

Glimpse into guts: overview of the feeding of larvae of tropical shorefishes

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ABSTRACT: 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 (21° 49' S, 114° 14' E), effectively doubling the number of families for which there is dietary data available. 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 are 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.

KEY WORDS: Diet · Larval fish · Feeding ecology · Prey selectivity · Calanoid copepods · Northwest Australia

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INTRODUCTION

The importance of understanding 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 Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, and Atlantic 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 lar-

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vae 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). Here, we attempted to provide a broad overview of the feeding of larvae of tropical shorefishes from shallow waters (20 to 100 m depth) off the North West Cape of Australia (hereafter NWC) by: (1) describing the diets of 50 families of larvae of tropical shorefishes; (2) exploring 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) examining whether family level differences in the diet still occur when spatiotemporal variation is removed, by examining the larvae collected in one net tow; and (4) calculating prey selectivity for some of the prey items of 7 co-occurring larval shorefishes. We aimed to 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.

MATERIALS AND METHODS

Sample collection and processing. Ichthyoplankton were collected during cruises in the vicinity of the NWC (21° 49' S, 114° 14' 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); an additional inshore site (TB, ~16 m depth) was sampled further north on the shelf near Thevenard Island in the second summer (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 ind. 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 length (SL) and mandible length (ML) were measured with an ocular micrometer. The guts were carefully excised from the body

with electrolytically sharpened tungsten needles and placed onto a microscope slide into a drop of glycerin. This assists dissection by dampening particle movement and aids the detection of food items due to its clearing properties (Arthur 1976). A subjective measure of gut fullness (GF) ([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.

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:

$$\text{IRI} = \%N \times \%FO$$

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

Data analysis was conducted in PRIMER v6 beta and Statistica 6.1 using the results from non-empty guts. We used ANOVA on the Shannon-Wiener 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 examined data at various scales of prey identification and spatio-temporal occurrence of fish larvae, to elucidate relationships among the fish families and their prey. We first removed unidentified prey as a category (~3% of total prey items) as these occurred across many families and thus did not contribute to our understanding of the dietary difference among families. An average of each prey category 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, we first standardised the data by converting the prey to a percentage composition of the total prey categories 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 2-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 3-dimensional plots of the datasets provided a better representation of relationships (i.e. lower stress values). However, these were best when viewed on the computer screen where they could be manipulated, but translated poorly to print and were difficult to plot with cluster analyses. Consequently, we chose to display only 2-dimensional plots, which followed the same trends as the 3-dimensional plots. We 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 categories 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, we repeated these analyses on a subset of the data for families of fish larvae that fed predominately on these prey. We 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 categories 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, we 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 we 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):

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

where r_i and p_i are the proportion of prey category i in the diet and in the water column respectively and m is the number of prey categories. 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 2 vertical net tows, while the proportion of prey categories in the diet was esti-

mated using an average count of prey categories 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 categories not present in the guts (e.g. *Acrocalanus gibber*) and prey categories 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 our conclusions to the relative selectivity of some components of the plankton. We considered $\alpha > 4$ to indicate high selectivity for a particular prey category, $4 > \alpha > 1$ to indicate moderate selectivity and $\alpha < 1$ to indicate low selectivity. To look in more detail at differences within a family the gobiids were able to be split into 2 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).

RESULTS

Fish lengths, gut fullness and digestion ratings

We examined whole gut contents of 591 individuals from 50 taxa of predominately early post-flexion larvae of ~4 mm 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 GF ranged from empty (1 ± 0 , engraulids, berycids, and scarids) to full (5 ± 0 , aploactinids, opisthognathids, pomacanthids, priacanthids, and samarids), i.e. all individuals examined 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.

Prey composition of diets

Prey diversity, measured as the Shannon diversity index (H'), 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 re-

Table 1. Families of larval fishes, collected with plankton nets near the North West Cape of Australia (NWC) (21° 49' S, 114° 14' E), used for gut content analysis. TGE: Total guts examined; EG: number of empty guts; SL and ML: standard and mandibular length, respectively; GF: Gut fullness (1: empty; 2: ¼; 3: ½; 4: ¾; 5: full); *H'*: Shannon-Wiener diversity index, (log_e); ST: Spatiotemporal collection details (B: in-shore 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: Larval development stage (Pe: Pre-flexion; F: Flexion; Po: Post-flexion). SL, ML, GF given as mean ± SD

No.	Family	Common name	TGE	EG	SL (mm)	ML (mm)	GF	<i>H'</i>	ST	Stage
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 ^a	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
Scorpaeniformes										
13	Aploactinidae	velvetfishes	4 ^a	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 ^{a(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 ^a	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 ^a	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 ^a	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 ^a	0	4 ± 0	0.5 ± 0	5 ± 0	0	BF9	Po
32	Pinguipedidae	grubfishes & sandfishes	20 ^a	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	damsel-fishes	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	Sphyrnidae	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	0	4 ± 0	1 ± 0	3 ± 0	0	EO7	Po
Pleuronectiformes										
46	Bothidae	left-eye flounders	22 ^{a(2)}	11 ^{a(2)}	9 ± 3	0.8 ± 0.4	2 ± 1	1.1	BN7F9	Po
47	Cynoglossidae	tongue soles	20 ^a	0	5 ± 2	0.5 ± 0.2	4 ± 1	1.3	BF9	Po
48	Samaridae	crested flounders	1 ^a	0	4 ± 0	0.8 ± 0	5 ± 0	0.6	BF9	Po
Tetraodontiformes										
49	Monacanthidae	leatherjackets & filefishes	28 ^{a(8)}	6	5 ± 3	0.4 ± 0.2	3 ± 1	1.6	BF9	Po
50	Tetraodontidae	puffers	11	0	4 ± 1	0.6 ± 0.2	4 ± 1	1.3	BN7D8EN8TD8	PeFPo

^aLarvae from 1 sample at Station B, February 1999. Number in parentheses indicates the number of individuals if different from total examined

Table 2. 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.

Prey category	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.			476	65	14167	74		348		573		140				3520			9		1063			
Corycaeidae				478						2	3462	18							321		166			
Harpacticoids								35					11											
Large calanoids																								
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																								
Mollusc																80						17		
Polychaetes																				2		66		
Protists																								
Appendicularia														10000								17		
Chaetognaths																								
Fish eggs/larvae								35																
Other															67									
Unidentified remains																								
Prey category	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										23		
Copepod nauplii	720	2314	2294	1673			857	103	234		3319	3625		517	8196		222		341		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	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						6		519	16			240	23	34	44		56					23		
Decapod larvae	80	408		255		272							46					38					136	
Euphausiid larvae										40														
Mollusc														137										
Polychaetes																						23	4909	
Protists																					6			
Appendicularia																					51	364		
Chaetognaths		212		194				31			3840									947				
Fish eggs/larvae				12									23											
Other													68											
Unidentified remains		39	118	982				141		360	11	10	91				56	10000	152			23	91	

corded an index of relative importance (IRI) of 10 000 as only one 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 ind.) and chaetodontids (2 ind.).

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

A generalist feeding strategy was indicated for only 3 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, which preyed on small calanoids and copepod fragments (IRI 833 for both prey groups); and tripterygiids, which preyed on *Oithona* spp. (IRI 667), copepod juveniles (IRI 556), copepod nauplii, small calanoids and appendicularia (all IRI 222).

Some prey species were only 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 65 mm (IRI 68, 56, and 35 respectively). Protists (*Dynophysis* sp. and a radiolarian) were recorded from callionymids, monacanthids and tetraodontids (IRI 5, 51 and 363).

Dietary differences among fish families

Clustering and nMDS analyses of all families produced 6 groups at 30% similarity (Fig. 1). 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 categories).

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 formed only 5 groups (Groups 7 to 11) at 30% similarity (Fig. 2). 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), teraponids (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 Group 10 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 (18%, mostly *Oithona* juveniles) and copepod juveniles (19%). The families in this group appear to have little in common with each other and in the 3-dimensional plots Group 11 sits above the others in a vertical plane, but this detail has been lost in the 2-dimensional plots.

The analysis of co-occurring families (from inshore site B, 17 February 1999) produced a dendrogram that split these into 3 groups (Groups 12 to 14) at 30% similarity (Fig. 3). Samarids (Family 48, Group 12, 1 ind.) 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 ind.), callionymids (Family 5, 21 ind.), gobiids (Family 22, 39 ind.), cynoglossids (Family 47, *Cynoglossus* sp., 20 ind.) and

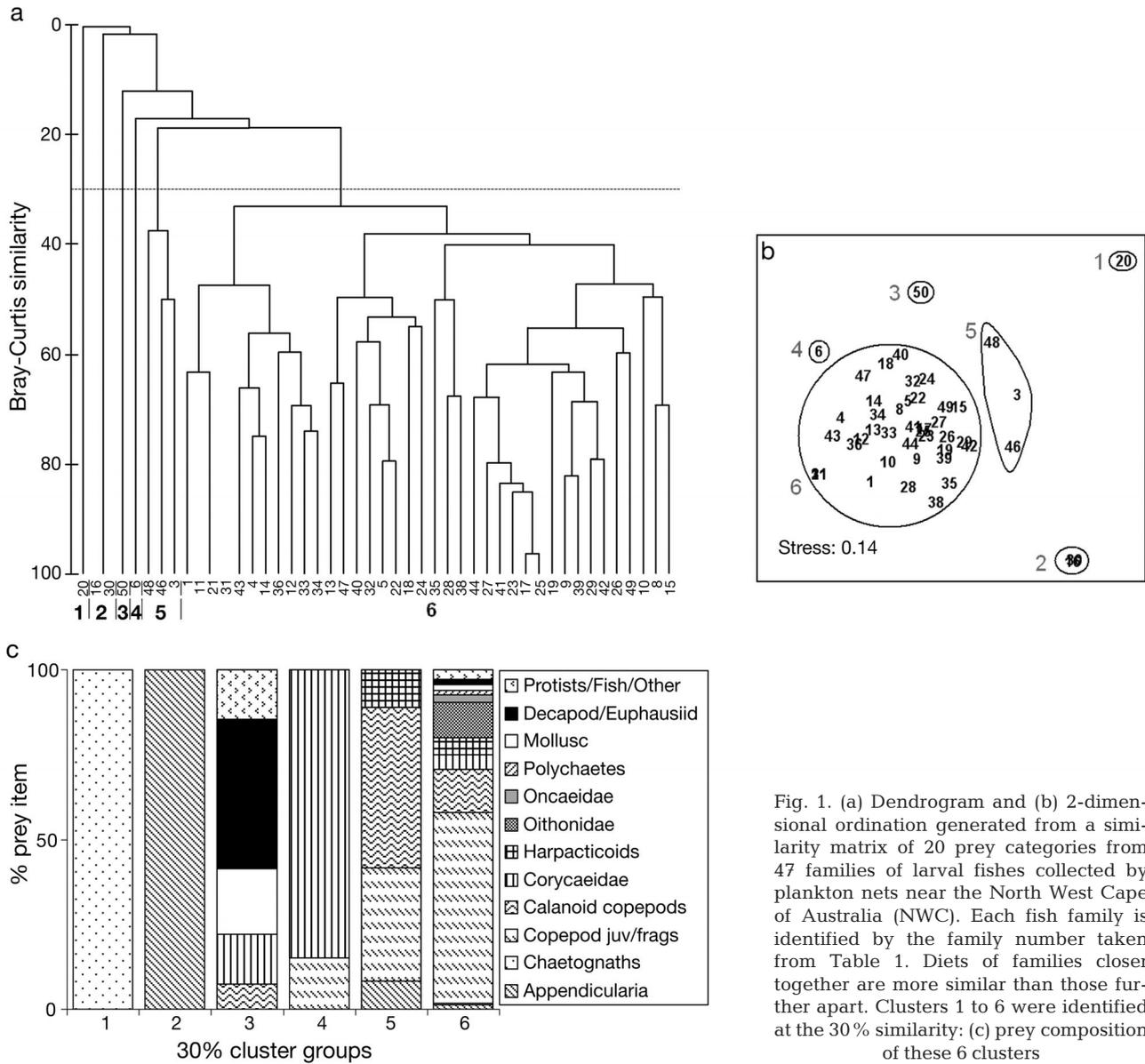


Fig. 1. (a) Dendrogram and (b) 2-dimensional ordination generated from a similarity matrix of 20 prey categories from 47 families of larval fishes collected by plankton nets near the North West Cape of Australia (NWC). Each fish family is identified by the family number taken from Table 1. Diets of families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

pinguipedids (Family 32, 20 ind.). This group ate a mixed diet of harpacticoids (22.5%, *Euterpina acutifrons* and *Microsetella* spp.), *Oithona* spp. (18%, adults and copepodites), 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 ind.) 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 ind.), leiognathids (Family 25, 20 ind.) and monacan-

thids (Family 49, 8 ind.) (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).

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 category (260 000 per 100 m³)

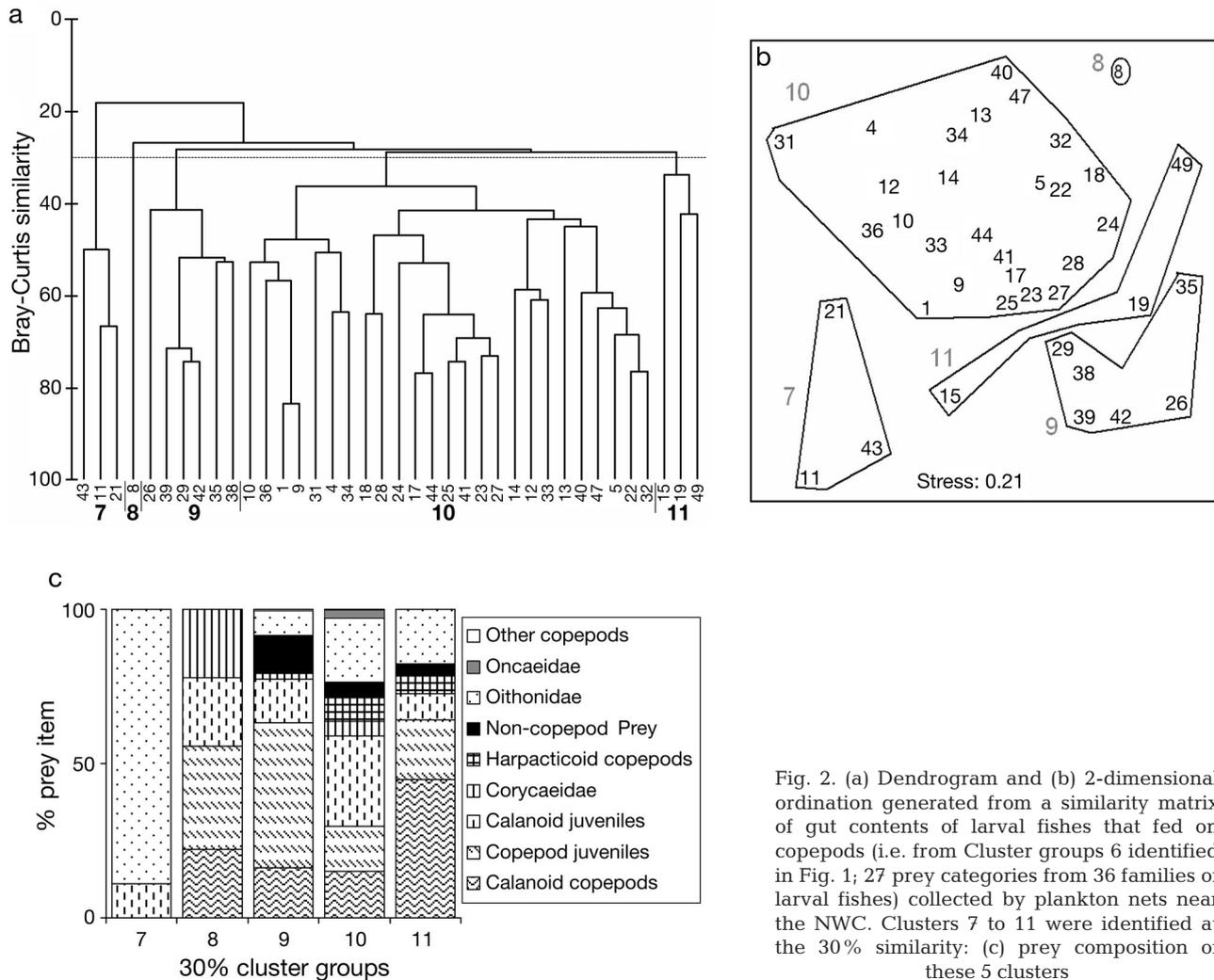


Fig. 2. (a) Dendrogram and (b) 2-dimensional ordination generated from a similarity matrix of gut contents of larval fishes that fed on copepods (i.e. from Cluster groups 6 identified in Fig. 1; 27 prey categories from 36 families of larval fishes) collected by plankton nets near the NWC. Clusters 7 to 11 were identified at the 30% similarity: (c) prey composition of these 5 clusters

and *Acrocalanus gibber* and *Corycaeus andrewsi* were the least abundant (600 per 100 m) (Table 3). Calionymids were the most abundant larvae (40 per 100 m³) and samarids and opisthognathids the least abundant (0.2 per 100 m³). Some prey taxa (e.g. *Clausocalanus farrani*), which were eaten by some larvae, could not be included in the prey selectivity analysis as they were not present in sufficient concentrations to show in the sorted fraction of the zooplankton sample. A total of 17 prey categories 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; Figs. 4 & 5, Table 3). Other preys were avoided, such as harpacticoid juveniles by *Cynoglossus* 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%, $\alpha = 2.1$; Figs. 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% respectively). Monacanthids showed a moderate selectivity for polychaetes (33%, $\alpha = 2.3$), which were another rare prey category (2% of available prey).

DISCUSSION

We 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 lar-

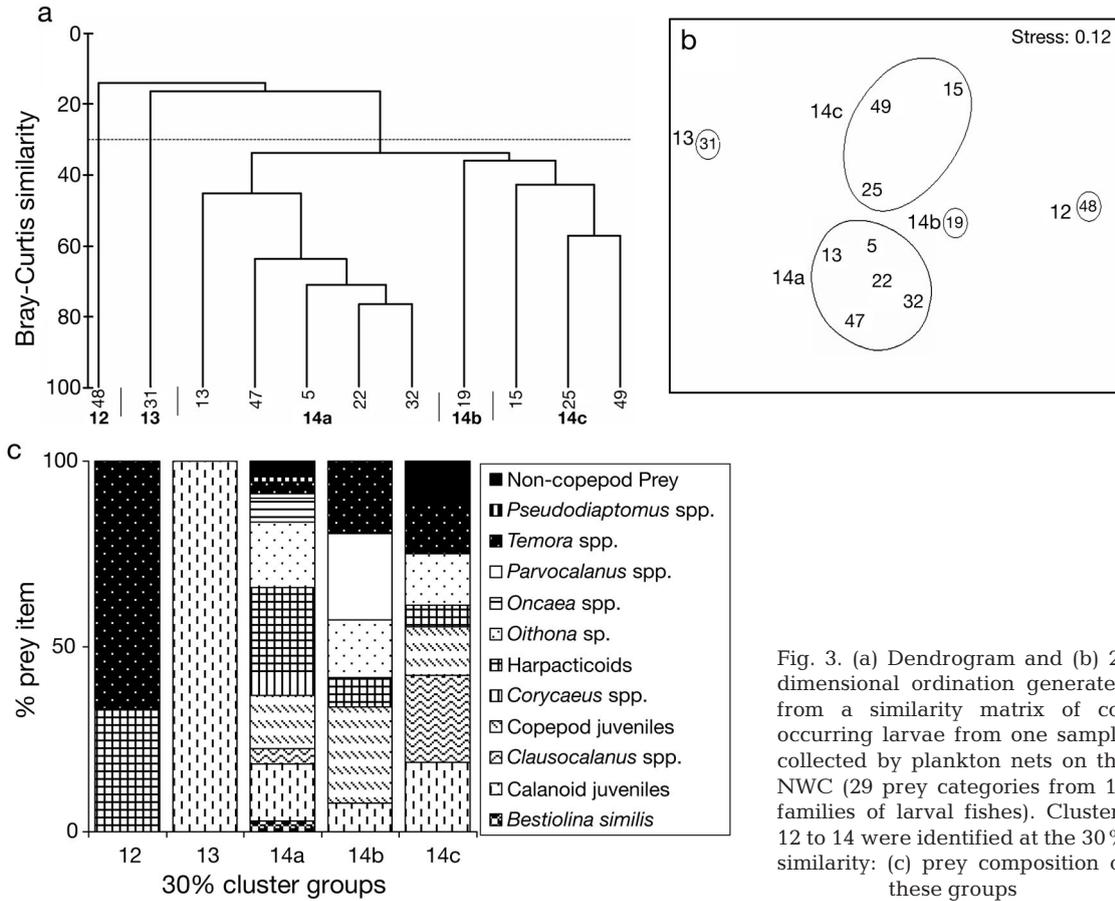


Fig. 3. (a) Dendrogram and (b) 2-dimensional ordination matrix generated from a similarity matrix of co-occurring larvae from one sample collected by plankton nets on the NWC (29 prey categories from 11 families of larval fishes). Clusters 12 to 14 were identified at the 30% similarity: (c) prey composition of these groups

val fishes in temperate waters (Hunter 1981). Our 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. calionymids 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 interspecific 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). We 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 we have had to compro-

mise the number of replicate individuals examined within each family. Consequently our 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 (A. D. McKinnon unpubl.); 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, we 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 we have been able to identify to species. Differences in naupliar behaviour between genera render them differentially susceptible to predation (Titelman & Kjørboe 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 we have been unable to discriminate.

Table 3. Density (no. 100 m⁻³) of zooplankton and fish larvae collected by plankton nets at site B near the NWC on 17 February 1999. Hp: harpacticoid copepods, Ca: calanoid copepods, Cy: cyclopoid copepods, NC: non-copepod. Prey items present in guts but not recorded in plankton counts are listed

Taxon	Prey type	Density
Prey		
Cyclopoid juveniles ^a		260000
Bivalves ^a	NC	99600
Calanoid juveniles		94500
Gastropods ^a	NC	91900
harpacticoid juveniles		72400
Larvaceans ^a	NC	56500
Microsetella sp.	Hp	26800
<i>Oithona nana</i> ^a	Cy	18900
<i>Euterpina acutifrons</i>	Hp	18900
Chaetognaths ^a	NC	18800
<i>Corycaeus</i> spp.	Cy	14300
<i>Parvocalanus crassirostris</i>	Ca	12600
<i>Oithona attenuata</i>	Cy	12600
<i>Oithona simplex</i>	Cy	9500
<i>Oncaea</i> spp.	Cy	6400
<i>Parvocalanus dubia</i> ^a	Ca	6300
Polychaetes	NC	6200
Decapod larvae	NC	3200
<i>Oithona</i> spp.	Cy	3200
<i>Acartia fossae</i> ^a	Ca	3100
<i>Canthocalanus pauper</i> ^a	Ca	3100
Euphausiid larvae ^a	NC	3100
<i>Bestiolina similis</i>	Ca	1600
<i>Corycaeus dahli</i>	Cy	1200
<i>Temora turbinata</i>	Ca	1200
<i>Paracalanus indicus</i> ^a	Ca	900
<i>Acrocalanus gibber</i> ^a	Ca	600
<i>Corycaeus andrewsi</i>	Cy	600
<i>Clausocalanus farrani</i>	Ca	–
copepod nauplii		–
<i>Corycaeus asiaticus</i>	Cy	–
<i>Dynophysis</i>	NC	–
Mite	NC	–
<i>Oithona</i> juveniles	Cy	–
<i>Oithona rigida</i>	Cy	–
<i>Parvocalanus</i> sp.	Ca	–
poecilostome juveniles	Cy	–
<i>Pseudodiaptomus</i> spp.	Ca	–
Fish larvae		
Callionymidae		40
<i>Cynoglossus</i> sp.		20
Gobiidae sp. 6		20
Pinguipedidae		10
Leiognathidae		5
Gobiidae mixed spp.		3
Monacanthidae		1
Aploactinidae		1
Platycephalidae		1
<i>Engyspiron</i> sp.		0.5
Carangidae		0.5
Samaridae		0.2
Opistognathidae		0.2

^aNot eaten by the fish larvae examined in this sample.

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. We could not identify the scombrids in our 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 & Kjørboe 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 is influenced by characteristics of their prey and the inherent preferences of particular taxa.

Prey characteristics — copepod prey

The characteristics of copepods as prey for larval fishes differed 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 preda-

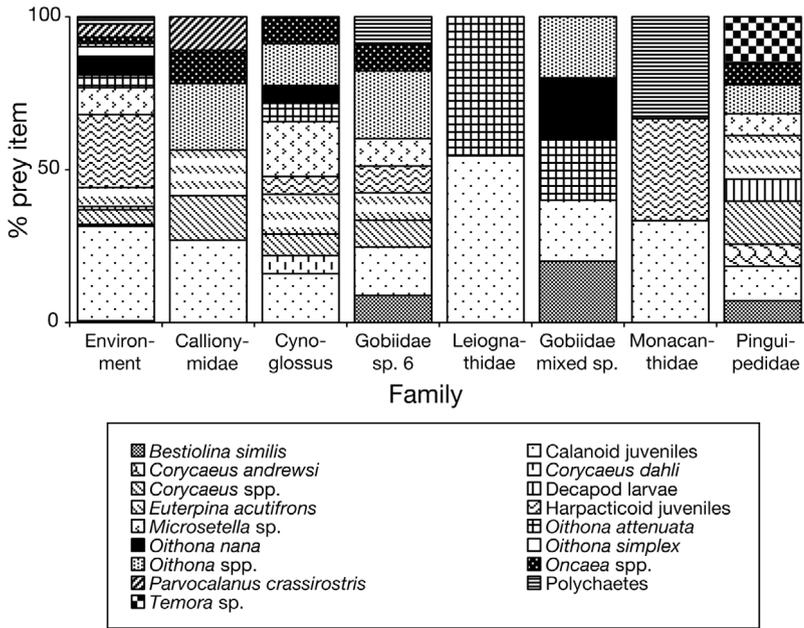


Fig. 4. Composition of prey items in the zooplankton community ('Environment') compared to that found within the guts of larvae of tropical shore fishes collected by plankton nets near the NWC

tion 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 we examined. These may

be preferred items simply because their size is within the size range of prey preferred by the larvae in our 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). Our 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 laboratory-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). We 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 families, calanoids constituted >50 % of their diet. In comparison, 72 % of the families fed on oithonid prey but only in 6 % of the cases did oithonids form >50 % of the diet. Thus, it appears that larval fishes in the tropics will preferentially select calanoid copepods as prey.

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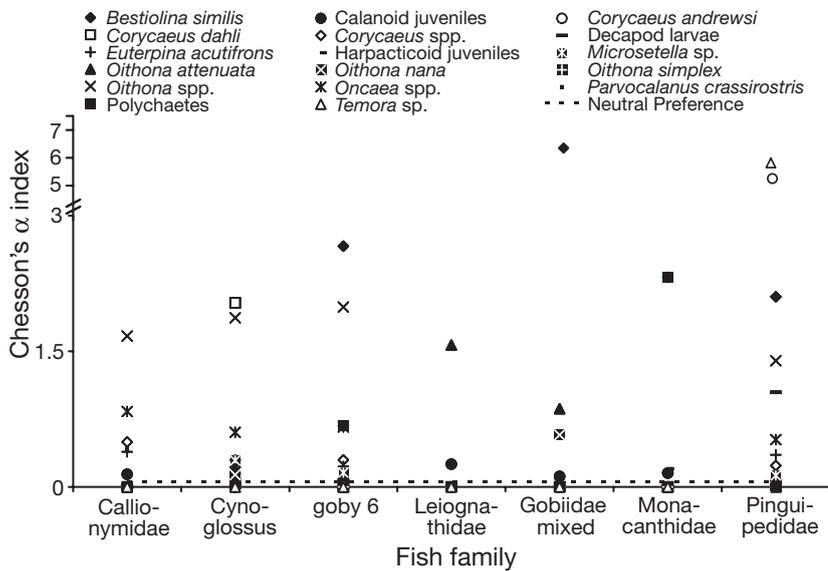


Fig. 5. Prey selectivity values (Chesson's α index) for 7 co-occurring taxa of larval fishes collected in a single plankton net near the NWC

Prey characteristics — non-copepod prey

Mollusc veligers, chaetognaths, appendicularians and protists were only eaten

Table 4. Comparison of diets for selected families from our study with the results from previous studies. Since the diets of larval fishes alter with size (Østergaard et al. 2005), the data are limited to tropical larvae with dietary information for larvae of similar sizes to those sampled in our study. Only dominant prey items are listed. N = no. of individuals examined

Taxa	N	Location	Diet	Source
Clupeidae				
Mixed species	392	Florida	Copepods	Houde & Lovdal 1984
Unidentified species	20	NW Shelf	Calanoid copepods	Present study
Callionymidae				
<i>Callionymus decoratus</i>	17	Hawaii	Cyclopoid copepods probably <i>Oithona</i>	Watson 1974
<i>Callionymus pauciradiatus</i>	770	Florida	Copepod nauplii	Houde & Lovdal 1984
Unidentified species	21	NW Shelf	Harpacticoid, cyclopoid (<i>Oithona</i>) copepods	Present study
Scorpaenidae				
<i>Scorpaenodes</i> sp.	89	Andaman Sea	Calanoid, corycaeid, oncaeid copepods	Østergaard et al. 2005
Unidentified species	10	NW Shelf	Calanoid, oithonid, corycaeid copepods	Present study
Acanthuridae				
<i>Acanthurus triostegus</i>	3	Hawaii	Appendicularians, larval polychaete	Randall 1961
Unidentified species	1	NW Shelf	Appendicularians	Present study
Apogonidae				
<i>Foa brachygrammus</i>	34	Hawaii	Tintinnids	Watson 1974
Unidentified species	130	Florida	Copepods	Houde & Lovdal 1984
Unidentified species	10	NW Shelf	Copepod juveniles, calanoids	Present study
Blennidae				
<i>Omobranchus elongatus</i>	15	Hawaii	Copepods	Watson 1974
<i>Blennius</i> sp.	4	Hawaii	Tintinnids	Watson 1974
Unidentified species	10	NW Shelf	Corycaeid, oithonid copepods, bivalves	Present study
Carangidae				
<i>Atule (Caranx) mate</i>	48	Hawaii	Cyclopoid copepods probably <i>Oithona</i>	Watson 1974
<i>Carangoides</i>	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				
<i>Orthopristis chrysoptera</i>	242	Florida	Copepods	Houde & Lovdal 1984
Unidentified species	12	NW Shelf	Oithonid copepods	Present study
Pomacentridae				
<i>Abudefduf abdominalis</i>	3	Hawaii	Tintinnids at <3mm SL, copepods >3mm	Watson 1974
<i>Amblyglyphidodon aureus</i>		PNG	Calanoid & oithonid copepods	Mitchell 1991
<i>Amphiprion polymnus</i>		PNG	Calanoid & oithonid copepods	Mitchell 1991
<i>Pomacentrus</i> or <i>Chrysiptera</i> sp.	12	NW Shelf	Calanoid & oithonid copepods	Present study
Scaridae				
<i>Leptoscarus vaiqiensis</i>	9	Japan	Copepods	Ohta & Tachihara 2004
Scombridae				
<i>Scomberomorus semifasciatus</i>	90	GBR	Fish larvae	Jenkins et al. 1984
<i>Scomberomorus queenslandicus</i>	181	GBR	Appendicularians, fish larvae	Jenkins et al. 1984
<i>Scomberomorus commerson</i>	51	GBR	Appendicularians, fish larvae	Jenkins et al. 1984
<i>Thunnus</i> spp.	1000+	Indian Ocean	<i>Coryceus</i> sp., <i>Evadne</i> sp.	Uotani et al. 1981
<i>Katsuwonus pelamis</i>	300+	Indian Ocean	Appendicularians, fish larvae	Uotani et al. 1981
<i>Auxis</i> spp.	300+	Indian Ocean	Appendicularians, <i>Evadne</i> sp.	Uotani et al. 1981
<i>Thunnus maccoyi</i>	583	Indian Ocean	Calanoid, cyclopoid, copepod nauplii, <i>Evadne</i>	Young & Davis 1990
<i>Thunnus alalunga</i>	275	Indian Ocean	<i>Coryceus</i> , <i>Farannula gibber</i> , copepod nauplii	Young & Davis 1990
<i>Katsuwonus pelamis</i>	65	Indian Ocean	Appendicularians, calanoids, nauplii, fish larvae	Young & Davis 1990
Unidentified sp.	20	NW Shelf	Copepod nauplii, appendicularians	Present study
Bothidae				
<i>Psettodes erumei</i>	11	GBR	Copepods	Liew 1983
<i>Pseudorhombus arsius</i>	34	GBR	Appendicularians, copepods	Liew 1983
<i>Pseudorhombus elevatus</i>	28	GBR	Copepods	Liew 1983
<i>Pseudorhombus spinosus</i>	28	GBR	Copepods, appendicularians, chaetognaths	Liew 1983
<i>Pseudorhombus diplospilus</i>	28	GBR	Appendicularians, chaetognaths	Liew 1983
<i>Grammatobothus</i> spp.	46	GBR	Paracalanid copepods	Liew 1983
<i>Engyprosope grandisquama</i>	24	GBR	Appendicularians	Liew 1983
<i>Asterorhombus intermedius</i>	26	GBR	Appendicularians	Liew 1983
Unidentified species	20	NW Shelf	Appendicularians, calanoid copepods	Present study
Cynoglossidae				
<i>Cynoglossus</i> sp.	32	Andaman Sea	Harpacticoid, oncaeid, copepod nauplii	Østergaard et al. 2005
<i>Cynoglossus</i> sp.	20	NW Shelf	Calanoid, cyclopoid, oncaeid copepods	Present study

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 thus limit their desirability 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 3 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 preyed 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.

Larval fish feeding and pelagic food webs on the North West Shelf of Australia

During the period of our study the waters of the North West Shelf of Australia had intermittently high primary production, particularly during the 1997-98 El Niño event (Furnas 2007). 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, 100s of km from land, whereas others such as most pomacentrids are rarely captured in oceanic waters (Victor 1987, Clarke 1995, Mora 2002, Lo Yat et al. 2006). However, our 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.

CONCLUSIONS

Our 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 4 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 our 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.

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