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# Does coastal topography constrain marine biogeography at an oceanographic interface?

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**Abstract.** Our understanding of the physical factors driving fine-scale structuring of marine biodiversity remains incomplete. Recent studies have hypothesised that oceanography and coastal geometry interact to influence marine biogeographic structure on small spatial scales. The coastal waters of eastern Tasmania, located at the oceanographic interface between two major boundary current systems (the East Australia Current (EAC) and the Leeuwin Current (LC)) represent an informative system for assessing this hypothesis. Parallel biogeographic and oceanographic analyses, focusing on the relative abundance of two widespread, larval-dispersed *Nerita* gastropods, suggest that the relative influences of the EAC and LC at this interface are modulated by coastal topographical variation. Specifically, east-facing coastal sites are dominated by the EAC-derived *N. melanotragus*, whereas south-facing bays are dominated by LC-derived *N. atramentosa*. These combined oceanographic and biological data imply that coastal topography and hydrodynamics can combine to influence the local distributions and abundances of planktotrophic-developing taxa at coastal convergence zones.

Additional keywords: boundary current, climate change, connectivity, conservation, dispersal, invasion, marine invertebrate, marine protected areas (MPAs), recruitment.

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## Introduction

Understanding the processes that drive spatial heterogeneity in the distribution of coastal species remains an intriguing challenge in marine biology. Whereas it has long been recognised that larval supply, recruitment and community composition can vary over fine geographic and temporal scales (e.g. Gaines and Roughgarden 1985; Underwood and Chapman 1996; Lagos et al. 2005; Hidas et al. 2010), a diversity of biotic and abiotic phenomena can underlie such patchiness. For instance, diverse factors such as temperature, topography, upwelling, hydrodynamics, predation, disturbance and competition have all been suggested to play roles in the spatial structuring of marine biodiversity (e.g. Underwood and Fairweather 1989; Sabatés 1990; Graham and Largier 1997; Guichard et al. 2001). However, our understanding of the biological effects of coastal geometry, particularly at oceanographic convergence zones, remains limited.

An initial hint that coastal geometry can influence local biodiversity patterns emerged from a study of the St Lawrence Estuary (Archambault and Bourget 1999), which noted that topographical variation was correlated with biological variability over >1-km scales, suggesting 'a possible relationship

between configuration of shoreline, hydrodynamics, recruitment and community characteristics' (p. 330). Despite the clear need for confirmation of this phenomenon, our understanding of the marine biological effects of coastal topography remains limited (but see Wolanski and Hamner 1988; McCulloch and Shanks 2003; Banks *et al.* 2007). Although numerous studies have recognised that deep embayments retain locally produced larvae (e.g. Bucklin *et al.* 2000; Perrin *et al.* 2004), and that oceanographic variability can influence retention of planktonic-developing species (Graham and Largier 1997; Banks *et al.* 2007; Condie *et al.* 2011), the biological effects of shoreline orientation still receive little attention. In particular, there is a need for more detailed analysis of marine biogeography at coastal convergence zones (but see Dawson 2001; Wares 2002).

On the basis of previous data (Archambault and Bourget 1999), we predict that the biological distributions at oceanographic interface zones (where currents meet) are influenced by coastal geometry. Eastern Tasmania sits at the interface between Australia's major eastern and western boundary current systems. The East Australia Current (EAC) is the main western boundary current of the South Pacific, with eddies extending as



**Fig. 1.** Map of southern Australia, showing distributions of intertidal gastropods *Nerita atramentosa* (red line) and *N. melanotragus* (yellow line). Dashed arrows provide a schematic representation of the region's major boundary current systems: the East Australian Current (EAC; yellow), and the Leeuwin Current (LC), South Australian Current (SC) and Zeehan Current (ZC) (hereafter referred to together as the LC; red).

far as south-eastern Tasmania in summer (Ridgway 2007*a*, 2007*b*). The Leeuwin Current (LC) is arguably the longest boundary current in the world, following the western coast and then southern coast of Australia, before linking with the Zeehan Current (ZC) in winter to flow counter-clockwise around southern Tasmania (Ridgway and Condie 2004).

The rocky shores of southern Australia are dominated by two widespread Nerita gastropod species (Waters et al. 2005; Waters 2008), one of which is abundant in south-eastern Australia (N. melanotragus) and the other in southern and western Australia (N. atramentosa) (Fig. 1). Although these species seem ecologically identical, and live together in close proximity at sites of sympatry, they can be quickly and reliably distinguished by genetic analysis (Waters et al. 2005), and also distinguished in the field by their opercular coloration (Spencer et al. 2007). Both species range widely from the subtropics to the cool temperate, and both also occur in a wide range of exposed and sheltered rocky habitats. Biogeographic data (Waters 2008) imply that Nerita melanotragus larvae (~5-month duration; Underwood 1975) are dispersed via the EAC, whereas N. atramentosa larvae are dispersed via the LC (Fig. 1). A recent study (J. M. Waters, S. A. Condie, M. Cirano, P. R. Teske and L. B. Beheregaray, unpubl. data) demonstrated that inter-annual shifts in Nerita biogeography in Bass Strait (Fig. 1) are attributable to short-term temporal oceanographic variation. By contrast, the current study focuses on abiotic factors underlying fine-scale spatial variation in biodiversity.

On the basis of the broad correlation between Australian oceanography and *Nerita* biogeography (Fig. 1), we expect the interface of the LC and EAC to produce a mixture of *N. melanotragus* and *N. atramentosa* in south-eastern Tasmania. Specifically, under a sink–source model, larvae of *N. atramentosa* are expected to arrive in eastern Tasmania from the southwest, via the ZC (the southern portion of the LC (Figs 1, 2). Here, we use this biological oceanographic system to assess the hypothesis that coastal topography and hydrodynamics influence species distributions at a coastal convergence zone.

# Materials and methods

# Biology

In early-mid 2012, Nerita specimens were sampled from 12 intertidal sites in eastern Tasmania (Table 1), and from two sites in western Tasmania (Fig. 2). The eastern sites were selected to provide a replicated suite of east-facing and south-facing coastal sites. Sampling was conducted so as to assess proportional abundances of the two taxa with respect to one another, as opposed to absolute abundance estimates. In total, 3271 specimens were morphologically assessed in the field, with each individual being categorised as N. atramentosa or N. melanotragus on the basis of operculum coloration (Waters et al. 2005; Spencer et al. 2007). Using the approach of Waters (2008), representative sampling of Nerita specimens was performed across each rocky-shore locality. Specifically, clusters of Nerita specimens were sampled from the upper to the lower intertidal zone, with large numbers of specimens (including a range of size classes) taken from a broad range of the potential microhabitats available at each site, including from rock crevices, underneath stones, from rock pools and from exposed vertical and horizontal rocky surfaces. Biased sampling of these two taxa with respect to one another is unlikely, because they exhibit no apparent ecological or size-differentiation (Waters et al. 2005; Spencer et al. 2007; J. M. Waters, S. A. Condie, M. Cirano, P. R. Teske and L. B. Beheregaray, unpubl. data), and indeed, to our knowledge, it is not possible to establish an individualspecies status in the field before opercular inspection (which was performed here after sampling). Notably, their status as distinct taxa went unnoticed until 2007, despite their abundance and prominence on Australian rocky shores.

Shell size was measured to help account for any temporal (interannual) variation in relative recruitment rates between the species (see Waters *et al.* in prep). The shell length of each specimen was measured to the nearest 0.1 mm with digital calipers. On the basis of the normal distributions observed for these size-frequency data, in most cases, we used a parametric

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Fig. 2. Proportional abundance of *Nerita atramentosa* (red) and *N. melanotragus* (yellow) in coastal Tasmania, 2012. Sample size and locality details are provided in Table 1. The proportional abundance of *N. melanotragus* is indicated for each locality.

statistical approach to test for significant size variation among the samples of *Nerita* population (Fig. 3). Specifically, we tested for differences in mean shell length among taxa within localities, using a two-tailed, heteroscedastic (unequal variance) Student's *t*-test. We used a generalised linear mixed model to determine whether the proportion of *N. melanotragus* in eastern Tasmania differs between east-facing and south-facing localities (Table 1, Fig. 2). The model was fitted using R 3.0.1 package lme4 (Bates and Maechler 2009), where species was the response variable (*N. melanotragus* = 1, *N. atramentosa* = 0), coastal orientation was the fixed predictor (east-facing = 1, south-facing = 0) and location was the random factor.

# Oceanography

To test whether local biological variation observed in eastern Tasmania can potentially be explained by oceanographic current patterns, we developed a fine-scale hydrodynamic model for the south-eastern Tasmanian region. This was nested within a data-assimilating global model that has been demonstrated to capture the characteristics of the EAC and LC, including sea-level anomalies and transport patterns (Schiller *et al.* 2008). The operational version of this model run by the Australian Bureau of Meteorology (OceanMAPS: Brassington *et al.* 2007) was used to obtain outputs most relevant to the data-collection period (i.e. within the first half of 2012).

Within the global model (0.1-degree resolution in latitude and longitude and 10-m vertical resolution near the surface), we nested a fine-scale model (0.02-degree resolution in latitude and longitude and 1-m vertical resolution near the surface), using the methodology of Herzfeld (2009). The finer-scale model was based on the sparse hydrodynamic ocean code (SHOC) modelling system, which has been successfully applied to many

Locality	Coordinates	Coastal orientation	Date	N (N. mel)	N (N. atr)
The Gardens*	41°10′43″S, 148°16′26″E	East	24 Jan. 2012	277	0
Binalong Bay*	41°15′00″S, 148°18′29″E	East	24 Jan. 2012	236	3
Bicheno*	41°52′06″S, 148°17′39″E	East	24 Jan. 2012	267	4
Sleepy Bay	42°08′02″S, 148°19′11″E	East	30 June 2012	200	3
Coles Bay	42°07′27″S, 148°16′56″E	South	23 Jan. 2012	87	170
Hazards View	42°06′26″S, 148°14′41″E	South	30 June 2012	114	98
Swansea	42°08′36″S, 148°04′54″E	South	30 June 2012	20	14
Mayfield	42°14′59″S, 148°00′58″E	South	23 Jan. 2012	123	284
Tessellated Pavement	43°00'32"S, 147°55'58"E	East	22 Jan. 2012	578	106
Pirates Bay*	43°01′59″S, 147°56′50″E	East	22 Jan. 2012	175	13
Safety Cove	43°11′09″S, 147°51′40″E	South	22 Jan. 2012	5	48
Nubeena	43°06′35″S, 147°43′41″E	South	8 July 2012	8	74
Trial Harbour	41°55′45″S, 145°10′26″E	(West)	26 Jan. 2012	0	187
Couta Rocks*	41°10′34″S, 144°40′52″E	(West)	26 Jan. 2012	0	177
Total				2090	1181

Table 1. Intertidal sampling of Nerita melanotragus (N. mel) and N. atramentosa (N. atr) in coastal Tasmania

Sites also previously sampled in 2007 (Waters 2008) are indicated by asterisks. Eastern localities are broadly categorised as either 'south-facing' or 'east-facing' (see Fig. 2)

coastal regions around Australia (e.g. Herzfeld 2006; Condie 2011). Its domain extended from the coast to beyond the edge of the continental shelf around eastern and south-eastern Tasmania (Fig. 4). Surface wind forcing was estimated from the regional atmospheric modelling system (RAMS; Pielke *et al.* 1992). Tides estimated from a global model (Eanes and Bettadpur 1995) were also added to the low-frequency sea level provided by the global model around the open boundaries. The model run used in the study covered the period from 1 February 2012 to 31 March 2012. However, to ensure that any transient features associated with the model start-up had dissipated, only results from March 2012 have been presented (corresponding to the period of peak recruitment). Results of the oceanographic modelling will focus on the current patterns responsible for transporting *Nerita* larvae along the eastern coast of Tasmania.

# Results

#### Spatial biodiversity patterns

As predicted from regional oceanography (Figs 1, 2), the oceanographic interface zone of eastern Tasmania yielded a mixture of N. atramentosa and N. melanotragus, reflecting the merging of two distinct larval 'pools' in this region. However, we also detected an apparent association between coastal topography and species proportional abundance. Specifically, all six east-facing (i.e. directly exposed to the EAC) coastal sites were dominated by EAC-associated N. melanotragus (mean proportional abundance 0.956; range 0.845-1.000), whereas the six inshore, south-facing localities (Table 1) were generally dominated by LC-associated N. atramentosa (mean proportional abundance 0.674; range 0.412-0.906; Fig. 2). This difference in proportional frequencies between the two sample groupings was highly significant (effect size 4.70, s.e. 0.73; P < 0.0001). The 'east-facing versus south-facing' phenomenon was replicated across two different regions of Tasmania's eastern coast, namely, across the Freycinet Peninsula (Bicheno

and Sleepy Bay dominated by *N. melanotragus*; Mayfield, Swansea, Coles Bay, Hazards View with substantial numbers of *N. atramentosa*), and also across the Tasman Peninsula (Pirates Bay and Tessellated Pavement dominated by *N. melanotragus*; Nubeena and Safety Cove dominated by *N. atramentosa*) (Fig. 2).

Most localities yielded broad ranges of Nerita size classes (Fig. 3), although few small specimens were sampled from the two southern-most sites (Safety Cove, Nubeena), which are both dominated by large rocks and boulders that restrict sampling success. Of the eight localities at which substantial proportions of both Nerita taxa were detected (both with a relative abundance of >0.05), only three yielded significant size differences between taxa (Mayfield, Tessellated Pavement, Safety Cove), whereas all other localities showed no interspecific size differentiation (Fig. 3). Furthermore, the sites yielding size differentiation showed inconsistent patterns, with N. melanotragus being larger than N. atramentosa at Mayfield, but the converse being the case at Tessellated Pavement and Safety Cove. There was thus little evidence that temporal fluctuations in recruitment success might underlie the observed broad regional variation in proportional abundance of the two species. Indeed, more recent field observations from the Freycinet Peninsula region have confirmed that this 'east-facing versus south-facing' pattern had persisted until December 2013 (J. M. Waters, unpubl. data).

# Oceanography

Results from the fine-scale circulation model are presented for March 2012 (Fig. 5), which is likely to be around the peak in seasonal recruitment for these *Nerita* taxa (Underwood 1975). We described three flow regimes that occur under different wind conditions and broadly represent the dominant patterns in this region during the *Nerita* settlement period.

The north-westerly winds on 4 March 2012 are representative of conditions most commonly encountered over the late



**Fig. 3.** Size frequency of *Nerita atramentosa* (red) and *N. melanotragus* (yellow) samples at the eight eastern Tasmanian localities where substantial frequencies of both species were detected (Table 1). The horizontal axis indicates shell length (in mm), and the vertical axis indicates frequency of occurrence. Shell-length differences between species in sympatry were assessed using a Student's *t*-test, with *P*-values provided for each site.

summer–autumn period (Fig. 5). Under these conditions, there was strong potential for the EAC to deliver larvae to east-facing localities, as inferred from biological data (Fig. 2), and also for the LC to deliver larvae to southern-most south-facing sites,

again consistent with biological observations (Fig. 2). However, the circulation was unfavourable to near-surface transport of larvae into Great Oyster Bay (the large embayment enclosed by Freycinet Peninsula; Fig. 2).



**Fig. 4.** Domain and computation grid of a high-resolution oceanographic circulation model for the coastal waters of eastern Tasmania. The colour provides an example of the surface-salinity field.

The model data from 16 March suggested a substantial inflow of surface EAC water into Great Oyster Bay (Fig. 5). During this period, the south-facing sites continued their exposure to the LC. When winds swung around to the south-east and intensified (24 March), conditions favoured northward excursion of the LC as far as Great Oyster Bay, where LC larvae are likely to have mixed with an inflow of EAC larvae, consistent with the observed mixtures of *Nerita* taxa in this region.

Over the course of the model run, circulation patterns comparable to that of 4 March (Fig. 5) occurred on ~51% of the days, with patterns from 16 and 24 March accounting for ~26% and 23%, respectively. This hydrodynamic model is broadly consistent with the relative abundances of *Nerita* species observed in the field (Fig. 2). Whereas the smaller contributions (<10%) of *N. melanotragus* to the southern south-facing sites are unlikely to have occurred on any of the days shown in Fig. 5, on two other days, a large clockwise EAC eddy extended beyond the southern tip of Tasmania and could potentially have delivered larvae of this species to these south-facing sites.

#### Discussion

The biological 'snap-shot' presented in the present study indicates that east-facing coastal sites of eastern Tasmania are presently dominated by abundant EAC recruits (*N. melanotragus*), whereas south-facing sites are generally dominated by LC recruits (*N. atramentosa*). Although longer-term data are required to better elucidate these features, the results suggest an intriguing association between geography and marine biogeography at this coastal convergence zone. Specifically, the data imply that recruitment patterns at an oceanographic J. M. Waters et al.

interface may be predictable on the basis of coastal orientation. This finding thus lends support to the hypothesis that coastal geometry can influence the composition of larval-dispersed marine assemblages over small spatial scales (Archambault and Bourget 1999).

If oceanographically mediated recruitment is indeed constrained by coastal topography, then we should expect to see evidence for such patterns in a range of larval-dispersed coastal taxa. Interestingly, previous studies of invertebrate population structure and distribution from eastern Tasmania have indeed detected biological contrasts between open coasts versus embayments. Specifically, Ling *et al.* (2009) recorded high abundances of the EAC-associated invasive urchin, *Centrostephanus rodgersii*, recruits on east-facing, but not on southfacing, shores. In explaining the relatively high density of recruits in exposed eastern sites, Ling *et al.* (2009) noted the difficulty of discriminating between the entangled effects of temperature and larval supply. This dilemma encapsulates the 'temperature versus transport' debate previously highlighted by Gaylord and Gaines (2000).

Although the present study does not assess environmental features such as temperature and salinity, we suggest that interspecific physiological differences among adults of these *Nerita* species may be unlikely to underlie this biogeographic pattern. Indeed, there is as yet no evidence for any substantial ecological or physiological differentiation between these taxa, with both ranging from the subtropics to cool-temperate, and occupying a wide range of exposed and sheltered habitats. Additionally, the detection of substantial numbers of both *Nerita* taxa at cool, inshore localities (Ling *et al.* 2009) suggests that temperature alone is unlikely to explain the observed mesoscale biogeographic structure.

The finding that the 'east-facing versus south-facing' biogeographic contrast is replicated across two distinct regions of Tasmania's eastern coast suggests that this phenomenon may not be an isolated or localised occurrence. Indeed, previous biogeographic data from Australia's mainland coast suggest similarly sharp biogeographic transitions associated with local topographic features (e.g. Wilsons Promontory; Cape Conran: Waters *et al.* 2005). More broadly, the proposed interaction between oceanography, topography and biodiversity may be of major biogeographic importance for numerous coastal taxa with extended pelagic development at oceanographic interface regions (e.g. Point Conception, USA Pacific coast: Dawson 2001; Cape Cod, USA Atlantic coast: Wares 2002).

Although further hydrodynamic modelling will be required to explore potential seasonal and interannual variability in relative contributions of the EAC and LC to recruitment, our preliminary modelling results are broadly consistent with relative abundances detected for *Nerita* species in eastern Tasmania (Figs 2, 5). Over most of the model domain, the circulation changed relatively little over the upper 20 m of the water column (Fig. 5). However, in semi-enclosed areas, such as Great Oyster Bay (inshore from Freycinet Peninsula), overturning cells tended to form. For *Nerita* larvae, which are expected to stay near the surface (although detailed knowledge of their potential for vertical migration is lacking), these conditions would be expected to enhance retention on the side of the bay where downwelling occurs (Condie and Sherwood 2006; Condie



**Fig. 5.** Modelled surface wind stress (left), surface currents (centre) and currents at 20-m depth (right) at 1200 hours on 3 days in March 2012. The wind-rose for average March conditions is shown in the top left map. The surface-current maps include the biological sampling sites (colour-coded to indicate the dominant *Nerita* species, as per Fig. 2) and arrows indicative of the broad oceanographic transport patterns (colour coded for the EAC and LC). LC water (bearing *N. atramentosa*; red) is regularly transported to south-facing bays, whereas EAC water (bearing *N. melanotragus*; yellow) regularly reaches east-facing localities.

2011). In this embayment, strong recruitment might therefore be expected under the conditions demonstrated for 16 and 24 March when there is downwelling in the north-western and north-eastern areas of the bay, respectively (Fig. 5). In contrast, the upwelling conditions on 8 March were likely to be less favourable to larval retention and local recruitment.

South-eastern Australia represents a 'hotspot' for marine climate change (Waters et al. in prep). Although the interface between the LC and EAC in eastern Tasmania migrates seasonally over several hundred kilometres (Condie and Dunn 2006; Ridgway 2007a), oceanographers have documented a major southward expansion of the EAC over recent decades, increasing sea-surface temperatures (SST) at a remarkably high rate (Ridgway 2007a, 2007b). Associated with this increasing southward influence of the EAC, numerous warm-temperate marine taxa have expanded south to south-eastern Tasmania (Ling et al. 2009; Pitt et al. 2010; Last et al. 2011; Wernberg et al. 2011), which is the geographic focus of the current study. In particular, the southward invasion of the urchin, C. rodgersii, has driven dramatic habitat modification and loss of marine biodiversity (Ling 2008; Ling et al. 2009). In the present study, we did not detect evidence for any dramatic recent biogeographic shifts in this region. Specifically, the four eastern sites previously sampled in 2007 (Binalong Bay, The Gardens, Bicheno, Pirates Bay; Waters 2008) all yielded similar species frequencies over a 5-year period. Nevertheless, the broad evidence for multidecadal southward shifts in species distributions is compelling (Pitt et al. 2010). We speculate that south-facing bays may potentially represent local refugia for indigenous southern, temperate marine communities that are otherwise threatened by southward invasions.

In summary, parallel biogeographical and oceanographic analyses from eastern Tasmania highlight the potential for complex interactions between coastal topography and biology at an oceanographic interface. Future studies should build on this informative system by analysing detailed, temporal, physical and ecological data to further assess oceanographic drivers of marine biogeographic pattern, and to assess sink–source population dynamics.

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