Small-scale differences in blue cod length distribution, growth, and trophic ecology in New Zealand

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ABSTRACT: Growth and reproduction in marine fish populations can be strongly influenced by local habitat quality and nutritional resources. Habitat degradation can alter prey composition and availability, and, consequently, trophic position and dietary niche breadth of marine fish. In the present study, we compared length-frequency distributions, growth, stomach contents, and isotopic values ($\delta^{13}C$ and $\delta^{15}N$) of blue cod *Parapercis colias* subpopulations from biogenic reef habitats and habitats that were more strongly influenced by shellfish dredges and fine sediment in New Zealand. Blue cod inhabiting more degraded regions were significantly smaller and relied on different prey items than blue cod from biogenic reef habitats. Results indicated that the isotopic niche areas of blue cod occupying degraded habitats were smaller than those of blue cod inhabiting relatively undisturbed biogenic reefs. Isotope mixing models demonstrated that blue cod from one of the biogenic reef regions relied predominantly on suspended particulate organic matter, while blue cod from the other biogenic and degraded regions primarily relied on macroalgae as their organic matter source. Dietary niche overlap was likely higher for blue cod from degraded habitats, with potential consequences for growth and reproduction. Blue cod inhabiting biogenic reefs showed a high degree of individual specialisation. The present study demonstrated that differences in length distribution, growth, and trophic ecology among blue cod subpopulations coincided with differences in habitat degradation. Ecosystem-based management solutions can help regenerate high-quality biogenic habitats while reducing fisheries mortality within these critical habitats.

KEY WORDS: *Parapercis colias* · Marlborough Sounds · Tasman Bay · Stable isotopes · SIBER · 'simmr' · Isotopic niche · Stomach contents

1. INTRODUCTION

Coastal marine ecosystems are among the most productive marine environments globally (Halpern et al. 2007, Wernberg et al. 2019). They provide resources and ecosystem services such as important feeding grounds, breeding, and nursery habitats for many species. However, these ecosystems are also among the most exploited (Halpern et al. 2007), through the direct harvest of living marine resources as well as incidental mortality and habitat destruction associated with fishing (Crain et al. 2009, Wernberg et al. 2019). Land-based influences of sedimentation and nutrient pollution can also cumulatively affect diversity and productivity of exploited coastal ecosystems (e.g. Schiel 2013, Wing et al. 2022b). The combination of land- and sea-based anthropogenic activities, such as forestry, farming, and fishing,

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threatens important coastal habitats and species composition and biomass, thereby altering the trophic structure (Pauly et al. 1998, 2005, Thrush et al. 2004, Diaz & Rosenberg 2008, Crain et al. 2009, Gilarranz et al. 2016, Schlieman et al. 2022). Understanding the impacts anthropogenic stressors have on the trophic ecology of species is fundamental for effective ecosystem-based management, as trophic interactions have profound influences on demographic structures and fishery yields (Estes et al. 2011, Hamilton et al. 2011, Udy et al. 2019a,b,c).

Population demographics and life history traits are strongly influenced by habitat quality and trophic interactions (Jack et al. 2009, Wing & Jack 2013, Persson et al. 2014, Kolodzey & Wing 2022). For example, fecundity and somatic growth in coastal marine fish and invertebrate subpopulations can be determined by the quality of the local habitat, e.g. availability of nutritional resources, abundance of predators, nursery habitat, and the available nutritional resources (Jack & Wing 2010, Beer & Wing 2013). For generalist species, spatiotemporal variability in diet among populations may be a response to geographical or seasonal variations in prey availability and quality (Foy & Norcross 1999, Bacha & Amara 2009). The variability in resource use, or niche breadth, may change if resources become rare or the quality of the habitat changes (Fry et al. 1999, McLeod et al. 2010, Vander Zanden et al. 2010). Niche breadth can vary due to individual specialisation (Bolnick et al. 2003), resulting in the natural intraspecific variability of trophic structures among distinct populations (Marshall et al. 2014). Spatial variation in niche breadth, prey availability, or nutritional value may influence growth rates, condition, reproductive success, and survival among geographically distinct subpopulations (McCormick 2003, Lawton et al. 2010, Beer & Wing 2013, Kolodzey et al. 2021, Kolodzey & Wing 2022).

In New Zealand, blue cod *Parapercis colias* are common generalist predators that feed on a variety of benthic taxa as well as small fish and pelagic invertebrates, including salps (Jiang & Carbines 2002, Rodgers & Wing 2008, Beer & Wing 2013). Previous work has indicated that the food webs supporting blue cod vary geographically. For example, a stomach content study from Otago Harbour (south-eastern New Zealand) reported that blue cod mainly fed on crustaceans, fish, and molluscs (Graham 1939), whereas studies from Cook Strait (central New Zealand) and the Chatham Islands indicated that blue cod predominantly fed on pelagic fish and octopus (Rapson 1965). These differences in diet were attrib-

uted to the specific locally available habitat and associated prey community. Accordingly, crustaceans were the primary prey for blue cod in Foveaux Strait (southern New Zealand) inhabiting areas with a disturbed seabed due to oyster dredging. In contrast, blue cod from undredged areas within the same region primarily fed on polychaetes, molluscs, and crustaceans (Jiang & Carbines 2002). Small-scale geographic differences in trophic ecology may result in demographic variations among subpopulations, as differences in prey abundance and quality may directly affect growth rates (Jiang & Carbines 2002, Beer & Wing 2013) and indirectly affect related life-history traits, such as survivorship and reproduction (Jack & Wing 2010, Kolodzey & Wing 2022).

In the present study, the trophic ecology of blue cod subpopulations from the Marlborough Sounds (3 regions, biogenic reef habitat) and Tasman Bay (2 regions, degraded habitat) was compared (Fig. 1; Table S1 in the Supplement at www.int-res.com/articles/suppl/m708p125_supp.pdf). The distance between habitats was ca. 20 km. In the Marlborough Sounds (D'Urville Island, Pelorus Sound, and Queen Charlotte Sound), the habitat comprised multispecies biogenic and rocky reefs (Shears & Babcock 2007, Davidson et al. 2010, 2011, Morrison et al. 2014). Sea-based anthropogenic impact in these regions was relatively low; however, both rocky reefs, including kelp forests, and biogenic reefs are threatened by climate change, increased sedimentation, and turbidity due to forestry and agriculture, and the formation of sea urchin barren habitat (Hay 1990, Handley & McLean 2016, Urlich & Handley 2020). In Tasman Bay (Inner and Outer Tasman Bay), the seabed was dominated by soft-sediment habitats with some shallow rocky reefs or boulders along the coastline (Newcombe et al. 2015). Tasman Bay has been subjected to commercial and recreational shellfish dredges and fish trawls, drastically reducing the presence of biogenic reef habitats, particularly bryozoan and horse mussel *Atrina zelandica* reefs. The majority of the remaining benthic taxa comprised infaunal bivalves and crustaceans (Thrush et al. 1995, Handley 2006, Gillespie et al. 2011, Urlich & Handley 2020).

Information about habitat-dependent differences in trophic ecology are important in order to understand how spatially structured populations may respond to changes in their environment, both in light of climate change and to provide adequate conservation and management advice for exploited species. The present study aimed to resolve differences in length-frequency distributions, growth, and
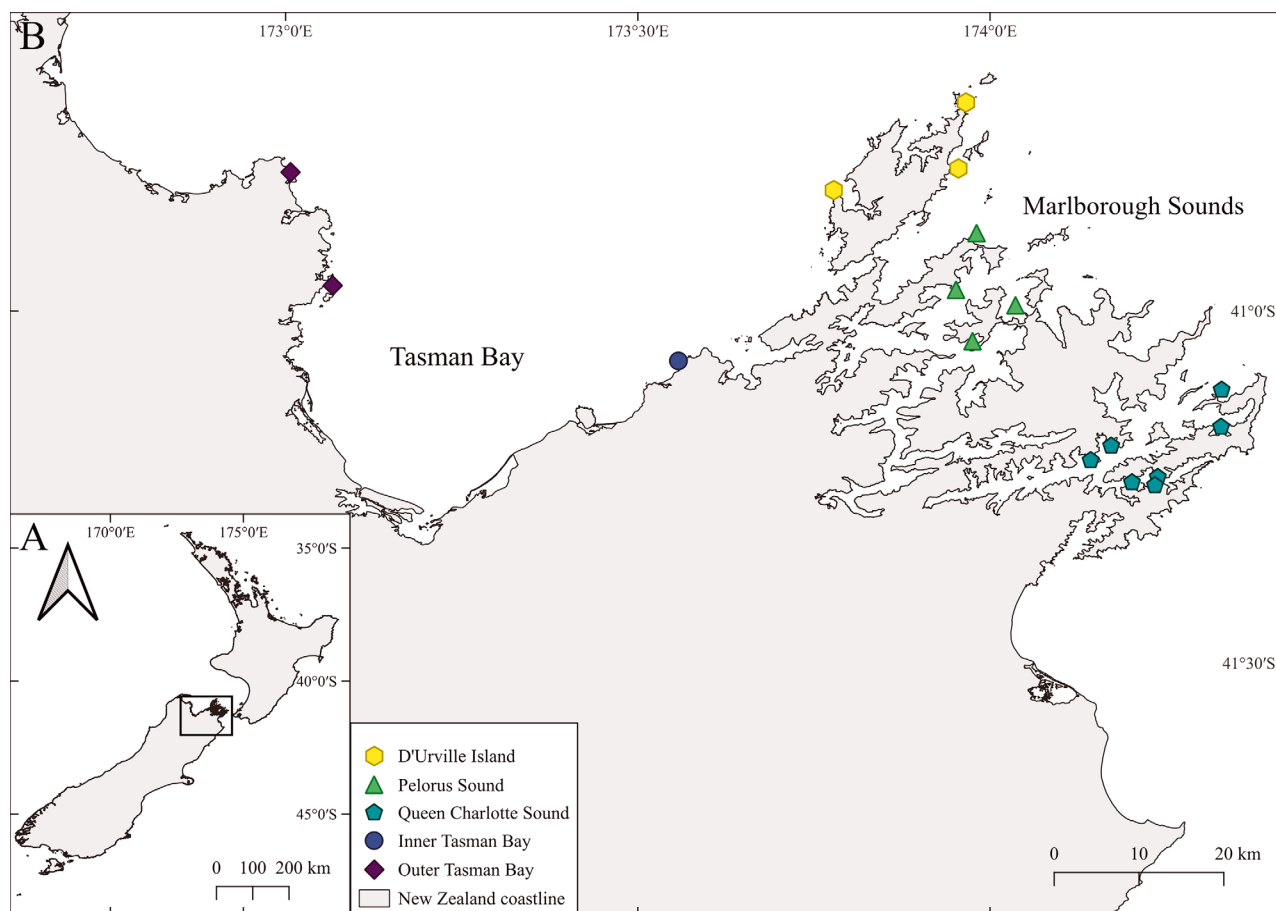
Fig. 1. (A) New Zealand and the sample sites in the (B) Marlborough Sounds (D'Urville Island, Pelorus Sound, Queen Charlotte Sound) and Tasman Bay (Inner and Outer Tasman Bay) (for specific coordinates, see Table S1 in the Supplement)

trophic ecology of blue cod subpopulations sampled from coastal areas with different habitat types. Specifically, the study aimed (1) to compare length-frequency distributions and growth among subpopulations; (2) to analyse the composition of diet; and (3) to analyse stable isotope values (δ^{13}C and δ^{15}N) of blue cod from 5 distinct regions in the Marlborough Sounds and Tasman Bay. Additionally, the research was designed to resolve differences in (4) the isotopic niche breadth and in (5) the basal organic matter source pools of food webs supporting blue cod based on the analysis of δ^{13}C and δ^{15}N in the context of differences in the local benthic habitats.

2. MATERIALS AND METHODS

2.1. Sampling sites and collection

Blue cod were sampled using modified commercial cod pots. In New Zealand, cod pots are widely used to target blue cod in commercial and recreational fisheries, as well as during scientific surveys to estimate abundance, sex ratio, length, and age distributions of this fish (Cole et al. 2004, Beentjes & Carbines 2009, Carbines & Beentjes 2011, Beentjes et al. 2018). In the present study, cod pots were modified to decrease the mesh gage from the commercially allowed 54 mm to a fine gage mesh of 10 and 20 mm in order to target a broad range of sizes. Three cod pots were baited with squid, placed on sandy bottoms along reef edges 15 to 20 m apart at 3 to 6 m depth, and left in the water for 30 to 45min (Cole et al. 2004). Cod pots were deployed once at each site. Smaller blue cod are not thought to avoid pots due to the presence of larger individuals (Cole et al. 2004, S. Kolodzey pers. obs.). Five regions were chosen for the present study, namely D'Urville Island (DUR), Inner Tasman Bay (ITB), Outer Tasman Bay (OTB), Pelorus Sound (PEL), and Queen Charlotte Sound (QCS), during 2 research cruises on board the RV 'Polaris II' in February and November 2018 (Fig. 1).

After measuring the total length (mm) of all blue cod, the majority were released alive. Subsamples were retained for age, stomach content, and stable isotope analysis, which were taken immediately after sampling the fish. Blue cod were humanely euthanized using the Iki method (Close et al. 1997) under the University of Otago ethics protocol AUP-18-193.

2.2. Age and growth

Sagittal otoliths were removed by cranial dissection to determine the age (yr) of blue cod. Otoliths were rinsed in deionised water and transferred to sterile Eppendorf tubes. One of each pair of otoliths was embedded in K36 epoxy resin (Epoxy Kit, Nuplex Industries), and transverse sections (~1.5 mm thickness) were cut through the primordium using a Buehler Isomet low-speed diamond-bladed saw. The sections were mounted on glass slides using Crystalbond 509 (Amerco Products). The otoliths were then ground using wet–dry sandpaper (grades P600 and P800) until the yearly growth increments were clearly visible. The slides were polished using ultra-fine sandpaper (grade P1500) along with alumina silicate polishing powder. Ages were estimated from photomicrographs of sectioned otoliths under transmitted light. Only opaque zones (winter growth) bordered by translucent zones (summer growth) on both sides were counted. Image processing software (ImageJ) was used to improve the contrast and clarity of images and to allow for a more accurate reading of the annual growth increments. Growth models were constructed using the von Bertalanffy growth model:

$$\mathrm{TL}_t = L_\infty \left(1 - e^{-k[t-t_0]}\right) \tag{1}$$

where TL_t is the total length at time t (in yr), L_∞ is the asymptotic length (in mm, i.e. the length an individual would reach if it would grow to an infinite age), k is the growth constant expressing the rate at which length approaches the asymptote, and t_0 is the theoretical age from settlement of an individual at zero size (this can be negative for species with large larvae). The von Bertalanffy growth models and confidence intervals (CIs) were constructed using the 'FSA' package (Ogle et al. 2022) in R v. 4.1.1 (R Core Team 2021). The von Bertalanffy growth models were compared using the Kimura likelihood ratio test (Kimura 1980) using the 'growthlrt' function in the 'fishmethods' package in R (Nelson 2022).

2.3. Stomach content analysis

Stomachs and viscera were dissected on board the RV 'Polaris II'. Due to time constraints during the research cruises, blue cod were sampled during different times of the day, which might impact the stomach content. The stomach and intestinal contents were examined macroscopically on board the RV 'Polaris II' by the same 2 people during both research cruises. Prey items were identified into broad taxonomic groups: Pisces, Polyplacophora, Gastropoda, Cephalopoda, Bivalvia, Tunicata, Crustacea, Echinodermata, and other benthic invertebrates. Prey items that were not easily identifiable were discussed between the 2 identifiers before recording. When partly digested, only prey items with a head were accounted for, as a measure of the minimum number of individuals. The stomach content was recorded as the presence/absence of dietary groups. The proportion of empty stomachs was calculated, and these were excluded from further analysis. The number of stomachs (n) in which each item i occurred was recorded and expressed as the proportion of occurrence ($\%O$) of the total number of stomachs of fish containing prey items (N_F):

$$\%O = \frac{n_i}{N_F} \times 100 \tag{2}$$

2.4. Stable isotope analysis

A dorsal muscle tissue sample was taken from behind the head and frozen in sterile Eppendorf tubes at −20°C. The dorsal muscle tissue samples were rinsed with deionised water, transferred to sterile Eppendorf tubes, and oven-dried at 60°C for 48 h. When fully dried, the samples were ground into a fine powder, using a mortar and pestle, which were rinsed with deionised water and dried with lint-free tissues (Kimwipes, KimTech Science, Kimberly-Clark Professional) between samples. Samples of 1 mg were weighed into 5 × 3.5 mm tin capsules (Elemental Analysis). Lipids were not extracted prior to stable isotope analysis from blue cod muscle tissue, as the C:N ratio was relatively low, varying between 3 and 3.7. It has been shown that these low concentrations of lipids have no significant effect on the values of $\delta^{13}C$ (Post et al. 2007, Rodgers & Wing 2008, Skinner et al. 2016).

Suspended particulate organic matter (SPOM) and macroalgae were sampled during the February and November 2018 research cruises. SPOM samples,

collected from just below the water surface, were taken using a rosette equipped with 10 l Niskin bottles (Ocean Test Equipment®), pre-filtered with a 300 μm mesh to remove large zooplankton, and then filtered through a pre-combusted (400°C for 4 h) 47 mm, 0.7 μm GF/F filter (Whatman®). Multiple species of macroalgae were sampled during dive surveys. Both macroalgae samples and SPOM samples on filters were oven-dried at 60°C for 48 h. Stable isotope analysis was conducted on whole SPOM filters. Macroalgae were ground into a fine powder, and 2 mg were weighed into tin capsules. For the mixing model and calculation of the trophic position, $\delta^{13}C$ and $\delta^{15}N$ values of macroalgae were pooled across species (Tables 1 & S2).

Stable isotope analysis was conducted by IsoTrace Research (Department of Chemistry, University of Otago, Dunedin, New Zealand) using the Europa 20-20 updated mass spectrometer (Europa Scientific) interfaced with a Carlo Erba NC 1500 elemental analyser (NA1500, Carlo Erba) in continuous flow mode (precision: 0.2‰ for $\delta^{13}C$, 0.3‰ for $\delta^{15}N$). The isotopic ratios of raw samples were standardized by calibrating against international standards (USGS-40 and USGS-41). An in-house laboratory reference material (ethylenediaminetetraacetic acid; Elemental Microanalysis; EDTA-OAS, $\delta^{13}C$ = −38.93 ± 0.2‰, $\delta^{15}N$ = −0.73 ± 0.12‰) of known carbon and nitrogen isotope values was measured after every 12th sample to correct for instrument drift. The natural isotope ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed in δ notation as $\delta^{13}C$ and $\delta^{15}N$ in ‰ (Peterson 1999, Fry 2006).

2.4.1. Isotopic niche

Stable isotope values of a consumer can be used to characterise its isotopic niche in a standardised, repeatable way (Newsome et al. 2007, Layman et al. 2012). The isotopic niche of a consumer is defined as the area occupied by its isotope values from coordinates in a 2-dimensional isotope bi-plot (Newsome et al. 2007). Even though it is not precisely equivalent to a dietary niche based on prey diversity, the isotopic niche is often used as a generalised proxy for the dietary niche of a consumer (Newsome et al. 2007, Quevedo et al. 2009). To quantify differences in the isotopic niche sizes of blue cod among regions, Stable Isotope Bayesian Ellipses in R (SIBER) (Jackson et al. 2011) was used in R v. 4.1.1 (R Core Team 2021). SIBER uses a multivariate ellipse-based approach to estimate the isotopic niche space of blue cod subpopulations based on the total area (TA) and the standard ellipse areas (SEA) of the stable isotope data. SEA represents the core (40%) isotopic niche space, and is used as a proxy of the richness/evenness of consumed resources (Bearhop et al. 2004).

2.4.2. Mixing model

In order to quantify the contribution of SPOM and macroalgae as basal organic matter sources for blue cod from the 5 sampled regions, we used a Bayesian mixing model implemented in the R package 'simmr' (Stable Isotope Mixing Models in R) (Parnell 2021). The 'simmr' model outputs are posterior probability distributions representing the likelihood of a specific source being part of the diet of the consumer. Individual 'simmr' models were run for each region using $\delta^{13}C$ and $\delta^{15}N$ values of consumers (i.e. blue cod), average and standard error (SE) $\delta^{13}C$ and $\delta^{15}N$ values of the basal organic matter sources (i.e. SPOM and macroalgae, Table 1), and average and standard deviation estimates for trophic enrichment factors (TEFs) of $\delta^{13}C$ and $\delta^{15}N$. TEFs were chosen based on literature values after Post (2002): +0.4 ± 1.3‰ for $\Delta^{13}C$, and +3.4 ± 1.0‰ for $\Delta^{15}N$.

2.4.3. Trophic position

The calculated average $\delta^{13}C$ and $\delta^{15}N$ values of organic matter derived from SPOM and macroalgae for each region, with variance among regions (Table 1), were used to calculate individual trophic position for blue cod. For each fish, a 2-step iterative procedure

Table 1. Average ± SE $\delta^{13}C$ and $\delta^{15}N$ values of suspended particulate organic matter (SPOM) and macroalgae, sampled from the 5 regions in Marlborough Sounds and Tasman Bay used for the mixing model and trophic position calculations. DUR: D'Urville Island; PEL: Pelorus Sound; QCS: Queen Charlotte Sound; ITB: Inner Tasman Bay; OTB: Outer Tasman Bay

Region	Source	$\delta^{13}C$	$\delta^{13}C$ SE	$\delta^{15}N$	$\delta^{15}N$ SE
DUR	SPOM	−24.46	0.09	6.29	0.19
	Macroalgae	−18.39	0.90	7.43	0.35
PEL	SPOM	−22.13	0.21	7.17	0.26
	Macroalgae	−18.25	0.79	5.69	0.29
QCS	SPOM	−21.67	0.13	7.18	0.38
	Macroalgae	−15.37	0.72	6.95	0.16
ITB	SPOM	−22.57	0.39	8.43	1.51
	Macroalgae	−16.23	0.55	7.09	0.29
OTB	SPOM	−23.05	0.37	9.74	1.53
	Macroalgae	−17.95	0.48	7.18	0.41

was used to determine trophic position. First, a 2-source mass balance mixing model after Phillips & Gregg (2001) was used to estimate the relative contribution of organic matter derived from SPOM and macroalgae to each individual using δ^{13}C. An initial approximation of the trophic position was used to estimate the trophic discrimination of δ^{13}C. These results were then used to estimate the corresponding δ^{15}N of the mixture of organic matter sources at the base of the food web ($\delta^{15}N_{base}$). The individual trophic position was then calculated as (McCutchan et al. 2003):

$$\text{Trophic position} = \left(\frac{\delta^{15}N_{consumer} - \delta^{15}N_{base}}{\Delta^{15}N}\right) + 1 \quad (3)$$

where $\delta^{15}N_{consumer}$ is the nitrogen isotope ratio of the consumer, and $\Delta^{15}N$ is the trophic discrimination factor (3.4‰) for δ^{15}N after Post (2002). The resulting estimate of the trophic position was then iterated back into the mass balance mixing model until a stable solution was obtained. TEFs of +0.4 ± 1.3‰ for Δ^{13}C and +3.4 ± 1.0‰ for Δ^{15}N after Post (2002) were used. TEFs can vary between taxa and systems (Newsome et al. 2010); however, as we compared the same species among regions, errors introduced by using average enrichment factors should not affect the detection of regional differences in trophic position.

2.5. Statistical analysis

Only 1 and 2 sites each were sampled for ITB and OTB, respectively; therefore, all data were pooled across sites (Fig. 1), and all comparisons were made among and between regions. Average total lengths were compared using Kruskal-Wallis and post hoc pairwise Mann-Whitney U-tests. The length-frequency distributions were compared using a Kolmogorov-Smirnov (K-S) test within the 'FSA' package (Ogle et al. 2022) in R v. 4.1.1 (R Core Team 2021). To test the hypothesis that the diet composition of blue cod varied among regions, multivariate comparisons of the diet composition were carried out. Stomach content was recorded as the presence/absence of a dietary group; therefore, a resemblance matrix was constructed based on the Jaccard index of similarity. The composition of dietary groups was then compared among regions (5 levels, fixed) using permutational analysis of variance (PERMANOVA) in PERMANOVA+ version 1.0.2 as an add-on for PRIMER v6 (PRIMER-E). PERMANOVA was performed using 9999 permutations. PERMANOVA, based on Euclidean distance, was then used to compare the frequency of occurrence (%O) of each dietary group among and between regions. The hypotheses that δ^{13}C and δ^{15}N values and the trophic position of blue cod varied among regions were tested using ANOVA, or, when the data were not normally distributed, Kruskal-Wallis tests. Post hoc Tukey's HSD tests or, for data that were not normally distributed, pairwise Mann-Whitney U-tests were carried out. Normality was tested using the Shapiro-Wilk test. The significance level for all analyses was α = 0.5. Unless otherwise stated, analyses were conducted in R v. 4.1.1 (R Core Team 2021).

3. RESULTS

3.1. Length-frequency distribution

Overall, blue cod sampled from the Marlborough Sounds and Tasman Bay ranged from 111 to 435 mm total length. The largest average (±SE) total length was observed in PEL (306 ± 2 mm) (Fig. 2), while the largest individual was observed in DUR (435 mm). The average total length differed significantly among regions (Kruskal-Wallis: χ^2 = 138.77, p < 0.0001). Blue cod from ITB and OTB were significantly smaller than blue cod from DUR, PEL, and QCS (Fig. 2). Similarly, K-S tests showed that ITB and OTB had sig-
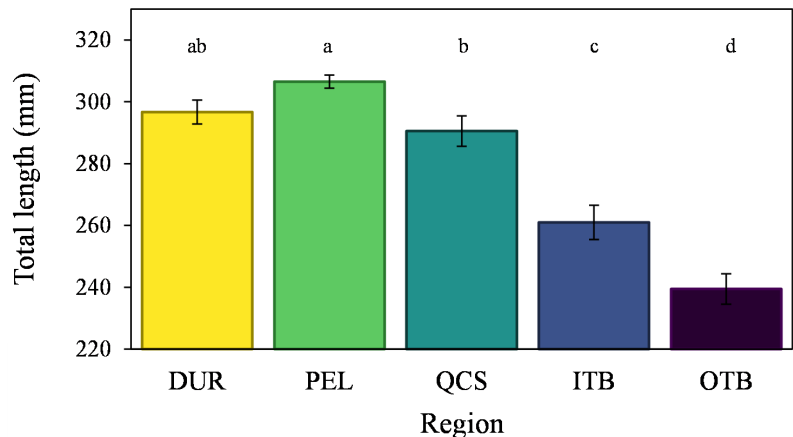

Fig. 2. Average ± SE total length of blue cod from D'Urville Island (DUR, n = 211), Pelorus Sound (PEL, n = 244), Queen Charlotte Sound (QCS, n = 60), Inner Tasman Bay (ITB, n = 52), and Outer Tasman Bay (OTB, n = 103). Shared letters above bars indicate that groups did not differ significantly (p > 0.05)

nificantly fewer large individuals and a higher number of smaller individuals than DUR, PEL, and QCS (Fig. 3, Table 2).

3.2. Age and growth

Due to the small number of otoliths that were retrieved from blue cod from PEL (n = 24) and QCS (n = 14), blue cod were pooled across DUR (n = 102), PEL, and QCS (Marlborough Sounds, n = 140) and across ITB (n = 38) and OTB (n = 69) (Tasman Bay, n = 107) for growth analysis. There were no statistical differences in growth between blue cod from DUR and the 3 regions in the Marlborough Sounds (DUR, PEL, QCS) pooled (Table S3) or the 2 regions in Tasman Bay (ITB and OTB) (Table S4).

In the Marlborough Sounds, blue cod ages ranged from 1 to 15 yr, while in Tasman Bay, they ranged from 1 to 16 yr. The average (±SE) age was 6.0 ± 0.2 yr in the Marlborough Sounds and 4.6 ± 0.2 yr in Tasman Bay. The von Bertalanffy growth model indicated that blue cod from the Marlborough Sounds grew at a faster rate and to larger sizes than those from Tasman Bay (Table 3, Fig. 4). The Kimura likelihood ratio test found significant differences in growth between blue cod from the Marlborough Sounds and Tasman Bay (χ^2 = 21.23, p < 0.0001) (Table 4).

3.3. Stomach content

Overall, 320 stomachs of blue cod were sampled. Of those, 54 stomachs (16.87 %) were empty (Table 5). The highest proportion of empty stomachs was found in blue cod sampled from QCS, while no empty stomachs were found in PEL (Table 5). The multivariate
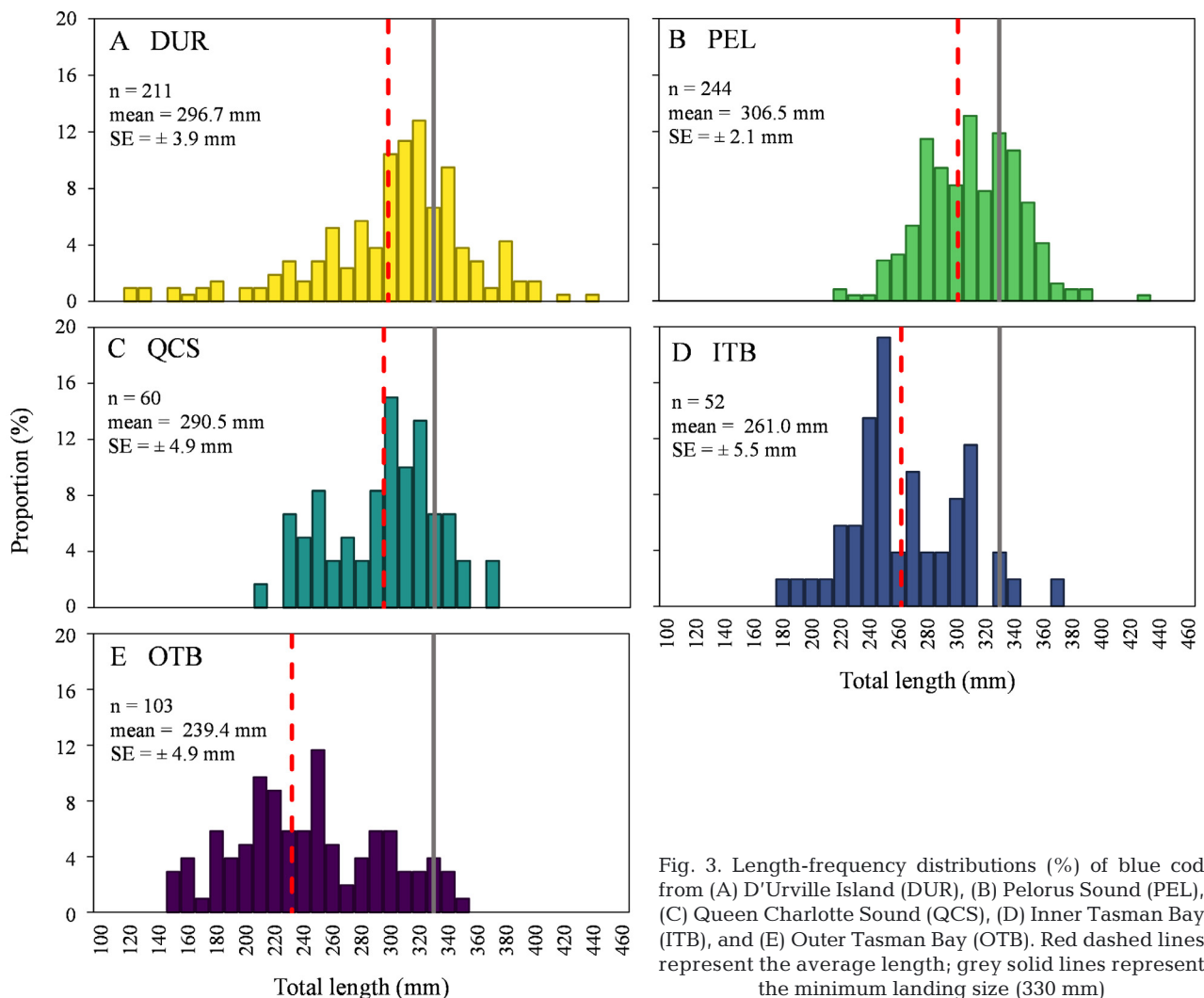

Fig. 3. Length-frequency distributions (%) of blue cod from (A) D'Urville Island (DUR), (B) Pelorus Sound (PEL), (C) Queen Charlotte Sound (QCS), (D) Inner Tasman Bay (ITB), and (E) Outer Tasman Bay (OTB). Red dashed lines represent the average length; grey solid lines represent the minimum landing size (330 mm)

Table 2. Results of the Kolmogorov-Smirnov test comparing the length-frequency distributions between paired regions. Significant (p < 0.05) differences are in **bold**. DUR: D'Urville Island; PEL: Pelorus Sound; QCS: Queen Charlotte Sound; ITB: Inner Tasman Bay; OTB: Outer Tasman Bay

Region	Test	D	p
DUR	ITB	0.417	**<0.0001**
DUR	OTB	0.489	**<0.0001**
DUR	PEL	0.140	**0.023**
DUR	QCS	0.144	0.291
ITB	OTB	0.311	**<0.01**
ITB	PEL	0.523	**<0.0001**
ITB	QCS	0.378	**<0.001**
OTB	PEL	0.613	**<0.0001**
OTB	QCS	0.456	**<0.0001**
PEL	QCS	0.189	0.0633

diet composition differed significantly among blue cod from the 5 regions (pseudo-$F_{4,260}$ = 7.719, p = 0.0001). Pairwise comparisons indicated that the multivariate diet composition did not differ between DUR and QCS (Table 6). The %O of Gastropoda, Bivalvia, Tunicata, and Crustacea differed significantly in the stomachs of blue cod from the sampled regions (Fig. 5, Table 7). Blue cod from DUR had relatively equal amounts of Gastropoda (28.2%), Bivalvia (37.3%), Tunicata (24.6), and Crustacea (40%) in their stomachs (Fig. 5). For blue cod from ITB, Gastropoda (60.5%) was the main prey, while those from OTB had predominantly Crustacea (62.8%) in their stomachs (Fig. 5). Blue cod from PEL had mostly Bivalvia (82.8%) in their stomachs, while those from QCS had equal amounts of Tunicata (37.5%) and Crustacea (37.5%) in their stomachs (Fig. 5, Table S5).

3.4. Stable isotope analysis

There were significant differences in the $\delta^{13}C$ values among blue cod from the 5 sampled regions (Kruskal-Wallis: χ^2 = 73.7, p < 0.0001). Blue cod sampled from PEL had on average (± SE) higher $\delta^{13}C$ values ($\delta^{13}C$ = −17.0 ± 0.14‰) than blue cod from DUR ($\delta^{13}C$ = −18.4 ± 0.07‰), ITB ($\delta^{13}C$ = −18.6 ± 0.06‰), OTB ($\delta^{13}C$ = −18.2 ± 0.03‰), and QCS ($\delta^{13}C$ = −18.3 ± 0.20‰) (Fig. 6A). Similarly, $\delta^{15}N$ values were significantly different among blue cod from the 5 regions (Kruskal-Wallis: χ^2 = 189.99, p < 0.0001). Blue cod sampled from DUR were significantly more depleted ($\delta^{15}N$ = 13.6 ± 0.05‰) in $\delta^{15}N$ than those from the other 4 regions, while blue cod from OTB ($\delta^{15}N$ = 15.1 ± 0.05‰) had significantly higher $\delta^{15}N$ values than those from DUR, ITB ($\delta^{15}N$ = 14.4 ± 0.08‰), PEL ($\delta^{15}N$ = 14.2 ± 0.08‰), and QCS ($\delta^{15}N$ = 14.1 ± 0.12‰) (Fig. 6B).

3.4.1. Isotopic niche

The widest range of $\delta^{13}C$ values was observed in blue cod from QCS (−20.3 to −16.8‰), in contrast to blue cod from ITB (−19.4 to −17.4‰) and OTB (−19.0 to −17.4‰), which had the narrowest range of $\delta^{13}C$ values. Blue cod from DUR had the largest range of $\delta^{15}N$ values, ranging from 11.9 to 15.2‰. The lowest ranges of $\delta^{15}N$ values were observed among blue cod from PEL (13.5 to 15.1‰) and ITB (13.6 to 15.5‰). Accordingly, SIBER estimates for TA and SEA indicated differences in the trophic niche among regions (Fig. 7, Table 8). The largest TA and SEA were observed for blue cod from QCS, followed by blue cod from DUR, and the smallest isotopic niche was estimated for blue cod sampled from ITB (Fig. 7, Table 8).

3.4.2. Mixing model

The isotope values of blue cod fell within the range of the isotope values for SPOM and macroalgae among all 5 regions, indicating that these are the constraining basal organic matter sources for blue cod in the Marlborough Sounds and Tasman Bay (Fig. 8). The relationship between consumer and basal organic matter source values is a precondition

Table 3. Von Bertalanffy growth model parameter estimates (L_∞, k, and t_0) for blue cod populations pooled across larger regions (Marlborough Sounds = DUR, PEL, QCS; Tasman Bay = ITB, OTB; abbreviations as in Table 1). Upper and lower 95% CIs for L_∞, k, and t_0 and the sample size (n) are given

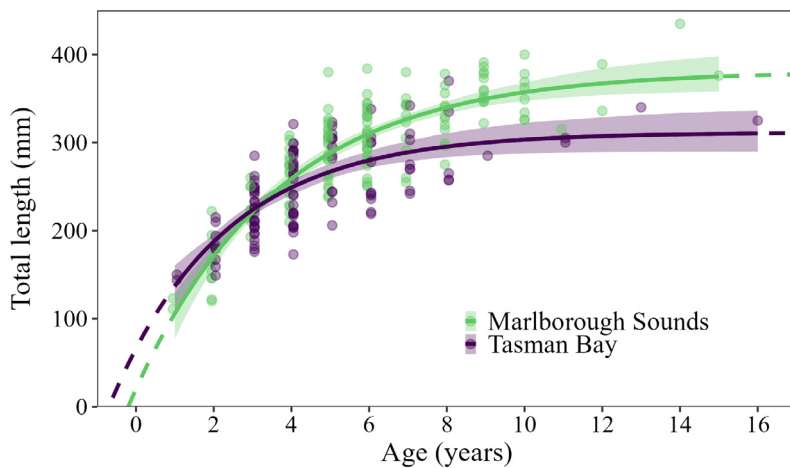| Pooled regions	L_∞ (mm)		k		t_0		n
	Estimate	CI	Estimate	CI	Estimate	CI	
Marlborough Sounds	381.09	361.5, 412.8	0.27	0.19, 0.34	−0.20	−0.97, 0.28	140
Tasman Bay	311.3	288.8, 353.7	0.34	0.19, 0.53	−0.69	−2.36, 0.14	107

Fig. 4. Raw length-at-age data and von Bertalanffy growth models for pooled blue cod populations from the Marlborough Sounds and Tasman Bay. Shaded areas indicate the 95% confidence intervals. Sample size and von Bertalanffy growth parameters are given in Table 3

3.4.3. Trophic position

Overall, the estimated trophic position of blue cod ranged between 2.8 and 3.6 and differed significantly among the 5 regions (Kruskal-Wallis: $\chi^2 = 143.94$, p < 0.0001).

Blue cod from PEL had a significantly higher average ($\pm$SE) trophic position (3.53 ± 0.03) than blue cod from DUR (2.87 ± 0.02), QCS (3.04 ± 0.04), OTB (3.09 ± 0.02), and ITB (2.94 ± 0.02). There was no significant difference in the trophic position of blue cod from QCS and OTB (Fig. 9).

4. DISCUSSION

The data and results of the present study provide evidence for spatial variability in length-frequency distributions, growth, diet, and isotopic niches, as well as the composition of the basal organic matter sources in food webs supporting blue cod subpopulations across regions with different degrees of anthropogenic activities in the Marlborough Sounds and Tasman Bay. The results are consistent with the idea that blue cod are generalist omnivores, and that their diet closely reflects availability of prey among habitats with different degrees of disturbance (Jiang & Carbines 2002).

Stomach content analysis indicated significant spatial differences in the variety and occurrence of

for the 'simmr' Bayesian mixing model to work adequately. The 'simmr' model output predicted that macroalgae were the major organic basal matter source for blue cod from DUR, OTB, and PEL (Fig. 8, Table 9). Blue cod from ITB and QCS likely relied on macroalgae and SPOM as their basal organic food sources in equal parts (Fig. 8, Table 9).

Table 4. Likelihood ratio tests (Kimura 1980) for the scenario Marlborough Sounds vs. Tasman Bay for growth parameters estimated (L_∞, k, and t_0) for blue cod populations pooled across larger regions (Marlborough Sounds = DUR, PEL, QCS; Tasman Bay = ITB, OTB; abbreviations as in Table 1). Significant (p < 0.05) differences are in **bold**

Test	Hypothesis	χ^2	p
$H0$ vs. $H1$	L_∞(Marlb.) = L_∞(Tasman)	5.03	**0.025**
$H0$ vs. $H2$	k(Marlb.) = k(Tasman)	0.11	0.740
$H0$ vs. $H3$	t_0(Marlb.) = t_0(Tasman)	0.98	0.322
$H0$ vs. $H4$	L_∞(Marlb.) = L_∞(Tasman), k(Marlb.) = k(Tasman), t_0(Marlb.) = t_0(Tasman)	21.23	**>0.0001**

Table 5. Proportion of sampled blue cod stomachs that were empty. Total sample size (n) is reported. DUR: D'Urville Island; PEL: Pelorus Sound: QCS: Queen Charlotte Sound; ITB: Inner Tasman Bay; OTB: Outer Tasman Bay

Region	n	% Empty stomachs
DUR	125	12.8
PEL	29	0
QCS	18	55.5
ITB	46	8.7
OTB	102	24.5

Table 6. Permutational analysis of variance (PERMANOVA) comparing the diet composition of blue cod between paired regions (empty stomachs excluded). Permutations (Unique perms.) and degrees of freedom (df) are given. Significant differences (p < 0.05) are in **bold**. DUR: D'Urville Island; PEL: Pelorus Sound; QCS: Queen Charlotte Sound; ITB: Inner Tasman Bay; OTB: Outer Tasman Bay

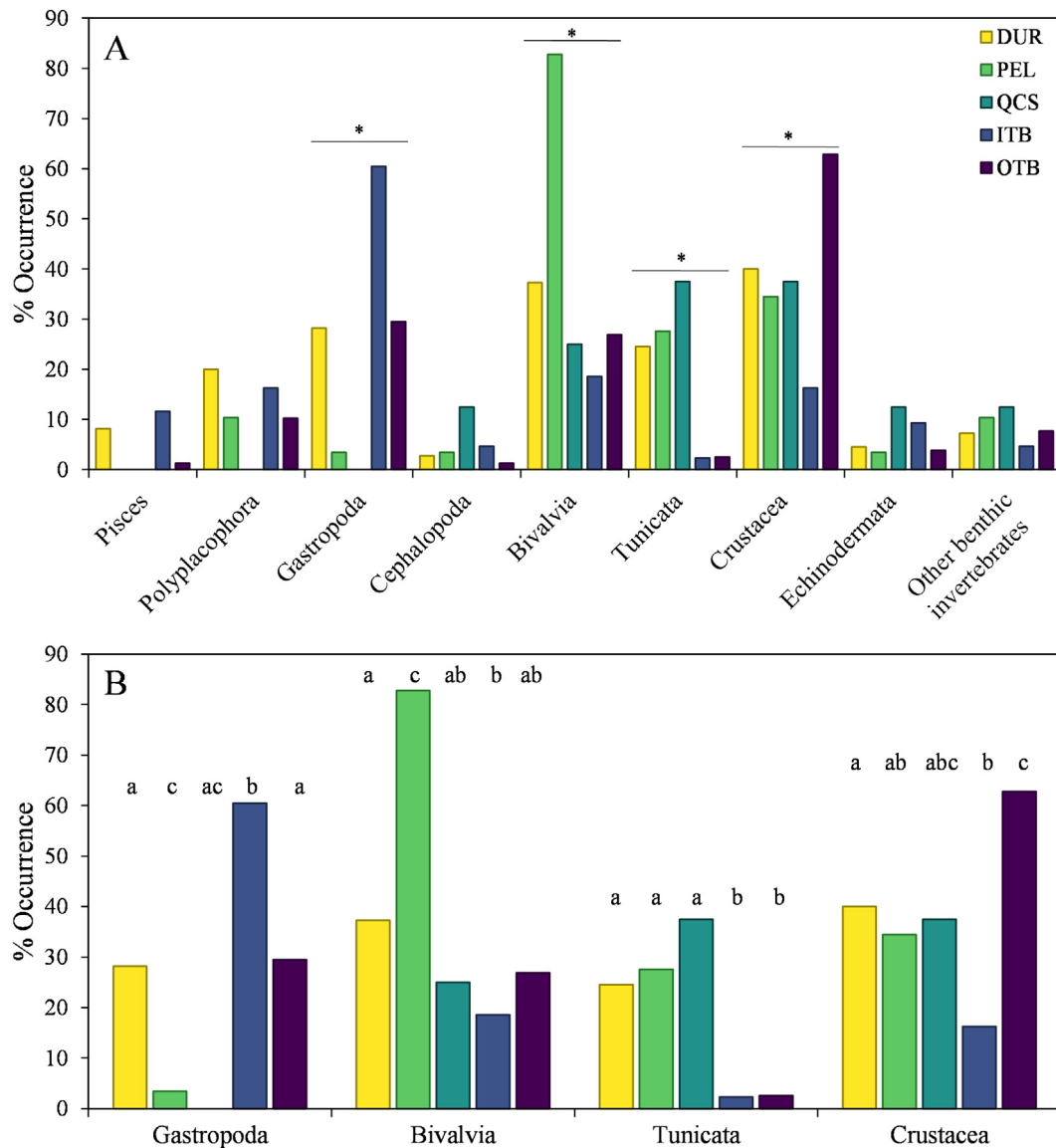| Region	Test	df	p	Unique perms.	t
DUR	ITB	1, 149	**<0.0001**	9950	2.883
DUR	OTB	1, 184	**<0.0001**	9940	2.683
DUR	PEL	1, 136	**<0.0001**	9946	2.675
DUR	QCS	1, 115	0.383	9827	1.026
ITB	OTB	1, 117	**<0.0001**	9930	3.469
ITB	PEL	1, 69	**<0.0001**	9940	4.093
ITB	QCS	1, 48	**<0.002**	7729	2.088
OTB	PEL	1, 104	**<0.0001**	9952	3.789
OTB	QCS	1, 83	**<0.05**	7165	1.629
PEL	QCS	1, 35	**<0.05**	5321	1.786

Fig. 5. (A) Proportion of occurrence of dietary groups in stomachs of blue cod among the regions: D'Urville Island (DUR), Pelorus Sound (PEL), Queen Charlotte Sound (QCS), and Inner and Outer Tasman Bay (ITB, OTB). * Indicates significant differences among regions based on PERMANOVA results ($p > 0.05$) (Table 7). (B) Close-up of significantly different dietary groups. Shared letters above bars indicate that groups did not differ significantly (pairwise PERMANOVA, $p > 0.05$) (Table S5). Note that the sum of % occurrence can be larger than 100, as one stomach can contain more than one prey group

specific dietary groups in stomachs of blue cod in the Marlborough Sounds and Tasman Bay. However, these results must be interpreted with care. Due to time constraints during research cruises, blue cod were sampled during different times of the day and states of the tide, which can have an impact on the presence of prey items depending on feeding time and digestibility. Prey items were identified by the same 2 people during both cruises and uneasily identified items were discussed prior to recording, but there may still be some variability between identi-

fiers. While the majority of the identified dietary groups were consumed by blue cod in all 5 regions, the %O of particular prey items varied significantly among regions. Blue cod from PEL had significantly higher occurrences of bivalves in their stomachs than blue cod from the 4 other regions. Gastropoda occurred significantly more often in the diet of blue cod from ITB, while crustaceans were the predominant prey of blue cod from OTB. Blue cod from DUR preyed equally on crustaceans, bivalves, and gastropods. Differences in the occurrence of specific

Table 7. Permutational analysis of variance (PERMANOVA) comparing the frequency of occurrence of each dietary group in samples among the 5 regions (DUR, ITB, OTB, PEL, and QCS; abbreviations as in Table 6). Permutations (Unique perms.) are given. Significant differences (p < 0.05) are in **bold**

Prey group	df	p	Unique perms.	Pseudo-F
Pisces	4, 260	0.049	809	2.392
Polyplacophora	4, 260	0.236	2825	1.389
Gastropoda	4, 260	**<0.0001**	4769	9.328
Cephalopoda	4, 260	0.421	281	0.924
Bivalvia	4, 260	**<0.0001**	5325	10.134
Tunicata	4, 260	**<0.0001**	2848	7.892
Crustacea	4, 260	**<0.0001**	5292	7.243
Echinodermata	4, 260	0.541	717	0.729
Other benthic invertebrates	4, 260	0.919	1224	0.269

prey items likely indicated differences in the abundance and composition of benthic organisms among the Tasman Bay and Marlborough Sounds regions.

Habitat degradation in Tasman Bay has had particularly strong negative effects on epifaunal organisms such as horse mussels, sponges, bryozoans, and colonial ascidians and has drastically reduced the abundance of these biogenic reef-forming groups (Handley 2006, Newcombe et al. 2015, Tuck et al. 2017). In contrast, within the inner and outer Marlborough Sounds, colonial ascidians, next to a variety of different taxa and species, including rhodoliths, barnacles, tubeworms, bryozoans, horse mussels, and sponges, form important constructors of biogenic habitats (Davidson et al. 2010).

In contrast to stomach content analysis, which provided a snapshot of the recent diet, stable isotope values of $\delta^{13}C$ and $\delta^{15}N$ of muscle tissue provide information on food resources assimilated over the time frame of months to years (Suring & Wing 2009). Blue cod from PEL were on average less depleted in $\delta^{13}C$ than blue cod from DUR, ITB, OTB, and QCS. The average $\delta^{15}N$ value was highest for blue cod from the OTB region, which suggested that the subpopulation fed at a relatively high trophic position. Blue cod were sampled close to shore and in relatively close proximity to several rivers emptying into Tasman
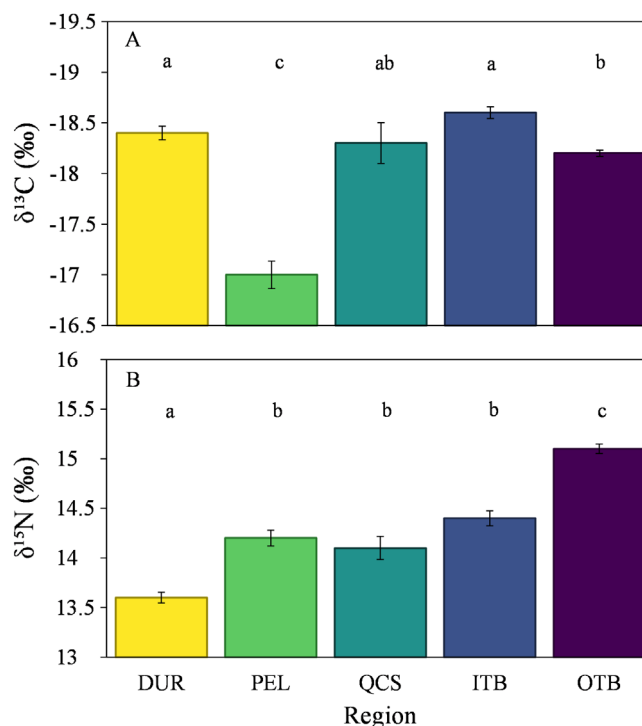

Fig. 6. Average ± SE (A) $\delta^{13}C$ and (B) $\delta^{15}N$ values of blue cod samples from D'Urville Island (DUR, n = 124), Pelorus Sound (PEL, n = 28), Queen Charlotte Sound (QCS, n = 49), Inner Tasman Bay (ITB, n = 45), and Outer Tasman Bay (OTB, n = 101). Shared letters above bars indicate that groups did not differ significantly (p > 0.05)
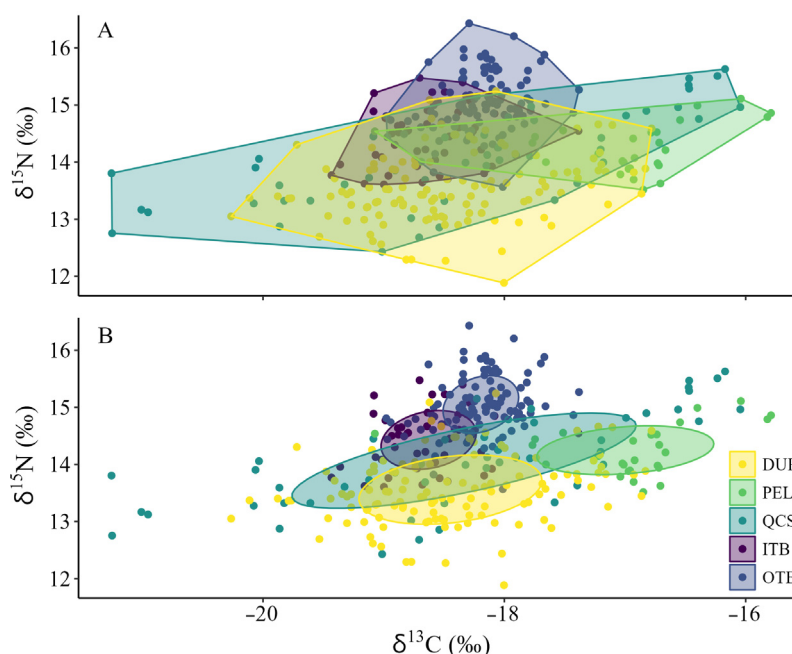

Fig. 7. Stable isotope biplot showing (A) the total area (TA) (polygons) of niche space occupied and (B) the standard (40%) ellipse area (SEA) of the isotopic niche for blue cod from D'Urville Island (DUR), Pelorus Sound (PEL), Queen Charlotte Sound (QCS), and Inner and Outer Tasman Bay (ITB, OTB). Note the scaled x- and y-axes

Table 8. SIBER estimates for the total area (TA) and standard ellipse area (SEA) for blue cod from the 5 sampled regions (abbreviations as in Table 6)

Region	TA	SEA
DUR	7.41	1.36
PEL	2.93	0.92
QCS	8.99	2.46
ITB	2.39	0.60
OTB	2.92	0.47

Bay (e.g. Torrent, Motueka, Riuwaka, Falls, and Marahau Rivers). A possible explanation for the elevated $\delta^{15}N$ values could be nutrient enrichment through anthropogenic sources of pollution and its effect on the value of $\delta^{15}N$ in basal organic matter source pools (e.g. Schlieman et al. 2022). Accordingly, nutrient run-off from agricultural land, sewage, and stormwater ammonium can enhance $\delta^{15}N$ values in marine systems (Hansson et al. 1997, Dailer et al.

2010, Sabadel et al. 2020). The elevated $\delta^{15}N$ values of blue cod from ITB and OTB could also be an indication of long-term nutritional stress (Bowes et al. 2014, Hertz et al. 2015, Doi et al. 2017). Fasting and starving animals may show a progressive increase in $\delta^{15}N$ due to catabolic processes when they start using their own protein resources to survive (Waterlow 1968). Weight and condition were not analysed in the present study; however, growth models demonstrated significant slower growth among blue cod from the degraded Tasman Bay region. While differences in growth rates can also be attributed to fishing mortality and its effects on the life cycle of blue cod (Kolodzey & Wing 2022), depressed growth could also indicate nutritional stress among blue cod from Tasman Bay.

Using SIBER, the isotopic niche for each blue cod subpopulation was estimated. The results of the analysis of the SEA demonstrated that blue cod from QCS had the largest isotopic niche, followed by blue cod from DUR and PEL. Blue cod from ITB and OTB
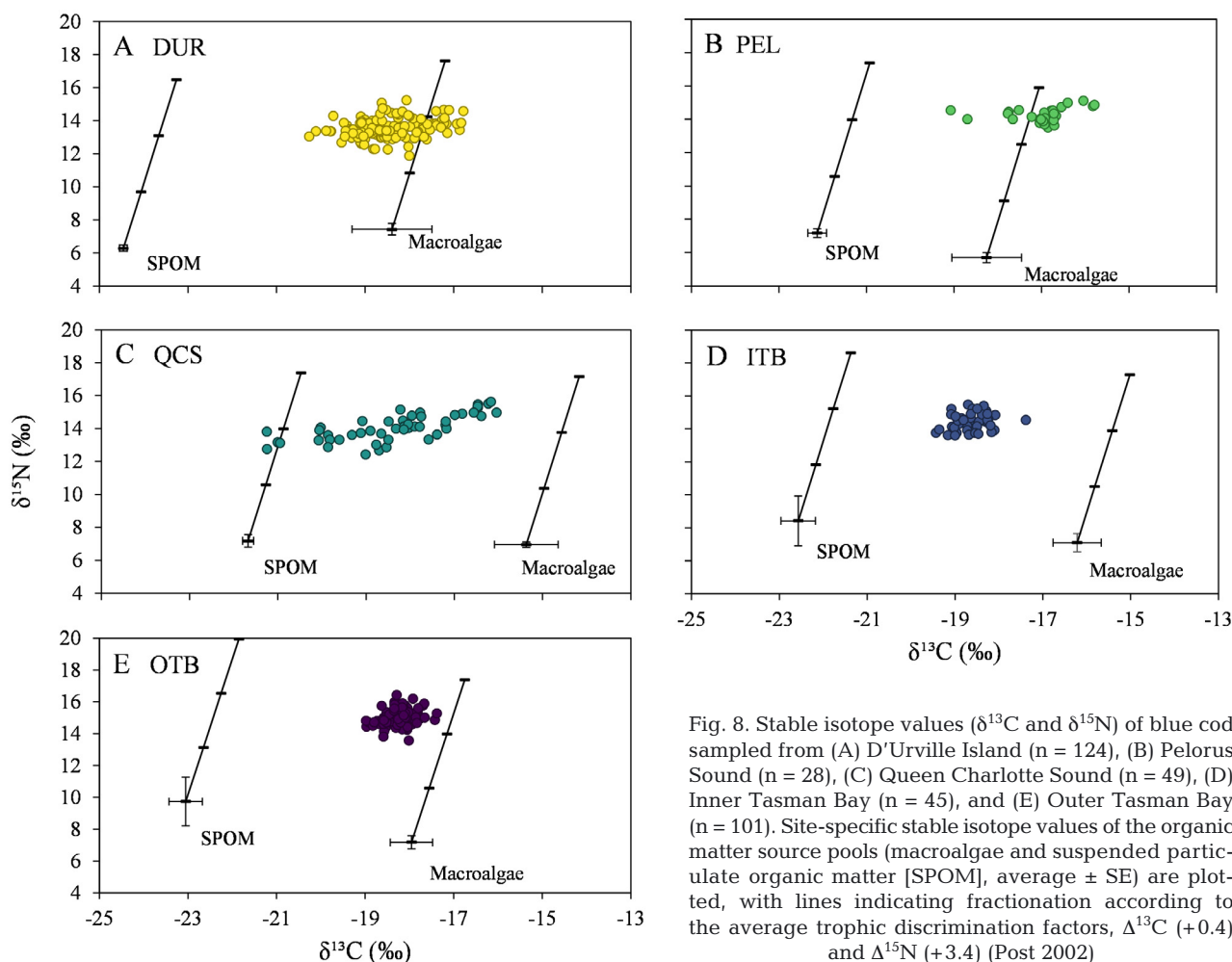

Fig. 8. Stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of blue cod sampled from (A) D'Urville Island (n = 124), (B) Pelorus Sound (n = 28), (C) Queen Charlotte Sound (n = 49), (D) Inner Tasman Bay (n = 45), and (E) Outer Tasman Bay (n = 101). Site-specific stable isotope values of the organic matter source pools (macroalgae and suspended particulate organic matter [SPOM], average ± SE) are plotted, with lines indicating fractionation according to the average trophic discrimination factors, $\Delta^{13}C$ (+0.4) and $\Delta^{15}N$ (+3.4) (Post 2002)

Table 9. Result of 'simmr' Bayesian mixing models run using blue cod $\delta^{13}C$ and $\delta^{15}N$ isotopes to estimate a probability distribution for suspended particulate organic matter (SPOM) and macroalgae. Average ± SD values for estimated proportion of contribution by SPOM and macroalgae and 97.5% credibility intervals (CI) are given. In **bold** is the predominant source for each region (abbreviations as in Table 6)

Region	SPOM	SPOM CI	Macroalgae	Macroalgae CI
DUR	0.136 ± 0.028	0.079–0.189	**0.864** ± 0.028	0.811–0.921
PEL	0.107 ± 0.051	0.026–0.218	**0.893** ± 0.051	0.782–0.974
QCS	**0.536** ± 0.031	0.475–0.597	0.464 ± 0.031	0.403–0.525
ITB	0.471 ± 0.026	0.421–0.523	**0.529** ± 0.026	0.477–0.579
OTB	0.216 ± 0.022	0.174–0.258	**0.784** ± 0.022	0.742–0.826

had small isotopic niches compared to those from DUR, PEL, and QCS. The small isotopic niches observed in blue cod from ITB and OTB are an indication of limited resources or a high reliance on limited prey. In contrast, the larger isotopic niches of blue cod from DUR and QCS could indicate high prey diversity and a higher degree of individual specialisation (Wing et al. 2022a). High individual specialisation within a population may be beneficial, as it can buffer the population against the loss of a particular habitat (Bolnick et al. 2003) and loss in resources due to climate change or habitat destruction (Möllmann et al. 2005, de Carvalho et al. 2019). For example, individual specialisation may reduce intraspecific competition for resources (Bolnick et al. 2003). In the case of blue cod, individual specialisation may also occur due to their territorial and small-ranging nature, as they are generally confined to local reef habitat as adults (Mace & Johnston 1983, Cole et al. 2000). Individuals may only feed within their relatively small home range, resulting in a high degree of individual specialisation and a broader range of basal organic matter sources for a subpopulation inhabiting diverse reef habitats. In contrast, blue cod with a small isotopic niche may be sharing the same preferred resource or only have access to a limited resource pool.

The observed differences in dietary specialisation and isotopic niches of blue cod from the Marlborough Sounds and Tasman Bay were likely the results of differences in the availability of prey items within an individual's foraging range. Large inputs of fine sediment as well as extensive trawling for finfish and commercial and recreational dredging for scallops and oysters have substantially modified the habitat and reduced biogenic reef structures within Tasman Bay (Newcombe et al. 2015, Tuck et al. 2017). Large kelp forests were absent from this region (e.g. Wing et al. 2022b), and studies have demonstrated

that the diversity of benthic infauna has decreased over the last decade, from 29 to 18 taxa dominated by crustaceans, molluscs, and annelids (Gillespie & Keeley 2007, Johnston & Gillespie 2016). The dietary specialisation and small isotopic niche breadth of blue cod in ITB and OTB are likely consequences of the disappearance of biogenic reef habitats and benthic invertebrates in these areas. Similarly, blue cod in Foveaux Strait that occupied habitats with reduced species abundance and diversity due to oyster dredges had a less diverse diet compared to blue cod inhabiting intact biogenic reefs (Jiang & Carbines 2002).

The results of the 'simmr' mixing model demonstrated that macroalgae were the main source of primary production for blue cod from OTB, while blue cod from ITB relied equally on SPOM and macroalgae. The habitat in both regions was severely disturbed due to scallop and oyster dredges, with little to no occurrence of biogenic reefs (Handley 2006, Newcombe et al. 2015). Some small patches of macroalgae of the genus *Carpophyllum* were present in OTB. The high proportion of macroalgae as the primary source of carbon could be due to blue cod feeding directly in and around those patches of macroalgae. A different explanation could be that OTB has an input of kelp detritus from other regions. Kelp detritus can provide an important nutritional food source in otherwise resource-poor habitats. Nevertheless, the detritus can be similar in isotopic value to both SPOM and fresh macroalgae and therefore can
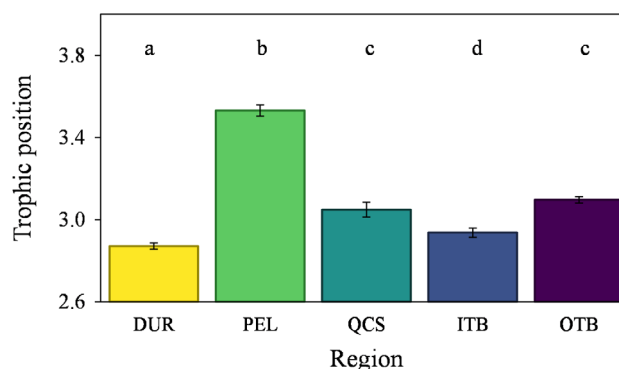

Fig. 9. Average ± SE trophic position of blue cod samples from D'Urville Island (DUR, n = 124), Pelorus Sound (PEL, n = 28), Queen Charlotte Sound (QCS, n = 49), Inner Tasman Bay (ITB, n = 45), and Outer Tasman Bay (OTB, n = 101). Shared letters above bars indicate that groups did not differ significantly (p > 0.05)

be difficult to distinguish from live material in some systems (Miller & Page 2012, Elliott Smith & Fox 2022).

Food availability can directly affect growth and reproduction in fishes (Anderson & Sabado 1995, Ouellet et al. 2001, Möllmann et al. 2005), as different types of prey can have different energetic values (Steimle & Terranova 1985). For example, pelagic prey, such as zooplankton and fish, are often of higher energetic values than benthic invertebrates (Steimle & Terranova 1985). In Fiordland (west coast of New Zealand), differences in growth and condition of blue cod inhabiting inner and outer fjord habitats have been attributed to differences in their basal organic matter sources and diet composition (Beer & Wing 2013). Blue cod from the outer fjords that fed on a diet fuelled by organic matter derived from macroalgae had higher growth rates and were in better condition compared to blue cod in the inner fjords, where a large proportion of the diet comprised diverse but energetically low benthic species linked to chemoautotrophic production (Wing et al. 2012, Beer & Wing 2013). Further, blue cod inhabiting dredged habitats in the Foveaux Strait had reduced somatic growth compared to those inhabiting biogenic reefs (Carbines et al. 2004).

In the present study, we demonstrated significant differences in the length-frequency distributions and growth among the Marlborough Sounds and Tasman Bay subpopulations. Blue cod from ITB and OTB were on average significantly smaller than blue cod from DUR, PEL, and QCS, with length distribution dominated by smaller individuals and only a few larger than the legal minimum landing size (330 mm). Additionally, blue cod from the Tasman Bay region grew significantly slower to smaller maximum lengths than blue cod from the Marlborough Sounds regions. In both areas, blue cod have been overexploited for decades and have undergone various management attempts to counteract the impact of overfishing with little success (Cole et al. 2000, Davidson 2001, Davey et al. 2008, Hartill et al. 2017, Fisheries New Zealand 2019). Particularly in the Tasman Bay region, the observed truncated length distributions towards large proportions of smaller individuals and slow growth could be an indication of higher mortality as consequences of long-term overexploitation. However, the observed differences in prey consumption and basal organic matter sources among habitats may have further limited growth, adding to the pattern observed (e.g. Roney et al. 2018). Interestingly, the 'simmr' mixing model output demonstrated high proportions of macroalgae at the base of the food

web of blue cod from OTB, which has been shown to support growth and condition of blue cod (Beer & Wing 2013). However, the observed smaller sizes and slower growth of blue cod in the region could be an indication that prey availability was insufficient, intraspecific competition was higher, and/or fishing mortality was higher (Cuenco et al. 1985).

Our results demonstrated significant fine spatial-scale differences in the trophic ecology among blue cod subpopulations from the Marlborough Sounds and Tasman Bay. While the analysis of the stomach contents did not resolve differences in the range of prey types that were consumed by blue cod among the regions, certain prey was prioritised by blue cod within regions. Isotopic niche analysis demonstrated that blue cod from the Marlborough Sounds (DUR, PEL, and QCS) had large isotopic niches, indicating that prey diversity may have been high, allowing a high degree of individual specialisation within generalist subpopulations. In contrast, the isotopic niche sizes of blue cod from Tasman Bay (ITB and OTB) were small, indicating that blue cod shared similar resources with low prey diversity as a likely result of the long history of dredging and trawling and loss of biogenic reefs in the region. Isotopic mixing model outputs suggested that blue cod from ITB were the only subpopulation with a majority of SPOM comprising the basal organic matter source in the food web, while food webs of blue cod from DUR, OTB, PEL, and QCS were based primarily on organic matter derived from macroalgae. The result was not anticipated for OTB, where macroalgae are scarce and blue cod were significantly smaller and grew slower than blue cod in the other regions, indicating that blue cod here may be accessing organic matter originating from kelp detritus.

Habitat degradation and the loss of complex biogenic reef structures had a significant impact on the trophic ecology of blue cod in Tasman Bay. The loss of food web complexity may directly decrease population stability, resistance, and resilience to anthropogenic or natural disturbances. Additionally, a low nutritional value of the diet has the potential to reduce individual growth rates, which in turn can result in a decrease in the egg production of the population, as smaller individuals carry fewer eggs or larvae than larger individuals (Beer et al. 2013). The habitat within Tasman Bay has been severely degraded due to extensive dredging and trawling. While the scallop fishery is closed, a small dredge oyster fishery remains in the area. Wing & Jack (2013) demonstrated that through the establishment of marine reserves in Fiordland, fish communities stabilised, and complex food webs were maintained, as

biodiversity was conserved. In Foveaux Strait, where oysters have been harvested for over 130 yr, only some, if any, undisturbed seafloor remained (Carbines & Cole 2009). However, after some areas were closed to oyster fishing, the habitat regenerated and blue cod abundance increased, highlighting the link between suitable habitat and diversity (Cranfield et al. 2001). In the case of Tasman Bay, the placement of marine protected areas and particularly trawl and dredge exclusion may aid the recovery of high-quality, diverse biogenic habitat and correspondingly productive subpopulations of blue cod.

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