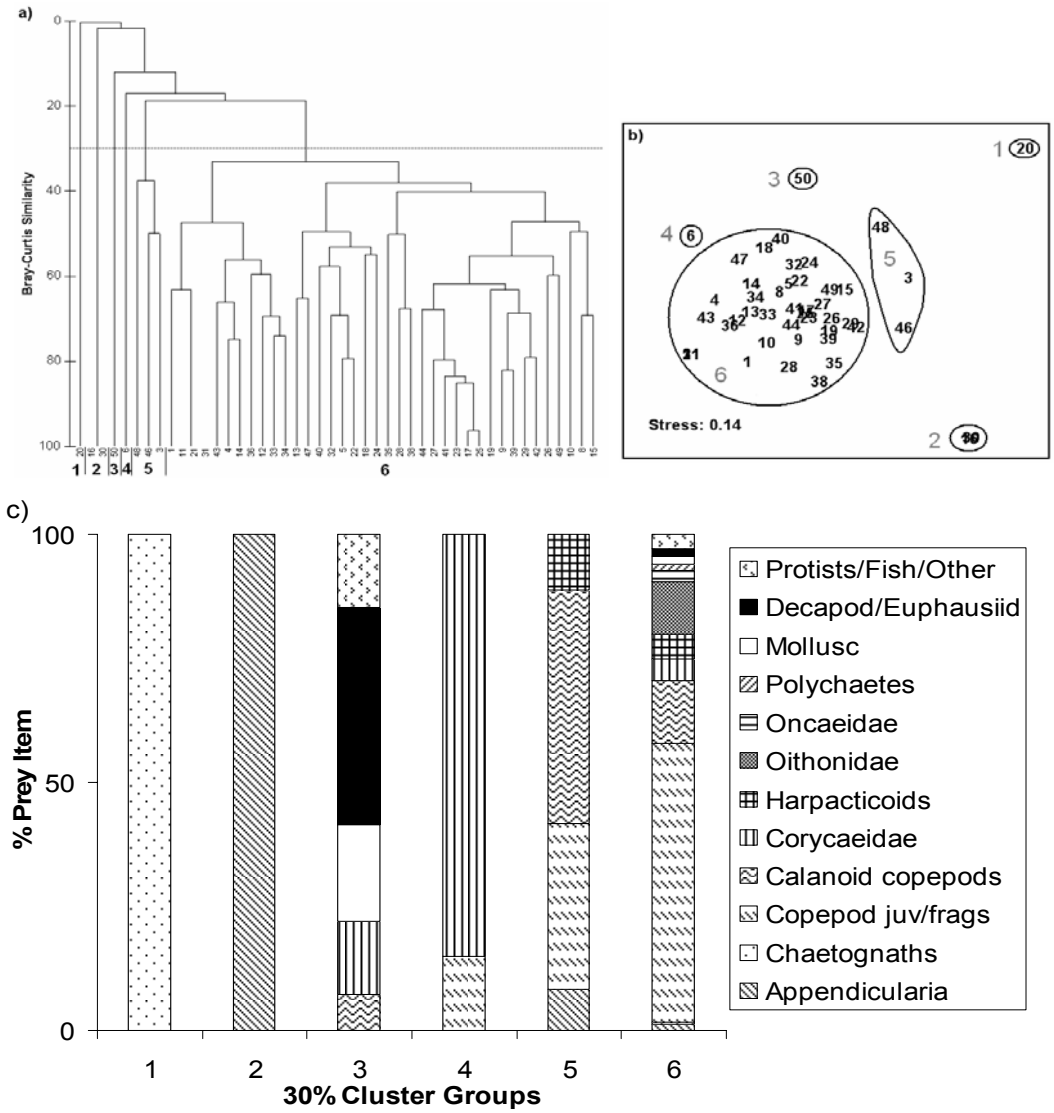

Figure 16. Dendrogram (a) and 2-dimensional ordination (b) generated from a similarity matrix of 20 prey items from 47 families of larval fishes collected by plankton nets near the North West Cape of Australia (NWC).
Each fish family is identified by the family number taken from Table 1. Diets of families closer together are more similar than those further apart. Clusters 1 to 6 were identified at the 30% similarity and the prey composition of these 6 groups is illustrated (c).

The majority of the larvae examined fed on copepods (Group 6, Fig. 1), but the types of copepods eaten differed among taxa. A more detailed examination of this group only formed 5 groups (group 7-11) at 30% similarity (Fig. 2a-c). Trichonotids (Family 43), solenostomids (Family 11) and cirrhitids (Family 21) (Group 7) ate predominately *Oithona* sp. (88% of diet, mostly juveniles). Holocentrids (Family 8, Group 8) ate

copepod juveniles (mostly poecilostomes, 33%, and calanoids, 22%) and copepod adults (*Clausocalanus* spp. and *Farranula* spp., each 22%). Lethrinids (Family 26), serranids (Family 3), mullids (Family 29), terapontids (Family 42), priacanthids (Family 35) and scombrids (Family 38) (Group 9) specialised on copepod nauplii (47% contribution to the group). The 25 fish families that composed Group10 ate calanoid copepodites (20%), *Oithona* sp. (21%), calanoid copepods (15%) and copepod juveniles (14%). Monacanthids (Family 49), carangids (Family 19), and platycephalids (Family 15) (Group 11) ate calanoid copepods (44%, mostly *Temora* spp.), Oithonidae (mostly *Oithona* juveniles, 18%) and copepod juveniles (19%). The families in this group appear to have little in common with each other and in three-dimensional plots it sits above the others in a vertical plane but this detail has been lost in the two-dimensional plots.

The analysis of co-occurring families (from inshore site B, 17 February 1999) produced a dendrogram that split these into 3 groups (group 12-14) at 30% similarity (Fig. 3a-c). Samarids (Family 48, Group 12, 1 individual) ate *Temora* spp. (67%) and *Euterpina acutifrons* (33%). One opistognathid (Family 31, Group 13) ate calanoid juveniles. Group 14 can be further broken down into 3 groups at the 40% similarity. Group 14a, consisted of aploactinids (Family 13, 4 individuals), callionymids (Family 5, 21 individuals), gobiids (Family 22, 39 individuals), cynoglossids (Family 47, *Cynoglossus* sp., 20 individuals) and pinguipedids (Family 32, 20 individuals). This group ate a mixed diet of harpacticoids (22.5%, *Euterpina acutifrons* and *Microsetella* spp.), *Oithona* spp. (adults and copepodites, 18%), copepod nauplii and copepodites (15%), and calanoid copepods (15%). These larvae were the only predators of *Bestiolina similis* and *Pseudodiaptomus* spp., although these were only consumed in small amounts (3% and 1.5% of diet respectively).

Carangids (Family 19, Group 14b, 3 individuals) ate a mixed diet including copepod nauplii (26%), *Parvocalanus* spp. (23%), *Oithona* spp. (adults and copepodites, 16%), *Temora* spp. (19.5%), harpacticoids (8%) and calanoid juveniles (8%). Platycephalids (Family 15, 4 individuals), leiognathids (Family 25, 20 individuals) and monacanthids (Family 49, 8 individuals) (Group 14c) also ate a mixed diet including *Clausocalanus farrani* (23%), calanoid juveniles (19%), *Oithona* spp. (adults and copepodites, 14%), copepod nauplii (13%), *Temora* spp. (13%). Non–copepod prey (12%) formed the diet

of monacanthids (molluscs, polychaetes and protists) and platycephalids (decapod larvae).

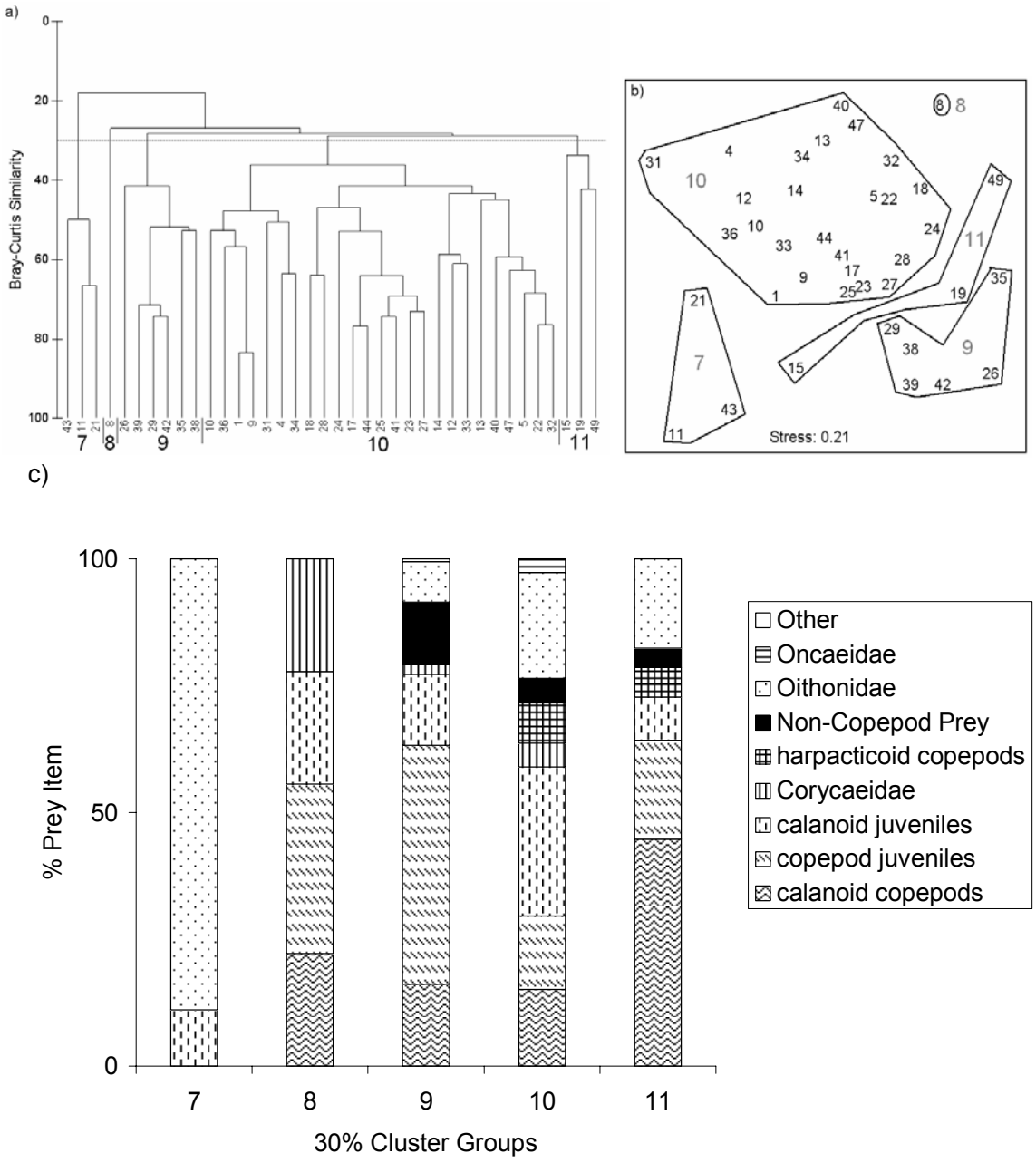

Figure 17. Dendrogram (a) and 2-dimensional ordination (b) generated from a similarity matrix of gut contents of larval fishes that fed on copepods (i.e. from cluster group 6 identified in Fig. 16; 27 prey items from 36 families of larval fishes) collected by plankton nets near NWC.
Clusters 7 to 11 were identified at the 30% similarity and the prey composition of these 5 groups is illustrated (c).

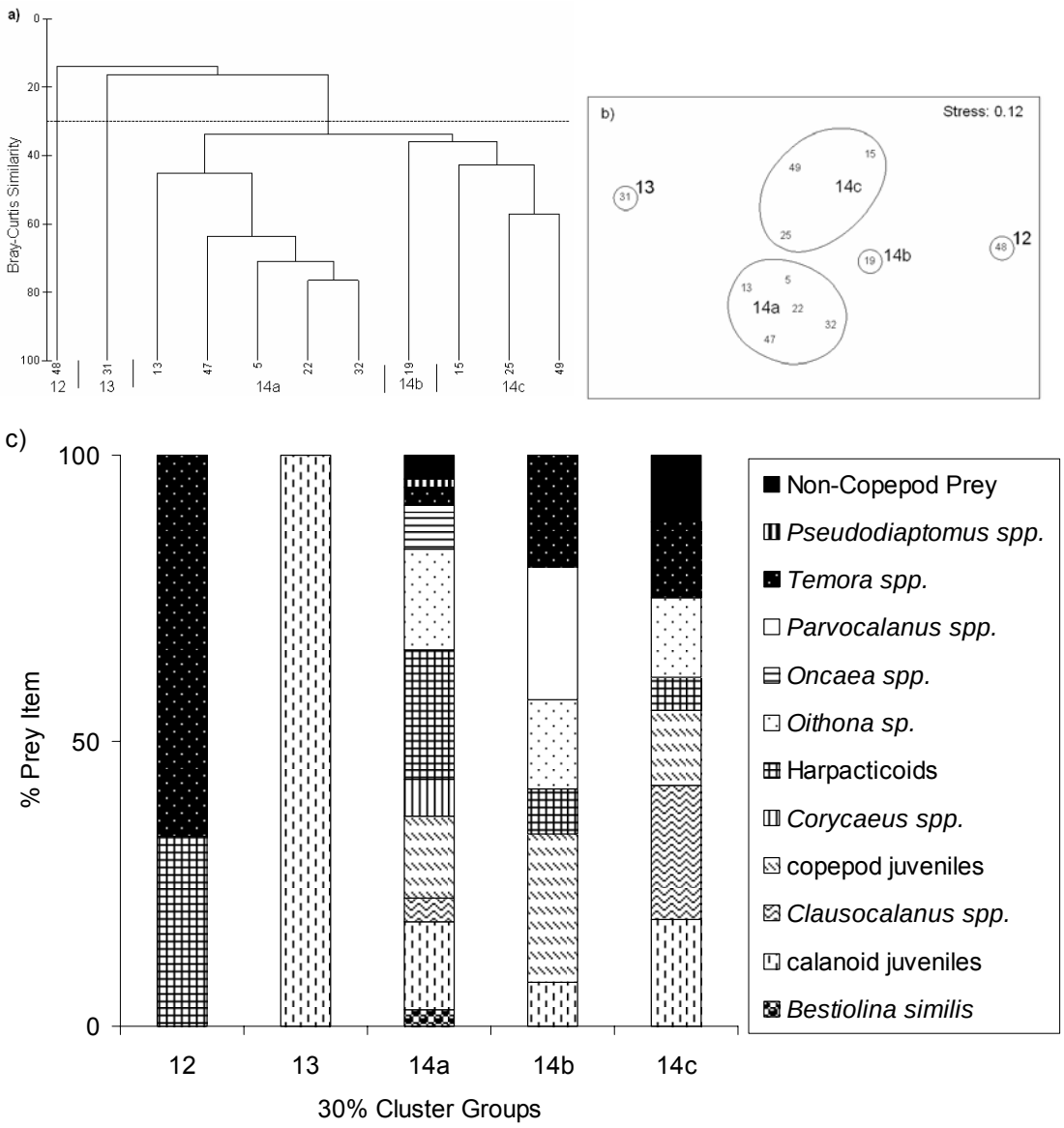

Figure 18. Dendrogram (a) and 2-dimensional ordination (b) generated from a similarity matrix of co-occurring larvae from one sample collected by plankton nets on the NWC (29 prey items from 11 families of larval fishes).
Clusters 12 to 16 were identified at the 30% similarity and the prey composition of these 5 groups is illustrated (c).

4.4.4 Zooplankton abundance and prey selectivity for co-occurring larvae

Analysis of zooplankton and fish larvae sampled at the same station showed that cyclopoid juveniles were the most abundant prey item (260 000 $100m^{-3}$) and *Acrocalanus gibber* and *Corycaeus andrewsi* were the least abundant (600 $100m^{-3}$) (Table 3). Callionymids were the most abundant larvae (40 $100m^{-3}$) and samarids and opistognathids the least abundant (0.2 $100m^{-3}$). Some prey taxa (e.g. *Clausocalanus farrani*), which were eaten by some larvae, could not be included in the prey selectivity analysis as they did not occur in sufficient concentration to occur in the sorted fraction of the zooplankton sample. A total of 17 prey items were assessed for selectivity for 7 taxa of larval fishes.

Larvae of shorefish families differed in their pattern of selectivity. Some prey were strongly selected, such as *Oithona attenuata* ($\alpha = 1.6$) by leiognathids (present in 45% of guts, but 4% of available prey; Figure, 4 & 5, Table 3). Other preys were avoided, such as harpacticoid juveniles by *Cynglossus* sp. (6% of prey items in guts but 24% of prey in the environment. *Bestiolina similis* was rare in the water column (0.5%) but a highly preferred prey item for two families (Gobiidae, both mixed species, 20%, $\alpha =$ 6.8, and Goby sp. 6, 9%, $\alpha = 2.7$, Pinguipedidae, 7%, 2.1; Figure, 4 & 5, Table 3). Pinguipedids showed high selectivity for both *Temora* sp. (15%, $\alpha = 5.6$) and *Corycaeus andrewsi* (7%, $\alpha = 5.3$), and these prey items were also rare in the water column (0.4% and 0.2% respectably). Monacanthids showed a moderate selectivity for polychaetes (33%, $\alpha = 2.3$), which were another rare prey item (2% of available prey).

Table 8. Density (No.100m^{-3}) of zooplankton and fish larvae collected by plankton nets at site B near the NWC on the 17th February 1999. * not eaten by the larvae examined in this sample. [Hp]Harpactocoid copepods, [Ca]Calanoid copepods, [Cy]Cyclopoid copepods, [NC] Non-Copepod. Prey items present in guts but not recorded in plankton counts are listed.

Prey	Concentration	Fish Larvae	Concentration
Cyclopoid juveniles*	260000	Callionymidae	40
Bivalves* [NC]	99600	*Cynoglossus* sp.	20
Calanoid juveniles	94500	Gobiidae sp. 6	20
Gastropods* [NC]	91900	Pinguipedidae	10
harpacticoid juveniles	72400	Leiognathidae	5
Larvaceans* [NC]	56500	Gobiidae mixed spp.	3
Microsetella sp.[Hp]	26800	Monacanthidae	1
*Oithona nana**[Cy]	18900	Aploactinidae	1
Euterpina acutifrons[Hp]	18900	Platycephalidae	1
Chaetognaths* [NC]	18800	*Engyspiron* sp.	0.5
Corycaeus spp. [Cy]	14300	Carangidae	0.5
Parvocalanus crassirostris[Ca]	12600	Samaridae	0.2
Oithona attenuata[Cy]	12600	Opistognathidae	0.2
Oithona simplex[Cy]	9500		
Oncaea spp. [Cy]	6400		
*Parvocalanus dubia**[Ca]	6300		
Polychaetes [NC]	6200		
Decapod larvae [NC]	3200		
Oithona spp. [Cy]	3200		
*Acartia fossae**[Ca]	3100		
*Canthocalanus pauper** [Ca]	3100		
Euphausid larvae* [NC]	3100		
Bestiolina similis[Ca]	1600		
Corycaeus dahli [Cy]	1200		
Temora turbinata[Ca]	1200		
*Paracalanus indicus**[Ca]	900		
*Acrocalanus gibber**[Ca]	600		
Corycaeus andrewsi [Cy]	600		

Prey items eaten but not recorded in zooplankton

Prey	Concentration
Clausocalanus farrani[Ca]	-
copepod nauplii	-
Corycaeus asiaticus[Cy]	-
Dynophysis [NC]	-
Mite [NC]	-
Oithona juveniles[Cy]	-
Oithona rigida[Cy]	-
Parvocalanus sp. [Ca]	-
poecilostome juveniles[Cy]	-
Pseudodiaptomus spp. [Ca]	-

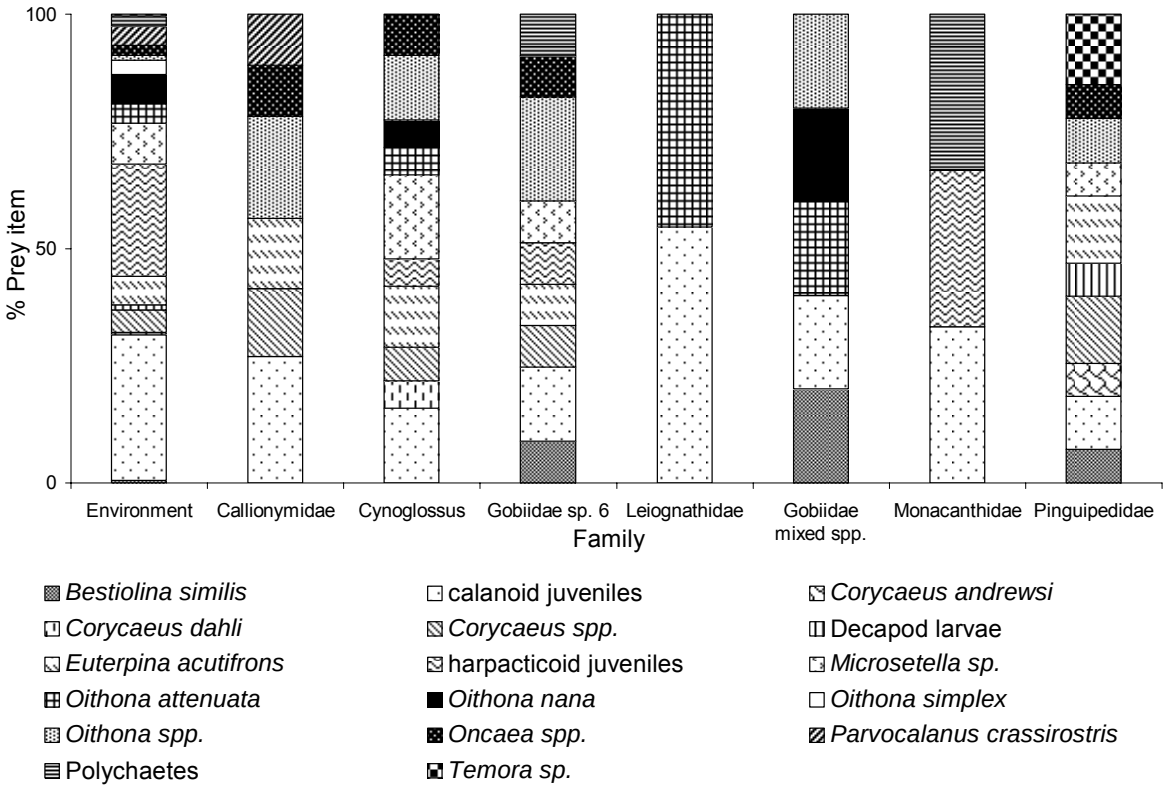

Figure 19. Composition of prey items in the zooplankton community compared to that found within the guts of larvae of tropical shorefishes collected by plankton nets near the NWC.

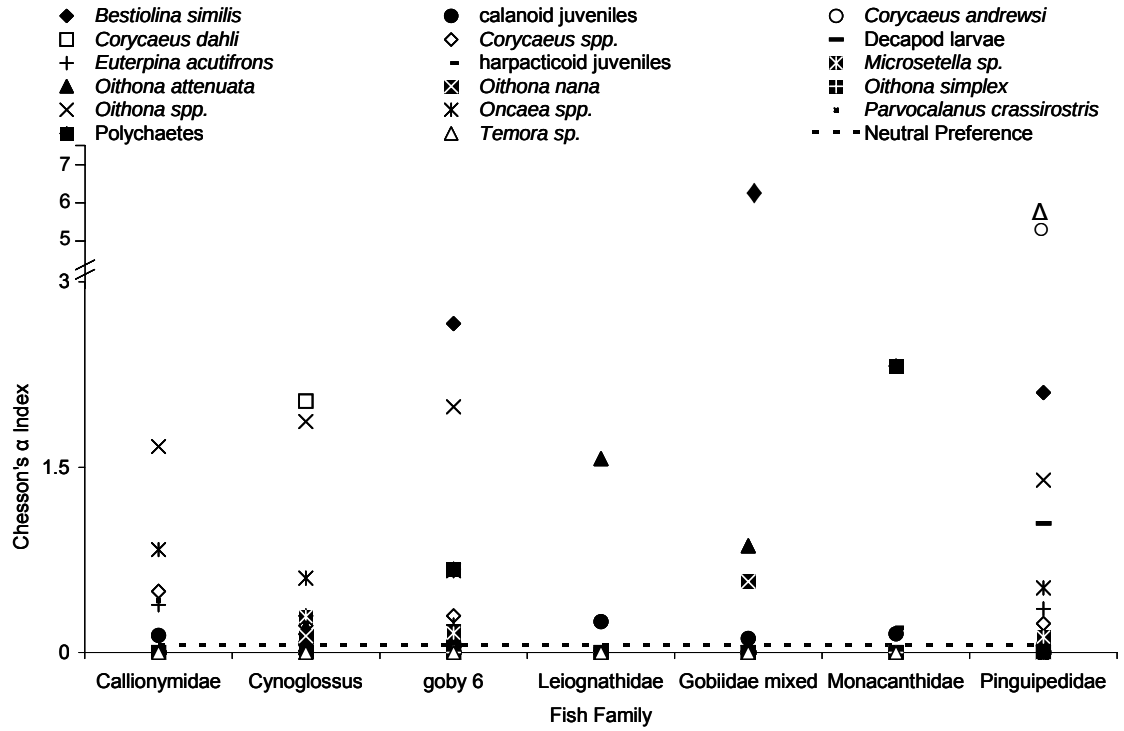

Figure 20. Prey selectivity values (Chesson's α index) for 7 co-occurring taxa of larval fishes collected in single plankton net near the NWC. Horizontal line represents neutral preference.

4.5 DISCUSSION

4.5.1 Diets of tropical larval shorefishes

I have described the diets of 50 families of tropical larval shorefishes from the NWC, effectively doubling the number of families for which we now have some knowledge of prey types and feeding patterns. Copepods have been shown to be the main prey item of larval fishes in temperate waters (Hunter 1981). My study reinforces the conclusion of previous work (Leis, 1991; Østergaard, 2005) that this is also the case in tropical systems. Clupeids, apogonids, blennids, gobiids, haemulids, pomacentrids, scorpaenids, scarids and carangids specialise on copepod prey (Table 4). Moreover, the orders of copepods eaten by some families were remarkably consistent across studies e.g. callionymids ate cyclopoid copepods and scorpaenids ate calanoid and corycaeid copepods (Table 4). There were some differences; carangids sampled in Hawaii ate predominately *Oithona* spp, whereas those from the Andaman Sea and NWC showed a preference for calanoid copepods. This may be due to either inter-specific differences in morphology, physiology and behaviour of larvae or could simply reflect a variation in the spatiotemporal occurrence of the prey types among locations and habitat types sampled by each study (bays, coastal or oceanic waters).

Fish larvae from over 76 families occurred in our collections (Sampey et al. 2004). I have had to restrict our examination to the 50 families for which there was suitable material available and to cover the range of taxonomic diversity I have had to compromise the number of replicate individuals examined within each family. Consequently my data do not capture the full range of variability of feeding by larvae within a family, either spatiotemporal (daily, monthly, yearly, inshore, offshore, alongshore) or ontogenetic (size and stage; pre-, post-, and flexion). Over 130 species of pelagic copepods occur in the area (McKinnon unpublished); discrimination of the naupliar and copepodite stages to a higher taxonomic resolution than order (calanoid, cyclopoid etc) is logistically difficult in well preserved plankton samples and more so within the guts of larval fish where evidence of the prey is often restricted to pieces of exoskeleton. For these reasons, I have been forced to pool diverse assemblages of organisms into single taxonomic units and to treat these in our analyses in the same way as taxa that I have been able to identify to species. Differences in naupliar behaviour

between genera render them differentially susceptible to predation (Titelman & Kiørboe 2003) and the same is likely to be true for copepodites. Therefore, for any particular family of fish larvae there is an underlying level of prey selection that I have been unable to discriminate.

4.5.2 Inter-specific differences within families

Dietary information is available for at least 7 species of scombrids and 9 species of bothids (Uotani et al. 1981, Jenkins et al. 1984, Young & Davis 1990, this study). This limited database suggests that inter-specific differences are no greater than inter-family differences in diet. I could not identify the scombrids in my study confidently to genus but they all appeared to be representatives of one species. These larvae were mostly ~ 5 mm and ate copepod nauplii and appendicularians, which is consistent with the findings of other studies (see Table 4). *Auxis* spp, *Scomberomorus* spp., and *Katsuwonus* spp. larvae examined in three different studies (Uotani et al. 1981, Jenkins et al. 1984, Young & Davis 1990) all showed a preference for appendicularians when less than 5.5 mm long, with only *Thunnus* spp. showing a preference for copepod nauplii and cladocerans (*Evadne* spp.) at a similar size. Bothids also ate appendicularians and calanoid copepods, with some species eating both of these prey items and others preferring only one. Variation in diet among species within a family was recorded in our study where one goby (goby 6) showed slightly different prey preference to other co-occurring gobiid species. All of these larvae showed strong preference for *Bestiolina similis*, but goby 6 ate polychaetes, *Euterpina acutifrons* and *Corycaeus* sp, in contrast to the remaining species that ate *Oithona nana* and *O. attenuata*. Such differences in prey choices within families may be related to differences in encounter rates between larvae and prey, which will be affected by prey patchiness (Jenkins 1988) and small scale turbulence (Gallego et al. 1996, MacKenzie & Kiørboe 2000) and may also be affected by variation in the morphology, physiology and behaviour among species within a family. However, the consistency of prey choices across families collected at different locations and times suggests that prey selection by fish larvae are influenced by characteristics of their prey and the inherent preferences of particular taxa.

4.5.3 Prey characteristics - copepod prey

The characteristics of copepods as prey for larval fishes differ between and within orders. Some families of fishes preferred calanoid copepods, others ate more cyclopoid copepods (including species in the families Oncaeidae, Corycaeidae and Oithonidae; Boxshall & Halsey 2004). These prey types have very different characteristics, with *Oithona* spp. being small, cryptic (clear) with a strong escape response thus rendering them less susceptible to visual predation when compared to many of the calanoid copepods such as *Centropages* spp., *Paracalanus* sp., *Pseudocalanus* sp., and *Calanus* spp., which are slower moving, larger and sometimes pigmented (Kimmerer 1991). Small calanoids of the genera *Clausocalanus*, *Pseudodiaptomus*, *Canthocalanus*, *Calanopia*, *Temora*, *Paracalanus*, *Parvocalanus* and *Bestiolina* were greatly favoured by the fish larvae I examined. These may be preferred items simply because their size matches the size window of prey preferred by the larvae in my samples or due to other attributes of the prey, such as behavior and nutritional content. *B. similis* has been suggested as a good candidate for tropical larval fish diets in aquaculture due to the size of its developmental stages, susceptibility to predation, growth rate and nutritional composition (McKinnon et al. 2003). My study shows that *B. similis* can be a highly preferred food item for some larval fishes in the field. Gobiid and pinguipedid larvae had a medium to high selectivity for *B. similis*; however, the actual numbers eaten were low compared to other prey as *B. similis* was rare in the plankton at the time of sampling.

Larval fish may act to optimise growth by utilising high calorific foods when available. Calanoid copepods have been found to preferentially select food with the highest nutritional content (Kleppel & Burkart 1995) suggesting that for predators, they may in turn be predictably high in nutritional content. Preferential selection of calanoid copepods has been recorded in both temperate (Pepin & Penney 1997) and tropical environments (Mitchell 1991) when prey was not limited. In aquarium trials of lab reared larvae fed different concentrations of field captured zooplankton, two species of pomacentrids, *Amphiprion polymnus* and *Amblyglyphidodon aureus* showed positive selection for calanoid species and negative selection for oithonid copepods, despite the higher numbers of oithonids in the plankton offered (Mitchell 1991). I provide further support for this interpretation as 85% of families examined (i.e. 40 of 47 with prey in

the guts) contained calanoid copepods and for 43% of these calanoids constituted > 50% of their diet. In comparison, 72% of the families fed on oithonid prey but only in 6% of the cases did they form > 50% of the diet. Thus, it appears that larval fishes in the tropics will preferentially select calanoid copepods as prey.

4.5.4 Prey characteristics - non-copepod prey

Mollusc veligers, chaetognaths, appendicularians and protists were only eaten by a small number of fish families, but when consumed they were often a preferred prey. Mollusc veligers are highly visible and slow moving but their shell may make them harder to digest and may limit their availability as prey. Tetraodontids were the only larvae to consume mollusc veligers as a major part of their diet in this study, whereas, blennids, siganids and labrids ate mollusc veligers as only a minor part of the diet. Chaetognaths are ambush predators (Kimmerer 1991) and have been known to eat larval fishes (Hunter 1981), although their main diet is copepods (Alvarez Cadena 1993). They are preyed upon by larval fishes (Hunter 1981) but generally do not form a major component of their diet. Larvae of three families of tropical fishes are known to utilise chaetognaths as prey: chaetodontids (this study), scombrids (Young & Davis 1990) and bothids (Liew 1983). Appendicularians are long, thin, soft-bodied tunicates of limited mobility, which are encased in a mucus house and as a result may be difficult for many larvae to detect and capture (Liew 1983). These were also only eaten by a small number of families including scombrids (Uotani et al. 1981, Jenkins et al. 1984, Young & Davis 1990, this study), bothids (Liew 1983, this study), and acanthurids (Randall 1961, this study). Mollusc veligers, chaetognaths and appendicularians are not predated by many families of fish larvae, implying that specialised physiological and morphological adaptations are required for these prey types. Laboratory experiments to determine the ability of larvae to handle different prey types would advance our understanding of larval fish life history strategies and food webs in tropical environments.

4.5.5 Larval fish feeding and food chains on the North West Shelf of Australia

During the period of my study the waters of the North West Shelf of Australia had intermittently high primary production, particularly during the 1997/98 El Niño event (Furnas *et al.* in press). The concurrent study of Meekan *et al*. (2003) found differences in both ambient temperature and zooplankton biomass between years, with the summer of 1997/98 characterised by cooler water temperatures, higher concentrations of chlorophyll *a* and higher zooplankton biomass. The composition of the larval fish community also varied between these years (Sampey *et al*. 2004). For example, carangids were more abundant in 1997/98 than in 1998/99, and increased in abundance during the summer of 1997/98 (Sampey *et al*. 2004); a pattern mirrored by the small calanoids (McKinnon & Duggan 2003) predominant in their diet. The small calanoid prey fraction were severely food-limited during the period of this study (McKinnon & Duggan 2003), as were the adults of the paracalanid copepods important amongst the small calanoid fraction (McKinnon & Duggan 2001). Food limitation of copepod growth appears to generally be the case in tropical shelf environments (McKinnon & Duggan 2003). Subsequent low transfer efficiencies through the phytoplankton-copepod-larval fish food chain may therefore contribute to food limitation of the components of the larval fish community dependant on copepod prey.

Protists have generally been neglected or underestimated as potential prey items in investigations of larval fish diets either due to the specific methodology required to identify them or because they have already been digested (de Figueiredo *et al*. 2005). Some taxa of larval fishes in the area can feed directly on the protist community (see diets of callionymids, monacanthids and tetraodontids) and others may link into the microbial food web through other prey items such as appendicularia (scombrids. bothids and acanthurids), polychaetes (lethrinids, monacanthids and gobiids) and molluscs (tetraodontids, blennids, labrids, siganids and monacanthids). However, generally protistan microzooplankton on the NWS appear unlikely to be important in the transfer of energy to larval fishes since they consume <5% of primary production (Moritz et al. 2006). Engraulids and scarids (amongst others) were recorded as having empty guts, but this may only reflect the absence of the more easily identified metazoans in their guts and these families could conceivably have been feeding on delicate micro-organisms such as ciliates. An ability to feed either directly or indirectly (e.g. via picoplankton

grazers such as appendicularia) on components of the microbial food web might explain why the larvae of some reef fishes such as acanthurids, chaetodontids and labrids are frequently found offshore, 100's of km from land, whereas others such as most pomacentrids are rarely captured in oceanic waters (Victor, 1987; Clarke, 1995; Mora, 2002; Lo Yat, in press). However, my results, although intriguing and consistent with those of other studies (e.g. acanthurids, Randall 1961) are based on the analysis of only a few individuals. Confirmation of these ideas will require targeted sampling of larval reef fishes on broad cross-shelf and oceanic transects. The development of molecular probes to identify gut contents (e.g. Nejstgaard *et al*. 2003; Suzuki *et al*. 2006) represents a powerful new tool to quantify predation on protists and other easily digested organisms. Such tools will be necessary to fully appreciate the diversity of larval fish diets.

4.5.6 Conclusions

My aim was to provide some insight into the feeding of as many taxa as possible of tropical fish larvae. Dietary preferences were broadly similar to those found in studies of fish larvae from temperate ecosystems. Despite the limited numbers of individuals examined in some families, there were clear differences between families of larval fish in prey types eaten. Most families of larval fish preferred copepod prey, and only four families were restricted to non-copepod prey. Calanoid rather than cyclopoid copepods were the preferred prey of most families of fish larvae, possibly because of their size, pigmentation, escape responses and nutritional value, and some calanoid genera (e.g. *Bestiolina*) were preferred prey items. Comparison of my data with studies of fish from the same families found elsewhere indicates that there are inter-specific differences in dietary preference. The selectivity displayed by fish larvae specialising on copepods reinforces the value of identifying prey to a low taxonomic level and highlights the need to develop more powerful tools towards this end. The ability of fish larvae to access components of the microbial food webs predominant in tropical waters is likely to determine their differential feeding success and subsequent distribution within the plankton.

Table 9. Comparison of diets for selected families from our study with the results from previous studies. Results are limited to tropical larvae with dietary information for larvae of similar sizes to those sampled in our study. The number in superscript is the number of individuals examined.

Taxa	Location	Diet	Reference
Clupeidae			
Mixed species [392]	Florida	Copepods	Houde & Lovdal 1984
Unidentified species [20]	NW Shelf	Calanoid copepods	Present study
Callionymidae			
Callionymus decoratus[17]	Hawaii	cyclopoid copepods probably *Oithona*	Watson 1974
Callionymus pauciradiatus [770]	Florida	copepod nauplii	Houde & Lovdal 1984
Unidentified species[21]	NW Shelf	Harpacticoid, cyclopoid (*Oithona*) copepods	Present study
Scorpaenidae			
Scorpaenodes sp. [89]	Andaman Sea	Calanoid, corycaeid, oncaeid copepods	Østergaard *et al.* 2005
Unidentified species [10]	NW Shelf	Calanoid, oithonid, corycaeid copepods	Present study
Acanthuridae			
Acanthurus triostegus [3 (2 empty)]	Hawaii	appendicularians, larval polychaete	Randall 1961
Unidentified species[1]	NW Shelf	appendicularians	Present study
Apogonidae			
Foa brachygrammus[34]	Hawaii	tintinnids	Watson 1974
Unidentified species [130]	Florida	copepods	Houde & Lovdal 1984
Unidentified species[10]	NW Shelf	copepod juveniles, calanoids	Present study
Blennidae			
Omobranchus elongatus[15]	Hawaii	copepods	Watson 1974
Blennius sp. [4]	"	tintinnids	"
Unidentified species[10]	NW Shelf	corycaeid, oithonid copepods, bivalves	Present study
Carangidae			
Atule (Caranx) mate[48]	Hawaii	cyclopoid copepods probably *Oithona*	Watson 1974
Carangoides[80]	Andaman Sea	oncaeid, corycaeid, calanoid copepods	Østergaard *et al.* 2005
Unidentified species[3]	NW Shelf	copepod nauplii, calanoid copepods	Present study
Gobiidae			
Unidentified species [525]	Florida	Copepod nauplii, bivalves, tintinnids	Houde & Lovdal 1984
Mixed species [39]	NW Shelf	Copepods	Present study
Haemulidae			
Orthopristus chrysoptera [242]	Florida	copepods	Houde & Lovdal 1984
Unidentified species [12]	NW Shelf	oithonid copepods	Present study

Table 9 cont.

Taxa	Location	Diet	Reference
Pomacentridae			
Abudefduf abdominalis[3]	Hawaii	tintinnids at <3mm SL, copepods >3mm	(Watson 1974)
Amblyglyphidodon aureus	PNG	Calanoid & oithonid copepods	(Mitchell 1991)
Amphiprion polymnus	"	"	"
Pomacentrus/Chrysiptera sp.[12]	NW Shelf	"	Present study
Scaridae			
Leptoscarus vaigiensis[9]	Japan	copepods	(Ohta & Tachihara 2004)
Scombridae			
Scomberomorus semifasciatus[90]	GBR	fish larvae	(Jenkins *et al.* 1984)
Scomberomorus queenslandicus[181]	"	appendicularians, fish larvae	"
Scomberomorus commerson[51]	"	"	"
Thunnus spp. [1000+]	Indian Ocean	*Coryceus* sp., *Evadne* sp.	(Uotani *et al.* 1981)
Katsuwonus pelamis[300+]	"	appendicularians, fish larvae	"
Auxis spp. [300+]	"	appendicularians, *Evadne* sp.	"
Thunnus macoiyi[583]	"	calanoid, cyclopoid, copepod nauplii, Evadne	(Young & Davis 1990)
Thunnus alalunga[275]	"	*Coryceus, Farannula gibber*, copepod nauplii	"
Katsuwonus pelamis[65]	"	appendicularians, calanoids, fish larvae	"
Unidentified sp. [20]	NW Shelf	copepod nauplii, appendicularians	Present study
Bothidae			
Psettodes erumei[11]	GBR	copepods	(Liew 1983)
Pseudorhombus arsius [34]	"	appendicularians, copepods	"
Pseudorhombus elevatus [28]	"	copepods	"
Pseudorhombus spinosus [28]	"	copepods, appendicularians, chaetognaths	"
Pseudorhombus diplospilus [28]	"	appendicularians, chaetognaths	"
Grammatobothus spp. [46]	"	paracalanid copepods	"
Engyprosopon grandisquama[24]	"	appendicularians	"
Asterorhombus intermedius [26]	"	appendicularians	"
Unidentified species [20]	NW Shelf	appendicularians, calanoid copepods	Present study
Cynoglossidae			
Cynoglossus sp. [32]	Andaman Sea	harpacticoid, oncaeid, copepod nauplii	(Østergaard *et al.* 2005)
Cynoglossus sp. [20]	NW Shelf	calanoid, cycloipod, oncaeid copepods	Present study

5 General Discussion

5.1 Major Findings

5.1.1 Distributions

The summer ichthyoplankton assemblages off the North West Cape of Australia included both oceanic (e.g. myctophids) and coastal fishes (e.g. carangids) but were dominated by small demersal shorefishes (e.g. gobiids, pomacentrids, apogonids), which may be typical of tropical shelf environments. These communities In general, assemblages grouped into one neritic assemblage but there was a gradient in change in the assemblages from inshore to offshore, with some taxa occurring in higher abundance at inshore sites (e.g. monacanthids and syngnathids) and others being more abundant offshore (e.g. myctophids). In comparison to cross shelf studies in other localities (e.g. Cowen *et al.* 1993, Thorrold & Williams 1996, Gray & Miskiewiecz 2000), the weak differences in the larval fish assemblages at inshore and offshore sites on this part of the shelf maybe due in part to the sampling protocol, which sampled only two sites and only the surface waters at the deeper site, and may thus have been unable to detect inshore-offshore changes in assemblage structure. Thus, the conclusions of my study are limited to the surface ichthyoplankton assemblages. Additionally, the waters between the inshore and offshore sites are affected by tidal motion and internal waves, resulting in mixing of these waters (Meekan *et al.* 2005), which is likely to have affected the structure of larval fish assemblages in the area.

The biophysical environment experienced by developing larval fishes differed both within and between the two years of sampling. Temperature, chlorophyll *a* and zooplankton biomass increased from October to February and also varied between years. In the first summer the shelf experienced El Niño water conditions whereas in the second summer La Niña conditions prevailed. Water temperatures were approximately 1˚C cooler in 1997/98 than in 1998/99, but chlorophyll *a* and zooplankton biomass were higher. Seasonal increases in the abundance and diversity of fish eggs and larvae occurred from October to February in each year. These seasonal increases in abundance have been recorded from other tropical localities, for example on the Great Barrier Reef (see Thorrold & Williams 1996). Despite the environmental

differences between the two years of sampling there were small differences in assemblages between years. However, the component taxa did show differences between years, with some taxa being more abundant in the first summer (e.g. carangids) and others more in the second (e.g. pomacentrids). These interannual variations in abundances may be related to the response of species within these families to the prevailing environmental conditions with some species' growth and survivorship being more affected by physical factors such as temperature, while others may be influenced by different prey fields. But this needs to be tested further as with only two summers of data I can say nothing definitive about the causes of these differences.

Comparison of my data with that from the only previous study in the area (Young *et al*. 1986) showed similar (i) rank abundance of larvae; (ii) increases in the abundance and diversity of taxa from October to December; (iii) spatial patterns, with some taxa being more abundant inshore (e.g. monacanthids) and others offshore (e.g. myctophids). These similarities, despite the use of different nets and sampling protocols, support the synoptic picture of larval fish community structure on the NWS.

5.1.2 Diets

In order to provide an overview of the diets of larvae of tropical shorefishes I described the diets of fifty families of mostly percoid larvae, although some families were represented by only one or two individuals. The majority of larvae ate copepods of various developmental stages with preference being shown for calanoid copepods by many taxa. Interesting exceptions to this were found with some taxa eating non-copepod preys such as chaetognaths, appendicularians, mollusc larvae and protists. Surprisingly high preference was shown for some species of calanoid copepods such as *Bestiolina* and *Temora*, which were rare in the plankton at the time. Comparisons with other published studies of tropical larvae with a similar size range to my larvae showed consistency with the prey eaten for many families, which may be related to predator or prey characteristics. For example, the preference for calanoid over cyclopoid copepods may be due to calanoid copepods being larger, slower moving and more pigmented compared to oithonid copepods, which may make them an easier prey item to detect and capture for larval fishes. Differences in the prey types eaten by individuals from the

same family may be related to the behaviour and morphology of different species within a family or variation in the spatiotemporal distributions of prey.

The prey types eaten by larval fishes give us an insight into the food chains operating in an area. Despite intermittently high primary productivity near NWC (Furnas *et al.* in prep), growth rates of copepods in the area appear to be food-limited (McKinnon & Duggan 2003). Larval fishes in the area predominately ate copepods, suggesting that they may also be food limited. Larval fishes that ate non-copepod prey such as protists, appendicularians or mollusc larvae may be able to gain energy through microbial food chains and this may be why the larvae of some reef fishes (e.g. acanthurids) are able to survive many kilometres from reefs. This requires further examination through targeted sampling programs.

5.2 Future Directions

5.2.1 Ichthyoplankton near NWC

Tidal or shelf fronts may offer better feeding opportunities to larval fishes (Le Fevre 1986, Kingsford et al. 1991, Brandt 1993, Govoni 1993, Kingsford & Suthers 1994, Thorrold & McKinnon 1995, Grimes & Kingsford 1996, Rissik & Suthers 1996, Dempster et al. 1997, Lochman et al. 1997). The presence of tidal currents operating between NW Cape and Muiron Islands may aggregate larval fishes and their prey, thereby enhancing feeding. Late stage larval fishes captured in light traps during the same cruises showed highest abundance at two stations (C & D), inside the area of the maximum tidal front (Meekan et al. 2005), and located between the inshore and offshore sites sampled for ichthyoplankton. Unfortunately, these stations were not sampled for ichthyoplankton in this study so I was unable to explore this hypothesis further.

In temperate waters, larvae feeding in different water masses (e.g. oceanic vs shelf) may encounter different prey and biophysical environment and consequently their survival may be influenced by different processes. Within a species this may result in vastly different growth rates and consequently survival of different groups of larvae and these can influence recruitment variations (e.g. larval walleye pollock, *Theragra*

chalcogramma, Napp et al. 2000). My data on the diets of tropical larval fishes presented in chapter 3 did not allow the examination of dietary differences among sampling locations. Larvae chosen for dietary analysis were not consistently chosen with regard to location as the aim of the study was to explore dietary differences among families. The examination of how much variation in prey types consumed, growth rates and survival of tropical larvae is attributable to differences among locations remains a promising avenue for further research.

5.2.2 Feeding ecology of tropical larval fishes

In temperate waters, workers have used condition measures to identify a variety of factors that influence growth rates and thus recruitment success. These include water mass associations (Jeffrey & Taggart 2000), vertical distribution (Grønkjær *et al.* 1997), availability of preferred prey (Anderson 1994), genetic factors (Purchase & Brown 2000) and parasites (Sirois & Dodson 2000a, b). Tropical fish larvae are known to display variable larval growth rates (Cowen & Sponaugle 1997, Searcy & Sponaugle 2000), but the planktonic processes that affect these are virtually unknown. Future research into the feeding ecology of tropical larvae needs to consider the feeding environment in association with individual condition measures (e.g. age and growth rates from otoliths) to assess the effect that different feeding experiences have on the growth of larval fish.

The vertical distributions of larval fishes reflects their ability to maintain position within the water column and varies between species and developmental stages according to their visual capabilities (Job & Bellwood, 1996, 2000, Job & Shand, 2001), swimming abilities (Leis *et al.* 1996, Fisher etal. 2000, Fisher & Bellwood 2001) and swim bladder development. Prey is not uniformly distributed and a number of factors influence the success of fish larvae in locating patches of prey. Biological factors, such as larval behaviour and the ability of the prey to evade capture, will influence encounter rates, as will physical factors, such as turbulence (Rothschild & Osborn 1988, Sclafani *et al.* 1993, Dower *et al.* 1997, MacKenzie & Kiorboe 2000, Peters & Marrase 2000, Seuront *et al.* 2001, Dower *et al.* 2002, Reiss *et al.* 2002, Reiss *et al.* 2005). Laboratory behavioural studies of tropical larval fishes are needed to determine if different species

have different predatory strategies (e.g. ambush or cruising predation) as these may affect the types of prey they are best able to capture. An understanding the behaviour of both larval fishes and their prey will aid the interpretation of predator-prey relationship in the field. Documenting the vertical distributions of larval fishes and their prey may aid our understanding of the optimal foraging strategy of different species in patchy environments (e.g. Fortier & Harris 1989).

Studies on digestion and assimilation abilities of tropical fish will be crucial to help calculate growth energetics. Tropical larvae live at higher temperatures than better known temperate species, and their rates of digestion may be very rapid. Digestion rates and assimilation of different prey types need to be determined in laboratory experiments for larvae of different species, in order to make inferences on the impact that tropical larval fishes may have on the prey in the field, and thus allow us to calculate energy budgets for an area (eg. Cui *et al.* 1996).

Useful information can be derived from considering larval assemblages at coarser taxonomic resolution (such as family), especially when considering large spatial or temporal scales. However, this level of resolution is inadequate when considering factors operating at the scale of the individual larva, where species level and even population/cohort information is required in order to track factors affecting survival. Recent work has started to shed light on the immense variety in ecological niches occupied by larval fish and it is no longer appropriate to consider the larval environment as unstructured, or to assume that all pelagic larvae behave and respond to environments similarly.

There is a critical need to increase taxonomic knowledge of the early developmental stages of tropical larvae in order to understand their biology. This is particularly so for percoid fishes, as it is extremely difficult to identify larvae on the basis of morphology in pre-flexion and immediately post-flexion stages. Genetic identification may be a way forward in identifying these stages of larval fishes, but this also has problems due to the state of adult fish taxonomy in some groups (e.g. labrids) and the fact that relatively few genetic markers have so been identified for many fish groups at the sub-family level (although this database is growing). Despite these problems, techniques using PCR and genetic markers already exist, and research using these tools could potentially increase

our taxonomic abilities. Such information is essential if distribution patterns and survivorship of the larvae of coral reef fishes is to be examined at the level of species or individuals.

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Appendix 1. Abundance of all fish families for each month and site.

Table A1. Mean (SD) abundance (number 10 000m^{-3}) of each fish family for each site and month combination.

	1997/98							
	Inshore (B)				Offshore (E)			
Taxon	**Oct**	**Nov**	**Dec**	**Feb**	**Oct**	**Nov**	**Dec**	**Feb**
Acanthuridae	-	-	-	-	-	-	-	10 (0)
Acropomatidae	-	9 (0)	-	-	-	-	-	-
Aploactinidae	-	10 (0)	11 (5)	-	-	-	-	-
Apogonidae	-	62 (60)	100 (0)	36 (0)	10 (0)	216 (0)	204 (226)	123 (86)
Berycidae	-	9 (0)	-	-	-	-	-	-
Blenniidae	10 (0)	26 (0)	51 (61)	9 (0)	12 (0)	72 (0)	33 (40)	9 (1)
Bothidae	6 (0)	183 (246)	40 (35)	31 (6)	10 (0)	32 (0)	90 (97)	30 (0)
Bregmacerotidae	20 (0)	70 (0)	-	-	32 (11)	19 (0)	74 (74)	9 (1)
Callionymidae	6 (0)	47 (34)	23 (1)	26 (23)	12 (0)	21 (16)	47 (0)	16 (6)
Carangidae	-	197 (267)	57 (28)	160 (176)	-	-	149 (187)	229 (72)
Centriscidae	-	-	-	-	-	-	-	-
Chaetodontidae	-	9 (0)	-	-	-	-	-	-
Champsodontidae	-	-	-	-	-	-	32 (0)	-
Cirrhitidae	-	-	-	-	-	-	-	-
Clupeidae	-	15 (10)	167 (162)	-	-	-	-	-
Creediidae	-	61 (0)	-	-	-	-	-	-
Cynoglossidae	6 (0)	35 (0)	7 (0)	9 (0)	-	9 (0)	32 (0)	-
Dactylopteridae	-	-	-	-	-	-	-	10 (0)
Eel leptocephalii	-	13 (6)	-	-	36 (0)	-	-	-
Engraulidae	-	-	-	9 (0)	-	-	-	-
Exocoetidae	-	-	-	-	-	8 (0)	-	-
Fistulariidae	-	12 (7)	-	-	-	-	-	10 (0)
Gempylidae	-	-	-	-	-	-	-	9 (0)
Gerreidae	-	-	-	27 (0)	-	8 (0)	16(0)	-
Gobiesocidae	-	-	-	9 (0)	-	-	-	9 (0)
Gobiidae	25 (0)	58 (584)	57 (38)	98 (123)	31 (27)	165 (220)	1050 (1448)	253 (218)
Gonostomatidae	25 (0)	-	-	-	57 (46)	17 (2)	-	25 (0)
Haemulidae	25 (0)	9 (0)	-	-	-	8 (0)	16 (0)	-
Holocentridae	-	-	-	-	-	-	-	-
Howellidae	6 (0)	-	-	-	-	-	-	-
Kraemeriidae	-	17 (0)	-	-	-	-	-	-
Labridae	-	52 (0)	-	-	16 (6)	-	29 (26)	20 (14)
Leiognathidae	-	9 (0)	-	-	-	-	-	-
Lethrinidae	-	95 (130)	7 (0)	-	-	41 (32)	16 (0)	-
Lutjanidae	6 (0)	19 (11)	-	38 (37)	-	25 (22)	63 (0)	68 (0)
Melamphaidae	-	-	-	-	-	-	-	-
Melanostomiidae	-	-	-	-	-	-	-	-
Microdesmidae	-	17 (12)	7 (0)	-	-	32 (0)	12 (5)	492 (668)
Monacanthidae	-	144 (190)	33 (37)	116 (139)	-	-	28 (27)	20 (0)
Mullidae	-	9(0)	30 (31)	-	-	16(0)	9 (0)	60 (0)
Myctophidae	220 (0)	9 (1)	-	-	212(201)	133 (52)	16 (0)	9 (0)
Nemipteridae	-	18 (15)	30 (10)	61 (73)	24 (0)	-	-	10 (0)
Nomeidae	-	-	-	-	30 (0)	-	-	-

Table A1 continued

	1997/98							
	Inshore (B)				Offshore (E)			
Taxon	**Oct**	**Nov**	**Dec**	**Feb**	**Oct**	**Nov**	**Dec**	**Feb**
Ophidiidae	-	-	-	-	-	8 (0)	16 (0)	-
Opistognathidae	-	35 (0)	-	-	-	-	-	-
Paralichthyidae	-	-	-	13 (6)	-	-	11 (0)	-
Pegasidae	-	-	-	9 (0.4)	-	-	-	-
Pempheridae	-	-	-	-	-	-	-	-
Pinguipedidae	-	9 (0)	7 (0)	-	-	-	-	-
Platycephalidae	-	14 (5)	7 (0)	15 (10)	-	24 (0)	-	9 (0)
Pomacanthidae	-	-	-	9 (0.4)	-	-	-	-
Pomacentridae	10 (0)	84 (89)	60 (21)	17 (0)	84 (0)	460 (584)	42 (28)	99 (55)
Priacanthidae	-	9 (0)	15 (0)	9 (0)	10 (0)	-	47 (0)	-
Psettodidae	-	9 (0)	-	-	-	-	-	-
Pseudochromidae	6 (0)	52 (0)	-	-	-	-	20 (3)	-
Samaridae	-	-	-	-	-	-	-	-
Scaridae	-	9 (0)	-	-	-	-	-	-
Schindleriidae	-	-	-	-	-	-	-	-
Scombridae	12 (0)	53 (14)	-	18 (0)	41 (41)	120 (0)	38 (49)	104 (165)
Scorpaenidae	-	35 (0)	-	-	-	8 (0)	-	17(0)
Serranidae	-	190 (0)	7 (0)	9 (0)	-	32 (0)	22 (0)	17(0)
Siganidae	-	-	-	-	-	-	16 (0)	-
Sillaginidae	-	-	-	-	-	-	-	-
Soleidae	-	-	-	-	-	-	13 (4)	10 (0)
Solenostomidae	-	-	-	-	-	-	-	-
Sparidae	-	9 (0)	-	-	-	24 (0)	-	30 (0)
Sphyraenidae	-	17 (0)	15 (13)	-	-	19 (0)	16 (0)	25 (7)
Syngnathidae	-	39 (19)	32 (23)	13 (6)	-	-	16 (0)	10 (0)
Synodontidae	-	35 (0)	-	-	-	-	-	9 (1)
Terapontidae	-	-	40 (0)	-	-	-	-	-
Tetraodontidae	-	52 (0)	-	-	-	-	63 (0)	-
Trichonotidae	-	-	-	9 (0)	-	-	-	10 (0)
Triglidae	-	9 (0.2)	-	-	-	-	-	-
Tripterygiidae	6 (0)	30 (0)	-	-	12 (0)	-	26 (0)	-
Uranoscopidae	-	-	-	-	12 (0)	-	-	-
Xenistmidae	-	-	-	-	-	-	-	10 (0)
unidentified	11 (2)	15 (6)	149 (188)	71 (38)	97 (151)	200 (271)	70 (36)	107 (68)

Table A1 continued.

	1998/99							
	Inshore (B)				Offshore (E)			
Taxon	**Oct**	**Nov**	**Dec**	**Feb**	**Oct**	**Nov**	**Dec**	**Feb**
Acanthuridae	-	-	-	-	-	-	-	-
Acropomatidae	-	-	-	-	-	-	-	-
Aploactinidae	-	-	-	80 (0)	-	-	-	-
Apogonidae	-	50 (47)	78 (0)	26 (0)	-	10 (0)	72 (0)	21 (9)
Berycidae	-	-	-	-	-	-	-	-
Blenniidae	8 (0)	12 (0)	-	9 (0)	24 (0)	42 (0)	108 (0)	26 (0)
Bothidae	-	12 (0)	-	31 (18)	12 (0)	52 (0)	-	16 (5)
Bregmacerotidae	-	-	157 (0)	-	47 (0)	42 (0)	-	-
Callionymidae	8 (0)	-	-	1225 (2105)	-	-	-	-
Carangidae	8 (0)	20 (5)	-	115 (110)	-	31 (0)	-	118 (89)
Centriscidae	-	-	-	44 (0)	-	-	-	-
Chaetodontidae	-	-	-	-	-	-	-	-
Champsodontidae	-	-	16 (0)	-	-	-	-	-
Cirrhitidae	-	-	-	9 (0)	-	-	-	-
Clupeidae	-	-	16 (0)	51 (25)	-	-	-	9 (0)
Creediidae	-	-	-	-	-	-	-	-
Cynoglossidae	-	17 (0)	-	847 (1174)	-	21 (0)	-	-
Dactylopteridae	-	-	-	-	-	-	-	-
Eel leptocephalii	-	-	-	-	-	-	-	10 (0)
Engraulidae	-	-	-	-	-	-	-	-
Exocoetidae	-	-	-	-	-	10 (0)	-	-
Fistulariidae	-	-	-	-	-	10 (0)	-	11 (3)
Gempylidae	-	-	16 (0)	-	-	-	-	13 (0)
Gerreidae	-	-	-	-	-	-	-	
Gobiesocidae	-	-	-	-	-	-	-	
Gobiidae	-	245 (276)	2983 (0)	861 (945)	9 (0)	135 (0)	233 (0)	22 (6)
Gonostomatidae	-	-	31 (0)	11 (9)	-	42 (0)	18 (0)	59 (36)
Haemulidae	-	-	110 (0)	-	-	-	-	-
Holocentridae	-	-	-	-	-	-	-	31 (30)
Howellidae	-	-	-	-	12 (0)	-	-	-
Kraemeriidae	-	-	-	-	-	-	-	-
Labridae	-	-	16 (0)	-	-	-	-	-
Leiognathidae	-	-	-	242 (329)	-	-	-	-
Lethrinidae	-	-	-	-	-	10 (0)	-	9 (0)
Lutjanidae	-	12 (0)	-	-	-	10 (0)	-	31 (7)
Melamphaidae	-	-	-	-	9 (0)	-	-	-
Melanostomiidae	-	-	-	-	-	10 (0)	-	-
Microdesmidae	-	36 (0)	16 (0)	60 (0)	12 (0)	10 (0)	18 (0)	90 (55)
Monacanthidae	-	12 (0)	-	250 (281)	-	10 (0)	-	-
Mullidae	-	12 (0)	-	-	23 (0)	-	-	18 (0)
Myctophidae	-	24 (0)	235 (0)	9 (0)	11 (2)	156 (0)	-	91 (91)
Nemipteridae	-	-	-	76 (76)	-	-	-	-
Nomeidae	-	-	-	-	-	10 (0)	-	-
Ophidiidae	-	-	16 (0)	-	-	-	-	9 (0)
Opistognathidae	-	-	-	16 (0)	-	-	-	-
Paralichthyidae	-	-	-	-	-	-	-	-
Pegasidae	-	17 (0)	-	17 (0)	-	-	-	-
Pempheridídae	-	-	-	-	-	-	9 (0)	-
Pinguipedidae	-	-	-	854 (0)	-	-	-	-

Table A1 continued

	1998/99							
	Inshore (B)				Offshore (E)			
Taxon	**Oct**	**Nov**	**Dec**	**Feb**	**Oct**	**Nov**	**Dec**	**Feb**
Platycephalidae	-	-	-	63 (0)	-	-	-	-
Pomacanthidae	-	-	-	9 (0)	-	-	-	-
Pomacentridae	9 (0)	90 (92)	94 (0)	10 (2)	12 (0)	240 (0)	323 (0)	105 (35)
Priacanthidae	-	-	-	-	-	-	-	52 (0)
Psettodidae	-	-	-	-	-	-	-	-
Pseudochromidae	-	-	-	-	-	10 (0)	9 (0)	-
Samaridae	-	-	-	16 (0)	-	-	-	-
Scaridae	-	-	-	-	12 (0)	-	-	13 (0)
Schindleriidae	-	-	78 (0)	-	-	52 (0)	-	-
Scombridae	-	-	16 (0)	17 (0)	-	-	9 (0)	79 (35)
Scorpaenidae	-	-	-	9 (0)	-	10 (0)	-	-
Serranidae	-	-	-	-	-	10 (0)	9 (0)	-
Siganidae	-	-	-	43 (0)	-	-	-	-
Sillaginidae	-	-	-	11 (0)	-	-	-	-
Soleidae	-	-	-	-	-	-	-	-
Solenostomidae	-	-	-	-	-	-	-	-
Sparidae	-	-	-	-	-	-	-	-
Sphyraenidae	-	48 (0)	-	-	-	-	18 (0)	97 (0)
Syngnathidae	-	24 (0)	16 (0)	10 (2)	-	-	-	-
Synodontidae	-	-	-	-	-	-	-	-
Terapontidae	9 (0)	357 (0)	-	-	-	-	-	-
Tetraodontidae	-	-	31 (0)	-	-	21 (0)	-	-
Trichonotidae	-	-	-	-	-	-	-	-
Triglidae	-	-	-	-	-	-	-	-
Tripterygiidae	-	-	16 (0)	17 (0)	-	-	18 (0)	-
Uranoscopidae	-	-	-	-	-	-	-	-
Xenistmidae	-	-	-	-	-	-	-	-
unidentified	-	12 (0)	63 (0)	378 (512)	-	10 (0)	99 (0)	41 (55)

Table A1 continued

	1988/89 Inshore (TB)	
Taxon	**Nov**	**Dec**
Acanthuridae	-	-
Acropomatidae	-	-
Aploactinidae	-	-
Apogonidae	-	185 (0)
Berycidae	-	-
Blenniidae	16 (9)	17 (9)
Bothidae	39 (0)	58 (0)
Bregmacerotidae	-	-
Callionymidae	-	34 (34)
Carangidae	-	58 (0)
Centriscidae	-	11 (0)
Chaetodontidae	-	11(0)
Champsodontidae	-	-
Cirrhitidae	-	-
Clupeidae	-	-
Creediidae	-	-
Cynoglossidae	-	23 (0)
Dactylopteridae	-	-
Eel leptocephalii	10 (0)	-
Engraulidae	-	493 (680)
Exocoetidae	-	-
Fistulariidae	-	-
Gempylidae	-	-
Gerreidae	-	-
Gobiesocidae	-	-
Gobiidae	-	200 (239)
Gonostomatidae	-	-
Haemulidae	-	10 (0)
Holocentridae	-	-
Howellidae	-	-
Kraemeriidae	-	-
Labridae	-	-
Leiognathidae	-	-
Lethrinidae	11 (0)	-
Lutjanidae	-	-
Melamphaidae	-	-
Melanostomiidae	-	-
Microdesmidae	-	-
Monacanthidae	20 (0)	272 (284)
Mullidae	-	-
Myctophidae	-	-
Nemipteridae	-	-
Nomeidae	-	-
Ophidiidae	-	-
Opistognathidae	-	-
Paralichthyidae	-	-
Pegasidae	-	11 (0)
Pempheridae	-	-
Pinguipedidae	-	-

Table A1 Continued

	1988/89 Inshore (TB)	
Taxon	**Nov**	**Dec**
Platycephalidae	-	11 (0)
Pomacanthidae	-	23 (0)
Pomacentridae	11 (0)	92 (115)
Priacanthidae	-	-
Psettodidae	-	-
Pseudochromidae	-	-
Samaridae	-	-
Scaridae	-	-
Schindleriidae	-	-
Scombridae	-	11 (0)
Scorpaenidae	-	10 (0)
Serranidae	-	-
Siganidae	10 (0)	-
Sillaginidae	-	-
Soleidae	-	-
Solenostomidae	11 (0)	-
Sparidae	-	-
Sphyraenidae	-	11 (0)
Syngnathidae	15 (6)	105 (48)
Synodontidae	-	-
Terapontidae	-	35 (0)
Tetraodontidae	-	10 (0)
Trichonotidae	-	20 (0)
Triglidae	-	-
Tripterygiidae	-	-
Uranoscopidae	-	-
Xenistmidae	-	-
unidentified	11 (0)	39 (26)

Appendix 2. Summary of all prey items for each fish family examined.

Table A2. Prey items eaten by each fish family (a) %N and (b) %FO. Family number is from Table 6 in Chapter 4, p62.

	Family No.																									
	1		3		4		5		6		8		9		10		11		12		13		14		15		16	
SpeciesName	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**
Copepods																												
Acartia fossae																			2	8								
Acartia pacifica															5	14												
Acartia sp.															7	14			12	33								
Bestiolina similis																			1	8			2	10	2	6		
Calanoid egg													5	20														
calanoid juveniles	77	25			71	67	46	81			6	13	32	20	54	71			67	92	38	100	60	90	21	53		
Calanopia sp.																												
Canthocalanus pauper																			1	4					2	6		
Clausocalanus sp.																			1	4			2	10	2	6		
Clausocalanus arcuicornis																												
Clausocalanus farrani			50	17			4	19			35	75	5	20	5	29			1	8					17	24		
Clausocalanus furcatus															5	29							5	20				
copepod fragments			50	17			4	19			35	75	5	20	5	29			1	8					17	24		
copepod nauplii	8	5					8	19					26	40	10	43					4	25						
copepod juveniles							1	5																				
Corycaeus agilis									33	50																		
Corycaeus andrewsi																												
Corycaeus asiaticus																												
Corycaeus crassiusculus																												
Corycaeus dahli																							4	10				
Corycaeus pacificus																												
Corycaeus spp.					14	33	4	14	6	50													4	10				
Euchaeta spp.															2	14												
Euterpina acutifrons							12	38											1	4	35	100	2	10				
Evadne tergestina																												

Table A2 Continued.

	Family No.																											
	1		3		4		5		6		8		9		10		11		12		13		14		15		16	
SpeciesName	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**
Copepods continued																												
Farranula concinna																												
Farranula gibbulus											6	13																
Farranula spp									56	50																		
harpacticoid juveniles																			1	4								
Microsetella sp.																												
Oithona attenuata																			1	21								
oithona juveniles	15	10					9	29	6	50			26	60			100	100	5	21			2	10	17	12		
Oithona nana																			1	21								
Oithona rigida							1	5											1	4								
Oithona simplex																			2	21	4	25						
Oithona spp.					14	33	2	10											2	29			19	40				
Oncaea spp.							3	14																				
Oncaea venusta																												
Paracalanid species																												
Paracalanus aculeatus																			2	4								
Paracalanus aculeatus major																									2	6		
Paracalanus indicus																			1	8			2	10				
parasitic copepod																												
Parvocalanus sp.							2	10											1	8								
Parvocalanus crassirostris																			1	13								
poecilostome juveniles							1	5			18	25									19	75						
Pseudodiaptomus sp.							1	5																				
Temora sp.																									17	24		
Undinula vulgaris																									2	6		
Non-Copepod Prey																												
Appendicularia																												
Larvaceans																											100	100
Chaetognaths																												
Amphipod																												
Barnacle cyprid																												
Crab Zoea															2	14												

Table A2 Continued.

	Family No.																													
	1		3		4		5		6		8		9		10		11		12		13		14		15		16			
SpeciesName	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**
Non Copepods continued																														
Decapod larvae															2	14									2	6				
Euphausid larvae																														
Mite																														
Fish Larvae- Gobiidae															2	14														
Fish Egg																														
Dynophysis sp.							1	5																						
Radiolarian																														
Bivalves																														
Gastropods																														
Pteropod																														
Polychaetes																														
Worm																														
Unidentified remains																														

Table A2 Continued.

	Family No.																											
	17		18		19		20		21		22		23		24		25		26		27		28		29		30	
SpeciesName	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**
Copepods																												
Acartia fossae																												
Acartia pacifica																												
Acartia sp.																												
Bestiolina similis											2	5																
Calanoid egg																					1	10	3	5				
calanoid juveniles	47	60	4	10	4	33			33	100	25	46	24	42			22	25			4	25	21	35	2	7		
Calanopia sp.																												
Canthocalanus pauper													4	8														
Clausocalanus sp.			4	10																								
Clausocalanus arcuicornis																												
Clausocalanus farrani	13	20									9	26	4	8	2	7	4	5	8	10	14	30			13	20		
Clausocalanus furcatus																												
copepod fragments	13	20									9	26	4	8	2	7	4	5	8	10	14	30			13	20		
copepod nauplii	13	20			42	100					10	18	16	17	7	7	37	40	24	30	36	65	38	60	42	40		
copepod juveniles																	4	5	8	10								
Corycaeus agilis																												
Corycaeus andrewsi																												
Corycaeus asiaticus															2	7												
Corycaeus crassiusculus																												
Corycaeus dahli															2	7												
Corycaeus pacificus															2	7												
Corycaeus spp.											2	5			5	14					2	15						
Euchaeta spp.																												
Euterpina acutifrons											3	8																
Evadne tergestina																												
Farranula concinna															2	7												
Farranula gibbulus															2	7												
Farranula spp			44	80											2	7												
harpacticoid juveniles					4	33					1	3																
Microsetella sp.											8	23			12	14												

Table A2 Continued.

	Family No.																											
	17		18		19		20		21		22		23		24		25		26		27		28		29		30	
SpeciesName	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**
Copepods continued																												
Oithona attenuata			12	30	4	33					1	3					4	5					3	5				
oithona juveniles			4	10	4	33			67	100	12	31	4	8	7	14	26	25			8	20	18	20	5	13		
Oithona nana					4	33					1	3																
Oithona rigida											2	5			30	21												
Oithona simplex					4	33															1	5						
Oithona spp.	7	10	16	30							10	21	44	50							14	15						
Oncaea spp.			4	10							3	8			2	7												
Oncaea venusta															2	7												
Paracalanid species																												
Paracalanus aculeatus																												
Paracalanus aculeatus major																												
Paracalanus indicus																												
parasitic copepod																												
Parvocalanus sp.																												
Parvocalanus crassirostris					13	33																						
poecilostome juveniles			4	10							1	3			2	7					1	5	6	10				
Pseudodiaptomus sp.																												
Temora sp.					21	67																						
Undinula vulgaris																												
Non-Copepod Prey																												
Appendicularia															2	7									7	27	100	100
Larvaceans																												
Chaetognaths							100	100													5	45			2	7		
Amphipod																												
Barnacle cyprid																												
Crab Zoea																												
Decapod larvae																												
Euphausid larvae															2	7												
Mite											1	3																
Fish Larvae- Gobiidae																												
Fish Egg																												

Table A2 Continued.

	Family No.																													
	17		18		19		20		21		22		23		24		25		26		27		28		29		30	
SpeciesName	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**
Non Copepods continued																														
Dynophysis sp.																														
Radiolarian																														
Bivalves																														
Gastropods			8	10											9	7														
Pteropod																							12	10						
Polychaetes											1	3							52	35										
Worm																														
Unidentified remains	7	10									1	3									3	15			16	60				

Table A2 Continued.

	Family No.																													
	31		32		33		34		35		36		38		39		40		41		42		43		44		45		46	
SpeciesName	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**
Copepods																														
Acartia fossae																														
Acartia pacifica																	1	17												
Acartia sp.																	1	17												
Bestiolina similis			1	5	7	40											3	33	3	10										
Calanoid egg									6	20			4	10	19	40													25	14
calanoid juveniles	100	100	21	60	34	80	64	92	2	10	72	60	2	5			27	83	33	45					28	20				
Calanopia sp.																														
Canthocalanus pauper					2	20																								
Clausocalanus sp.																														
Clausocalanus arcuicornis					2	20																								
Clausocalanus farrani			1	5			7	75	2	10					10	25	1	17	3	10	4	10			6	10			8	5
Clausocalanus furcatus					2	20																			6	10				
copepod fragments			1	5			7	75	2	10					10	25	1	17	3	10	4	10			6	10			8	5
copepod nauplii					11	80	3	33	23	10			51	65	56	65			17	30	86	95			11	20				
copepod juveniles																					1	15								
Corycaeus agilis									2	10																				
Corycaeus andrewsi			2	10																										
Corycaeus asiaticus			1	5					2	10																				
Corycaeus crassiusculus									6	20																				
Corycaeus dahli																	3	33												
Corycaeus pacificus																														
Corycaeus spp.			10	45			7	42	2	10							12	17												
Euchaeta spp.																														
Euterpina acutifrons			20	45	2	20											11	17												
Evadne tergestina									2	10																				
Farranula concinna									6	30																				
Farranula gibbulus									9	20																				
Farranula spp									6	20																				
harpacticoid juveniles																														
Microsetella sp.	2	10			1	8									3	17	2	5												

Table A2 Continued.

	Family No.																													
	31		32		33		34		35		36		38		39		40		41		42		43		44		45		46	
SpeciesName	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**
Copepods continued																														
Oithona attenuata					2	20											1	17	2	5										
oithona juveniles			2	5	23	60					4	10			4	10	1	17	31	50	3	20	50	25						
Oithona nana					2	20											10	50												
Oithona rigida									2	10									5	5										
Oithona simplex					2	20																								
Oithona spp.			4	15	6	40	7	67									3	17					50	25	22	30				
Oncaea spp.			3	15			2	17			4	10					3	33												
Oncaea venusta																														
Paracalanid species					4	20																								
Paracalanus aculeatus																														
Paracalanus aculeatus major																														
Paracalanus indicus					4	20					4	10																		
parasitic copepod									2	10																				
Parvocalanus sp.																	1	17												
Parvocalanus crassirostris																														
poecilostome juveniles			1	5			3	17	22	50																				
Pseudodiaptomus sp.																														
Temora sp.			21	45					2	10							1	17												
Undinula vulgaris																														
Non-Copepod Prey																														
Appendicularia													40	95											11	20			42	23
Larvaceans									3	10																				
Chaetognaths																	1	17												
Amphipod									2	10																				
Barnacle cyprid																														
Crab Zoea																	3	17												
Decapod larvae			8	35																										
Euphausid larvae											4	10																		
Mite																														
Fish Larvae- Gobiidae																														
Fish Egg																	4	17							6	10				

Table A2 Continued.

	Family No.																																			
	31		32		33		34		35		36		38		39		40		41		42		43		44		45		46								
SpeciesName	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**						
Non Copepods continued																																				
Dynophysis sp.																																				
Radiolarian																																				
Bivalves																	4	33																		
Gastropods																																				
Pteropod																																				
Polychaetes																																				
Worm													2	5																						
Unidentified remains											12	30			2	5	3	33							6	10	100	100	17	9						

Table A2 Continued.

	Family No.							
	47		48		49		50	
SpeciesName	a	b	a	b	a	b	a	b
Copepods								
Acartia fossae								
Acartia pacifica								
Acartia sp.								
Bestiolina similis								
Calanoid egg					3	7		
calanoid juveniles	22	70			11	25		
Calanopia sp.					2	4		
Canthocalanus pauper								
Clausocalanus sp.								
Clausocalanus arcuicornis								
Clausocalanus farrani					3	7		
Clausocalanus furcatus								
copepod fragments					3	7		
copepod nauplii					25	46		
copepod juveniles								
Corycaeus agilis								
Corycaeus andrewsi								
Corycaeus asiaticus								
Corycaeus crassiusculus								
Corycaeus dahli	1	5						
Corycaeus pacificus								
Corycaeus spp.	6	45					5	9
Euchaeta spp.								
Euterpina acutifrons	13	50	33	100	2	4		
Evadne tergestina								
Farranula concinna								
Farranula gibbulus								
Farranula spp								
harpacticoid juveniles	4	35			2	4		
Microsetella sp.	31	90						
Oithona attenuata	1	5						
oithona juveniles	3	20			5	7		
Oithona nana	1	5						
Oithona rigida								
Oithona simplex								
Oithona spp.	12	45						
Oncaea spp.	7	40						
Oncaea venusta								
Paracalanid species								
Paracalanus aculeatus								
Paracalanus aculeatus major								
Paracalanus indicus								
parasitic copepod								
Parvocalanus sp.								
Parvocalanus crassirostris								
poecilostome juveniles	1	5			17	7		
Pseudodiaptomus sp.								
Temora sp.			67	100	17	7	3	9
Undinula vulgaris								
Non-Copepod Prey								
Appendicularia								
Larvaceans								
Chaetognaths								
Amphipod								
Barnacle cyprid							3	9
Crab Zoea							15	9

Table A2 Continued.

	Family No.							
	47		48		49		50	
SpeciesName	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**
Non Copepods continued								
Decapod larvae								
Euphausid larvae								
Mite								
Fish Larvae- Gobiidae								
Fish Egg								
Dynophysis sp.								
Radiolarian					5	11	10	36
Bivalves					3	7	8	18
Gastropods							53	64
Pteropod								
Polychaetes					2	4		
Worm								
Unidentified remains							6	18