

Occurrence of tropical fishes in temperate southeastern Australia: Role of the East Australian Current

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Abstract

Dispersal of larval propagules is the major mechanism facilitating connectivity of marine populations. However, only a fraction of larvae settle in suitable habitat. For coral reef fishes, many larvae are advected away from coral reefs, often despite strong behavioural mechanisms (including swimming), and some may travel long distances away from the tropics. Here we document the occurrence of tropical reef fishes along the southeast coast of Australia between 2003 and 2005 and evaluate the role of the East Australian Current (EAC) in driving this pattern. In total we observed 47 species of tropical fishes from 11 families during the summer recruitment season (January to May) at locations spanning most of the length of the New South Wales coast (28° S–37.5° S latitude, ~1700 km from the southern end of the Great Barrier Reef). Southern locations tended to have reduced richness and density relative to northern ones. In general, the southward extent of distribution of the most commonly observed species was well explained by their planktonic larval durations. Recruitment events tended to be much more episodic in Merimbula (37° S) than Sydney (34° S), but there was little evidence for interannual similarity in the spatial patterns of recruitment of individual species with exception of the numerical dominance of *Abudefduf vaiigiensis* and *Abudefduf sexfasciatus* (Pomacentridae) at the Sydney location and of *Chaetodon auriga* and *Chaetodon flavirostris* (Chaetodontidae) at the Merimbula location. Despite strong evidence for the role of the EAC in the transport of these species at a coastal scale, we found little evidence that individual recruitment events were correlated with local increases in water temperature that would be associated with EAC ingress.

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1. Introduction

The production of pelagic larvae is a nearly ubiquitous feature of the life history of marine fish (Leis, 1991). While recent work has demonstrated the often substantial sensory (Leis et al., 2002; Leis and Carson-Ewart, 2003) and locomotory abilities (Stobutzki and Bellwood, 1997; Bellwood and Fisher, 2001) of larvae of several species of fish, these abilities are most pronounced near the end of the pelagic larval phase (Fisher et al., 2000) and thus there will be some portion of this phase during which the larvae are subject to the vagaries of ocean currents. The potential for long distance transport in

ocean currents during this period is tremendous (Roberts, 1997). Particularly apparent is the expatriation (removal from “typical” biogeographic range; Hare and Cowen, 1991) of tropical fish larvae into temperate waters by means of poleward-flowing boundary currents. Tropical fish have been consistently observed since at least 1964 along the east coast of Japan as far north as Tsuyazaki (northern coast of Kyushu Island, 33°47' N latitude, Nakazono, 2002). Along the east coast of North America the seasonal (summer) arrival of tropical fish has been documented as far north as Long Island, New York (40° N latitude, McBride, 1996; McBride and Able, 1998). The powerful Gulf Stream is the primary mechanism by which these larvae are moved from the subtropical reefs of the South Atlantic Bight into the temperate regions of the mid-Atlantic Bight (Grothues et al., 2002).

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Fish initially entrained in the Gulf Stream at lower latitudes are eventually transported shoreward to the shelf break by warm-core eddies that break off from the main current flow (Hare et al., 2002).

This phenomenon occurs along the east and west coasts of Australia as well. Hutchins and Pearce (1994) have documented the transport of tropical fish along the coast of western Australia as far as 32° S latitude (Rottneest Island) by the Leeuwin current. Along the east coast of Australia fish collectors and divers routinely spot juvenile tropical fish throughout the austral summer and isolated surveys around Montague Island (36°15' S) and Merimbula (37° S) have revealed large numbers of tropical species (75 and 50 species respectively, Hutchins, 1991). In this case, the boundary current responsible for the delivery of these fishes is the East Australian Current (EAC). Like the Gulf Stream, the EAC is a western boundary current; however it is slightly less powerful in terms of maximum velocities (up to ~90 cm/s) and volumes of water moved (Grothues et al., 2002; Ridgway and Dunn, 2003). It is a dominant force driving the oceanography and ecology of the entire coastal shelf region from its origin as a series of jet offshoots of the South Equatorial Current around 22° S latitude to its eventual existence as coastal fingers and eddies as far south as 38° S latitude (Church and Craig, 1998). Tropical larvae initially entrained in the powerful current may be transported along the coast until about 32° S latitude where the EAC turns sharply to the east to eventually join the Tasman Front. A combination of self-generated instabilities (Marchesiello and Middleton, 2000) as well as flow responses to the wind field (Ridgway and Dunn, 2003) cause the EAC to separate from the coast at this point and in so doing to shed a continuous series of cyclonic and anti-cyclonic eddies. These eddies are produced at a period of between 90 and 180 days (Bowen et al., 2005) and can serve as a mechanism for the transport of larvae previously entrained in the EAC further down the southeast Australian coast and across the shelf break (in a manner analogous to what occurs in the North Atlantic with the Gulf Stream, Hare et al., 2002).

While the EAC may be primarily responsible for the transport of these tropical fish to temperate latitudes, there are several factors that ultimately determine the post-settlement distribution of these fish. We group these broadly into four categories: (1) timing and location of production (spawning), (2) processes of physical transport (currents), (3) processes of biological transport (swimming), and (4) factors associated with settlement (e.g., availability of suitable habitat, settlement behaviour). The timing and location of spawning is obviously critical for the availability of dispersing larvae (e.g. Shapiro et al., 1997; Sponaugle and Pinkard, 2004). Once produced, the larvae will be under some level of influence from physical transport via often quite variable ocean currents (e.g. Limouzy-Paris et al., 1997). In addition to physical transport, larvae will be subjected to a host of biological processes during the transport phase. Many larval fish have the ability to move themselves over substantial distances within these moving water masses (Stobutzki and Bellwood, 1994; Stobutzki and Bellwood, 1997; Wolanski et al., 1997; Dudley et al., 2000;

Bellwood and Fisher, 2001) generally in response to stimulus gradients of some sort (e.g. salinity and noise, Leis and Carson-Ewart, 1998; Stobutzki and Bellwood, 1998; Kingsford et al., 2002; Leis et al., 2002; Leis and Carson-Ewart, 2003). The growth and survival of larval fish during this pelagic phase will be a function of factors such as their physiological and behavioural responses to food and water temperature (e.g. Green and Fisher, 2004), predation and, of course, the overall length of the pelagic larval phase. Lastly the availability of suitable settlement habitat (e.g. Booth, 1992), the ability of the larva to locate this habitat (sensory ability and behaviour responses, e.g. Montgomery et al., 2001; Kingsford et al., 2002; Codling et al., 2004), and survival during the post-settlement phase (e.g. Tupper and Boutilier, 1997; Booth and Wellington, 1998) will ultimately dictate where and in what numbers these fish will occur.

With exception of isolated surveys in specific locations, the process of tropical fish expatriation along the east coast of Australia has not been thoroughly studied. It is assumed, as discussed above, that the EAC plays the dominant role in the transport of these fish and thus processes falling into our second category (physical transport) drive the distribution and abundance of these species in high latitudes. While perhaps a reasonable assumption, it has not been tested to date. Here we present the results of a three-year study of the occurrence and recruitment of tropical reef fish along the coast of temperate New South Wales (NSW). Recruitment is defined here as the settlement of pelagic larvae to benthic substrate and thus represents the occurrence of new or unaccounted for individuals in our regular censuses. If we hypothesize that physical transport processes (particularly the EAC in this case) dominate, several predictions arise. Firstly, as larval mortality will be a function of transport time and physiological constraints such as temperature tolerance we would expect to see both the density as well as richness of tropical species reduce with latitude. Secondly, if transport is via the same route from the same place for all species, we would expect that the planktonic larval duration (PLD) will be a good predictor of species distributions, with those having longer PLDs being found further to the south. Thirdly, if the EAC is acting as a conveyor-belt for transport of these larvae, we would expect to see strongly correlated temporal patterns of recruitment and that spatially, these patterns will be lagged at southern relative to northern locations at intervals corresponding to the lag in the arrival of EAC water masses. Lastly, at local scales, recruitment should be highly correlated with variability in EAC strength and proximity to shore as represented by variability in local water temperatures.

We use a combination of coastwide sampling at coarse temporal scales (1–3 times per season) and weekly sampling at two specific locations (Sydney and Merimbula) along with water temperature data to evaluate these predictions. Failure to meet predictions implies at least one of the other three processes (supply, biological transport, or settlement) is likely also involved. While we are not able to control or account for either production or biological transport processes, we chose locations with similar habitat to remove settlement

processes, as far as possible, as a factor. Thus where results do not support our predictions, either biological transport or supply issues are likely to be important.

2. Methods

2.1. Study locations

The 11 survey locations used in this project are areas located along the coast of New South Wales, SE Australia, at which tropical fish have been regularly observed over the past 10 years by the authors as well as other researchers and amateur fish counters and collectors. The use of only locations where tropical fish are known to occur minimizes the potential for bias in the analysis due to a lack of suitable habitat at a location. All locations were either on headlands or at the mouths of rivers and lakes and habitat was exposed rock with low levels of macroalgal growth. Locations ranged over 8 degrees of latitude and about 1000 km of coast from Red Rocks in the north to Bittangabee in the south (Fig. 1). Two of these locations were used for in-depth temporal analyses (see below): Shelly Beach in Sydney and Bar Beach in Merimbula.

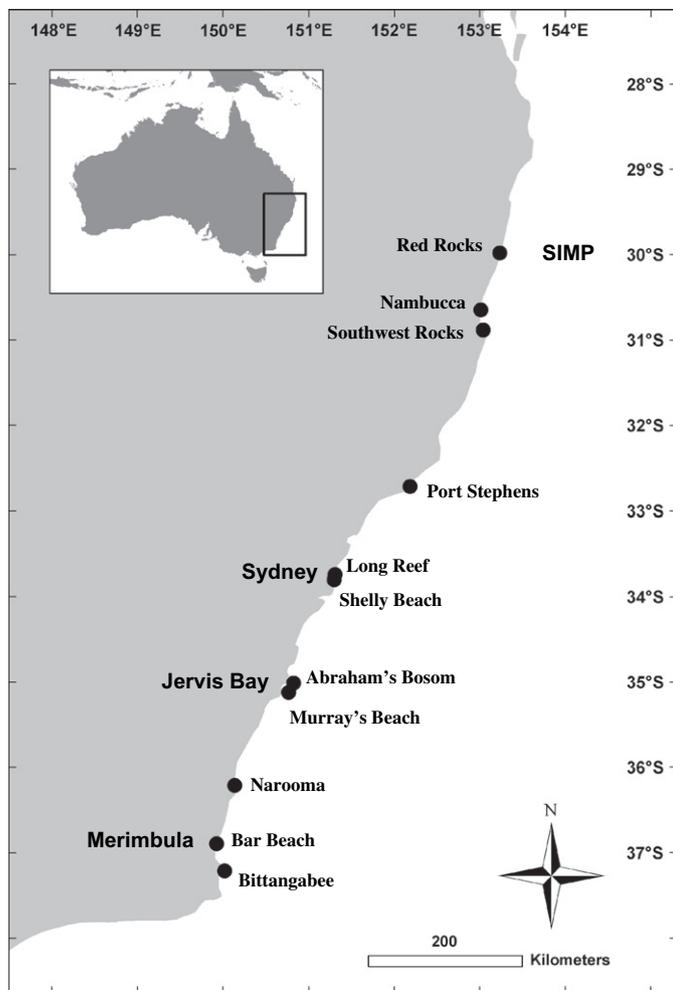


Fig. 1. Map of coastal New South Wales, Australia with study locations (●). “SIMP” indicates the location of the Solitary Islands Marine Park.

Shelly Beach is north facing with a rocky headland to the west and a seawall to the east. Its depth range is from 1 to 6 m. Bar Beach is west facing with a headland to the south and intermittent rocky and sandy habitat upstream to the north. It too varies in depth from about 2 to 6 m. Habitat at both locations was similar consisting of medium to large sized (~ 0.5 – 1.0 m diameter) exposed rocks with low levels of macroalgal growth.

2.2. Surveys

We collected data on fish species abundance and size via repeated visual census surveys at each location. The use of standard visual census transects for surveys proved inefficient due to the rarity of these tropical species. Instead we systematically surveyed a large area at each location using landmarks to define its borders. The total area surveyed at each location was determined using GPS and this same area was surveyed each visit. During each survey a single individual on SCUBA or snorkel would methodically transit the entire area noting on waterproof paper the species and size class of tropical fish seen. Individuals carrying size reference templates and trained in species identification and underwater size estimation conducted the surveys. The same individuals surveyed the same locations for the duration of the project and consistency between observers was controlled via at least annual comparisons of concurrent survey results between the observer and DJB.

The identification of species as “tropical” was based upon distributional information from the literature (Hutchins and Swainston, 1986; Kuiter, 2000). There are of course inherent problems with such a dichotomy as range limits are typically gradients rather than punctuated demarcations. Thus species were only considered to be “tropical” if, by weight of evidence, breeding aged individuals did not occur south of the south end of the Great Barrier Reef (GBR, $\sim 24^\circ$ S latitude). This definition works quite well for the study here with only a few exceptions and these are discussed in the results. Size classes used in this study were: “recruit” (new settler: less than 1–2 weeks old), “juvenile” (young-of-the-year juvenile: recruited in the present season), and “adult” (older juvenile/adult: survived at least since the last recruitment season, i.e., had overwintered at least once). These categories were assigned based on general length-age information for each species (Hutchins and Swainston, 1986; Kuiter, 2000). The recruit/juvenile and juvenile/adult boundary sizes were (in mm and organised by family): Acanthuridae 25/60; Balistidae 30/65; Caesionidae 25/60; Chaetodontidae 25/60; Labridae 15/50; Ostraciidae 15/55; Pomacanthidae 20/55; Pomacentridae 15/45; Serranidae 25/65; Tetraodontidae 20/50; Zanclidae 25/60. While these size cut-offs would not be appropriate for every member of the given family, they are for the members observed in this study.

We initiated surveys at the onset of the 2003 recruitment season (here defined as January–May), and the ensuing temporal resolution of sampling varied from location to location. All locations were visited at least once, but more typically

2–3 times, during the middle of the recruitment season each year. Exceptions were Bittangabee and Port Stephens for which no 2003 samples were available. Two locations, Shelly Beach in Sydney and Bar Beach in Merimbula, were visited approximately weekly during the recruitment season (except for the Sydney location in 2003 where sampling was monthly).

2.3. Trends in density and richness with latitude (Prediction 1)

We evaluated our first hypothesis concerning the coastal trends in richness and density using the data collected from locations across NSW. For simplicity, some of the adjacent locations were combined (Long Reef and Shelly Beach in Sydney and Murray's Beach and Abraham's Bosom in Jervis Bay) yielding a total of nine locations along the coast. We used data on the counts of all tropical species (as identified above) as well as estimates of their densities (individuals/m²) at each census to examine the trends in species richness and density. The significance ($p < 0.05$) of north–south trends in each of these coastwide variables were tested using linear regressions with latitude. As recruitment each season represents the results of unique biophysical processes, we have used seasonal averages for each year of the study at each location as the unit of replication for these regression analyses (giving $n = 24$; as indicated above, Bittangabee and Port Stephens don't have 2003 estimates).

2.4. Species distributions and PLD (Prediction 2)

We addressed the second prediction concerning PLDs using only the distributions of the seven most regularly-seen tropical fish in this study (to eliminate possible habitat effects with latitude, Table 1); bengal sergeant (*Abudefduf bengalensis*), Indo-Pacific sergeant (*Abudefduf vaigiensis*), scissortail sergeant (*Abudefduf sexfasciatus*), Whitley's sergeant (*Abudefduf whitleyi*), neon damselfish (*Pomacentrus coelestis*), threadfin butterflyfish (*Chaetodon auriga*) and dusky butterflyfish (*Chaetodon flavirostris*). We compared the proportional distributions of these species with latitude using linear regression as above. We also compared the observed coastal distribution of these species with that expected based on average PLD values for each species from the literature (as given in Brothers and Thresher, 1985; Thresher, 1989; Wellington and Victor, 1989; Wilson and McCormick, 1999). Distributions were plotted for each species based on the average density observed at each location over the three years of the study relative to the sum of that species' total coastwide density. We then compared this to the expected southern limit to their distribution determined by assuming passive transport in EAC waters moving with an average current speed of around 0.5 m/s (Ridgway and Dunn, 2003) and originating near the southern end of the GBR at One Tree Island (23.506° S 152.092° E).

2.5. Temporal and spatial patterns in recruitment (Prediction 3)

In order to more specifically consider the impact of the EAC on local recruitment over time, we monitored recruitment patterns at two locations with approximately weekly samples throughout the recruitment season: Shelly Beach in Sydney and Bar Beach in Merimbula. We focused specifically on the seven species highlighted above to ensure that any observed patterns were not the result of irregular settlement of rarely observed species. These data are used to address our third hypothesis that should the EAC be acting as a conveyor belt for tropical larvae, highly synchronous settlement of all species is expected at each location but that there should be some temporal lag in settlement between the two locations which corresponds to the transit time for EAC waters between the locations. Below we describe first how we identified recruitment events from the dataset and then discuss the techniques for each of these analyses separately.

2.5.1. Estimating recruitment

A challenge to any recruitment study conducted via regular visual census is determining recruitment from the background persistence of individuals. Because the interval between surveys was often slightly longer than the length of our "recruit" size class, there was potential for underestimation of recruitment if we relied only upon this size class as our measure of recruitment. Thus we have pooled the small and medium size classes and used the differences in this pooled amount from survey to survey to determine the net gain or loss of individuals. Gains are then interpreted as recruitment events and losses as mortality. We then established a recruitment index, which was the recruitment for each species at each census divided by its total seasonal recruitment; thus having a value between 0 and 1. Use of the recruitment index allowed for temporal recruitment comparisons between species regardless of the actual magnitude of overall seasonal recruitment.

Both locations were surveyed about 15 times per year between January and May except for Sydney in 2003 which was only surveyed four times. Because the absolute number of surveys is likely to affect the observed recruitment, especially when only a few are done, we have adjusted the raw recruitment numbers across locations and years to allow for comparison. The adjustment involved multiplying the raw recruitment number by the ratio of the maximum number of surveys in either location in any year (which was 17) by the number of surveys done at a given location in a given year. In general the differences between raw and adjusted numbers were quite small as most locations had close to this number of surveys, the exception being Sydney in 2003. These values were used for all comparisons of overall seasonal recruitment.

2.5.2. Patterns of recruitment: location and species differences

We looked for evidence of coincident annual patterns of variation in recruitment among species using the adjusted census data (by number of surveys, as described above) in two

Table 1
 Frequency of sightings of all tropical species (organised by family) from 2003 to 2005 at each of the coastwide study locations in NSW Australia. Locations are listed left to right by latitude (north to south) and abbreviated as: Red Rocks (RR, 30.0° S), Nambucca (NB, 30.6° S), SR (Southwest Rocks, 30.9° S), PS (Port Stephens, 32.7° S), SY (Sydney, 33.8° S), JB (Jervis Bay, 35.1° S), NR (Narooma, 36.2° S), ME (Merimbula, 36.9° S), and BT (Bittangabee, 37.2° S). Frequency of sightings coded for species seen in: 50% or more of all census at a location (black), less than 50% of all census at a location (grey), only on one census during all three years (○)

Family	Scientific name	North		LOCATIONS					South	
		RR	NB	SR	PS	SY	JB	NR	ME	BT
Acanthuridae	<i>Acanthurus olivaceus</i>		○	○		■	○			
	<i>Acanthurus triostegus</i>	■	■	■		■			■	○
	<i>Naso unicornis</i>					■				
Balistidae	<i>Rhinecanthus rectangulus</i>					■				
Caesionidae	<i>Caesio</i> sp.					○				
Chaetodontidae	<i>Chaetodon auriga</i>	■		○	○	■	○	■	■	○
	<i>Chaetodon citrinellus</i>	○		○		■		■	■	
	<i>Chaetodon flavirostris</i>		■		○	■	■	○	■	○
	<i>Chaetodon guentheri</i>					■			○	
	<i>Chaetodon kleinii</i>					■			○	
	<i>Chaetodon lordhowensis</i>								○	
	<i>Chaetodon lunula</i>	○	○						○	
	<i>Chaetodon melannotus</i>					○			○	
	<i>Chaetodon truncatus</i>		○	■		■			■	
	<i>Chaetodon vagabundus</i>	■	○	■		■	○	○		
	<i>Chelminops truncatus</i>						■		○	
	<i>Heniochus acuminatus</i>					○				
	<i>Heniochus chrysostomus</i>								○	
Labridae	<i>Labroides dimidiatus</i>	○	■			■	■	○		
	<i>Macropharyngodon meleagris</i>					■				
	<i>Thalassoma lunarae</i>	■	■	■		■				
Ostraciidae	<i>Ostracion cubicus</i>					○	○	○	■	
Pomacanthidae	<i>Centropyge tibicen</i>	○				■				
	<i>Centropyge vroliki</i>						○			
Pomacentridae	<i>Abudefduf bengalensis</i>	■		○		■		■	■	
	<i>Abudefduf sexfasciatus</i>	■		○		■		■		
	<i>Abudefduf sordidus</i>					■				
	<i>Abudefduf vagiensis</i>	■	■	■		■	■	■	■	○
	<i>Abudefduf whitleyi</i>		■			■				
	<i>Chromis margaritifer</i>					○				
	<i>Chromis nitida</i>		○						■	
	<i>Chrysiptera leucopoma</i>		■	○						
	<i>Dascyllus trimaculatus</i>					■				
	<i>Neopomacentrus azysron</i>					○				
	<i>Neopomacentrus nigroris</i>				○					
	<i>Plectroglyphidodon lacrymatus</i>					■				
	<i>Plectroglyphidodon leucozonus</i>							○		
	<i>Pomacentrus bankanensis</i>									
	<i>Pomacentrus chrysurus</i>									
<i>Pomacentrus coelestis</i>		○	■	○	■	■	■	■		
<i>Pomacentrus wardi</i>		○	○		■					
<i>Stegastes apicalis</i>										
<i>Stegastes brachialis</i>					○					
<i>Stegastes gascoyni</i>		■			■					
Serranidae	<i>Pseudanthias squamipinnis</i>					○				
Tetraodontidae	<i>Canthigaster bennetti</i>	○				○				
Zanclidae	<i>Zanclus cornutus</i>					■				

ways. The recruitment of individual species relative to the other six was analysed to see whether certain species tended to numerically dominate in certain areas. We compared the annual proportional recruitment (recruitment of a species divided by the sum of recruitment of all seven species; arcsine-square root transformed) of the seven species using one-way ANOVAs for each location separately. Differences in proportional recruitment between Sydney and Merimbula for individual species were evaluated using *t*-tests. Secondly, we assessed the patterns of proportional recruitment over time for these species individually to see if strong recruitment years for one species were associated with those of another and if this pattern was consistent across locations. This was done by comparing graphically the recruitment of each species at each site as a proportion of that species's three-season total at that site.

2.5.3. Recruitment synchrony

Patterns of synchronous recruitment over time were determined in two ways: (1) by examining the co-occurrence of recruitment peaks (present/absent) among species and (2) by correlating the magnitude of recruitment peaks among species. For the first analyses we simply coded each census according to the presence or absence of a recruitment peak (recruitment index > 0) occurring between that census and the previous one. From this, we tabulated the total number of co-occurring recruitment peaks between all combinations of species pairs. We next generated an expected number of co-occurring peaks between species pairs. This was calculated by multiplying the total number of census days by the joint probability of the two species pairs having a peak on the same day (which is simply the product of the daily probability of recruitment for each species). We then tested for significant co-occurrence of recruitment peaks in the whole data set for each location separately using Chi-squared tests. In order to test for synchrony between individual species, we calculated the probability of obtaining the observed number of shared recruitment peaks between each species pair (21 total species pairs). This was done by assuming the distribution would be Poisson (random) with a mean value equal to the expected value calculated above. Both the aggregate Chi-squared test as well as the individual species pair tests were applied, by location, using data from all three years combined.

For the second set of analyses we looked for temporal correlations of the magnitude of species recruitment peaks. We did this at each location by correlating the full recruitment index time series (in all three seasons) between individual species pairs.

2.5.4. Latitudinal lags in recruitment

We used time series analysis to evaluate the hypothesis that recruitment at more southerly locations might be lagged relative to northerly ones and that the lag amount would correspond to the lag in EAC waters as indicated by temperature differences between the locations. For these analyses we only used data from 2004 and 2005 as the sparse coverage at Sydney in 2003 did not allow for this year to be analysed.

We estimated the lag in temperature between the Sydney and Merimbula locations using cross-correlations of daily averaged temperature values from *in-situ* loggers placed at each location. Analyses were done individually on the relevant recruitment seasons (January–May in 2004 and 2005). While the recruitment index time-series data were sampled weekly, sample dates were not the same at both locations. We have therefore binned recruitment index data by week (Sunday to Saturday) during the recruitment season. We then conducted distributed lag analyses (a time series analysis technique equivalent to multiple regression; Lütkepohl, 2005) where the Sydney recruitment index time series was the independent variable and the Merimbula series, with lags of 0, 1, and 2 weeks, was the dependent. These values for lags were chosen based on the results of the temperature cross-correlations described above. Separate distributed lag analyses were run for each of the species as well as all combined and for each season (2004 and 2005).

2.6. Local association of recruitment with pulses in water temperature (Prediction 4)

Here we test our fourth prediction that recruitment consistently co-occurred with local increases in water temperature (indicative of the EAC moving onshore). For these analyses we associated either the magnitude or simply the presence or absence of a recruitment peak (recruitment index > 0) at a particular census with the characteristics of the water temperature over the interval between the previous census and the current one. Specifically we investigated the average water temperature over this interval and a measure of the existence of a pulse in water temperature over the interval. Pulses in water temperature were identified in the dataset by looking at the 3 day difference in water temperature (water temperature for each day minus the water temp 3 days previous to that day). As it only takes one pulse to cause a recruitment event, we use the maximum 3-day difference during an interval as our measure of the pulse. We note that we tried several other methods for estimating pulses including 1- and 2-day differences as well as daily deviations from 10- and 15-day running averages. As all results were similar we only present those related to the 3-day temperature difference.

The effect of water temperature on the magnitude of recruitment was evaluated using linear regressions of the recruitment index for individual focal species and all focal species combined against average and pulsed water temperature values. Due to variability in larval supply within the EAC waters, we did not necessarily expect the magnitude of the temperature and recruitment pulses to be always strongly linked; however there should be a relationship involving at least their co-occurrence (recruitment of any level timed with some sort of pulse in local water temperature). Thus we also tested for any disproportionate association of recruitment peaks (yes or no) with pulses in water temperature (yes or no) using simple Chi-squared contingency tables. Since it was possible that recruitment would only occur above certain intensities of a temperature pulse, we conducted these analyses across a range of

minimum pulse levels (0–5 °C) used to decide if a pulse had occurred or not (so for example, if the level was set at 2 °C, only pulses larger than 2 °C were counted as “yes”). Thus the number of recruitment peaks occurring in intervals with a given minimum level of a pulse was obtained along with the total number occurring outside of this range. From these values and the row/column totals, the expected values were generated in the typical fashion for contingency table analysis. This was done for each species (and all combined) in each location. This technique also allowed us to construct curves showing the cumulative proportion of recruitment for each species at each location that occurred with a given minimum level of temperature pulse (0–5 °C). From these data we looked for evidence of a threshold pulse level at which the majority of recruitment occurred. We compared these curves with the proportional cumulative distribution of pulse events, which represents the curve you would get if there was no association between recruitment and temperature pulse and thus recruitment simply occurred in direct proportion to the frequency of each pulse level. Comparisons between the observed and expected curves for each species at each location were made with Chi-squared tests.

3. Results

Over the course of the study we observed 47 species of tropical fish from 11 different families (see Table 1 for a complete listing including frequency of occurrence at each of our study locations).

3.1. Trends in density and richness with latitude (Prediction 1)

There was a significant reduction in both density ($r^2 = 0.27$, $p = 0.010$, Fig. 2a) and richness ($r^2 = 0.32$, $p = 0.004$, Fig. 2b) with increasing south latitude ($n = 24$ for each). The two locations with the highest richness, Nambucca (30.6° S latitude) and Southwest Rocks (30.9° S latitude), also had extremely high densities, with Southwest Rocks being close to 2 individuals per square metre. Although based on only annual samples, the Port Stephens (32.7° S latitude) location had low densities relative to those nearby. Our most northern site, Red Rocks (30.0° S) had anomalously low richness.

3.2. Species distributions and PLD (Prediction 2)

Analyses of data from the seven most commonly-occurring species (listed in the methods) indicated a trend of decreasing proportional abundance of the four *Abudefduf* species ($r^2 = 0.26$, $p = 0.012$; Fig. 3a) and concomitant increasing proportional abundance of the two Chaetodontids ($r^2 = 0.17$, $p = 0.048$; Fig. 3c) with increasing south latitude ($n = 24$ for each). The proportional abundance of *Pomacentrus coelestis* seems to have peaked around Jervis Bay (35.1° S latitude) decreasing rapidly thereafter with individuals not commonly observed at Merimbula and never at Bittangabee (Fig. 3c). Because of this modal shape, no regression was fit.

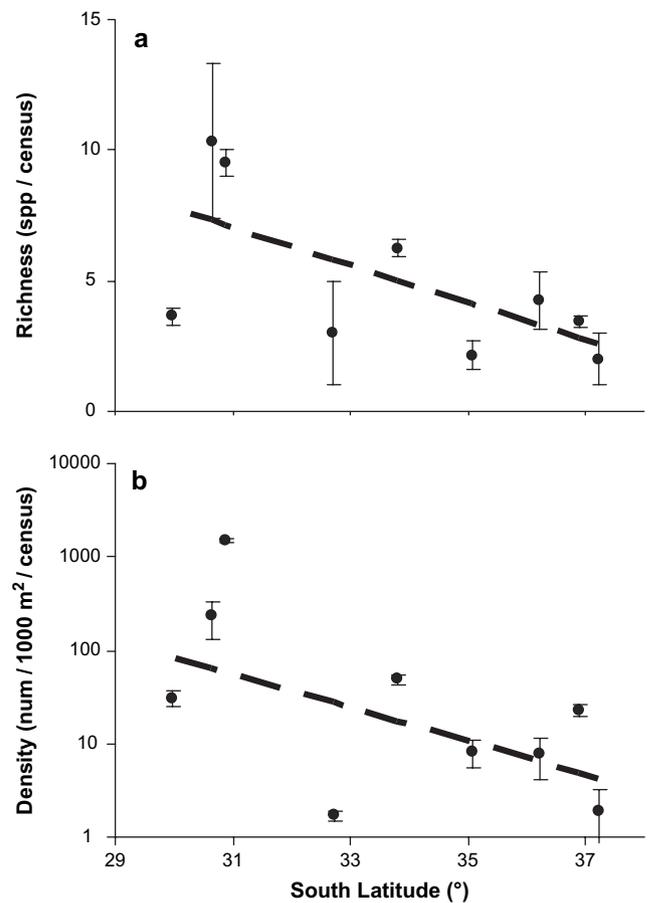


Fig. 2. Mean (\pm SE) annual richness (a) and density (b) per census given by study location latitudes from 2003 to 2005. Density has been log-transformed. Best fit lines from simple linear regressions (dashed line, $n = 24$) were: Richness = $-0.722 \times$ Latitude + 29.49, $r^2 = 0.32$, $p = 0.004$; $\log(\text{Density}) = -0.414 \times$ Latitude + 16.90, $r^2 = 0.27$, $p = 0.010$.

Literature estimates for species' PLDs were as follows; *Abudefduf vaigiensis* = 21 days, *Abudefduf sexfasciatus* = 20 days, *Abudefduf bengalensis* = 23 days, *Abudefduf whitleyi* = 18 days, *Pomacentrus coelestis* = 24 days, *Chaetodon auriga* = 47 days and *Chaetodon flavirostris* = 45 days (see references in legend to Fig. 4). The observed distribution was within the predicted southern extent (solid arrows in Fig. 4) for *C. auriga* and *C. flavirostris*; however, all the other species were found further south than expected.

3.3. Temporal and spatial patterns in recruitment (Prediction 3)

3.3.1. Temporal patterns of recruitment: location and species differences

In total we conducted 109 surveys during the recruitment season (January to May) at the two focal study locations (Sydney and Merimbula). Recruitment was not uniform for all seven species at either location (location-specific ANOVAs on arcsin-square root transformed proportional recruitment data, $n = 3$; Sydney: $F = 19.78$, $p < 0.001$; Merimbula: $F = 4.97$, $p = 0.011$; Fig. 5a). In Sydney, recruitment was

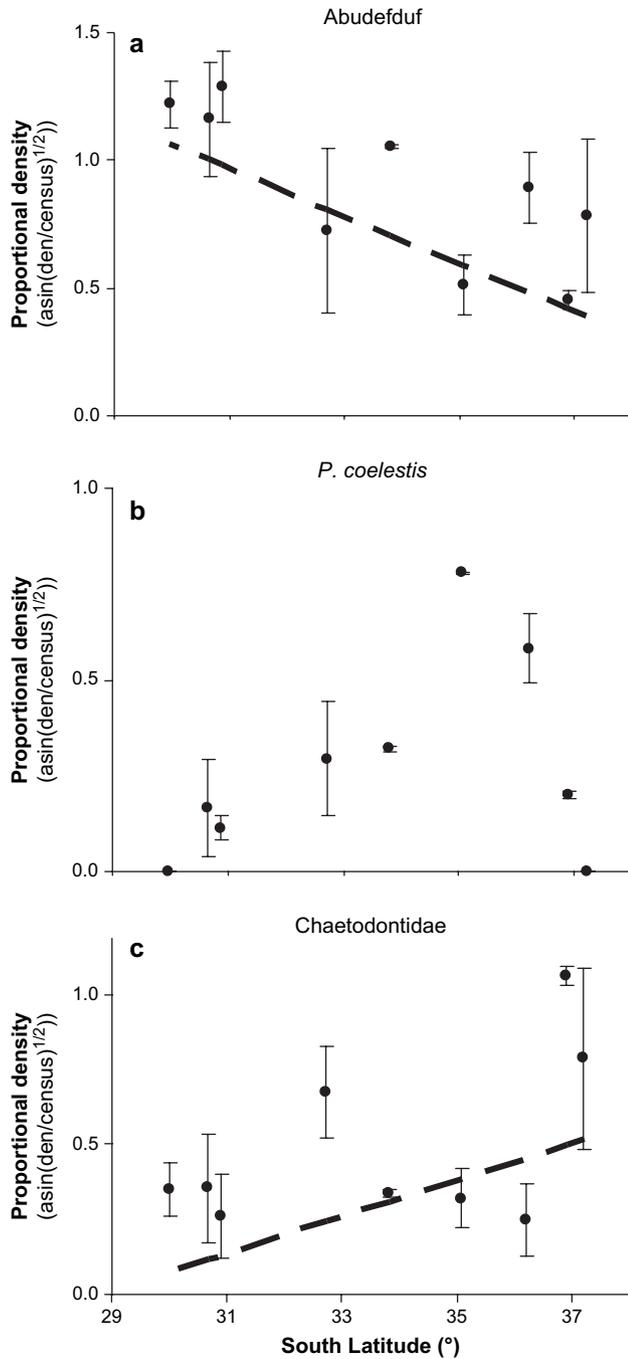


Fig. 3. Mean (\pm SE) annual proportional (of the total for all seven species) abundance (arcsin square-root transformed) of (a) *Abudefduf vaigiensis*, *Abudefduf sexfasciatus*, *Abudefduf bengalensis*, *Abudefduf whiteyi*, (b) *Pomacentrus coelestis* and (c) *Chaetodon auriga* and *Chaetodon flavirostris* given by study location latitude, from 2003 to 2005. Best fit lines from simple linear regressions (dashed line, $n = 24$) are: $\text{asin}(\sqrt{\text{prAbdu.}}) = -0.093 \times \text{Latitude} - 3.869$, $r^2 = 0.26$, $p = 0.012$; $\text{asin}(\sqrt{\text{prChaet.}}) = 0.061 \times \text{Latitude} + 1.734$, $r^2 = 0.17$, $p = 0.048$. No line was fit to the *P. coelestis* data as they do not appear linear.

dominated numerically by *Abudefduf vaigiensis* and *Abudefduf sexfasciatus* which together comprised an average of 80%, 80%, and 75% of the total seasonal (January–May) recruitment in 2003, 2004 and 2005, respectively. *Pomacentrus coelestis* had the third highest recruitment in Sydney in all years while *Abudefduf whiteyi*, *Abudefduf bengalensis*, *Chaetodon*

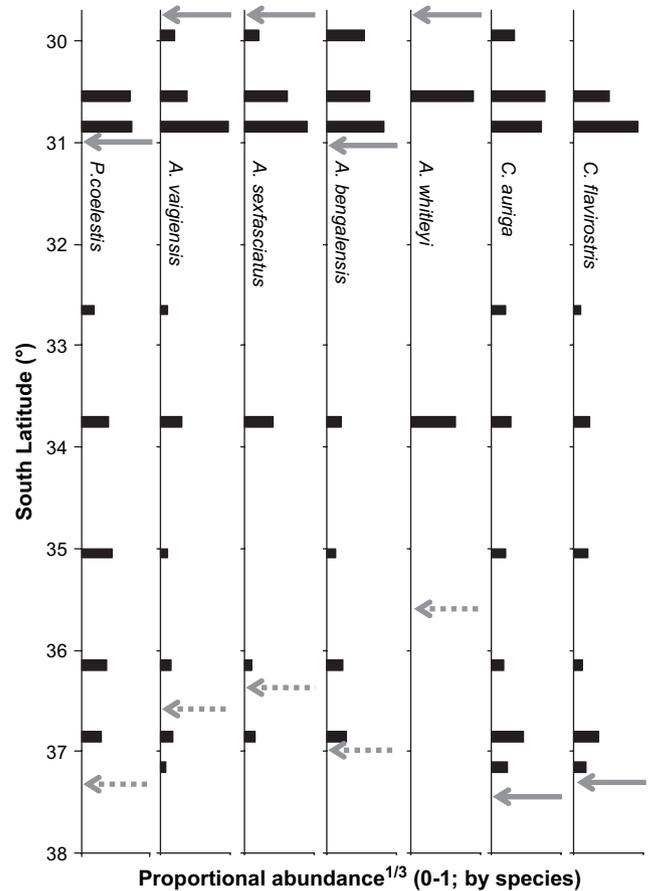


Fig. 4. Spatial distribution of recruitment (expressed as the proportion of the total three season recruitment for each species at each location) of each species by latitude and the expected southern limit to their distribution based on passive transport by an average current for a fixed planktonic larval duration (PLD) assuming they originated from the southern Great Barrier Reef (solid grey arrow) or from the Solitary Islands (dashed grey arrow, Pomacentrid species only). Proportion data have been expressed as the cube root for ease of visualization. PLD values (listed in text) were derived from published estimates (Brothers and Thresher, 1985; Thresher, 1989; Wellington and Victor, 1989; Wilson and McCormick, 1999) and an average East Australian Current flow speed of 0.5 m/s was used (Ridgway and Dunn, 2003).

auriga, and *Chaetodon flavirostris* were consistently present in only low proportions (0.5–11%; ranking orders based upon Tukey post hoc tests from above ANOVAs and summarized in the legend to Fig. 5).

Recruitment at the Merimbula location was dominated by the butterflyfish *Chaetodon auriga* and *Chaetodon flavirostris* which combined represented 83%, 55%, and 50% of the seasonal recruitment in 2003, 2004 and 2005 respectively. The remainder of the recruitment was primarily by *Pomacentrus coelestis* and *Abudefduf vaigiensis*, which ranged from 5% to 30% depending upon season. *Abudefduf bengalensis* was also present in 2004 and 2005 at around 13% of the total while *Abudefduf whiteyi* was not seen at this location (ranking orders based upon Tukey post hoc tests from above ANOVAs and summarized in the legend to Fig. 5). There was a higher proportional abundance in Sydney than Merimbula (all $n = 6$) for *A. vaigiensis* ($t = 3.41$, $p = 0.027$), *Abudefduf sexfasciatus* ($t = 2.83$, $p = 0.047$), and *A. whiteyi* ($t = 4.88$, $p = 0.008$) while the

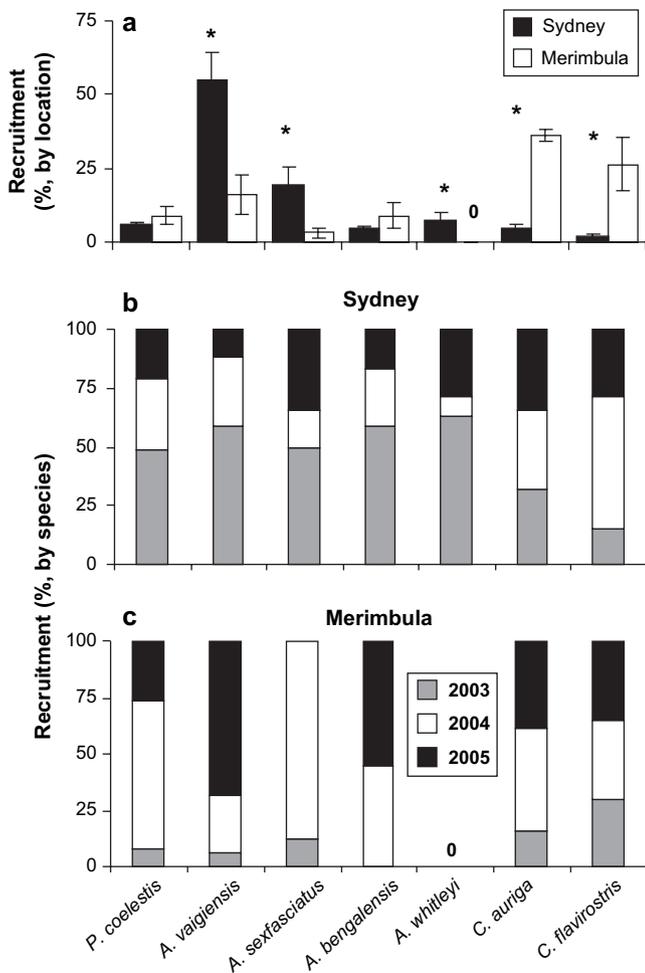


Fig. 5. Summary of recruitment of the seven most commonly observed tropical species at Sydney and Merimbula over the course of the study. The annual average (\pm SE) proportion of recruitment (of all 7 species) for each species at each location is given in panel a (so all bars for a given location sum to 1.0 for each year). One-way ANOVAs ($n = 3$) on square-root arcsin transformed data indicated that the proportional recruitment of species was different at both Sydney ($F = 19.78$, $p < 0.001$) and Merimbula ($F = 4.97$, $p = 0.011$). Tukey post hoc tests indicated rankings for Sydney as: *Abudefduf vaigiensis* > *Abudefduf sexfasciatus* \geq *Abudefduf whiteyi* = *Pomacentrus coelestis* = *Abudefduf bengalensis* = *Chaetodon auriga* \geq *Chaetodon flavirostris*; and for Merimbula as: *C. auriga* \geq *C. flavirostris* = *A. vaigiensis* = *A. bengalensis* = *P. coelestis* \geq *A. sexfasciatus* (no *A. whiteyi* in Merimbula). Asterisks indicate where locations differed ($p < 0.05$) for each species according to t -tests on square-root arcsin transformed data ($n = 6$). The annual temporal distribution of recruitment for each species is given for Sydney (b) and Merimbula (c). Legend for both panels is as in c.

opposite was true for *C. auriga* ($t = -10.72$, $p < 0.001$) and *C. flavirostris* ($t = -3.70$, $p = 0.021$).

Patterns of individual species recruitment over all three seasons showed considerable variability. Recruitment in 2003 was strong for all species in Sydney, however not in Merimbula (Fig. 5b,c). Patterns in Merimbula were mixed, with *Abudefduf vaigiensis* and *Abudefduf bengalensis* being strongest in 2005 and *Pomacentrus coelestis*, *Abudefduf sexfasciatus*, and *Chaetodon auriga* dominating in 2004. In the face of this variability, recruitment of the two Chaetodontid species was remarkably consistent from year to year at both locations.

3.3.2. Recruitment synchrony

Analysis of data from all years indicated that synchronous recruitment of the seven focal species in general tended to occur more often than would be expected by chance at both Merimbula ($\chi^2 = 19.7$, $p < 0.001$) and Sydney ($\chi^2 = 14.6$, $p < 0.023$). Analysis of individual species pairs across all seasons reinforced these results with Merimbula showing synchrony (both presence/absence and peak magnitude tests, $p < 0.05$) for six species pairs and Sydney for only three (Table 2). In Sydney there was synchrony for *Chaetodon auriga* with *Chaetodon flavirostris*, *Pomacentrus coelestis* with *Abudefduf sexfasciatus*, and *Abudefduf bengalensis* with *C. auriga*. At Merimbula there was synchrony for *P. coelestis* with *Abudefduf vaigiensis*, *P. coelestis* with *C. auriga*, *P. coelestis* with *C. flavirostris*, *A. vaigiensis* with *A. bengalensis*, and *C. auriga* with *C. flavirostris*. Across locations the only consistent pattern was the tendency of the two Chaetodontids to recruit with strong synchrony.

3.3.3. Latitudinal lags in recruitment

Cross-correlation analysis of seasonal temperature data from our loggers at the two locations indicated that in 2004 there was a significant ($p < 0.01$) lag of zero days ($r = 0.894$) between Sydney and Merimbula while in 2005 the lag was 5 days ($r = 0.710$). This suggests that the two locations were exposed to similar water masses (presumably the EAC) at nearly the same time in 2004 while in 2005 the transit time for these water masses between locations was much longer (about 5 days). If these water masses are the primary means by which the larval tropical fish are delivered, observed lags in recruitment events should be similar. While the recruitment data are restricted to weekly resolution, based upon the distributed lag analyses the patterns do in fact match quite well. In 2004, the lag for all species combined was zero weeks ($n = 24$, $F = 11.45$, $p < 0.001$) while in 2005 it was 1 week ($n = 24$, $F = 4.19$, $p = 0.016$). For the individual species for which there was enough data to conduct the analysis, in 2004 three of six (*Pomacentrus coelestis*, *Abudefduf vaigiensis* and *Chaetodon auriga*) showed a lag of zero weeks, one (*Chaetodon flavirostris*) had a lag of -2 weeks (meaning Sydney was lagged relative to Merimbula) and two (*Abudefduf bengalensis* and *Abudefduf sexfasciatus*) did not have any significant lag values. In 2005, there were only four species with enough data for analysis and of those, two (*A. vaigiensis* and *C. flavirostris*) showed a lag of 1 week and the other two (*A. bengalensis* and *C. auriga*) showed no significant lag.

3.4. Local association of recruitment with pulses in water temperature (Prediction 4)

Despite general positive trends, regressions of the recruitment index on average water temperature and temperature pulse magnitude (maximum 3-day difference in temperature) were not significant for any of the seven focal species at either location in either year ($n_{\text{Sydney}} = 36$, $n_{\text{Merimbula}} = 54$, all $p > 0.58$). Chi-squared tests also did not reveal any tendency for recruitment events to co-occur with any of a range of minimum temperature pulse magnitudes from 0 to 5 °C

Table 2

Results of recruitment synchrony analyses for individual species pairs at Sydney and Merimbula using all three seasons (2003–2005) of data. Shaded boxes indicate significant synchrony at the $\alpha = 0.05$ (black) or $\alpha = 0.10$ (grey) level for both the presence/absence and peak magnitude analyses (for which results were identical, see text for explanation of the two tests)

	<i>A. vaigiensis</i>	<i>A. sexfasciatus</i>	<i>A. bengalensis</i>	<i>A. whitleyi</i>	<i>C. auriga</i>	<i>C. flavirostris</i>
Sydney						
<i>P. coelestis</i>		█				
<i>A. vaigiensis</i>						
<i>A. sexfasciatus</i>						
<i>A. bengalensis</i>					█	
<i>A. whitleyi</i>						█
<i>C. auriga</i>						█
Merimbula						
<i>P. coelestis</i>	█		█		█	█
<i>A. vaigiensis</i>						
<i>A. sexfasciatus</i>						
<i>A. bengalensis</i>						
<i>A. whitleyi</i>						
<i>C. auriga</i>						█

($n_{\text{Sydney}} = 36$, $n_{\text{Merimbula}} = 54$, all $p > 0.18$). Temperature pulse cumulative recruitment curves do seem to indicate a threshold value of about 1 °C temperature increase over 3 days beyond which recruitment increases; however, in all cases curves are not significantly different from that expected with no association (Fig. 6, sample sizes varied from 3 to 18 for the different species at each location, all $p > 0.90$).

4. Discussion

This study documents the recurrent seasonal recruitment of tropical fish to temperate coastal habitats in SE Australia from northern New South Wales as far south as Bittangabee (37° S), a distance of over 1700 km from the southern end of the GBR. Also, in 2003, we found a tropical butterflyfish, *Chaetodon citrinellus*, even further to the south in Mallacoota, Victoria (an extra 50 km). However, the Mallacoota lagoon entrance had closed by the following year and has not reopened since, so we have not been able to survey there since. As was the case for butterflyfish found at extreme northerly latitudes off the east coast of the United States (McBride and Able, 1998), few of these tropical fish seem to survive over the winter to become adults and thus the majority of individuals sighted, especially at the most southerly locations, were recruits and juveniles (unpublished data). Below we discuss each of the initial predictions in turn.

4.1. Trends in density and richness with latitude (Prediction 1)

The importance of the EAC in shaping the distribution of these tropical fishes is evident by the general coastwide

trend towards lower richness and reduced density of tropical fish at the more southerly latitudes; however, there is considerable variability at local scales. Since the nature of the habitat was largely the same at all of the study locations, the spatial variability observed is most likely the result of local-scale differences in hydrodynamics that affect either the delivery of EAC water masses to the locations or perhaps directly influences the ability of entrained larva to sense and/or locate the nearby habitat (biological transport processes). Studies of larval fish assemblages off Sydney, for instance, have suggested the existence of recirculation cells which can serve to retain ichthyoplankton over the shelf and minimize long shore advection (Ault et al., 1999).

The extremely high richness and density of tropical fish observed at Nambucca and Southwest Rocks was not surprising given the proximity of these locations to the point at which the EAC curves rapidly to the east (around 31.5° to 32° S) and in so doing produces a large number of eddies (Bowen et al., 2005) which are capable of translocation entrained larval fish across the shelf (Hare et al., 2002). Larval fish distributions have been shown to respond quickly to cross-shelf advective processes (Dempster et al., 1997).

4.2. Species distributions and PLD (Prediction 2)

The prediction that species found consistently further south would have longer PLDs was supported by our data. Northerly locations were dominated by *Abudefduf vaigiensis* and *Abudefduf sexfasciatus*, species with PLDs of about 20 days, while *Chaetodon auriga* and *Chaetodon flavirostris*, who have PLDs of about 45 days, dominate the more southerly locations. This same pattern was true for the repeated surveys in Sydney and Merimbula. Thus although many of these species are known to have strong swimming (e.g. Stobutzki and Bellwood, 1994; Stobutzki and Bellwood, 1997; Bellwood and Fisher, 2001) and sensory (e.g. Kingsford et al., 2002; Leis et al., 2002; Leis and Carson-Ewart, 2003) abilities in the larval stage, it is possible that reduced sensory gradients of the offshore EAC waters prevent them from working against the advective forces of the strong current.

We note, however, that the distribution of these expatriated fishes was within the predicted southern extent (assuming passive EAC transport from the southern end of the GBR) for only the two Chaetodontid species. The other five species were observed well south of their predicted southern extent. Despite the use of simplifying assumptions regarding EAC transport dynamics, it is also possible that several of these species maintain breeding populations well to the south of the GBR. The authors have observed breeding of *Abudefduf vaigiensis* and *Pomacentrus coelestis* at North Solitary Island in the Solitary Islands Marine Park (SIMP, see Fig. 1 for location). Based on five years' worth of survey data at various locations all around the SIMP, adults of all of these species are regularly observed (though Chaetodontids are much more rare than the others; H. Malcolm, personal communication) and

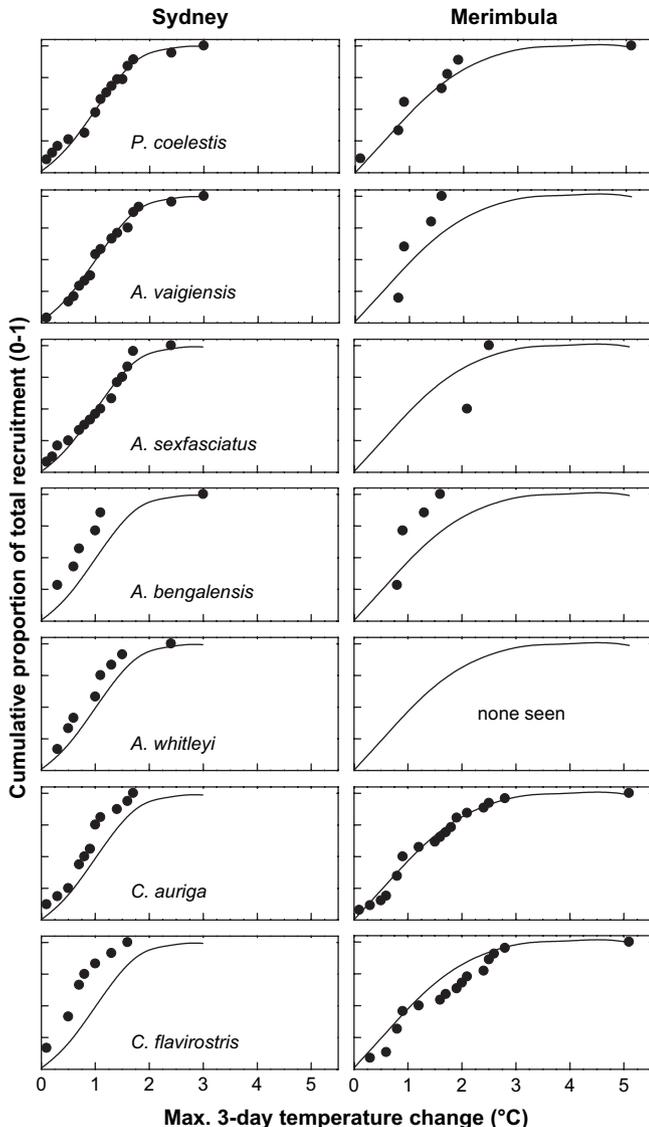


Fig. 6. The cumulative proportion of total seasonal recruitment occurring during intervals with a given level of temperature pulse for each of the seven focal species (solid circles) and the expected distribution based upon the frequency of occurrence of these intervals (solid line) for Sydney (left panels) and Merimbula (right panels). Values were calculated from all three seasons of data. The level of temperature pulse is represented by the maximum 3-day temperature difference occurring over the interval during which recruitment occurred. Observed values were not significantly different from expected for any species at either location (samples sizes ranged from 3 to 18 with all $p > 0.90$), indicating no tendency for recruitment to occur during intervals with higher magnitude temperature pulses.

thus there remains the possibility of active breeding. Recasting the transit distance estimates with the SIMP as the point of origin we get excellent agreement for *P. coelestis* and the four *Abudefduf* species (dashed arrows in Fig. 4). This suggests that the EAC is certainly playing a role in transport; however, there may be unknown issues of supply, which can serve to cloud this relationship. It also points out that some species thought to be “tropical” may in fact have small but viable and reproductively active populations in sub-tropic and even occasionally temperate latitudes.

4.3. Temporal and spatial patterns in recruitment (Prediction 3)

The lack of any clear pattern across species and locations (Sydney and Merimbula) with regards to the relative strength of any one recruitment season as well as the lack of a definitive lag period between recruitment events at the two locations is likely a product of the differences in the timing of recruitment patterns at the two locations. Recruitment was much more synchronous in Merimbula than in Sydney, which is supported by the recruitment index time-series from each location (data not shown). Recruitment in Merimbula typically occurred during a few (1–3) large events each season while in Sydney this can be spread over 3–5 events per season. The most likely explanation for this is that the Sydney location, due to its proximity to the EAC separation zone, is exposed to a much larger number of EAC eddies and the tropical fish larvae that they carry. Only a few of these eddies will make the entire distance to reach Merimbula. This variability in water mass connectivity is reflected in the temperature cross-correlation lags between the two locations (zero days one year and five days the next). Despite such variability, the role of the EAC in transporting larvae is supported by the lag estimates of recruitment between the two locations being zero weeks the first year and one week the second.

The extreme synchrony in recruitment of the two Chaetodontids was also unexpected. Since it occurred at both Sydney and Merimbula, it cannot be simply a by-product of the overall higher levels of synchrony at the Merimbula location as previously discussed. It is possible that this is simply the expected pattern for events whose likelihood is reduced with distance from the source. Thus only occasionally do patches of warm water from the tropics which contain living larvae make it that far south. If this were the case we would expect to see that recruits of the same species found further to the south would have longer PLDs relative to those found to the north. However, analysis of otoliths from fish collected all along the coast has not shown this (D. Booth, unpublished data). More likely, high synchrony of the two Chaetodontids is the product of single versus multiple sources for the larvae. As discussed above, *Pomacentrus coelestis* and *Abudefduf vaigiensis* are known to reproduce not only at the southern end of the GBR but also in the Solitary Island Marine Park (SIMP). This is not the case for *Chaetodon auriga* and *Chaetodon flavirostris*. In 5 years of surveys at 47 different locations within SIMP there have only been about six *C. auriga* and 64 *C. flavirostris* observed (H. Malcolm, personal communication). Reproduction there would be minimal or absent and thus unlikely to be supplying all propagules found at more southern locations. It is then likely that *P. coelestis* and the *Abudefduf* species will be present in water masses with different points of origin and therefore exhibit much less synchrony in their arrival time than the two Chaetodon species which will typically be transported only in masses of water that have made it all the way from the southern end of the GBR. Similar processes have been proposed for *P. coelestis* on the GBR based on natal region otolith element signatures

from post-settlement fish (Patterson et al., 2005). Fish collected from locations in the northern GBR had similar signatures implying a common natal environment while those from southern GBR locations were quite variable implying multiple points of origin.

4.4. Local association of recruitment with pulses in water temperature (Prediction 4)

Despite the evidence presented supporting the role of the EAC in the transport of these tropical fishes at the coastal scale, we were unable to detect any patterns linking the elevated temperatures that come with EAC ingress with our recruitment data at the two intensively censused locations. The data indicated that tropical fish only first arrive in mid January to early February when water temperatures first reach around 20–21 °C (data not shown); however, during the summer months after this point, simple spikes in water temperature do not seem good predictors of recruitment. This is no doubt due to variability in, and perhaps limited amounts of, larval production, but is also likely the product of complicated near-shore EAC flow patterns and cross-shelf transport. There is also a role for biological transport processes here with larval behaviour perhaps playing a larger role than during the early stages of transport when the fishes are advected away from the reef by the EAC.

This study has documented the phenomenon of tropical fish expatriation along the southeast coast of Australia and raised a number of interesting lines for future research. It seems clear that the relative transport abilities of the individual species is important; however, equally so are the aspects of their biology and ecology which determine the southern extent of their reproductive range. While the important role of the EAC in large-scale transport of these tropical fishes was evident (support of predictions 1–2 and partially of 3), its role in local scale recruitment is less clear (prediction 4). Clearly understanding the vagaries of the EAC dynamics and the processes involved with migration of eddies across the shelf will be important to comprehending the fine scale timing of recruitment for these species. We are currently using a combination of satellite-derived sea surface temperature, logger recorded local water temperatures, and fixed monitoring station wind data to look more closely at interannual differences in EAC strength and flow patterns as they relate to our recruitment data. We are also determining the distribution of larval durations for the fish captured at these locations with the aim of addressing issues of single versus multiple points of origin as well as to see if different larval durations may in any way reflect eddy entrainment versus rapid linear advection of larvae prior to recruitment.

It is becoming increasingly clear that many marine organisms, fishes in particular, have population dynamics that take place on scales much larger than previously considered. In our attempts to understand the dynamics of these metapopulations, the issue of connectivity has become paramount (e.g. Crowder and Figueira, 2006). Effective conservation and management requires this knowledge. The processes underlying the long-distance transport and recruitment of the tropical

vagrant fish species described here will be analogous to those for other sub-tropical and even temperate fish. Understanding the dynamics of this transport and how it is likely to be affected by things such as climate change may allow us to better track range shifts (e.g. Perry et al., 2005) and population dynamics of these stocks, which enables more effective management and conservation.

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