

FEEDING ECOLOGY OF MARINE FISH LARVAE: AN AUSTRALIAN PERSPECTIVE

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Abstract

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

generalisations are premature. Future research should aim to 1) collect larval feeding data on more species and 2) examine further the relationship between feeding ecology, recruitment success and seasonal and interannual variations in plankton production.

Introduction

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

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

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

Diet

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

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

quality may also contribute to a prey's suitability (Mitchell in press). For example, Mitchell (in press) found that tropical larvae selected the most pigmented nauplii and copepods.

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

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

Prey selection

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

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

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

Timing of feeding

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

feed continuously through the day, peaking at sunset. A similar pattern was also found for two species of pomacentrid larvae (Mitchell in press).

Digestion and food consumption

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

Impact of larval fish on their prey

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

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

The critical period concept

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

tant component of the diet of first-feeding larval blue grenadier. The whole question of the relationship of spawning and larval production to seasonal changes in nutrient production is not well understood. We have a good knowledge of when most marine fishes spawn in Australian waters and therefore when larvae are likely to be found, but the link with seasonal pulses of production has yet to be examined in detail.

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

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

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

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