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Growth variability and stable isotope composition of two larval carangid fishes in the East Australian Current: The role of upwelling in the separation zone

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ABSTRACT

The larvae of two carangid fishes, silver trevally (*Pseudocaranx dentex*) and yellowtail scad (*Trachurus novaezelandiae*), were compared among coastal water masses and the East Australian Current (EAC). Samples followed a north to south gradient including a southern region of upwelling, generated as the EAC separated from the coast. Mean larval carangid densities were greater in the mixed layer (10-30 m) than the surface, but there was no difference between inshore and offshore stations or along latitudinal gradients. Overall, *P. dentex* recent larval growth over two days pre-capture was faster than *T. novaezelandiae*, and faster at inshore, coastal stations than in the EAC. Integrated larval growth rate (mm d^{-1}) was usually faster at inshore stations for both species. *T. novaezelandiae* were enriched in both nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) stable isotopes relative to *P. dentex*. Larvae of both species captured within the upwelling region were enriched in $\delta^{15}N$ and depleted in $\delta^{13}C$ relative to other sites. Recent larval growth had a significant positive relationship with fluorescence (as a proxy of chlorophyll *a* biomass), and integrated larval growth rate had a significant positive relationship with fluorescence and larval isotope ($\delta^{15}N$) composition. Recent and integrated growth of larval *T. novaezelandiae* and *P. dentex* was enhanced by EAC separation and upwelling, and also in coastal water; stimulated by food availability, and potentially through exploitation of a different trophic niche.

1. Introduction

Nutrient limitation is one possible reason for the low yield of Australian fisheries, which despite having the third largest fishing zone, provides $<1\%$ of the total global production (ABARE, 2009; Anon., 2009). Both the eastern and western Australian coasts are dominated by tropical, low-nutrient, poleward currents, and coastal productivity is largely dominated by the sporadic influx of nutrients from seasonal freshwater flows or upwelling events. The East Australian Current (EAC) forms the western boundary current of the South Pacific sub-tropical gyre, and drives sporadic mesoscale oceanographic features such as upwelling, anticyclonic and cyclonic eddies (Ridgway and Dunn, 2003). Coastal upwelling plays an important role in nutrient enrichment of the oligotrophic waters of New South Wales, and is a regular oceanographic feature at the EAC separation point (at approximately 31.5°S) (Roughan and Middleton, 2002). Such upwelling events can have a substantial impact on the phytoplankton composition, and contribute to phytoplankton blooms both in the region of upwelling, and also further south (Dela-Cruz et al., 2002).

Links between productivity of coastal small pelagic fisheries and upwelling events have been described across coasts in all ocean basins (Santos et al., 2007; Wexler et al., 2007), although the underlying biological mechanism is species and region specific. For example, in the California Current ecosystem, upwelling due to equator-ward wind-stress supports production of large phytoplankters and zooplankters, which contribute to productivity of anchovy (*Engraulis* spp.) (Rykaczewski and Checkley, 2008). In the same ecosystem, upwelling due to cyclonic wind-stress curl may also result in greater production of small plankters, which contribute to the productivity of Clupeidae (*Sardinops* spp.). In contrast, growth of larval sardine (*Sardinops sagax*) in the EAC was lower within upwelling regions, and correlation with micro-zooplankton concentration was not consistent between months (Uehara et al., 2005). Upwelling has also been found to have a negative influence on recruitment, with higher mortality of larval European pilchard (*Sardina pilchardus*) and Atlantic horse mackerel (*Trachurus trachurus*) within upwelling regions off Portugal, due to offshore transport away from nursery grounds (Santos et al., 2001). Understanding the mechanisms that link upwelling with changes in larval growth and

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recruitment of valuable fishes such as *Pseudocaranx dentex* and *Trachurus novaezelandiae* (combined catch ~$AU1 million in 2007, ABARE, 2009) is crucial to understanding and predicting temporal variation in adult population abundance, and the effects of an increasingly strong EAC (Ridgway, 2007).

Determining recent larval growth is a conventional approach to assess the significance of oceanographic variability for various life stages of fish populations (Suthers et al., 1992; Buckley and Durbin, 2006; Takasuka and Aoki, 2006). There are few studies which use recent larval growth to specifically examine the role of upwelling, and most of these examples use recent otolith growth as a proxy for somatic growth (Santos et al., 2001; Uehara et al., 2005). Recent otolith growth can respond to environmental conditions (temperature and food availability) within 2-3 days (Suthers, 1998), and the small changes in growth during larval stages can have a dramatic effect on larval survival, and population abundance at later stages (Houde, 1987; Cushing and Horwood, 1994). Faster growth in larval fish reduces the duration of the vulnerable larval stage (Leggett and Deblois, 1993; Bergenius et al., 2002), and provides a mechanism by which upwelling can affect later recruitment to adult populations.

This study investigates potential effects of upwelling on the density, size and growth rates of two larval carangids, silver trevally (*Pseudocaranx dentex*) and yellowtail scad (*Trachurus novaezelandiae*). *P. dentex* and *T. novaezelandiae* early life history off eastern Australia is poorly known, despite these species comprising up to 28% of total summer larval fish density in the EAC (Syahailatua, 2005), and economically important fisheries for these species in the Southwest Pacific, Indo-Pacific Ocean, Atlantic Ocean and the Mediterranean Sea (Stewart and Ferrell, 2001; Afonso et al., 2009). We had four specific objectives:

1. Compare the recent and integrated growth rate of larval *P. dentex* and *T. novaezelandiae* along coastal gradients, and between upwelled, coastal and adjacent EAC water;
2. Compare the density of larval *P. dentex* and *T. novaezelandiae* along coastal gradients of EAC separation and upwelling;
3. Examine differences in the nitrogen and carbon isotopic composition of larval *P. dentex* and *T. novaezelandiae* along coastal gradients, and between upwelled, coastal and adjacent EAC water;
4. Determine the trophic and abiotic factors that may contribute to the growth of larval Carangidae.

2. Methods

2.1. Study area and prevailing oceanography

Upwelling at the EAC separation point forms part of a general upwelling situation on the northern New South Wales coast, which is characterized by a rapid decrease in temperature (3 °C) and salinity in 2-5 days, a large increase in surface nutrients, particularly nitrate, and a decrease in the surface oxygen concentration (Rochford, 1975). Upwelling is driven by the acceleration of the EAC as the continental shelf narrows to 17 km at Smoky Cape (at approximately 30.6°S), which lifts cold, nutrient-rich water, into the euphotic zone at Diamond Head (at approximately 31.4°S), and is generally a persistent feature during the Austral spring and summer when the EAC is flowing fastest (Fig. 1, Roughan and Middleton, 2002). Elevated nutrients lead to increased primary productivity, where regions of high fluorescence are associated with the colder water (Roughan and Middleton, 2002). South of the EAC separation point, upwelling is primarily driven by local winds, as opposed to Ekman driven advection of colder water onto the shelf zone (Gibbs et al., 1998).

Sampling was conducted along the 50 m (inshore station) and 100 m (offshore station) depth contours, at three sites (Urunga, Point Plomer and Diamond Head; in increasing order of latitude) along a 132-km-long section of the continental shelf between Urunga (30.54°S; 153.15°E) and Diamond Head (31.73°S; 152.89°E, Fig. 1). Sampling took place between 21–25 November 1998 and 21–26 January 1999. Upwelling was detected in both sampling periods at the inshore station off Diamond Head, with a front separating cool upwelled water from the EAC in the vicinity of the 153°E longitude (Fig. 1).

2.2. Sampling techniques

All sampling was conducted at night; after dusk and before dawn. Up to four replicate plankton tows were conducted at the

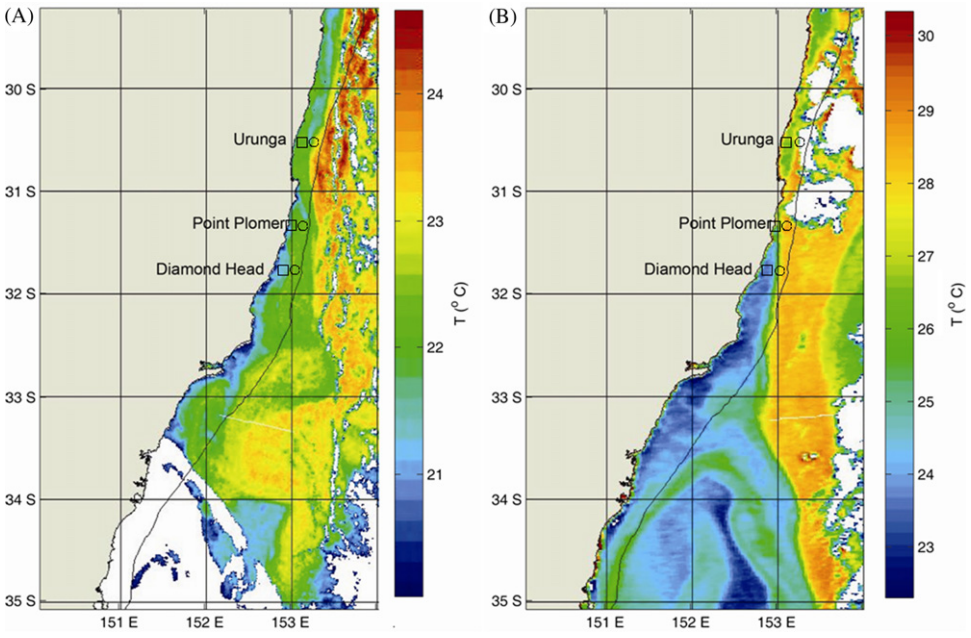

Fig. 1. Satellite images of sea surface temperature (SST, °C) on 15 November 1998 (a) and 18 Jan 1999 (b) (adapted from Roughan and Middleton, 2002). The 200 m isobath is indicated by the solid line, and inshore (□) and offshore (○) sites are shown.

Table 1
Oceanographic properties for sites and stations sampled during November 1998 and January 1999. The upwelling site (*) was distinct in that it had elevated fluorescence and lower temperature. Mean length and age are also shown for *Pseudocaranx dentex* (first line) and *Trachurus novaezelandiae* (second line) analysed during the November voyage, with the number of individual fish analysed indicated in brackets.

Voyage	Site	Station	Temperature (mean ± SE °C)	Salinity (mean ± SE)	Fluorescence (mean ± SE)	Length (mean ± SE mm)	Age (mean ± SE d)
November	Urunga	Inshore	23.8 ± 1.0	35.51 ± 0.01	54 ± 8	3.9 ± 0.2 (31)	9.3 ± 0.8
						3.5 ± 0.1 (69)	8.8 ± 0.4
		Offshore	22.1 ± 0.1	35.33 ± 0.01	26 ± 0	4.7 ± 0.2 (17)	12.5 ± 1.0
						4.3 ± 0.3 (28)	10.2 ± 0.8
	Point Plomer	Inshore	26.0 ± 0.8	35.49 ± 0.01	53 ± 6	4.7 ± 0.4 (17)	10.6 ± 1.3
						4.2 ± 0.2 (33)	8.9 ± 0.4
		Offshore	24.0 ± 0.7	35.38 ± 0.01	48 ± 1	4.8 ± 0.2 (16)	12.5 ± 1.1
						4.3 ± 0.1 (66)	11.5 ± 0.5
	Diamond Head	Inshore*	22.8 ± 0.2	35.38 ± 0.03	70 ± 4	5.3 ± 0.4 (35)	13.1 ± 1.1
						5.7 ± 0.8 (21)	13.3 ± 1.8
		Offshore	24.7 ± 0.9	35.38 ± 0.02	47 ± 6	5.0 ± 0.2 (38)	11.8 ± 0.7
						6.2 ± 0.4 (18)	15.4 ± 0.8
January	Urunga	Inshore	25.7 ± 0.8	35.50 ± 0.01	45 ± 5		
		Offshore	24.2 ± 0.8	35.42 ± 0.03	51 ± 9		
	Point Plomer	Inshore	26.2 ± 0.7	35.45 ± 0.02	62 ± 3		
		Offshore	24.7 ± 0.6	35.41 ± 0.01	45 ± 1		
	Diamond Head	Inshore*	22.8 ± 0.2	35.43 ± 0.02	56 ± 4		
		Offshore	25.2 ± 0.8	35.40 ± 0.02	47 ± 5		

surface, at two stations in each of three sites (Fig. 1). Two gear-types were used: a neuston net to sample surface water (0.75 × 0.7-m square opening, 500 μm mesh size) and a multiple opening and closing net (EZ net, 1 × 1-m square opening, 500-μm mesh size) to sample the upper mixed layer. Both the neuston, and multiple opening and closing net were deployed simultaneously; and each tow of the multiple opening and closing net sampled from 20 and 30 m depths at inshore and offshore stations respectively, up to a depth 10 m from the surface. Temperature, salinity and fluorescence at each sample site were recorded from the engine intake at 4 m depth by a regularly calibrated thermosalinograph, as well as by a CTD cast at each station (SeaBird Conductivity-Temperature-Depth, Table 1).

2.3. Laboratory procedure

Plankton samples were preserved in buffered formalin on board the research vessel, and sorted and identified within two months of capture. *P. dentex* and *T. novaezelandiae* present in the samples were identified using the Neira et al. (1998) guide to larval fish. Larvae across the entire size range present in the tow were sub-sampled, measured for notochord or standard length (± 0.01 mm), using a dissecting microscope attached to an image analysis system, and analysed for otolith increments (Table 1).

2.3.1. Otolith analyses

Sagittal otoliths of 389 individuals were identified and removed using a dissecting microscope with polarized light (Campana, 1992). The left sagitta was mounted onto a glass slide with nail polish, and examined under oil immersion at 64 × or 100 × with a compound microscope connected to an image analysis system. The total number of increments was counted twice, and the maximum radius was measured, before measuring the width of the daily growth increments along the maximum radius. Daily increment formation was verified through examination of marginal increment formation of individuals caught just after dusk and or just before dawn (Jordan, 1994; Syahailatua, 2005), and the total increment count was taken as the age since hatch.

2.3.2. Stable isotope analysis

Individuals within tows were pooled for stable isotope analysis (n=1-12) and body muscle tissue freeze dried for at least two days to yield >1 mg dried tissue. Freeze-dried tissue was thoroughly homogenized and weighed into a tin capsule on a microbalance (nearest 0.001 mg). Nitrogen and carbon isotopic compositions were determined for each species, for inshore and offshore stations at the three sites (n=3), using an Automated Nitrogen Carbon Analysis-Mass Spectrometer (Europa Scientific). Analytical precision was determined to be ± 0.2‰ for both nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$).

2.4. Statistical analyses

For samples captured in November, recent larval growth was determined using the biological intercept method; a modification of the Fraser-Lee equation which employs a biologically determined, rather than a statistically estimated intercept value (Campana, 1990; Campana, 1992). For each individual, recent larval growth during one and two days prior to capture was calculated from the width of the outer two most complete increments (W_1 and W_2, μm):

$$RG_i = \frac{0.5 \cdot W_i(SL_c - SL_h)}{R_c - R_h},$$

where RG_i is the average daily recent growth calculated for the two full days prior to capture (mm), $W_i=(W_1+W_2)$, SL_c and SL_h is the standard length at capture and hatch respectively, and R_c and R_h is the radius at capture and radius at hatch respectively. SL_h was determined through a search of the literature for values in similar taxa and similar oceanographic areas, and calculated as 1.6 mm for *P. dentex* (James, 1967; Neira et al., 1998) and 2.1 mm for *T. novaezelandiae* (Russell, 1976; Theilacker, 1980; Ochiai et al., 1982; Matarese et al., 1989; Jordan, 1994; Neira et al., 1998).

Separation of sites and stations on the basis of oceanographic variables was undertaken by an Analysis of Similarity (ANOSIM) of a Euclidian similarity matrix of normalized temperature, salinity and fluorescence values. Homogeneity of variance was evaluated using Levene's test, and normality assessed by visual inspection of a normal probability plot, for all parametric

analyses. RG_i and integrated larval growth rate were compared among species, sites and stations using the slope between RG_i (mm) and age (d); and length (mm) and age (d) respectively. Slopes were determined using the relationship between each set of parameters for all individuals captured within a single net deployment (or 'tow'), and thus represented a growth rate correct for the population sampled in each replicate tow. Using tow as the replicate unit, the relative difference in growth was evaluated through a three-factor analysis of variance (ANOVA), to detect differences amongst site (fixed; 3-levels, Urunga, Point Plomer and Diamond Head), and between species (fixed; 2-levels, *P. dentex* and *T. nozaezelandiae*) and stations (fixed; 2-levels, inshore-coastal waters and offshore-EAC waters).

The mean density of *P. dentex* and *T. nozaezelandiae* was calculated by dividing the number of larvae captured by the volume of water filtered and multiplying by 100, such that density is expressed as # larvae $100\,m^{-3}$. Larval density was evaluated for differences amongst site, between stations, and between depths (fixed; 2-levels, surface layer and mixed layer), with a separate three-factor ANOVA for each species. The relationship between integrated larval growth rate and density was tested with a separate simple linear regression for each species. A permutational multivariate ANOVA (PERMANOVA) was used to evaluate differences in the $\delta^{15}N$ and $\delta^{13}C$ isotopic composition between species. Pair-wise comparisons (PERMANOVA) tested differences in bivariate isotopic data between stations and amongst sites. Stepwise multiple linear regressions were undertaken on data from all stations and sites, to explore potential drivers of the differences observed in recent and integrated larval growth rate, and standardised independent variables including sea surface temperature (physiological activity), fluorescence (as a proxy for chlorophyll *a* biomass and food availability), and the $\delta^{15}N$ (trophic position at which fish were feeding). The best model was selected from competing models using Akaike's Information Criteria (Bozdogan, 1987). ANOVA were undertaken using SPSS v. 17.0, regressions and *t*-tests were undertaken in R (Ihaka and Gentleman, 1996), and non-parametric analyses were undertaken in PRIMER v. 6.1.11, with a PERMANOVA+v. 1.0.1 add-in (PRIMER-E, Plymouth, UK).

3. Results

3.1. Prevailing oceanography

Inshore sites were characterised by higher temperature and fluorescence than offshore sites (Table 1). For November 1998 data, ANOSIM indicated that hydrography at Urunga were significantly different to Point Plomer (R=0.402, P=0.034) and Diamond Head (R=0.533, P=0.020). Inshore stations were warmer and had higher fluorescence than offshore stations (Table 1, R=0.351, P=0.004). Comparisons were similar for January 1999 data, with Urunga having significantly lower temperature than Point Plomer (R=0.239, P=0.043) and Diamond Head (R=0.481, P=0.009), and inshore stations having higher temperatures and fluorescence than offshore stations (R=0.241, P=0.018).

3.2. Growth and upwelling

Over 1650 *Pseudocaranx dentex* and 2239 *Trachurus novaezelandiae* were captured throughout the study, and 13% of the samples captured in November were measured for length (SL) and had their otoliths analysed. The range in standard length of *P. dentex* and *T. novaezelandiae* captured in the study were similar, ranging from 1.6–15.8 mm SL, with most 5–15 mm SL. The otoliths of *P. dentex* and *T. novaezelandiae* exhibited clearly defined growth increments, with the hatch diameter at approximately 18.4 and 18.2 μm respectively. In both species, the initial 2-3 rings post-hatch were 2-3 μm wide, increasing to a width as great as 6 μm. There was a strong linear relationship between otolith radius (R_c, μm) and standard length (mm) for both *P. dentex* ($R^2=0.86$) and *T. novaezelandiae* ($R^2=0.87$). There was no significant difference in growth rates of fish between paired surface neuston and EZ net deployments undertaken simultaneously ($t=1.629$, P=0.142), so net deployments at different depths were pooled for subsequent analysis.

ANOVA revealed significantly faster recent larval growth at inshore relative to offshore stations ($F_{1,52}=20.342$, $P<0.001$), and that *P. dentex* recent larval growth was faster than *T. novaezelandiae* ($F_{1,52}=4.159$, P=0.048, Fig. 2). Integrated larval growth rates showed different relationships to those observed for recent larval growth, indicating growth was faster inshore that at offshore stations ($F_{1,52}=14.076$, P=0.001), but with a significant site x station x species interaction term ($F_{1,52}=11.884$, $P<0.001$, Fig. 3). The three-factor interaction term was interpreted by comparing inshore and offshore stations for each combination of species and sites separately, with the *F* value for each pairwise comparison calculated using the mean-square error from the full three factor ANOVA model (Quinn and Keough, 2002). Analysis of simple main effects revealed that growth at Urunga offshore station was faster than inshore stations for *P. dentex* ($F_{1,7}=11.538$, P=0.029, Fig. 3); *P. dentex* growth was faster at inshore than offshore stations at Point Plomer ($F_{1,7}=18.692$, $P<0.001$) and Diamond Head ($F_{1,7}=4.846$, P=0.048). *T. novaezelandiae* growth was faster at inshore than offshore stations at Diamond Head ($F_{1,7}=29.846$, $P<0.001$, Fig. 3). A comparison amongst levels

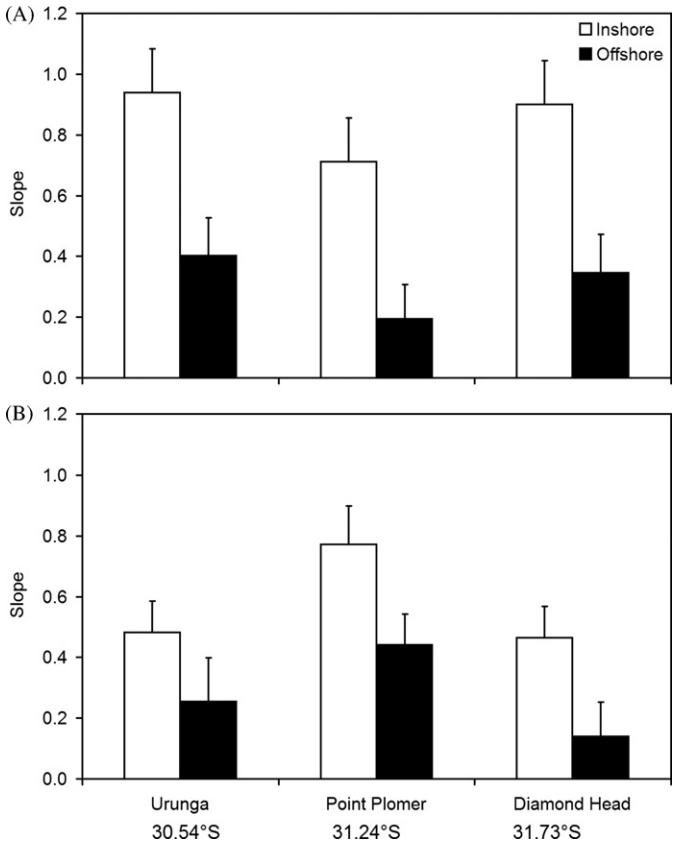

Fig. 2. Slope (mean ± SE) of the relationship between age and recent growth (RG_i) for *Pseudocaranx dentex* (a) and *Trachurus novaezelandiae* (b).

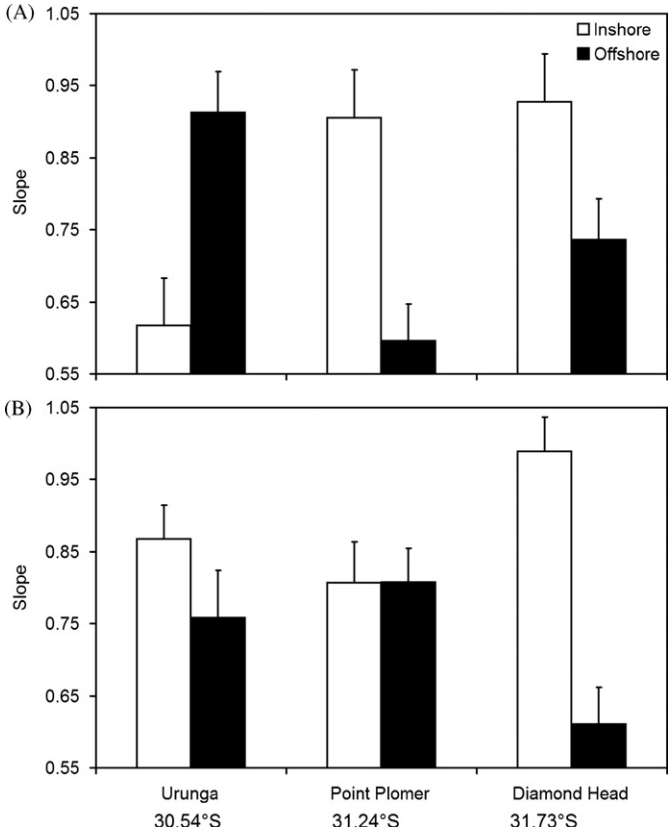

Fig. 3. Slope (mean ± SE) of the relationship between age and length for *Pseudocaranx dentex* (a) and *Trachurus novaezelandiae* (b).

within site for each combination of species and station indicated that for *P. dentex*, growth inshore at Diamond Head (Bonferroni, P=0.003) and Point Plomer (Bonferroni, P=0.002) was faster than Urunga ($F_{1,9}$=8.154, P=0.010, Fig. 3), and offshore growth was faster ($F_{1,13}$=8.538, P=0.010) at Urunga than Point Plomer (Bonferroni, P=0.044, Fig. 3); and that growth of *T. novaezelandiae* inshore was faster ($F_{1,16}$=3.385, P=0.050) at Diamond Head than Urunga (Bonferroni, P=0.050) and Point Plomer (Bonferroni, P=0.044, Fig. 3).

3.3. Density of *P. dentex* and *T. novaezelandiae*

Density data were normally distributed around the mean, although a $\log_{10}$ transformation of density values failed to stabilize variance in density. Data from both the November and January cruises were pooled for comparison of surface and mixed layer samples, amongst sites and stations. Densities of both *P. dentex* ($F_{1,67}$=5.849, P=0.019, Fig. 4a and b) and *T. novaezelandiae* ($F_{1,71}$=4.079, P=0.048, Fig. 4c and d) were significantly greater in the mixed layer than in surface waters. Overall, fish densities appeared greater for offshore samples than inshore surface samples (Fig. 4a and c), but this was not significant for *P. dentex* ($F_{1,67}$=3.058, P=0.086) or *T. novaezelandiae* ($F_{1,71}$=1.718, P=0.195). Similarly, there was no difference in density amongst sites for *P. dentex* ($F_{1,67}$=0.298, P=0.743) or *T. novaezelandiae* ($F_{1,71}$=1.273, P=0.287), indicating there was no north – south coastal gradient or any detectable effect of upwelling on the density of the two species. There was no significant relationship between $\log_{10}$ transformed larval density and integrated larval growth rate, for either *P. dentex* in surface samples (b=0.024, t=0.201, P=0.843); or *T. novaezelandiae* in surface (b=-0.025,

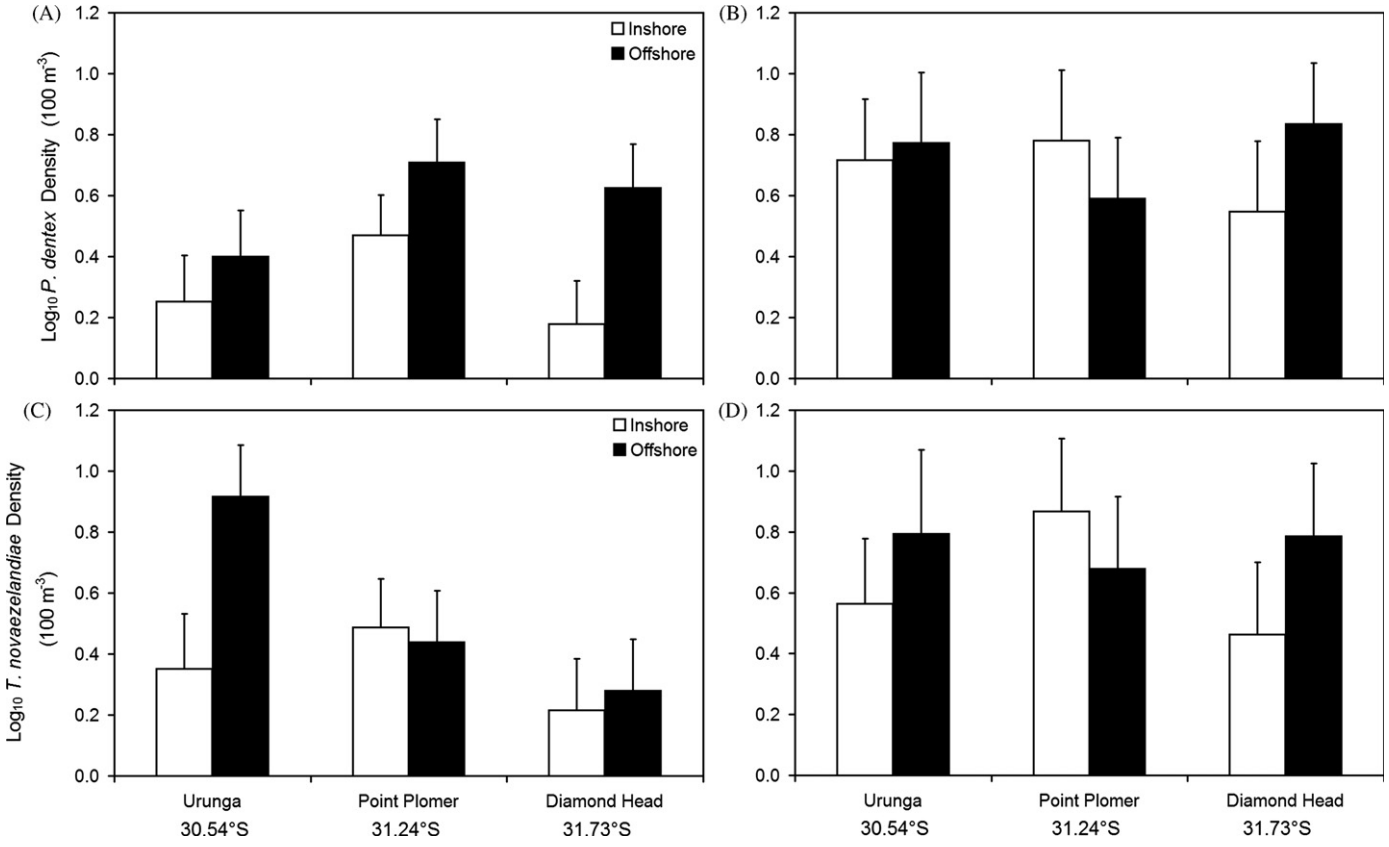

Fig. 4. $\log_{10}$ mean ± SE density of *Pseudocaranx dentex* (a, b) and *Trachurus novaezelandiae* (c, d) in surface (left panel) and mixed layer samples (right panel).

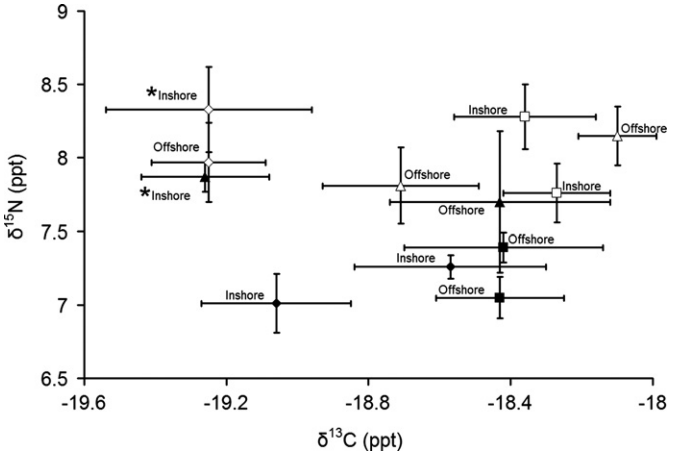

Fig. 5. Biplot of the isotopic composition (^{13}C and ^{15}N mean ± SE) of *Pseudocaranx dentex* (closed symbols) and *Trachurus novaezelandiae* (open symbols) captured inshore and offshore at Urunga (♦), Point Plomer (■) and Diamond Head (▲, ∗ denotes the inshore Diamond Head Site where upwelling occurred).

t=-0.515, P=0.603) or mixed layer samples (b=-0.085, t=-0.529, P=0.601). *P. dentex* mixed layer samples were excluded from this analysis as there were insufficient samples analysed for growth rate.

3.4. Isotopic composition

P. dentex and *T. novaezelandiae* showed geographically and oceanographically distinct isotopic composition (Fig. 5). Permutational MANOVA (PERMANOVA) detected a difference in the isotopic composition between *P. dentex* and *T. novaezelandiae* ($F_{1,45}$=7.790, P=0.006), with *T. novaezelandiae* enriched in both $\delta^{15}N$ and $\delta^{13}C$ relative to *P. dentex* (Fig. 5). Individuals captured within the upwelling region appeared to be enriched in $\delta^{15}N$ and depleted in $\delta^{13}C$ relative to other samples (Fig. 5). This was confirmed with pairwise comparisons (PERMANOVA) which showed significant differences in isotopic composition between Diamond Head and Point Plomer (t=2.912, P=0.005), and between inshore and offshore samples at Diamond Head (t=2.129, P=0.026).

Multiple regression diagnostics indicated the absence of collinearity for all parameters (Tolerance=0.888–0.924). Recent larval growth (Adjusted R^2=0.314, $F_{1,10}$=6.036, P=0.034) was positively related to fluorescence (b=0.165, t=2.457, P=0.034) only, and integrated larval growth rate (Adjusted R^2=0.509, $F_{2,9}$=6.692, P=0.017) was positively related to both fluorescence (b=0.068, t=2.305, P=0.047) and $\delta^{15}N$ (b=0.062, t=2.094, P=0.065), with all other parameters excluded.

4. Discussion

All sites and stations were oceanographically distinct, driven largely by temperature and fluorescence, and trends were consistent between years. Inshore sites were generally characterised by higher temperatures and fluorescence than offshore sites, with upwelled sites distinct in that they had elevated fluorescence but lower temperatures. In November, the Urunga inshore site experienced substantial wind driven upwelling two weeks prior to the current research voyage; however, this was not evident (i.e. high fluorescence and lower temperature) in the site hydrography at the time samples were taken. The lower EAC temperatures relative to coastal water measured in this study are unusual, especially during January when the EAC is at full strength. It is possible that offshore stations were not in the EAC proper, but rather located in a mixing zone between coastal water and the EAC.

The larvae of *Pseudocaranx dentex* and *Trachurus novaezelandiae* were more abundant deeper in the mixed layer, relative to the surface waters sampled by the neuston net. Inspection of the data indicates greater surface densities of *P. dentex* at offshore stations, however ANOVA indicated a non-significant effect of this factor. Densities of both *P. dentex* and *T. novaezelandiae* detected here were comparable to those detected previously in the EAC (Gray, 1993; Smith, 2003), and greater densities at depth compared to the surface agree with previous work for both species (Gray, 1993). Also, the lack of any significant differences in larval densities between inshore and offshore stations reflects distributions further south in the EAC. The lack of any difference in larval densities amongst sites was surprising, given the upwelling off Diamond Head and the significantly different oceanography amongst the water masses sampled. Larvae of taxa that are pelagic as adults (such as *P. dentex* and *T. novaezelandiae*) often show no trends in horizontal distribution (Kingsford and Choat, 1989); however, distribution of larval carangids in the EAC has previously been shown to be affected by mesoscale variability, such as coastal upwelling as observed in this study (Smith and Suthers, 1999; Smith, 2003). The role of mesoscale variability in driving larval *P. dentex* and *T. novaezelandiae* populations has been shown to relate to the strength of transport events (Smith and Suthers, 1999). In our study, it is possible that the horizontal distribution of larval carangids was not affected as the transport events were not sufficiently strong.

There were distinct differences in growth rate amongst sites and stations, and between *P. dentex* and *T. novaezelandiae*. The potential positive growth effect of upwelled water observed here is in contrast with a companion study, which showed significantly lower recent larval growth of *Sardinops sagax* in the Diamond Head upwelling region (Uehara et al., 2005). Similarly, other studies show lower larval *S. sagax* growth in coastal upwelling regions off the Kuroshio Current (Watanabe, 2002) and the California Current (Logerwell and Smith, 2001). Upwelling is generally thought to provide a good opportunity for faster growth, as nutrient enrichment stimulates primary productivity and increases food availability (Bakun, 2006). The results observed here show there are species-specific positive or negative effects on growth dependent on a number of factors. Some examples of these factors include the conditions inducing upwelling (i.e. wind stress or wind curl, Rykaczewski and Checkley, 2008), the age and size structure of the planktonic community in the upwelled region (Neira and Arancibia, 2004; Uehara et al., 2005), turbulence and flow disturbance (Rissik et al., 1997; Behrenfeld et al., 2006) and temperature (Wexler et al., 2007) within the upwelling region. Different combinations of these factors favor different species (Rykaczewski and Checkley, 2008), and consequently a consistent model is lacking. The trends in growth amongst inshore, offshore and upwelled sites in our study are partially explained by trophic factors, as discussed below.

Temperature and food availability are major determinants of growth (Suthers et al., 1989; Jenkins et al., 1991; Jordan, 1994), but do not always act exclusively of each other and relationships are not always consistent amongst taxa and across spatial scales. Multiple regression accounted for up to 50% of the variation in growth amongst samples in our data set, with significant positive relationships between recent larval growth rate and fluorescence; and between integrated larval growth rates, fluorescence and $\delta^{15}N$. These relationships indicate that, trophic factors, and not temperature, are important in carangid growth in the northern temperate EAC and its surrounding waters. Jenkins et al. (1991) found a strong positive correlation between food availability and

Thunnus maccoyii larval growth, and a negative relationship with fish density. There was no significant relationship between larval growth and temperature, which was attributed to the small temperature range sampled in the study (Jenkins et al., 1991). In contrast, Meekan et al. (2003) showed temperature to be the major factor driving growth in *Pomacentrus coelestis*, as opposed to food. The current study sampled larvae across a similar temperature range to Meekan et al. (2003), which suggests that the range in temperature was probably sufficient to detect a temperature effect if such a relationship existed. Houde (1989) suggests that faster growth at higher temperatures must be supported by increased food consumption, meaning that fish at higher temperatures may be more likely to starve than at lower temperatures. This provides an alternative explanation of the importance of food supply, and not temperature, in driving the growth of *P. dentex* and *T. novaezelandiae*; as the current study was undertaken in the northern half of the species' latitudinal (and temperature) range. The relationships detected here could be further verified by expanding the spatial range of sampling to better match the larval distribution for the two species (Jenkins et al., 1991).

Both *P. dentex* and *T. novaezelandiae* had different stable isotope signatures among some sites and stations. Whilst there was no distinct pattern in isotopic composition between inshore and offshore stations, both species were depleted in $\delta^{13}C$ within the upwelling area at the inshore station off Diamond Head, indicating a different carbon source at this site. Little comparative data exists to interpret these trends, however stable isotope characteristics of upwelled water are generally complex and depend upon the season and phytoplankton growth (Altabet and McCarthy, 1986; Wu et al., 1999). Similar isotopic relationships amongst sites were detected in *Sardinops sagax* sampled on the same research voyage (Uehara et al., 2005). These isotope signatures and the $\delta^{13}C$ of *P. dentex* and *T. novaezelandiae* correspond with previous analyses which demonstrate depleted $\delta^{13}C$ of particulate organic matter in upwelling cyclonic eddies, relative to non upwelled water (Waite et al., 2007).

Waite et al. (2007) reported that lipid-rich mesozooplankton have a heavy (or less negative) $\delta^{13}C$ signature, and zooplankton captured in upwelled water (within cyclonic eddies) were generally depleted in $\delta^{13}C$ relative to anticyclonic eddies. Lipid-poor zooplankton prey may lead to a depleted $\delta^{13}C$ signature in fish captured within upwelled water. It is possible that carangids may be partially compensating for this by feeding at a marginally higher trophic niche (as reflected by higher $\delta^{15}N$ where $\delta^{13}C$ is lower), but this would have to be verified by examination of diet. Factors contributing to a lower lipid content in upwelled water cannot be determined directly from this dataset; however, oil content of a key prey species of larval Carangidae (calanoid copepodites, Sassa and Konishi, 2006) can be lower at lower temperatures (Breteler and Gonzalez, 1988; Pasternak et al., 2001). Alternatively, if fish in the upwelled region were feeding within a trophic web supported by a phytoplankton community that was relatively early in the bloom phase, this could lead to a depleted $\delta^{13}C$ in both zooplankton and fish, relative to adjacent EAC and coastal water (Tamelander et al., 2009). Further chemical analysis of a wider range of trophic samples is needed to elucidate the trophic differences between upwelled and non-upwelled water in the EAC.

The inshore Urunga site experienced a wind driven upwelling event in the week prior to our sampling in 1998 (Roughan and Middleton, 2004), and this may have contributed to a depleted $\delta^{13}C$ for *P. dentex*. Elevated fluorescence at this site was not evident at the time of sampling, potentially as a result of subsequent downwelling and mixing the water masses. *P. dentex* captured at this site exhibited an integrated larval growth rate that was substantially higher relative to other offshore sites. The lack of a similar relationship for *T. novaezelandiae* suggests that this species may not have been exposed to upwelled water prior to the mixing and advection, and could have been transported to this site after the upwelling event. We speculate that upwelled water moved inshore at Urunga, as this could explain the high fluorescence and high recent larval growth experienced at this site.

This is the first report of the nitrogen isotopic composition in larval carangid fishes. $\delta^{15}N$ measurements of other planktonic fish larvae off south eastern Australia include *Sardinops sagax* ($>10.5‰$, Uehara et al., 2005) and an unidentified mix of clupeid larvae (9.3‰, Davenport and Bax, 2002); both of which are enriched in $\delta^{15}N$ relative to *P. dentex* and *T. novaezelandiae* in this study. A positive relationship between $\delta^{15}N$ and integrated larval growth rate implies that larval fish with faster growth are enriched in ^{15}N. This may indicate that feeding at a higher trophic position or exploiting a different trophic niche (i.e. larvae feeding as carnivores as opposed to detritivores) could lead to improved growth in larval carangids, but a baseline particulate organic matter (POM) measurement was not undertaken to standardize the relative trophic position amongst sites and stations. A similar relationship has been shown for juvenile striped bass (*Morone saxatilis*) in the Delaware River, where fish exploiting a different feeding niche had significantly faster growth (Wainright et al., 1996). The isotopic signature at the base of the food web (POM) varies spatially and seasonally. Future studies designed to confirm this relationship should provide simultaneous measurements of POM and larval fish muscle tissue $\delta^{15}N$ such that relative measures of trophic level can be compared amongst sites.

5. Conclusion

Overall, *T. novaezelandiae* had a higher $\delta^{15}N$ than *P. dentex*, and this corresponded with faster average integrated larval growth rate. Higher growth rates of both species, however, were detected within upwelled water regardless of the $\delta^{15}N$ signature. Regression analysis revealed positive relationships between integrated larval growth rates and both water fluorescence, and the $\delta^{15}N$ signature of the larvae. These findings imply that faster growth may be achieved when food availability is greater, and when fish are feeding at a higher trophic position. The enriched $\delta^{15}N$ signature of fish with faster growth rates is an important finding, and may help explain growth differences in Carangidae and other species outside of the EAC. In addition, a species-specific understanding of growth and productivity within the EAC is a new finding that needs to be investigated off other coasts. Future research should be bolstered with concomitant analysis of stomach contents and isotopic composition of both fish muscle and POM, to further examine which differences in prey consumption may be contributing to faster growth.

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