

# Ontogenetic shifts in resource use by the sea urchin *Evechinus chloroticus* across an ecotone

Stephen R. Wing\*, Lucy Wing

Department of Marine Science, University of Otago, PO Box 56, Dunedin 9054, New Zealand

**ABSTRACT:** Sea urchins exhibit dramatic changes in ontogenetic niche between newly settled recruits (many of which occupy cryptic habitats and feed on microalgae or detritus) and mature adults (that may catch drift kelp or actively graze on macroalgae and invertebrates). We examined patterns in the ontogenetic niche of *Evechinus chloroticus* within the New Zealand fjords, a system with a series of strong environmental and benthic productivity gradients. Using data from 15 long-term monitoring sites, we examined relationships between the diet of juvenile and adult sea urchins and the morphology of their preferred food, the kelp *Ecklonia radiata*. Stable isotope analysis ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of *E. chloroticus* stomach contents, muscle tissue and samples along the blades of *E. radiata* revealed evidence of large variation in nutritional conditions. The contribution of *E. radiata* to the diet of *E. chloroticus* declined from the wave-exposed sites near the entrances of fjords to the fully wave-sheltered sites of the inner fjords. Coincident with the decline in prevalence of *E. radiata* as a food source, the trophic level of *E. chloroticus* increased at inner fjord sites, indicating prey switching to grazing on invertebrates. Along this gradient, we observed a divergence in the trophic levels of adult *E. chloroticus* from those of juveniles, indicating that adults maintain a higher trophic level at sites where their preferred food resources are scarce. These results have important implications for understanding how sea urchin populations persist across strong gradients in primary productivity, and their role in subtidal food webs.

**KEY WORDS:** Sea urchin · Ecotone · Ontogenetic · Kelp forest · Trophic position · Fjord · Niche

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## INTRODUCTION

Sea urchins exhibit an extraordinary ability to persist under variable nutritional conditions, resulting in an effective decoupling of survivorship with the availability of their preferred food (Andrew 1989). Accordingly, population outbreaks of sea urchins can outstrip local resources resulting in strong modification of benthic habitats and communities (North & Pearse 1970, Scheibling et al. 1999, Steneck et al. 2004). On temperate coasts, intense and prolonged grazing by sea urchins can drive regime shifts between alternate ecosystem states (Simenstad et al. 1978, Dayton et al. 1998, Folke et al. 2004, Estes et al. 2011). Much of the observed

niche plasticity of sea urchins has been attributed to their considerable ability to survive under conditions of low food quality and quantity, effectively reducing density dependent mortality (Andrew 1993, Scheibling et al. 1999). Sea urchins may tolerate conditions of low food availability by lowering metabolic needs, or by actively reabsorbing tissues (e.g. Andrew 1989). In both cases, they maintain their trophic position but persist on limited resources. Alternatively, some species of sea urchins readily shift their diets, grazing on algae, invertebrates or even bacteria, exhibiting a high degree of omnivory (Vanderklift et al. 2006, Wing et al. 2008, Agnetta et al. 2013). Such prey switching is indicated by a marked shift in trophic position, and

\*Corresponding author: steve.wing@otago.ac.nz

provides a mechanism by which sea urchins are able to persist when their preferred food sources (in particular Laminarian algae) are exhausted.

Thus, the ontogenetic niche, or the progression of niches held throughout ontogeny, can vary among populations of sea urchins inhabiting habitats of different quality. Newly settled recruits typically occupy cryptic habitats and can persist on benthic microalgae or macroalgal-derived detritus. Upon maturity, sea urchins emerge from cryptic habitats and catch drift kelp, actively grazing on macroalgae or invertebrates (Tegner & Dayton 1977, Andrew 1989). When preferred foods become scarce, adult sea urchins are able to make use of a variety of food sources by maintaining a broad and flexible trophic niche. Plasticity in the progression of niches held throughout their life history is thus an important trait that enables populations of sea urchins to persist under apparent nutritional stress (Werner & Gilliam 1984).

Gradients in primary productivity associated with ecotones provide valuable scientific opportunities to resolve population level responses to the availability of resources, such as niche plasticity or prey switching (Oksanen et al. 1981, Morgan et al. 2000, Wing 2009). In this context, the ability to resolve trophic position within and among populations provides essential information about differences in resource use and life-history strategies that are driven by habitat quality.

The broad-ranging marine environments in Fiordland, New Zealand offer an excellent model system in which to tease apart the effects of the physical environment on benthic productivity and the associated marine food web. Fiordland is comprised of 15 large, 10 to 30 km long, deep water basins with numerous side arms and reaches. Strong gradients in ocean wave exposure, salinity and irradiance characterise a dramatic shift between wave-exposed, well-illuminated kelp forest environments at the entrance of the fjords to quiescent, topographically shaded conditions with strong influences of freshwater runoff in the inner fjords (Wing et al. 2007). As a result, the physical influences on benthic productivity of Laminarian kelps and other macroalgae create strong spatial gradients in the availability of food, and the basal sources of organic matter for sea urchins and other benthic consumers (Wing et al. 2008, Wing 2009). Here, the dominant perennial kelp species, *Ecklonia radiata*, forms persistent stands in the partially wave-exposed entrances of the fjords and provides a relatively stable source of organic matter to the subtidal com-

munity (Wing et al. 2007, Jack & Wing 2011). Multiple basins in the Fiordland system offer the opportunity to compare the effects of position along these environmental gradients among multiple relatively independent populations, and thus to resolve important trophic responses to nutritional limitation across an ecotone.

In this context, stable isotopic analysis provides a powerful tool for resolving the trophic position of consumers (Post 2002, Fry 2006). The ratio of stable isotopes of carbon  $^{13}\text{C}/^{12}\text{C}$ , expressed as the deviation from a limestone standard ( $\delta^{13}\text{C}$ ), offers a reliable way of resolving alternate sources of basal organic matter to consumers. For example, analysis of  $\delta^{13}\text{C}$  is a useful way to determine the mixture of macroalgae versus phytoplankton supporting a marine food web. Trophic discrimination of carbon  $\Delta^{13}\text{C}$  (the amount that  $\delta^{13}\text{C}$  changes with each trophic level) is on average low in aquatic environments (+0.4‰, SE 0.17) relative to the observed differences among organic matter sources (McCutchan et al. 2003, McLeod & Wing 2009). In contrast, the ratio of stable isotopes of nitrogen  $^{15}\text{N}/^{14}\text{N}$ , or  $\delta^{15}\text{N}$  as a deviation from the ratio in air, provides an effective measure of trophic level in consumers (Post 2002). Here,  $\Delta^{15}\text{N}$  increases on average +2.3‰ (SE 0.28) with each trophic level in aquatic systems (McCutchan et al. 2003).

In the present study, we ask: How does the trophic position of sea urchin subpopulations vary along strong gradients in availability of their preferred food? To answer this question, we used stable isotope analysis to investigate the contribution of *E. radiata* to the diet of *E. chloroticus* at multiple sites in Fiordland distributed from the wave-exposed entrances of the fjords to the inner fjord habitats. Furthermore, we analysed the effect of the amount of *E. radiata* in the diet of *E. chloroticus* relative to  $\delta^{15}\text{N}$  in muscle tissue; an effective proxy for trophic level. Finally, we modeled the trophic level of *E. chloroticus* and compared differences between adults and juveniles along the primary environmental gradients of the fjords. Here, we ask: How does variability in trophic position change as sea urchins emerge from cryptic habitats across the ecotone? The results provide a well-resolved measure of plasticity in the ontogenetic niche of sea urchins and provide a possible mechanism for population persistence along benthic productivity gradients. Results from the present study have important implications for understanding the consequences of plasticity in the trophic position of sea urchins, and for their role in subtidal marine ecosystems.

## MATERIALS AND METHODS

### Study sites

The study was conducted in 11 glacially-carved fjords along the southwest coast of the South Island of New Zealand at 15 long-term monitoring sites distributed across the strong environmental gradients of the Fiordland ecotone (Jack & Wing 2013) (Fig. 1). The position of these sites relative to the wave-exposed outer coast ranged from partially wave-exposed kelp forest habitats to quiescent inner fjord conditions heavily influenced by freshwater runoff. Each site was characterised by steep granite bathymetry with extensive invertebrate suspension feeding communities (Wing & Jack 2012) and abundant sea urchins (Wing 2009). *Ecklonia radiata* stands were present at 12 of the 15 sites (Wing et al. 2007).

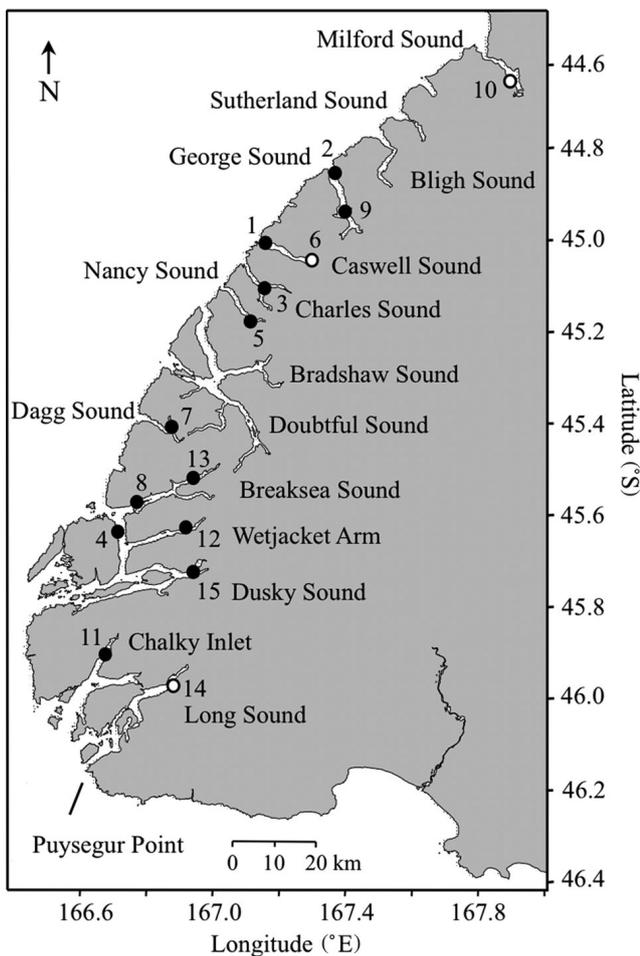


Fig. 1. Fiordland long-term study sites. ●: study sites with *Ecklonia radiata* present; ○: *E. radiata* absent. Numbers by each study site are ranked from the closest (1) to the farthest (15) from the open wave-exposed coast

### Data collection

Stomach contents and muscle tissue, from between the demi-pyramids of the Aristotle's lantern, were sampled from 5 adult (>100 mm test diameter) and 5 juvenile (<40 mm test diameter) *Evechinus chloroticus* collected at 5 to 10 m depth from each site during austral summer. Juveniles were found inhabiting cryptic habitats under boulders and in crevices, whereas adults were exposed. In addition, extensive information on the size frequency distributions of *E. chloroticus* was collected from each site during multiple years (see Wing 2009). Average test diameter of the adult mode of populations from each site was used as an index of population structure for the present analysis. Morphological data including blade width and samples for isotopic analysis were taken from the meristem region and eroding tip of the blade from 5 to 7 specimens of *E. radiata* haphazardly collected from 5, 10 and 15 m at 11 sites during austral summer (Fig. 1, see also Wing et al. 2007). Stratified sampling effectively accounts for differences in  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and morphology across the depth gradient at each site to best characterise *E. radiata* available for grazing and that produced as detrital material.

### Distance to fjord entrances

The distance from study sites to the outer coast was calculated in each fjord using a geographic information system (GIS) with 50 m horizontal resolution in the inner fjords. In this case, a mean coastline raster line served as a zero line for the distance algorithm 'r.cost' in GRASS 5.3 (Geographical Resources Analysis Support System) (ITC-irst), which uses a 'knight's move' distance calculation on a square grid to accurately provide distances around complex coastlines (Neteler & Mitasova 2002).

### Stable isotope analysis ( $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ )

Samples were freeze-dried and ground to a fine powder using a mortar and pestle. From each sample a 1 to 3 mg subsample was weighed, depending on sample type, and sealed into a tin capsule for stable isotope analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Samples were analysed at the Department of Chemistry, University of Otago by combustion in an elemental analyser (Carlo Erba NA1500) to  $\text{CO}_2$  and  $\text{N}_2$ . The isotopic compositions of the sample gases were measured by a Delta

Advantage isotope ratio mass spectrometer (Thermo-Finnigan) operating in continuous flow mode. Raw delta values were normalized and reported against the international scales for carbon and nitrogen, VPDB and air, respectively. Normalization was made by 3-point calibration with 2 glutamic acid international reference materials and an EDTA standard (Elemental Microanalysis) for carbon (USGS-40 =  $-26.2\text{‰}$ , USGS-41 =  $37.8\text{‰}$ , EDTA =  $-38.52\text{‰}$ ) and nitrogen (USGS-40 =  $-4.52\text{‰}$ , USGS-41 =  $47.57\text{‰}$ , EDTA =  $-0.73\text{‰}$ ). Time-based drift correction was calculated from the laboratory standard analysed at regular intervals with the samples. Analytical precision based on the replicate analyses of the quality control standard (EDTA,  $n = 12$ ) was  $0.2\text{‰}$  for  $\delta^{13}\text{C}$  and  $0.3\text{‰}$  for  $\delta^{15}\text{N}$ .

### Statistical analysis

We used general linear models (JMP Pro v.10) to test the relationship between (1) average test diameter (mm) for the adult mode of *E. chloroticus* at each site (from Wing 2009), (2) average blade width (mm) of *E. radiata* (from Wing et al. 2007) and (3) differences in  $\delta^{13}\text{C}$  between stomach contents of *E. chloroticus* and  $\delta^{13}\text{C}$  of *E. radiata* ( $\delta^{13}\text{C}_{\text{Diet}} - \delta^{13}\text{C}_{\text{Ecklonia}}$ ) as an indicator of the relative contribution of *E. radiata* to the diet. We analysed both adult and juvenile sea urchins from each site. We then used a general linear model to test the relationship between  $\delta^{13}\text{C}_{\text{Diet}} - \delta^{13}\text{C}_{\text{Ecklonia}}$  and  $\delta^{15}\text{N}$  from muscle tissue of *E. chloroticus* at each site.

### Trophic level

We used the average  $\delta^{15}\text{N}$  value of *E. radiata* observed at each site to estimate  $\delta^{15}\text{N}_{\text{base}}$ , or the  $\delta^{15}\text{N}$  value at trophic level zero. Trophic level was then calculated for each individual *E. chloroticus* from  $\delta^{15}\text{N}_{\text{base}}$ , defined as:  $(\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{base}}/\Delta_n) + 1$ , where  $\Delta_n$  is the trophic discrimination factor, after Post (2002). We used the average trophic discrimination factor for aquatic environments of  $+2.3\text{‰}$  (SE 0.28) for  $\Delta^{15}\text{N}$ , after McCutchan et al. (2003), for each enrichment step.

We then used a general linear mixed model to test the relationship between trophic level of juvenile and adult *E. chloroticus* with distance (km) along the axis of each fjord. Factors in this model were age (fixed, 2 levels), distance (random, continuous) and age  $\times$  distance (interaction term).

## RESULTS

The kelp *Ecklonia radiata* made up a larger proportion of the diet of urchins *Evechinus chloroticus* at sites where the average test diameter of the adult mode was larger ( $F_{11} = 15.58$ ,  $r^2 = 0.63$ ,  $p = 0.0034$ ) (Fig. 2). At sites where the *E. radiata* blade width was narrower, kelp made up a greater proportion of sea urchins' diet ( $F_{11} = 23.76$ ,  $r^2 = 0.73$ ,  $p = 0.0009$ ) (Fig. 3). *E. chloroticus* that had a smaller proportion of *E. radiata* in their diet had greater  $\delta^{15}\text{N}$  signatures in their muscle tissue ( $F_{11} = 25.76$ ,  $r^2 = 0.72$ ,  $p = 0.0005$ ) (Fig. 4).

Trophic level increased with distance into the fjords for adult *E. chloroticus*, but not for juveniles (Fig. 5). Our general linear mixed model detected significant effects of the factors age ( $t$ -ratio = 2.55,  $p = 0.018$ ) and distance ( $t$ -ratio = 4.08,  $p = 0.0005$ ) and a significant interaction term of age  $\times$  distance ( $t$ -ratio = 3.21,  $p = 0.004$ ). Whole model results demonstrated that much of the variability in trophic level can be attributed to the divergence in trophic level between adult and juvenile *E. chloroticus* ( $F_{26} = 11.14$ ,  $r^2 = 0.60$ ,  $p = 0.0001$ ) (Fig. 5).

## DISCUSSION

Prey switching and omnivory within food webs can stabilize population fluctuations and reduce competitive exclusion among consumers (Murdoch 1969, Worm & Duffy 2003, Vallina et al. 2014). Additionally, in grazing systems species richness of primary producers may be enhanced when consumers actively switch among prey types (e.g. Huntly 1991, Bruno et al. 2005). Marine food webs in particular exhibit a high prevalence of omnivory: integer trophic values are only observed for primary consumers, while higher trophic levels are characterised by a tangled array of omnivores (Shurin et al. 2006). In marine food webs, the trophic position of consumers may vary through life-history stages (e.g. Alexander et al. 2013), resulting in a higher prevalence of omnivory than would be predicted using species averages (e.g. Link 2002, Thompson et al. 2007). In kelp forest ecosystems, sea urchins are typically considered only as primary consumers of macroalgae. However, observations of omnivory within this guild demonstrate that a high degree of trophic plasticity is possible (Andrew 1989, Vanderklift et al. 2006, Agnetta et al. 2013). These results raise the interesting question of whether omnivory, rather than physiological tolerance of low food availability, may be the prevailing

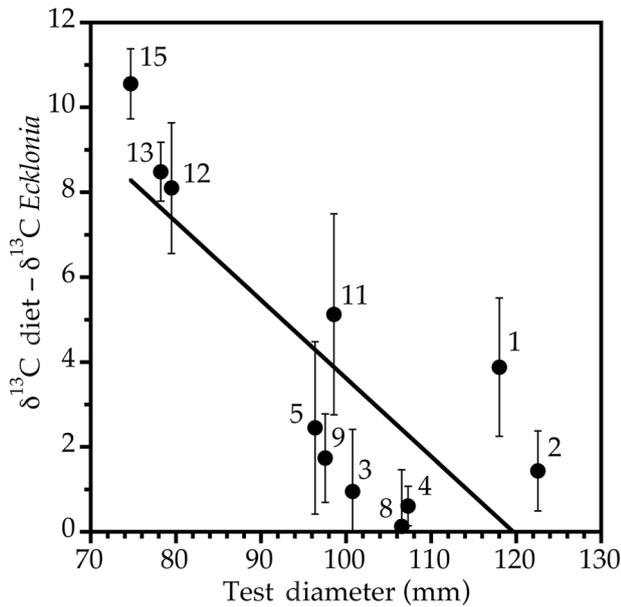


Fig. 2. Relationship between mean test diameter (mm) of *Evechinus chloroticus* populations and the difference between  $\delta^{13}\text{C}$  of *Ecklonia radiata* and  $\delta^{13}\text{C}$  of the stomach contents of *E. chloroticus*. Error bars:  $\pm 1$  SE. Numbers correspond to sites identified in Fig. 1

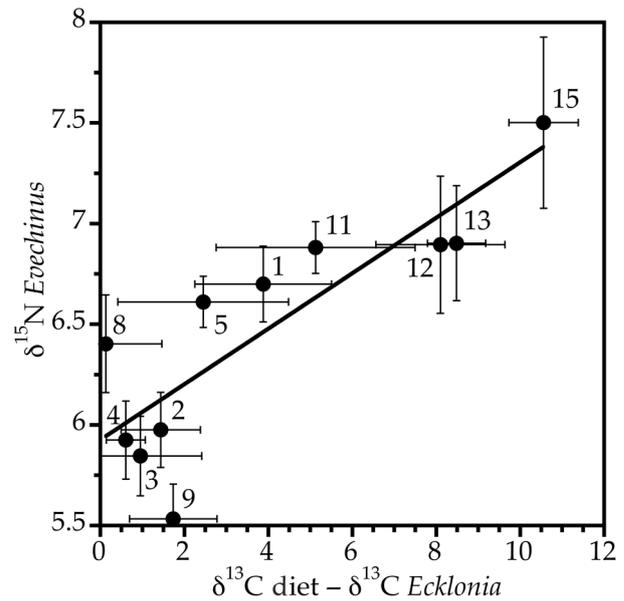


Fig. 4. Relationship between  $\delta^{15}\text{N}$  in muscle tissue of *Evechinus chloroticus* and the difference between  $\delta^{13}\text{C}$  of *Ecklonia radiata* and  $\delta^{13}\text{C}$  of the stomach contents of *E. chloroticus*. Error bars:  $\pm 1$  SE. Numbers correspond to sites identified in Fig. 1

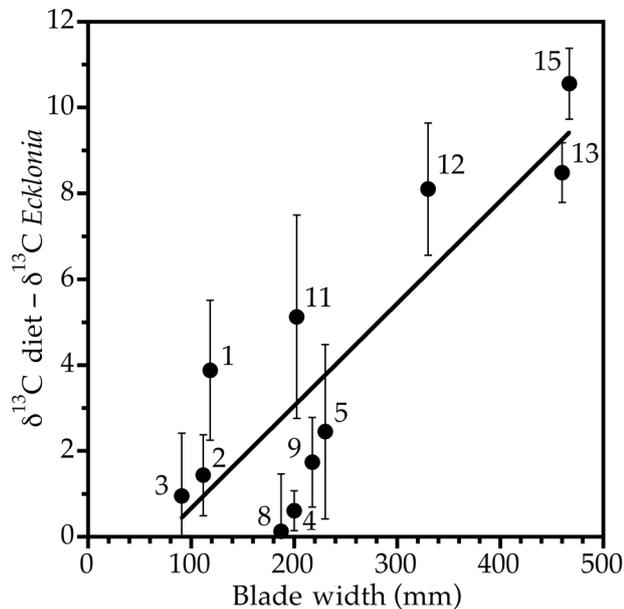


Fig. 3. Relationship between mean blade width (mm) of *Ecklonia radiata* (an indicator of photoadaptation under low light conditions; Wing et al. 2007), and the difference between  $\delta^{13}\text{C}$  of *Ecklonia radiata* and  $\delta^{13}\text{C}$  of the stomach contents of *Evechinus chloroticus*. Error bars:  $\pm 1$  SE. Numbers correspond to sites identified in Fig. 1

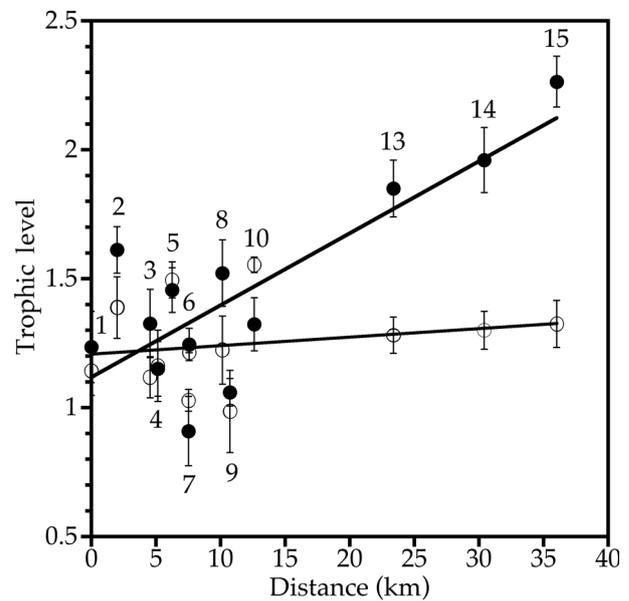


Fig. 5. Trophic level of adult ( $>100$  mm test diameter;  $\bullet$ ) and juvenile ( $<40$  mm test diameter;  $\circ$ ) along a gradient between outer coast wave-exposed sites and inner fjord wave-sheltered sites. Distances (km) are from the entrance of each fjord. Error bars:  $\pm 1$  SE. Numbers aligned with each pair of symbols correspond to sites identified in Fig. 1

mechanism for maintenance of sea urchin populations in subtidal environments.

In the present study, we measured the trophic position of the sea urchin *Evechinus chloroticus*, which persists as a conspicuous member of the subtidal

community and is distributed across a full range of shallow water habitats in the Fiordland region (Wing et al. 2001). High retention of larvae and recruitment in the inner fjord environment results in high density subpopulations in the absence of their preferred

food, subtidal Laminarian algae (Wing et al. 2003, Wing 2009). In the inner fjord, *E. chloroticus* persists on a range of alternative food sources. For example, Wing et al. (2008) measured plasticity in the diet of *E. chloroticus* along the axis of Doubtful Sound, a fjord with a large input of freshwater from a hydroelectric power plant. Consequentially, the inner fjord habitats in Doubtful Sound have been highly modified (Tallis et al. 2004), and there is a larger prevalence of organic matter from bacterial recycling of terrestrial material in the shallow marine food web than in other fjords (Jack et al. 2009, McLeod & Wing 2009). In Doubtful Sound, analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  revealed that sea urchins inhabiting the highly modified inner fjord habitats had a high prevalence of recycled terrestrial organic matter and chemoautotrophic bacteria in their diet (Wing et al. 2008). In the present study, we examined similar subpopulations of sea urchins inhabiting inner fjord environments of unmodified fjords.

In Fiordland, reductions in wave-induced flow and irradiance along the axis of each fjord has resulted in a steep gradient in density and productivity of the common kelp *Ecklonia radiata* (Miller et al. 2000, 2011, Wing et al. 2007). The result is a sharp transition from algal-dominated communities in the wave-exposed, well-illuminated entrances of the fjords to highly diverse sessile invertebrate communities in the inner fjord regions (Witman & Grange 1998, Smith & Witman 1999). Plasticity in the growth habit of *E. radiata* has resulted in strikingly different blade morphologies between dense, productive stands of kelp that have relatively narrow, thick blades on the wave-exposed outer coast, to more sparse, less productive stands of kelp that have wide, thin blades in the quiescent, dimly illuminated inner fjord environments (Wing et al. 2007). Using blade width as an indicator of the physiological condition of *E. radiata*, we tested for variability of blade width at each site with isotopic evidence for prevalence of *E. radiata* in the diet of sea urchins. We found a strong negative relationship between blade width and the prevalence of *E. radiata* in sea urchin diet among sites, consistent with the observed gradient in productivity of *E. radiata* and its availability as a food source. We then examined the relationship between average test diameter of sea urchins at the adult mode within size frequency distributions, collected over multiple years at each site, and the prevalence of *E. radiata* in their diet. We found that adult sea urchins were on average larger at sites where they consumed more kelp. This relationship is consistent with food limitation in the inner fjord habitats (e.g. Wing et al. 2003, Wing 2009). We then exam-

ined variability in trophic level of adult sea urchins in relation to the prevalence of *E. radiata* in their diet. We observed that as *E. radiata* became less prevalent in the diet, the trophic level of sea urchins increased. This pattern is consistent with a switch from an algal-based to an animal-based diet. The observed differences in trophic level were confined to adult sea urchins (>100 mm test diameter) while juveniles (<40 mm test diameter) displayed little difference in trophic position among sites distributed along the length of the fjords. The patterns we observed here demonstrate that adult *E. chloroticus* populations vary in trophic position along environmental gradients from the outer coast to the inner fjord habitats. As a corollary, the ontogenetic niche of this species varies among habitat types, providing a mechanism for their persistence in marginal habitats. This alternative mechanism enables sea urchins to alleviate starvation instead of merely altering their metabolism to survive while remaining under nutritional stress. In addition, our records of omnivory in this species have been expanded by this study from recycled microbial production to include predation on animals.

These observations are important for our understanding of how sea urchins maintain uniquely strong interaction strengths within food webs, and for their ability to influence patterns in diversity and habitat structure within subtidal ecosystems (Scheibling et al. 1999, Steneck et al. 2004, Filbee-Dexter & Scheibling 2014). In the Fiordland ecosystem, sea urchins effectively occupy trophic levels ranging from 1 to 2 as adults while juveniles are constrained to trophic level 1. Their apparent ability to switch between microbial, algal and animal-based diets as they mature likely results in persistence and influence within a wide range of subtidal communities. These observations of more extensive omnivory in sea urchins have important implications for understanding subtidal community structure and for managing temperate marine ecosystems, such as the Fiordland Marine Area and other similar systems with strong environmental and productivity gradients (Shears et al. 2008, Babcock et al. 2010). The Fiordland Marine Area (FMA, 'Te Moana o Atawhenua') is a region of globally significant natural and cultural heritage. An extensive analysis of patterns in the physical environment and of biological diversity in the region (Wing et al. 2004) was used to help support the community-led development of the Fiordland Marine Conservation Strategy in 2004, which was legislated as the Fiordland Marine Management Act (FMMA) in 2005. The FMMA closed the inner regions of 11 fjords to commercial fishing

(46 002 ha; 59% of the FMA) and established a network of 10 marine reserves nested within the commercial exclusion zones, encompassing 10 421 ha or 13.1% of the FMA (Wing & Jack 2014). In the context of spatial management and biodiversity conservation in Fiordland, the sea urchin *E. chloroticus* forms a critical part of the marine food web with a potentially strong influence on habitat structure and patterns in biodiversity.

Sea urchin barrens have been widely cited as an alternative to luxuriant seaweed communities within the marine literature and provide an example of alternate states of the subtidal ecosystem (see Filbee-Dexter & Scheibling 2014 for a review). While under many circumstances removal or decline in sea urchin abundance can result in re-growth of kelps, sea urchins may also persist in high density populations in regions where sessile invertebrates form the dominant community (Witman & Grange 1998, Smith & Witman 1999). The results presented here demonstrate that the *E. chloroticus* population in Fiordland persists across a dramatic gradient in availability of its preferred food, the common kelp *E. radiata*. Further, in multiple inner fjord habitats where organic matter from *E. radiata* is less available, adult sea urchins rely on a largely animal-based diet, as indicated by an increase in trophic level. This pattern indicates plasticity of the ontogenetic niche for this species and provides evidence for an ecological mechanism by which populations of sea urchins may persist along steep gradients in benthic productivity. The ability of adult sea urchins to switch diet from macroalgae to sessile suspension feeding invertebrates represents a shift in both its trophic level and in the basal organic matter source pools supporting subpopulations. These results have important implications for understanding the potential for *E. chloroticus* to influence and maintain biodiversity patterns in complex environments such as Fiordland, and provide impetus to further understand the trophic position of sea urchins in other temperate regions such as the Chilean, Scandinavian, and British Columbian fjord systems. Fjord systems such as these make up an important component of temperate marine environments worldwide.

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