Larval fishes off Western Australia: influence of the Leeuwin Current

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Manuscript received December 2007; accepted March 2009

Abstract

Although the poleward flow of the Leeuwin Current off Western Australia is unique among eastern boundary currents in the southern hemisphere, the biological oceanography of this system is comparatively poorly known. In this short review, the findings of the various studies on larval fishes completed off Western Australia are collated, synthesized and related to the influence of the Leeuwin Current. The studies range from light-trap experiments focusing on tropical fish larvae off the north-western coast to studies on larvae of commercially significant temperate clupeiod species in the Great Australian Bight. Larval fish assemblages within the Leeuwin Current appear to be composed of a mixture of oceanic, slope, tropical and temperate coastal species, with strong seasonal variation in species composition. Ichthyoplankton studies in progress off Western Australia are reported on and aim to address gaps in the knowledge about the influence of the Leeuwin Current and its meso-scale features upon larval fishes.

Keywords: Leeuwin Current, ichthyoplankton, sardines, water masses, eddies

Introduction

The Leeuwin Current is an atypical eastern boundary current in the Indian Ocean that flows poleward along the shelf-edge off Western Australia (WA) before turning eastward at Cape Leeuwin and crossing the Great Australian Bight (Cresswell & Golding 1980). This warm, low salinity current is driven by a strong alongshore steric height gradient that is sufficient to suppress the effects of coastal wind-driven upwelling (Ridgway & Condie 2004). This results in oligotrophic conditions, unlike the highly productive eastern boundary currents off South America and southern Africa (Pearce 1991; Feng *et al*. 2009).

Studies of larval fish assemblages have been conducted in most of the world's major boundary currents, for example, the California Current, Gulf Stream, Benguela Current and Agulhas Current (Doyle *et al*. 1993; Moser & Smith 1993; Olivar & Shelton 1993; Beckley 1998; Hare *et al*. 2001). Western boundary currents such as the Gulf Stream, Agulhas Current and East Australian Current provide a transport mechanism for larvae of tropical fishes to be dispersed towards temperate areas (Miskiewicz 1989; Gray 1993; Olivar & Beckley 1994; Beckley & Leis 2000; Hare *et al*. 2002; Booth *et al*. 2007). Although southward dispersal of larval fishes by the Leeuwin Current has been invoked in the literature (Maxwell & Cresswell 1981; Hutchins 1991; Lenanton *et al*. 1991; Hutchins & Pearce 1994; Caputi *et al*. 1996), there has been no specific study of the ichthyoplankton of the Leeuwin Current *per se*. However, there have been several localized studies which have investigated larval fishes in specific areas along the WA coast. In this short review, we will draw these together, synthesise their findings and relate them to the Leeuwin Current. The review will sequentially cover the three broad geographical areas off WA, namely the north-west, west and south coasts as well as the implications of meso-scale eddies of the Leeuwin Current on larval fishes.

North-west Shelf

The headwaters of the Leeuwin Current include the area off the north-west of Australia (D'Adamo *et al*. 2009). In this region, distributional patterns of larval fishes along two transects extending across the continental shelf near Dampier and to the east of Port Hedland (Figure 1) were described by Young *et al*. (1986). Although the results were somewhat confounded by use of different sampling gears between cruises, they noted a major discontinuity in larval fish composition just inshore of the shelf break. In general, larvae of fishes found as adults on the continental slope and open ocean characterised the deeper sampling sites (*e.g.*, Myctophidae, Gonostomatidae, Gempylidae, and Coryphaenidae) whilst larvae of species that were shelf-dwelling as adults (*e.g.*, Clupeiodei, Gobiidae, Carangidae, Apogonidae, Synodontidae and Lutjanidae) typified the shelf sites.

Further to the west, along a cross-shelf transect of stations in Exmouth Gulf that extended out past the Muiron Islands into the Leeuwin Current (15–75 m

Figure 1. Map of Western Australia showing coastal localities mentioned in the text where studies of larval fishes have been completed.

depth), studies using light traps and plankton nets have been conducted during the austral summer months (Meekan *et al*. 2001, 2003; Sampey *et al*. 2004). The light trap work focused on comparing the catches between two light trap designs and between drifting and moored traps (Meekan *et al*. 2001). Catches in drifting traps were dominated by post-flexion larvae of reef fishes (*e.g*., Pomancentridae, Blenniidae, Lethrinidae) whilst the moored traps caught predominantly Clupeidae. Despite differences in catch rates, multivariate analysis showed that cross-shelf patterns in catches were mapped equally well by both trap designs and Bray-Curtis classification analyses essentially split the inshore and mid-shelf stations from those stations further offshore. Larval fishes from bongo net tows conducted at one station in Exmouth Gulf (20 m depth) and another at 100 m depth west of the Muiron Islands were compared by Sampey *et al*. (2004). Although families such as Monocanthidae were more abundant at the inshore site, and Scombridae and Myctophidae were more abundant at the offshore site, they only discerned a weak cross-shelf pattern in the ichthyoplankton. This could probably be explained by the well-mixed water column at both stations and no evidence of lower salinity Leeuwin Current water at the deeper station.

At Ningaloo Reef, where the shelf is narrow and the inshore Ningaloo Current flows counter to the Leeuwin Current in summer (Woo *et al*. 2006; Hanson *et al*. 2007), flux of larval fishes across the crest of the reef during the summer months was examined by McIlwain (1997, 2002, 2003). Most of the larvae making the transition from the pelagic environment to the reef lagoon arrived during November and December. Time series analysis showed that semi-lunar periodicity was the most common pattern in larval supply, particularly for the abundant Blenniidae, Labridae, Synodontidae and Scorpaenidae which arrived on a 15 day cycle. Eel leptocephalii showed the strongest evidence of lunar cycling and the replenishment of Soleidae and Lethrinidae was also on a monthly basis. However, many larvae appeared to arrive completely stochastically. Cross-correlation techniques were used to compare differences in abundance at spatial scales of 500 m and 5 km and multi-specific patches of larvae at least 5 km wide were found to cross the reef crest into the lagoon habitat. The timing of these patches was often chaotic and rarely lasted longer than 24 h.

In summary, studies on larval fishes off the north-west region of WA are few and, with the exception of Young *et al*. (1986), they have only taken place in the summer months which is the time of weakest Leeuwin Current flow (D'Adamo *et al*. 2009). Nevertheless, offshore larval fish assemblages in Leeuwin Current headwaters appear to have distinctly different larval fish assemblages from those inshore on the shelf.

West coast

The marine ichthyoplankton assemblages off the west coast of Australia from Ningaloo to Cape Leeuwin remain poorly studied although some sampling programmes that focused on particular teleost species of commercial importance have been conducted by the WA Department of Fisheries. Gaughan & Mitchell (2000) investigated the biology of the tropical sardine (*Sardinella lemuru)* and this included enumeration of the eggs and larvae of this species from plankton samples collected across the shelf between Shark Bay and Dongara and out to the Abrolhos Islands. Summer spawning was confirmed and eggs were typically found over the outer half of the continental shelf. Although the influence of the Leeuwin Current was explored, they concluded that northward transport of early life history stages was more likely under the influence of the strong southerly winds that prevail during the summer months.

Numerical modelling of the dispersal of *Pagrus auratus* (pink snapper) eggs and larvae in Shark Bay (Nahas *et al*. 2003) concluded that the Leeuwin Current has a negligible influence on recruitment in gulf snapper populations and tides are the primary transport mechanism. The foraging ecology of five species of terns at the Abrolhos Islands has provided insight into larval fishes off the mid-West coast (Surman & Wooller 2003). They showed that the neustonic larvae of *Gonorhynchus greyii* (beaked salmon) and *Parupeneus signatus* (goatfish) were particularly important in the diet of lesser and brown noddies and sooty and roseate terns which foraged seaward of the islands in the vicinity of the Leeuwin Current.

Vertical and surface tows for plankton were conducted at 65 stations in shelf and slope waters between Fremantle and Exmouth by the Department of Fisheries in March 1996 (D Gaughan unpublished data). During two subsequent oceanographic cruises, CSIRO collected zooplankton samples using bongo nets along transects from North West Cape to the Abrolhos Islands in November 2000 and the Abrolhos Islands to Fremantle in October/November 2003 (J A Koslow unpublished data). Extraction of the fish larvae from these plankton samples was undertaken to try and locate the elusive larvae of tailor (*Pomatomus saltatrix).* Although very few tailor larvae were recorded from these samples (only six specimens from surface tows around Geraldton in March 1996), there was a clear trend of overall larval fish concentrations declining across the shelf and slope (Chisholm 2004). Some tailor larvae were extracted from surface plankton tows conducted around Rottnest Island by the Department of Fisheries in May 1999 (Chisholm 2004).

There were numerous, and extensive, surveys by the Department of Fisheries for the eggs and larvae of the commercially important sardine (*Sardinops sagax*) in shelf waters of the lower west coast over the period 1993–2004 (Fletcher *et al*. 1996; Gaughan *et al*. 2004, 2007). Muhling *et al*. (2008a) synthesised the data on the temporal and spatial distributions of sardine eggs and larvae off the south-western coast between Two Rocks and Cape Naturaliste and related them to the gonadosomatic index of adult sardines, daily growth rates of larvae and regional biological oceanography. While gonadosomatic index data suggested a distinct winter peak in sardine spawning activity, coincident with maximum seasonal surface chlorophyll concentrations, egg and larval distributions were not significantly higher in winter. This is likely due to the poor retention conditions for pelagic eggs and larvae on the mid-outer shelf during winter, as a result of the strength and location of the Leeuwin Current. Growth rates of larval sardines were unexpectedly high, averaging 0.70–0.89mm day^{-1} possibly because of the warmer water of the Leeuwin Current impinging on the shelf (Jones 2006; Muhling *et al*. 2008). Nevertheless, it was suggested that the coincidental timing of the modest seasonal maximum in primary productivity with the least favourable conditions for retention of pelagic larvae further compounds the restricted size of the sardine stock off south-western Australia.

Plankton samples taken over the continental shelf between Perth and Busselton confirmed that eggs and larvae of whitebait (*Hyperlophus vittatus*) occur primarily in shallow inner-shelf waters such as Cockburn Sound, Warbro Sound and Koombana Bay particularly in the winter months (Gaughan *et al*. 1996a,b). Studies conducted on the ichthyoplankton assemblages of the confined waters of Cockburn Sound (Jonker 1993; Kendrick 1993) and the Swan Estuary (Gaughan *et al*.

1990; Neira *et al*. 1992) revealed no evidence of any Leeuwin Current influence and the assemblages were dominated by larvae of teleosts found in temperate coastal waters.

SRFME programme

The Strategic Research Fund for the Marine Environment programme included the first detailed study of the biophysical oceanography off south-western Australia. This study focused on a transect extending offshore from Two Rocks (north of Perth) and, in addition to physical oceanography, covered nutrients, primary production, zooplankton and larval fish studies (Koslow *et al*. 2006, 2008; Muhling 2006). Muhling *et al.* (2008b) described the larval fish assemblages from inshore (18 m depth) to offshore waters (1000 m depth) off Two Rocks over a two and a half year period, and have related assemblage structure to oceanography. Assemblages showed strong spatial and temporal structure, which was well correlated to seasonality in water masses (Figure 2). The strength and position of both the Leeuwin and Capes Currents influenced variability in the marine environment, and, consequently, larval fish assemblages. In particular, the shoreward intrusion of the Leeuwin Current over the continental shelf in winter results in higher connectivity across the shelf, and greater similarity in larval fish assemblages between shelf and offshore waters, whereas in summer, larval fish assemblages were distinct between shelf and offshore stations.

Larval fish assemblages near the coast typically comprised larvae of inshore reef families, such as Blenniidae, Gobiidae and Monacanthidae. Shelf stations were dominated by larvae of pelagic families, such as Clupeidae, with *Sardinops sagax* and *Etrumeus teres* the most abundant species within this family. In summer, Labridae larvae were also abundant over the shelf, whereas in winter, larvae of oceanic fishes from the Myctophidae (*e.g.*, *Diogenichthys atlanticus*) and Phosichthyidae (mostly *Vinciguerria* spp.) were more abundant. Seaward of the shelf break, the larval fish assemblage was dominated by oceanic larvae throughout the year, with only slight seasonal changes in species composition. Some vagrant, tropical larvae, such as Pomacentridae and Ostraciidae were collected at stations on the outer shelf and slope during summer and autumn, within the southward flow of the Leeuwin Current.

Larval fish assemblages from within the Leeuwin Current generally had similar species, however, assemblages from shelf stations inundated by the Leeuwin Current were distinct from those taken in the core of the Leeuwin Current (Muhling *et al*. 2008b). This suggests that water depth and/or distance from shore has a structuring effect on assemblages not completely related to water mass and probably reflects differing spawning locations of the diverse species assemblage of fishes in south-western Australia.

Seasonal variability in cross-shelf transport, and thus larval fish assemblages, was investigated by Muhling & Beckley (2007). The horizontal and vertical distributions of larvae across the shelf and offshore were found to be strongly influenced by the current regime at the time of sampling. A winter cruise in August 2003 was undertaken during a time of strong, southward Leeuwin Current flow, while the northward flowing Capes Current, in combination with surface offshore Ekman transport, predominated during the summer cruise of January 2004. The southward flow of the Leeuwin Current extended to >150 m depth during winter, effectively limiting any retention of larvae on the shelf at

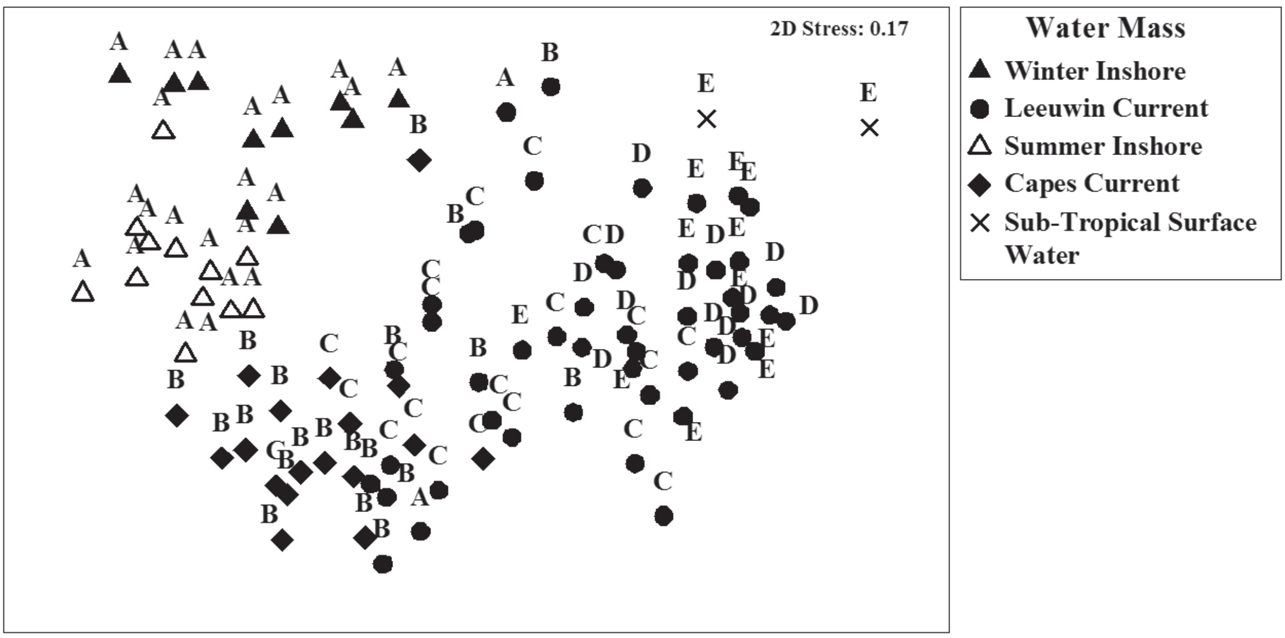

Figure 2. Multi-dimensional scaling ordination of larval fish assemblages and water masses along the Two Rocks SRFME transect across the shelf and Leeuwin Current off south-western Australia (2002–2004). Stations were at 18 m (A), 40 m (B), 100 m (C), 300 m (D) and 1000 m (E) depths.

this time. These factors, in combination with the vertical depth preferences of larvae of different taxa, largely determined their distribution patterns. A conceptual model of larval fish assemblages in relation to water masses off the lower West coast is given in Figure 3.

Leeuwin Current eddies

Meso-scale eddies are conspicuous features of the Leeuwin Current (Cresswell & Griffin 2004) and a dedicated, multi-disciplinary cruise to examine the oceanography and ecology of a pair of counter-rotating eddies off south-western Australia was conducted in October 2003 (Waite *et al*. 2007a; Feng *et al*. 2007). Muhling *et al*. (2007) examined the larval fish assemblages in both the cold-core, cyclonic eddy and the warm-core, anticyclonic eddy which had propagated seaward from the shelf edge. Despite the warm-core eddy being characterized by coastal diatoms (Thompson *et al*. 2007; Waite *et al*. 2007b), larval fishes in both eddies were dominated by oceanic families such as Myctophidae, Phosichthyidae, Gonostomatidae, Sternoptychidae, Paralepididae and Stomiidae. However, larval fish assemblages from the warm-core eddy were significantly different from those in the cold-core eddy. Larval fish assemblages were more variable within the warm-core eddy, both across eddy zones (centre, body and perimeter) and within depth strata, than in the cold-core eddy. Depth of the mixed layer was strongly correlated with assemblages in the warm-core eddy but not in the cold-core eddy. Stable isotope analysis (Waite *et al*. 2007c) suggested that larval fishes in the warm-core eddy were preferentially targeting food sources derived from large phytoplankton carbon such as that found in the diatoms of the warm-core eddy.

Pelagic larval duration among coastal fish species is typically a few weeks (MacPherson & Raventos 2006). Thus, as the eddies studied by Muhling *et al*. (2007) were located 300–600 km offshore and were already 4–5 months old when sampled, it was not possible to ascertain the influence of the eddies in entraining coastal fish larvae off the shelf. Gaughan (2007) hypothesised on potential influences of Leeuwin Current eddies on teleost

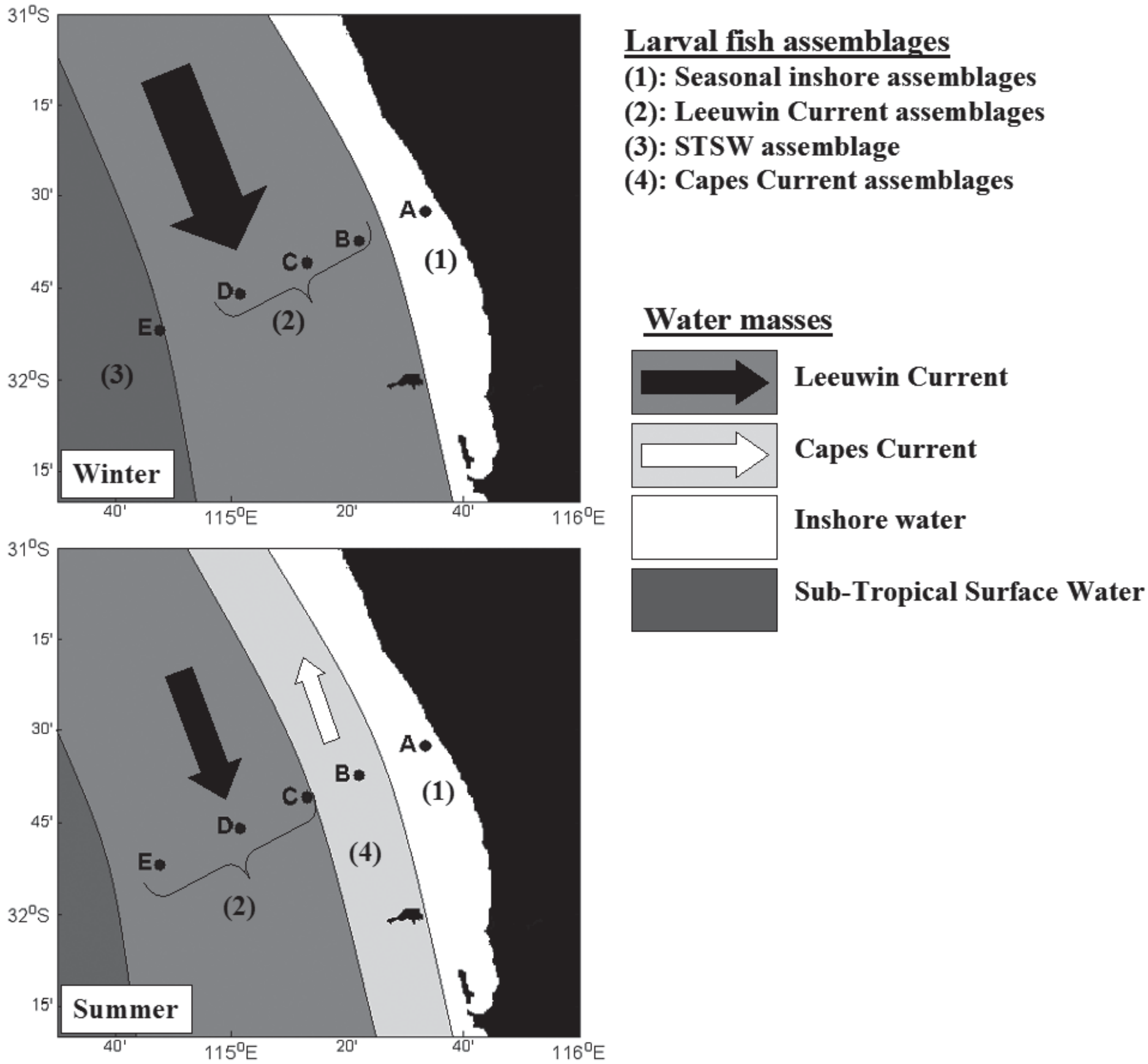

Figure 3. Conceptual diagram indicating seasonality in water masses and associated larval fish assemblages off the lower west coast of Australia.

recruitment to the Western Australian continental shelf suggesting that retention/loss of teleost eggs and larvae and positive/negative influences on feeding conditions for larvae were of importance.

South coast

Along the south coast of WA, ichthyoplankton studies have focused on eggs and larvae of sardines (*Sardinops sagax)*. Fletcher & Tregonning (1992) sampled out to the edge of the continental shelf off Albany and concluded that most spawning of sardines was inshore of the main influence of the Leeuwin Current. They found peaks in egg abundance in both July and December but only a December peak in larval abundance and speculated that this could reflect higher larval transport out of the study area in winter when the Leeuwin Current was strongest.

In a subsequent study, Fletcher *et al*. (1994) examined inter-seasonal variation in the transport of sardine eggs and larvae over the continental shelf along the south coast from Walpole to Bremer Bay by using a fleet of fishing vessels to sample the area over as short a time period as possible. They concluded that, during winter, the location of the Leeuwin Current had a direct effect on spawning as eggs were most abundant off Albany in a band of cooler coastal water and there were very few to the west where the Leeuwin Current was close to the coast. Larvae were distributed further to the east with highest numbers towards Bremer Bay. They determined that the consistent shifts in the abundance peaks of the different egg and larval stages indicated drift of 30–40 km d^{-1} corresponding to an easterly flowing current speed of 0.3–0.46 m s^{-1}. In summer, all stages of eggs and larvae were distributed throughout the study area with the peak in abundance on the shelf off Albany and there was no obvious local oceanographic influence on their abundance as the Leeuwin Current had weakened near Cape Leeuwin.

Using geo-statistical techniques, Fletcher & Sumner (1999) examined the fine scale spatial distribution of sardine eggs and larvae of various ages off Albany. They showed that sardine eggs have a patchy distribution which reflects the spawning behaviour of adults. For older larval stages, patch size increased and the level of cohesion decreased. Various studies to investigate aspects of sardine larval ecology were conducted during a research cruise from Adelaide to Albany across the Great Australian Bight in July 1994. Using a multiple opening and closing EZ net, Fletcher (1999) showed that recently spawned eggs were generally located in 40–60 m of water and that larvae were near the surface though during the night they tended to be slightly deeper in the water column (15–30 m). During this study an attempt was made to document the larval distributions of other selected fishes found during surface and vertical tows. The neustonic larvae of *Scombersox saurus*, *Cheilodactylus* sp. and *Gonorhyncus greyii* were most abundant on the shelf-edge and slope whilst larvae of neritic Labridae, *Scomber australasicus* and *Etrumeus teres* were most abundant on the shelf between Albany and Bremer Bay (Fletcher *et al*. 1996).

Gaughan *et al*. (2001a) determined the growth rate of *S. sagax* larvae from samples collected during this cruise across the Great Australian Bight and found the mean growth rate to be 0.48 mm d^{-1}. As indicated in their comparative table this value is less than that found for sardine larvae in other parts of the world. They concluded that the lower productivity off the oligotrophic south coast, partly induced by the Leeuwin Current, was responsible for this low growth rate.

The potential for transport of larval sardines between Western Australian and South Australian fishery management areas was assessed by examining the eastward movement of surface water and the age and hatch-date distributions of larvae in shelf waters across the Great Australian Bight (Gaughan *et al*. 2001b). Generally, the ages of larvae tended to increase from west to east but the mean estimated flow on the shelf of 0.1 m s^{-1} (calculated from ADCP and wind data during the cruise) was insufficient to support the hypothesis that larvae could passively advect from Western Australia to the eastern Great Australian Bight. However, the Leeuwin Current was particularly weak during the year of the study, and the authors contended that potential links between distant areas through larval dispersal requires consideration especially with regard to the scale of fisheries management units. Similarly, Dimmlich *et al*. (2000) explored the transport of larvae of Australian herring (*Arripis georgianus*) from WA where they spawn (Fairclough *et al*. 2000) to South Australia using a transport model incorporating wind-generated coastal currents and the Leeuwin Current. They concluded that in years of stronger transport, recruitment to South Australia was higher.

The results from numerous Department of Fisheries plankton surveys for sardine eggs that took place periodically between 1991 and 2005, and covered much of the southern coast of Western Australia, have allowed examination of the re-growth of sardine stocks following the mass mortality event of 1998/99 as a result of a widespread epizootic infection (Gaughan *et al*. 2004, 2007). Using the daily egg production method, estimates of spawning biomass, from before and after the epidemic, were integrated into an age-structured simulation model. The simulation model utilized information on factors that increase (*e.g*., recruitment, growth rate) and decrease (*i.e*., mortality due to fishing and natural causes) stock size to estimate changes in biomass over time. The analyses showed a strong recovery of sardine stocks in WA from the very low levels that remained after the mass mortality event of 1998/99.

Further research

At present there is considerable research effort being focused on the biological oceanography of Leeuwin Current eddies, in particular, the cross-shelf transport of larval fishes during the formation of eddies (Holliday & Beckley unpublished data). A four-week cruise was conducted in May 2006 and covered the area 30–34°S and westward from the coast to 112°E (Paterson *et al*. 2008). Vertical distribution patterns of larval fishes derived from depth-stratified sampling using an EZ net during this cruise combined with concurrent ADCP data and drifter tracks are being used to examine this process.

In May/June 2007, an intensive study of the biological oceanography of the Leeuwin Current was undertaken and included sampling across the shelf and slope out to a depth of 2000 m along transect lines at each degree of latitude from 34°S (Cape Leeuwin) to 22ºS (North West Cape) (Thompson *et al*. unpublished data). Along these transects, zooplankton and neuston samples were collected in oceanic, Leeuwin Current and shelf waters for elucidation of the larval fish assemblages (Beckley *et al*. unpublished data). This study took place during the autumnal increase in Leeuwin Current strength and primary production on the shelf (Lourey *et al*. 2006) and a repeat cruise during summer months when Leeuwin Current flow is weaker would provide an interesting contrast.

Identification of larval fishes requires the existence of appropriate descriptions of the larval stages. Larvae of widely distributed oceanic fishes have been relatively well described in the international literature and many of these publications can be used to identify those occurring in the Leeuwin Current (*e.g*., Moser *et al*. 1984; Olivar *et al*. 1999; Richards 2006). Similarly, the major treatise by Leis & Carson-Ewart (2000) is particularly useful for identification of the larvae of Indo-Pacific tropical fishes entrained in the Leeuwin Current. Larvae of many temperate Western Australian coastal fishes, especially those of commercially important species, are included in the volume by Neira *et al*. (1998). However, for some of the speciose inshore families (*e.g*., Labridae) lack of appropriate larval descriptions makes resolution to species level extremely difficult. This is somewhat of an impediment to studies on the influence on larval fish ecology of oceanographic processes associated with the Leeuwin Current and inshore counter currents (*e.g*., Capes Current) which appear to be important in retention of the larvae of coastal species spawning in the summer months.

Conclusion

In essence, larval fishes assemblages of the Leeuwin Current comprise a mixture of oceanic, slope, tropical and temperate coastal species, reflecting both the source waters and advection into the current on its 5 000 km-long trajectory around WA. Seasonality in strength and location of the Leeuwin Current appears to have a profound effect on the ecology of larval fishes in the region. There is considerable scope for investigations into the ecological processes associated with the Leeuwin Current as well as seasonal, inshore counter currents along the WA coast.

References

Beckley L E 1998 The Agulhas Current ecosystem with particular reference to dispersal of fish larvae. *In*: E Okemwa, M J Ntiba & K Sherman (eds). Status and Future of Large Marine Ecosystems of the Indian Ocean: A report of the international symposium and workshop. IUCN, Gland, Switzerland, 74–91.

Beckley L E & Leis J M 2000 Occurrence of tuna and mackerel larvae (Family: Scombridae) off the east coast of South Africa. Marine & Freshwater Research 51: 777–782.

Booth D J, Figueira W F, Gregson M A, Brown L & Beretta G 2007 Occurrence of tropical fishes in temperate southeastern Australia: role of the East Australian Current. Estuarine, Coastal & Shelf Science 72: 102–114.

Caputi N, Fletcher W J, Pearce A F & Chubb C F 1996 Effect of the Leeuwin Current on the recruitment of fish and invertebrates along the Western Australian coast. Marine & Freshwater Research 47: 147–155.

Cresswell G R & Golding T J 1980 Observations of a south-flowing current in the southeastern Indian Ocean. Deep-Sea Research 27A: 449–466.

Cresswell G R & Griffin D 2004 The Leeuwin Current, eddies and sub-Antarctic waters off south-western Australia. Marine & Freshwater Research 55: 267–276.

Chisholm W J 2004 Larval distribution of tailor (*Pomatomus saltatrix*: Pisces) off Western Australia. Honours thesis, Murdoch University, Perth, WA.

D'Adamo N, Fandry C, Buchan S & Domingues C 2009 Northern sources of the Leeuwin Current and the "Holloway Current" on the North-west Shelf. Journal of the Royal Society of Western Australia 92 (2): 53–66.

Dimmlich W F, Ayvazian S G, Allison R & Fleer D 2000 Development of an exploratory model of larval and juvenile Australian herring (*Arripis georgiana*) transport from Western Australian spawning grounds to coastal nursery habitats. *In*: Stock Assessment of Australian Herring, FRDC Final Report, Project 96/105, West Australian Fisheries Department, pp 94–114.

Doyle M J, Morse W W & Kendall A W 1993 A comparison of larval fish assemblages in the temperate zone of the northeast Pacific and northwest Atlantic Oceans. Bulletin of Marine Science 53: 588–644.

Fairclough D V, Dimmlich W F & Potter I C 2000 Reproductive biology of the Australian herring, *Arripis georgiana*. Marine & Freshwater Research 51: 619–630.

Feng M, Majewski L J, Fandry C B & Waite A M 2007 Characteristics of two-counter-rotating eddies in the Leeuwin Current system off the Western Australian coast. Deep-Sea Research II 54: 961–980.

Feng M, Waite A M & Thompson P A 2009 Climate variability and ocean production in the Leeuwin Current system off the west coast of Western Australia. Journal of the Royal Society of Western Australia 92 (2): 67–81.

Fletcher W J 1999 Vertical distribution of pilchard (*Sardinops sagax*) eggs and larvae off Southern Australia. Marine & Freshwater Research 50: 117–22.

Fletcher W J & Tregonning R J 1992 Distribution and timing of spawning by the Australian pilchard (*Sardinops sagax neopilchardus*) off Albany, Western Australia. Australian Journal of Marine & Freshwater Research 43: 1437–1449.

Fletcher W J, White K V, Gaughan D J & Sumner N R 1996 Analysis of the distribution of pilchard eggs off Western Australia to determine stock identity and monitor stock size. FRDC Final Report, Project 92/95, West Australian Fisheries Department.

Fletcher W J & Sumner N R 1999 Spatial distribution of sardine (*Sardinops sagax*) eggs and larvae: an application of geostatistics and resampling to survey data. Canadian Journal of Fisheries & Aquatic Science 56: 907–914.

Fletcher W J, Tregonning R J & Sant G J 1994 Interseasonal variation in the transport of pilchard eggs and larvae off southern Western Australia. Marine Ecology Progress Series 111: 209–224.

Gaughan D J 2007 Potential mechanisms of influence of the Leeuwin Current eddy system on teleost recruitment to the Western Australian continental shelf. Deep-Sea Research II 54: 1129–1140.

Gaughan D J & Mitchell R W D 2000 The biology and stock assessment of the tropical sardine, *Sardinella lemuru*, off the mid-west coast of Western Australia. Final Report FRDC Project 95/037, Fisheries Research Report, Fisheries Western Australia 119: 1–136.

Gaughan D J, Neira F J, Beckley L E & Potter I C 1990 Composition, seasonality and distribution of the ichthyoplankton in the lower Swan Estuary, south-western Australia. Australian Journal of Marine & Freshwater Research 41: 529–543.

Gaughan D J, Fletcher W J & Tregonning R J 1996a Spatial and seasonal distribution of the eggs and larvae of sandy sprat, *Hyperlophus vittatus* (Clupeidae), in south-western Australia. Marine & Freshwater Research 47: 971–979.

Gaughan D J, Fletcher W J, Tregonning R J & Goh J 1996b Aspects of the biology and stock assessment of whitebait, *Hyperlophus vittatus* (Clupeidae), in south-western Australia. Fisheries Research Report, Fisheries Department of Western Australia 108: 1–127.

Gaughan D J, Fletcher W J & White K V 2001a Growth rate of larval *Sardinops sagax* from ecosystems with different levels of productivity. Marine Biology 139: 831–837.

Gaughan D J, White K V & Fletcher W J 2001b The links between functionally distinct adult assemblages of *Sardinops sagax*: larval advection across management boundaries. ICES Journal of Marine Science 58: 597–606.

Gaughan D J, Mitchell R W D, Leary T I & Wright I W 2004. A sudden collapse in distribution of Pacific sardine (*Sardinops sagax*) in south-western Australia enables an objective re-assessment of biomass estimates. Fishery Bulletin 102: 617–633.

Gaughan D J, Craine M, Stephenson P, Leary T & Lewis P 2007 Regrowth of pilchard (*Sardinops sagax*) stocks off southern WA following the mass mortality event of 1998/99. Final Report, FRDC Project 2000/135, Fisheries Research Report No. 176, Department of Fisheries, Western Australia, 82 p.

Gray C A 1993 Horizontal and vertical distributions of larval fishes off central New South Wales. Marine Biology 1156: 649–666.

Hanson C E, Waite A M, Thompson P A & Pattiaratchi C B 2007 Phytoplankton community structure and nitrogen nutrition in the Leeuwin Current and coastal waters off the Gascoyne region of Western Australia. Deep-Sea Research II 54: 902–924.

Hare J B, Fahay M P & Cowen R K 2001 Springtime ichthyoplankton of the slope region of the north-eastern USA: larval assemblages, relation to hydrography and implications for larval transport. Fisheries Oceanography 10: 164–182.

Hare J B, Churchill J H, Cowen R K, Berger T J, Cornillion P C, Dragos P, Glenn S M, Govoni J J & Lee T N 2002 Routes and rates of larval fish transport from the southeast to the northeast United States continental shelf. Limnology & Oceanography 47: 1774–1789.

Hutchins J B 1991 Dispersal of tropical fishes to temperate seas in the southern hemisphere. Journal of the Royal Society of Western Australia 74: 79–84.

Hutchins J B & Pearce A F 1994 Influence of the Leeuwin current on recruitment of tropical reef fishes at Rottnest Island. Bulletin of Marine Science 54: 245–255.

Jones C M 2006 Growth rate of sardine (*Sardinops sagax*) larvae off the lower west coast of Australia. MSc thesis, Murdoch University, Perth WA.

Jonker L J 1993 Comparison of the larval fish assemblages in healthy and degraded seagrass meadows in Cockburn Sound, Western Australia. Honours thesis, Murdoch University, Perth, WA.

Kendrick A J 1993 Assemblages of larval fishes in coastal waters of south-western Australia. Honours thesis, Murdoch University, Perth WA.

Koslow J A, Fearns P, Feng M, Greenwood J, Hanson C, Harridan T, Lourey M, Mortimer N, Pearce A, Strzelecki J, Clementson L, Kloser R, Ryan T, Thompson P, Wild-Allen K, Paterson H, Pesant S, Waite A, Muhling B, Beckley L E, Majewski L & Begum A 2006 Coastal and shelf pelagic community structure: Pattern and processes. *In*: J K Keesing, J N Heine, R C Babcock, P D Craig, J A Koslow 2006 Strategic Research Fund for the Marine Environment (SRFME) Final report, CSIRO Marine Research, pp 55–122.

Koslow J A, Pesant S, Feng M, Pearce A, Fearns P, Moore T, Matear R & Waite A 2008. The effect of the Leeuwin Current on phytoplankton biomass and production off Southwestern Australia. Journal of Geophysical Research 113: C07050, doi10.1029/2007JC004102

Leis J M & Carson-Ewart B M (eds) 2000 The larvae of Indo-Pacific coastal fishes. Fauna Melanesia Handbook 2. Brill, Leiden. 850pp.

Lenanton R C, Joll L, Penn J & Jones K 1991 The influence of the Leeuwin Current on coastal fisheries of Western Australia. Journal of the Royal Society of Western Australia 74: 101–114.

Lourey M J, Dunn J R & Waring J 2006 A mixed-layer climatology of Leeuwin Current and Western Australian shelf waters: Seasonal nutrient dynamics and biomass. Journal of Marine Systems 59: 25–51.

Macpherson E & Raventos N 2006. Relationship between pelagic larval duration and geographic distribution of Mediterranean littoral fishes. Marine Ecology Progress Series 327: 257–265.

Maxwell J G H & Cresswell G R 1981 Dispersal of tropical marine fauna to the Great Australian Bight by the Leeuwin Current. Australian Journal of Marine & Freshwater Research 32: 493–500.

McIlwain J L 1997 Hydrodynamic flows and flux of larval fishes across the crest of Ningaloo Reef, Western Australia. Proceedings of the 8th International Coral Reef Symposium 2: 1133–1138.

McIlwain J L 2002 Link between reproductive output and larval supply and recruitment of a common damselfish species, with evidence of replenishment from outside the local population. Marine Ecology Progress Series 236: 219–232.

McIlwain J L 2003 Finescale temporal and spatial patterns of larval supply to a fringing reef in Western Australia. Marine Ecology Progress Series 252: 207–222.

Meekan M G, Wilson S G, Halford A & Retzel A 2001 A comparison of catches of fishes and invertebrates by two light trap designs, in tropical NW Australia. Marine Biology 139: 373–381.

Meekan M G, Carleton J H, McKinnon A D, Flynn K & Furnas M 2003 What determines the growth of tropical reef fish larvae in the plankton: food or temperature? Marine Ecology Progress Series 256: 193–204.

Miskiewicz A G 1989 The distribution of tropical coral reef fish larvae in temperate waters along the New South Wales coast of Australia. Rapp. P.-V. Reun.Ciem 191: 452 (The early life history of fish the third ICES symposium Bergen 3–5 October 1988 (eds J H S Blaxter, J C Gamble, & H von Westernhagen).

Moser H G & Smith P E 1993 Larval fish assemblages of the California Current region and their horizontal and vertical distributions across a front. Bulletin of Marine Science 53: 645–691.

Moser H G, Richards W J, Cohen D M, Fahay M P, Kendall A W & Richardson S L 1984 Ontogeny and systematics of fishes. Special Publication No. 1, American Society of Ichthyologists & Herpetologists, 760pp.

Muhling B A 2006 Larval fish assemblages in coastal, shelf and offshore waters of south-western Australia. PhD thesis, Murdoch University, Perth WA.

Muhling B A & Beckley L E 2007 Seasonal variation in horizontal and vertical structure of larval fish assemblages off south-western Australia, with implications for larval transport. Journal of Plankton Research 29 (11): 1–17.

Muhling B A, Beckley L E & Olivar M P 2007 Ichthyoplankton assemblage structure in two meso-scale Leeuwin Current eddies, eastern Indian Ocean. Deep-Sea Research II 54: 1113–1128.

Muhling B A, Beckley L E, Gaughan D J, Jones C M, Miskiewicz A G, & Hesp S A 2008a Spawning, larval abundance and growth rate of *Sardinops sagax* off south-western Australia: influence of an anomalous eastern boundary current. Marine Ecology Progress Series 364: 157–167.

Muhling B A, Beckley L E, Koslow J A & Pearce A F 2008b Larval fish assemblages and water mass structure off the oligotrophic south-western Australian coast. Fisheries Oceanography 17(1): 16–31.

Nahas E L, Jackson G, Pattiaratchi C B & Ivey G N 2003 Hydrodynamic modeling of snapper P*agrus auratus* egg and larval dispersal in Shark Bay, Western Australia: reproductive isolation at a fine spatial scale. Marine Ecology Progress Series 265: 213–226.

Neira F J, Potter I C & Bradley J S 1992 Seasonal and spatial changes in larval fish fauna of a large Australian estuary. Marine Biology 112: 1–16.

Neira F J, Miskiewicz A G & Trnski T (eds) 1998 Larvae of temperate Australian fishes: Laboratory guide for larval fish identification. University of Western Australia Press, Perth, 474pp.

Olivar M P & Shelton P A 1993 Larval fish assemblages of the Benguela Current. Bulletin of Marine Science 53: 450–474.

Olivar M P & Beckley L E 1994 Influence of the Agulhas Current on the distribution of lanternfish larvae off the southeast coast of Africa. Journal of Plankton Research 16: 1759–1780.

Olivar M P, Moser H G & Beckley L E 1999 Lanternfish larvae from the Agulhas Current (SW Indian Ocean). Scientia Marina 63: 101–120.

Paterson H L, Feng M., Waite A M, Gomis D, Beckley L E, Holliday D & Thompson P A 2008 Physical and chemical signatures of a developing anti-cyclonic eddy of the Leeuwin Current, Eastern Indian Ocean. Journal of Geophysical Research 113: C07049, doi:10.1029/2007JC004707.

Pearce A 1991 Eastern boundary currents of the southern hemisphere. Journal of the Royal Society of Western Australia 74: 35–45.

Richards W J (ed) 2006 Early stages of Atlantic fishes: an identification guide for Western Central North Atlantic. Volume 1. CRC Press, Taylor & Francis Group, Florida, pp1335.

Ridgway K R & Condie S A 2004 The 5500km long boundary flow off western and southern Australia. Journal of Geophysical Research 109: C04017, doi:10.1029/2003JC001921.

Sampey A, Meekan M G, Carleton J H, McKinnon A D & McCormick M I 2004 Temporal patterns in distribution of tropical fish larvae on the North-west Shelf of Australia. Marine & Freshwater Research 55: 473–487.

Surman C A & Wooller R D 2003. Comparative foraging ecology of five sympatric terns at a sub-tropical island in the eastern Indian Ocean. Journal of Zoology (London) 259: 219–230.

Thompson P A, Pesant S & Waite A M 2007 Contrasting the vertical differences in the phytoplankton biology of a dipole pair of eddies in the south-east Indian Ocean. Deep-Sea Research II 54: 1003–1028.

Waite A M, Thompson P A, Pesant S, Feng M, Beckley L E, Domingues C M, Gaughan D, Hanson C E, Holl C M, Koslow T, Meuleners M, Montoya J P, Moore T, Muhling B A, Paterson H, Rennie S, Strzelecki J & Twomey L 2007a The Leeuwin Current and its eddies: An introductory overview. Deep-Sea Research II 54: 789–796.

Waite A M, Pesant S, Griffin D A, Thompson P A & Holl C M 2007b Oceanography, primary production and dissolved inorganic nitrogen uptake in two Leeuwin Current eddies. Deep-Sea Research II 54: 981–1002.

Waite A M, Muhling B A, Holl C M, Beckley L E, Montoya J, Strzelecki J, Thompson P A & Pesant S 2007c Food web structure in two counter-rotating eddies based on d15N and d13C isotopic analyses. Deep-Sea Research II 54: 1055–1075.

Woo M, Pattiaratchi C & Schroeder W 2006 Summer surface circulation along the Gascoyne continental shelf, Western Australia. Continental Shelf Research 26: 132–152.

Young P C, Leis J M & Hausfeld H F 1986 Seasonal and spatial distribution of fish larvae in waters over the North West Continental Shelf of Western Australia. Marine Ecology Progress Series 31 :209–222.