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# ZOOTAXA

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**Systematic revision of the flatfish genus *Peltorhamphus* Günther, 1862  
(Teleostei: Pleuronectiformes: Rhombosoleidae), including description of  
a new species from Southeastern New Zealand, with biological and  
ecological summaries for the species**

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## Abstract

The flatfish genus *Peltorhamphus* Günther, 1862 (Pleuronectiformes: Rhombosoleidae) and its constituent species are redescribed based on examination of 1885 specimens. Four species are considered valid: three previously described (*P. novaezeelandiae* Günther, 1862, *P. latus* James, 1972, and *P. tenuis* James, 1972) and *P. kryptostomus* n. sp., described herein. *Peltorhamphus novaezeelandiae*, *P. latus*, and *P. tenuis* have widespread distributions on soft sediments in shallow coastal and inner continental shelf waters off both islands of New Zealand. *Peltorhamphus novaezeelandiae* has also been reported at the Chatham Islands. Previous reports of *P. novaezeelandiae* from Norfolk Island are erroneous. *Peltorhamphus kryptostomus* n. sp. has the most restricted geographic distribution in shallow coastal waters of the Otago-Southland region along the southeastern coast of South Island. The four species of *Peltorhamphus* are morphologically similar and overlap in many traditional meristic and morphometric features rendering identifications difficult, especially of juveniles and earlier life-history stages. Furthermore, throughout New Zealand waters, as many as three of the species possibly occur sympatrically, while in inshore areas of southeastern South Island, all four species may occur in sympatry. Novel morphological characters discovered in this study, combined with traditional diagnostic characters were used to identify and diagnose the species. *Peltorhamphus tenuis* is the most distinctive of the four, differing from congeners in the following combination of characters: greater length of second ocular-side pectoral-fin ray; its higher numbers of dorsal- and anal-fin rays and total vertebrae; having a series of small scales (best developed in specimens >70 mm SL) on blind sides of dorsal- and anal-fin rays (scales absent in congeners); its elongate body; and ocular-side pigmentation. The other three species are more similar morphologically and have frequently been misidentified both in fish collections and in some previous literature on these fishes. Of these three, *P. novaezeelandiae*, the largest in the genus, is distinguished from congeners by the combination of: its large size (reaching 510 mm SL vs. ≤ 200 mm SL); rounded head shape; blind-side squamation; the second ocular-side pectoral-fin ray shorter than body depth; ontogenetic variation in interorbital width; greater distance (4–8 scales wide) between ventral margin of lower eye and dorsal (upper) margin of rostral hood above the mouth; and 2–6 fleshy, finger-like filaments on the inner anteroventral margin of the fleshy skinfold on the ocular-side lower jaw. *Peltorhamphus latus* differs from congeners by the combination of: its short (maximum 150 mm SL), relatively deep body and bluntly pointed snout; blind-side squamation; relatively long, robust gillrakers on first gill arch, with upper limb gillrakers long, but not usually overlapping tips of dorsalmost gillrakers on the lower limb; black pigment on entire roof of mouth; relatively large eyes and narrow interorbital width (without significant ontogenetic variation); short diagonal distance (usually 2–3 scales wide) between ventral margin of lower eye and dorsal (upper) margin of rostral hood above the mouth; and absence of finger-like filaments on the inner anteroventral margin of the fleshy skinfold on the ocular-side lower jaw. *Peltorhamphus kryptostomus* n. sp. is distinguished from congeners by the combination of: its deep body and smoothly rounded snout; blind-side squamation; long, robust gillrakers on the first gill arch, with some posterior gillrakers on the upper limb overlapping tips of the first and second dorsalmost gillrakers on the lower limb; black pigment on the entire roof of the mouth; relatively large eyes and relatively narrow interorbital width; wide distance between ventral margin of lower eye and upper margin of rostral hood (3–6, usually 4–5, scales wide); and 1–4 finger-like filaments on the inner anteroventral margin of the fleshy skinfold on the ocular-side lower jaw. Ecological and life-history information are summarized for each species, and a key to juveniles > 40 mm SL and adults is also provided. Re-assessment of the number of valid species of *Peltorhamphus* provides better understanding of species diversity within this genus and within the Rhombosoleidae, as well as that for the flatfish assemblage residing in New Zealand waters.

**Key words:** New Zealand flatfishes, South Pacific flatfishes, taxonomy, species description, generic revision, synonymy, flatfish ecology, New Zealand Sole, Slender Sole, Speckled Sole, New Zealand Gray Sole

## Introduction

Rhombosoleid flatfishes (Pleuronectiformes: Rhombosoleidae) are small to large dextral flatfishes, and are prominent members of coastal marine demersal fish assemblages around New Zealand and southern Australia (Günther 1862; Norman 1926, 1934; Chapleau 1993; Guibord 2003; Gomon 2008; Munroe 2015a, 2015b). Among these flatfishes occurring in New Zealand waters is the genus *Peltorhamphus* Günther, 1862, originally described from at least 12 specimens and hypothesized by Günther (1862) as belonging to a single species, which he named, *P. novaezeelandiae*. Eleven of 12 syntypes included in the original description of this species were collected from several locations around New Zealand, whereas the twelfth syntype (BMNH 1848.3.18.216; 122.6 mm SL) was purportedly collected from an unspecified locality at Norfolk Island (Günther 1862). However, the capture location reported for this specimen is incorrect, and likely it too was also collected in New Zealand waters. Further comments regarding this Norfolk Island record are provided in the Distribution section in the generic account below.

Subsequent authors (Sherrin 1886; Hutton 1890; Jordan 1919, 1923; Phillipps 1927a, 1927b) considered *Peltorhamphus* to be monotypic, including Norman, first in his revision of flatfishes of the subfamily Rhombosoleinae (Norman 1926), and again in his detailed treatment of the subfamily (Norman 1934).

In the mid-20<sup>th</sup> century, Graham (1956) and Manikiam (1969) observed some differences among specimens of *Peltorhamphus* that suggested more than one species might be present. In 1972, James conducted a systematic revision of *Peltorhamphus* and recognized three species, *P. novaezeelandiae* Günther, and two new species, *P. tenuis* James, 1972 and *P. latus* James, 1972. He noted that these species are often captured simultaneously in many areas around New Zealand.

In redescribing *P. novaezeelandiae*, James discovered that of the 11 syntypes of *P. novaezeelandiae* he examined, only the largest (Fig. 1), earlier designated the lectotype of *P. novaezeelandiae* by Norman (1934), was actually that species. James re-identified 10 paralectotypes, including the specimen erroneously reported from Norfolk Island, as his newly described, *P. latus*. This is a much smaller species than *P. novaezeelandiae*, but shares morphological similarities with the latter species. James concluded that *P. novaezeelandiae* and *P. tenuis* are endemic to New Zealand waters, as is *P. latus*, with the exception of the one erroneously reported from Norfolk Island by Günther (1862). James (1972) also provided a key to identifying specimens of *Peltorhamphus* that he recognized. James' revision was accepted by subsequent authors until the species accounts presented in Munroe (2015b), wherein a fourth species of *Peltorhamphus* was identified.

One interesting result in James' analysis of morphometric data was the significant allometric growth observed in many morphological features of all three species. Only for *P. latus* did he report geographical variation in values for morphometric features, most of which was attributable to differences between specimens from the Blueskin Bay (southeast coast of the southern South Island) 'population' compared with those from other locations around New Zealand.

During the writing of the chapter on Rhombosoleid flatfishes for the book *The Fishes of New Zealand*, Munroe (2015b) examined specimens of *Peltorhamphus* from throughout New Zealand waters, including those from the Blueskin Bay region. These had previously been identified either as juvenile *P. novaezeelandiae* or adult and juvenile *P. latus*. After detailed study of this material, including several morphological features not previously used to differentiate species of *Peltorhamphus*, Munroe (2015b) concluded that an undescribed species was also present, which occurs sympatrically with juveniles and adults of *P. novaezeelandiae*, *P. latus* and *P. tenuis* in waters off the southeast coast of South Island.

Morphological similarities among the species (James 1972; Munroe 2015b), together with ecological sympatry, present difficulties when attempting to identify specimens (James 1972; Armitage *et al.* 1994; Banks *et al.* 2007). Juveniles (Roper 1979; Roper & Jillett 1981; Colman 1994) overlap more in many morphometric features than do adults (this study). Roper (1979) commented that juveniles of three species (*P. novaezeelandiae*, *P. latus* and *P. tenuis*) collected off southeastern South Island were difficult to identify, but that he could separate the species using a combination of morphometric features. Stevens *et al.* (2004) were unable to age juvenile *Peltorhamphus* because their samples included a mixture of species that were difficult to identify with accuracy. Similar problems

were encountered in the present study when attempting to identify juveniles, especially the smallest (< 30 mm SL) collected off the southeast coast of South Island. The magnitude of this issue became apparent in a subsample of 203 lots (1106 specimens) examined during the present study; 81 lots (40% of the total examined, including some paratypes), contained misidentified specimens. Such high frequencies of misidentifications, particularly in lots off the southeast coast of South Island with specimens of the new species co-mingled with *P. novaezeelandiae* or *P. latus*, or both, is problematic, and called into question some previous studies on distribution, ecology and abundance of juveniles of *P. novaezeelandiae* or *P. latus* from this region. Juveniles of *P. tenuis* are less frequently collected (based on number of specimens in museum collections and reported in literature) and are more easily identified, so have not contributed significantly to this problem.



**FIGURE 1.** Photographs of Ocular (A) and Blind (B) sides of the lectotype of *Peltorhamphus novaezeelandiae* (BMNH 1848.3.18.-, 245 mm SL); unknown location, New Zealand. Photos: S. Raredon.

For some larger, better known, and commercially important Rhombosoleids in New Zealand waters, including *P. novaezeelandiae*, limited information has been published on their ecology and fisheries. For *P. novaezeelandiae*, there is still little known about geographic and bathymetric distributions, life-history aspects, morphological variation and other biological parameters, ecology or population dynamics, including abundance or biomass estimates (Beentjes 2003). The smaller-sized, and commercially unimportant species of this family, including the smaller species of *Peltorhamphus*, are even less well studied.

The large number of misidentified specimens, compounded by discovery of a fourth, undescribed species, prompted re-evaluation of the systematics of species in this genus. Purposes of this paper are to: 1) evaluate the status and redescribe the previously named species, *P. novaezeelandiae*, *P. latus* and *P. tenuis*, including new information from additional specimens and morphological characters not previously used; 2) provide formal description and diagnosis of the undescribed species; 3) construct a key to assist in identification of larger juveniles (ca. > 40 mm SL) and adults of the four species; and, 4) collate and update information on the biology, ecology, size at maturity, and bathymetric and geographic distributions of the four species.

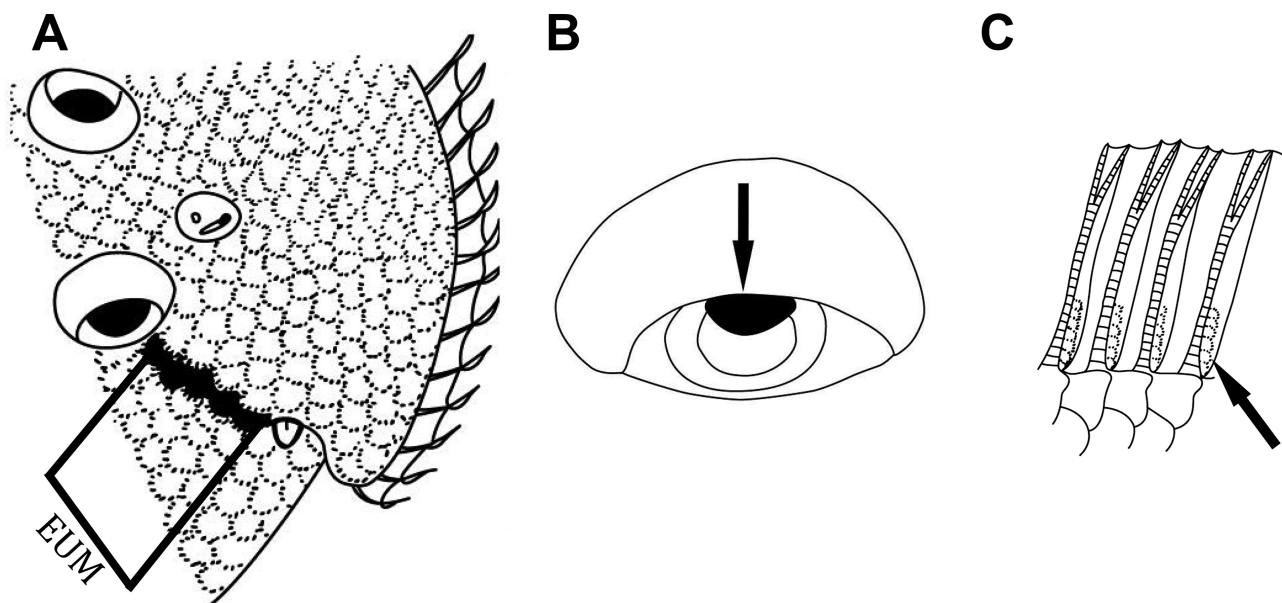
## Materials and methods

A total of 1885 specimens of *Peltorhamphus* was examined and identified in this study. Specimens examined were mostly those curated in the fish collection of the Museum of New Zealand Te Papa Tongarewa (Te Papa) Museum, but also included fresh and fresh-frozen specimens available at Te Papa, as well as specimens curated at other museums and institutions. Fish collections are listed by acronym in the Material examined section, following Fricke & Eschmeyer (2018). Material examined included primary types of *P. tenuis*, *P. novaezeelandiae*, *P. latus*, and *P. kryptostomus* **n. sp.** Based on Günther (1862), at least 12 specimens constitute the syntype series for *P. novaezeelandiae*, however, only 11 (lectotype and 10 paralectotypes) were available for the present study. All 13 paratypes of *P. tenuis* and 19 paratypes of *P. latus* were examined and included.

A subset of 486 specimens was radiographed: 119 *P. novaezeelandiae*, 134 *P. tenuis*, 158 *P. latus*, and 75 *P. kryptostomus* **n. sp.** Data of the following meristic features were recovered from radiographs: numbers of abdominal, caudal, and total vertebrae (including the hypural plate; PU1 vertebrae with two haemal or two neural spines were counted as two vertebrae); number of supracranial pterygiophores; counts of rays for dorsal, anal, caudal, and ocular- and blind-side pelvic fins; number of proximal dorsal-fin pterygiophores inserted into the first interneural space; and number of proximal anal-fin pterygiophores inserted anterior to the first haemal spine (HS1). Other meristic features counted through direct observation of 610 fishes (both radiographed and non-radiographed specimens) included: numbers of rays present in ocular- and blind-side pectoral fins, including the small transparent rays located at dorsal and ventral margins of these fins when they were visibly separate from other rays; number of lateral-line pores beginning with the pore located just slightly dorsoanterior to the vertical through the posterior margin of the opercle, and including the pore on the scale located on the posterior caudal peduncle at the flexure point of the caudal fin; interorbital scales were counted as the number of scales along the vertical row between midpoints of the eyes; number of scales between eye and mouth included those inserted along the diagonal row between the anteroventral margin of the lower eye and dorsal margin of the rostral flap above the mouth opening (Fig. 2A); number of head scales were counted along the vertical from midpoint of the upper eye to dorsal margin of head; number of finger-like filaments on inner anteroventral margin of the fleshy skinfold on the ocular-side lower jaw (Figs. 3A–B); gillraker counts made from the first blind-side gill arch included counts of upper limb gillrakers, lower limb gillrakers including the gillraker (when present) in the angle between upper and lower arches, and total gillrakers (sum of upper and lower gillraker counts). Terminology for scales followed that of Roberts (1993).

A set of 19 morphometric features was taken from 268 individuals, and selected measurements were taken from another 28 specimens of the four species (detailed information in Material examined section for each species). Morphometric features up to 150 mm were measured to the nearest 0.1 mm with dial calipers, or with a microscope fitted with an ocular micrometer. Measurements of 150 mm and larger were made using a measuring board to the nearest 1.0 mm. Morphometric features included: standard length (SL)—straight line distance on blind side from anterior tip of snout to flexion point of hypural plate at base of caudal fin; trunk length (TKL)—straight line distance on blind side from posterior angle of opercle to flexion point of hypural plate at base of caudal fin; body depth (BD)—greatest width across the body on blind side, exclusive of dorsal- and anal-fin rays; head

length (HL)—horizontal distance on ocular side from anterior tip of snout to posteriormost point on opercle; head width (HW)—vertical distance on ocular side across head at posteriormost point of opercle, including width of isthmus ventrally; ratio of head width to head length (HW/HL); dorsal head width (DHW)—straight line distance on ocular side between midpoint of upper eye and dorsal margin of body exclusive of fin rays; postorbital head length (POL)—horizontal distance on ocular side from posterior margin of lower eye to distal margin of opercle; snout length (SNL)—horizontal length on ocular side between anterior tip of snout and anterior margin of lower eye; eye diameter (ED)—greatest horizontal distance across lower (non-migrated) eye; interorbital width (IO)—vertical distance between midpoints of lower and upper eyes; upper jaw length (UJL)—straight line distance between posterior and anterodorsal ends of blind-side upper jaw; eye to mouth distance (EUM; Fig. 2A)—diagonal distance between ventral rim of lower eye at mid-eye and dorsalmost margin of rostral hood above the mouth; rostral hook length (RHL)—measured on blind side as width between horizontals at dorsal margin of blind-side upper jaw and at ventralmost tip of rostrum; upper head lobe (UHL)—straight line distance on ocular side between upper point of opercular opening and dorsal margin of body; lower head lobe (LHL)—straight line distance on ocular side between upper point of opercular opening and horizontal at ventral margin of opercle (not including isthmus or branchiostegals); ocular-side pectoral fin length (OSP)—straight line distance between base and distal tip of longest fin ray; blind-side pectoral fin length (BSP)—straight line distance between base and distal tip of longest fin ray; caudal-fin length (CFL)—straight line distance on blind side between base and distal tip of longest fin ray; caudal peduncle depth (CPD)—greatest vertical distance on blind side across caudal peduncle.



**FIGURE 2.** Selected anatomical features of *Peltorhamphus*. **A.** Scales (in black) in diagonal row between anteroventral margin of lower eye (EUM distance) and dorsal margin of rostral flap above mouth. **B.** Pupillary operculum (indicated by arrow) of *P. latus*. **C.** Scales on blind sides of dorsal- and anal-fin rays in *P. tenuis*. Drawn by: M. Freeborne.

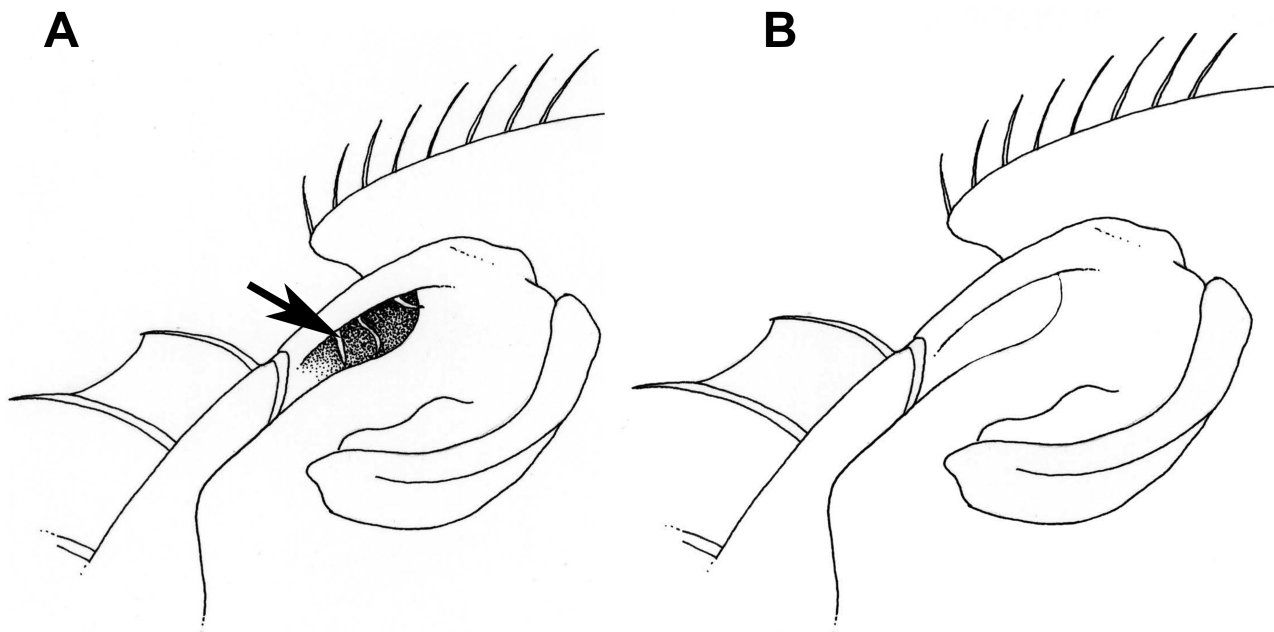
Morphometric data for individual species appear in the individual species accounts. Many morphometric features of all four species display allometric growth even after attempts to standardize measurements by converting to percent SL or HL. Plots of morphometric data for select features, converted to either percent SL or HL, are also presented for each species in their species account to show patterns of allometric growth in these features.

Size, sex, and location and depth of capture were tallied for all specimens examined where the data were available. Comparisons of sizes (mm SL) of males and females within a species were summarized for 598 specimens.

Sex was determined by macroscopic examination of the gonads, either by dissection to confirm sex or maturity stage of non-type specimens (usually for males, immature females, and some mature females with elongate ovaries, but without ova evident), or by direct external examination of ripe ovaries visible through the abdominal wall by shining a light through from the blind side (usually mature females with elongate, but not ripe ovaries, and females with ripening/ripe ovaries, where their fully extended ovaries were easily observed through the body wall).

Ovaries are tubular structures that elongate posteriorly as the fish matures. Ovaries of immature females are narrow and only slightly elongate posteriorly. At this stage, external appearance of the ovary is reminiscent of the testes in

males of comparable size. With dissection the ovary can be distinguished by its hollow interior. Maturing females have conspicuously elongate ovaries that extend much farther posteriorly, to a point about equal to 75% of SL, and have a broader, tubular shape compared with those of immature females. In mature ovaries developing ova are often evident upon external inspection, and are readily apparent with dissection.



**FIGURE 3.** Blind-side view of ventral mouth region illustrating anteroventral skin fold on ocular-side lower jaw in *Peltorhamphus*. **A.** Lower-jaw marginal skinfold with filaments present (*P. novaezeelandiae*, *P. tenuis*, and *P. kryptostomus* n. sp.). **B.** Lower-jaw marginal skinfold without filaments (only *P. latus*). Drawn by: M. Freeborne.

In *Peltorhamphus*, testes are solid, tubular structures, somewhat triangular anteriorly, more elongate posteriorly. Although testes elongate slightly posteriorly as males mature, they usually do not extend further posteriorly than the vertical through the midpoint of the standard length.

Size and stage of maturity (mature, immature) were determined for 355 females and discussed in greater detail in the individual species accounts. In this paper, juvenile refers to females with immature ovaries, and males of the same species of corresponding size. Because detectable external differences (e.g., size or shape) in the testes of mature and immature males are not evident macroscopically, maturity stages of males were assumed to be similar to those of females of corresponding sizes. Males possibly have a different maturation schedule, maturing at sizes smaller or larger than those of the females of a species. Maturity stages of males would best be determined through histological analyses, which was beyond the scope of the present study.

Depth of capture information was recorded for 1394 specimens and summarized. Where capture depths included a range of depths over which gear sampled, a mean depth of capture was used. Size at depth information for each species is discussed under the individual species accounts below.

Literature references pertaining to systematic subjects appear in the synonymies of each species in their respective species accounts. Biological, ecological, and fisheries-related literature references appear with annotated comments in Appendices 1–3 for *P. novaezeelandiae*, *P. tenuis*, and *P. latus*, respectively.

## Systematics Section

### Genus *Peltorhamphus* Günther, 1862

Figs. 1–28; Tables 1–13

Günther 1862:460 (original description without figures or illustrations; type species *Peltorhamphus novaezeelandiae* Günther, 1862 by monotypy; New Zealand; Norfolk Island record erroneous).

Macleay 1882:138 (generic redescription; New Zealand; Norfolk Island record erroneous).



Hutton 1890:32 (redescription following Günther 1862; counts, measurements, colour description; monotypic; valid genus in Pleuronectidae; New Zealand; Norfolk Island record erroneous).

Waite 1907:27 (listed, New Zealand).

Waite 1910:383 (listed, New Zealand; Norfolk Island record erroneous).

Waite 1911:213 (black & white drawing of type species; in key; synonymy; New Zealand, including Chatham Islands).

Waite 1916:454 (listed, New Zealand; Norfolk Island record erroneous; after Günther, 1862).

Jordan 1919:319 (listed in genera of fishes).

Jordan 1923:169 (listed among genera of Rhombosoleidae).

Norman 1926:257 (valid genus in Rhombosoleinae: Pleuronectidae; type species *Peltorhamphus novaezeelandiae* Günther, 1862 by monotypy; redescription based on 19 specimens including syntypes; counts, morphometrics, colour notes; New Zealand, Chatham Islands; Norfolk Island record erroneous).

Norman 1934:427 (valid genus in Rhombosoleinae: Pleuronectidae; line drawing; type species *Peltorhamphus novaezeelandiae* Günther, 1862 by monotypy; redescription; brief comment on relationships; brief synonymy; designation of lectotype; New Zealand, Chatham Islands; Norfolk Island record erroneous).

Whitley 1968:49 (listed, New Zealand; type species *Peltorhamphus novaezeelandiae* Günther, 1862).

James 1972:346 (valid genus in Rhombosoleinae: Pleuronectidae (following Norman 1934); synonymy; redescription and diagnosis; revision of species within genus including description of two new species; type species *Peltorhamphus novaezeelandiae* Günther, 1862; discussion of lectotype designation by Norman (1934); generic relationships; New Zealand, Chatham Islands; Norfolk Island record erroneous).

Ahlstrom *et al.* 1984:643 (listed; valid genus in Rhombosoleinae: Pleuronectidae).

Hensley & Ahlstrom 1984:684 (listed, valid genus in Rhombosoleinae: Pleuronectidae; morphological features distinguishing genus from other Rhombosoleids).

Sakamoto 1984:211 (valid genus in Rhombosoleinae: Pleuronectidae; osteology; discussion of relationships of genus based on phenetic classification; three species recognized in genus).

Eschmeyer 1990:306 (valid genus in Rhombosoleinae: Pleuronectidae; type species *Peltorhamphus novaezeelandiae* Günther, 1862 by monotypy).

Eschmeyer 1998a:2069 (valid genus in Rhombosoleinae: Pleuronectidae; type species *Peltorhamphus novaezeelandiae* Günther, 1862 by monotypy).

Eschmeyer 1998c:2492 (classification; valid genus in Rhombosoleinae: Pleuronectidae).

Guibord 2003:202 (osteology; morphology; monophyletic genus defined on apomorphic characters; relationships within Rhombosoleidae based on cladistic analyses; relationships among three species in genus unresolved).

Evseenko 2004:20 (valid genus in Rhombosoleinae: Pleuronectidae; type species *Peltorhamphus novaezeelandiae* Günther, 1862 by monotypy).

Nelson 2006:448 (valid genus in Rhombosoleidae).

Munroe 2015b:1695 (valid genus in Rhombosoleidae).

Fricke *et al.* 2020. Online version (valid genus in Pleuronectidae: Rhombosoleidae; type species *Peltorhamphus novaezeelandiae* Günther, 1862).

**TABLE 1.** Frequency distributions of 21 meristic features for four species of *Peltorhamphus*. Counts in bold-face type represent those for the holotype or lectotype (*P. novaezeelandiae*) of each species.

Species	Supracranial Pterygiophores											N
	21	22	23	24	25	26	27	28	29	30	31	
<i>novaezeelandiae</i>	–	–	1	<b>4</b>	34	37	37	13	5	–	–	131
<i>tenuis</i>	–	–	–	–	3	12	<b>53</b>	45	16	6	1	136
<i>latus</i>	–	–	2	10	23	36	59	<b>17</b>	5	–	–	152
<i>kryptostomus</i>	2	4	<b>37</b>	23	7	1	–	–	–	–	–	74

Species	Pterygiophores Inserted in Interneural Space 1				N
	1	2	3	4	
<i>novaezeelandiae</i>	–	<b>31</b>	97	3	131
<i>tenuis</i>	–	7	<b>115</b>	14	136
<i>latus</i>	–	93	<b>59</b>	3	155
<i>kryptostomus</i>	1	52	<b>21</b>	–	74

Species	Pterygiophores Anterior To Haemal Spine 1							N
	6	7	8	9	10	11	12	
<i>novaezeelandiae</i>	–	1	5	<b>35</b>	62	22	2	127
<i>tenuis</i>	–	–	9	36	<b>55</b>	7	–	107
<i>latus</i>	–	–	24	73	<b>46</b>	6	–	149
<i>kryptostomus</i>	2	3	26	<b>29</b>	12	2	–	74

Species	Abdominal Vertebrae			N
	3+6	3+7	3+8	
<i>novaezeelandiae</i>	4	<b>124</b>	4	132
<i>tenuis</i>	4	<b>126</b>	2	132
<i>latus</i>	1	<b>154</b>	2	157
<i>kryptostomus</i>	3	<b>71</b>	1	75

Species	Caudal Vertebrae								N
	26	27	28	29	30	31	32	33	
<i>novaezeelandiae</i>	–	<b>32</b>	84	16	–	–	–	–	132
<i>tenuis</i>	–	–	–	1	39	75	<b>16</b>	1	130
<i>latus</i>	28	<b>112</b>	18	–	–	–	–	–	158
<i>kryptostomus</i>	1	<b>44</b>	29	1	–	–	–	–	75

Species	Total Vertebrae									N
	35	36	37	38	39	40	41	42	43	
<i>novaezeelandiae</i>	–	–	<b>32</b>	83	17	–	–	–	–	132
<i>tenuis</i>	–	–	–	–	1	40	77	<b>18</b>	2	136
<i>latus</i>	1	27	<b>109</b>	20	–	–	–	–	–	157
<i>kryptostomus</i>	–	1	<b>45</b>	29	–	–	–	–	–	75

Species	Caudal-fin Rays				N
	17	18	19	20	
<i>novaezeelandiae</i>	1	<b>128</b>	2	–	131
<i>tenuis</i>	2	<b>131</b>	3	–	136
<i>latus</i>	2	<b>149</b>	7	1	159
<i>kryptostomus</i>	1	<b>69</b>	3	1	74

Species	Ocular-side Pectoral-fin Rays							N
	5	6	7	8	9	10	11	
<i>novaezeelandiae</i>	–	–	–	1	32	<b>65</b>	17	115
<i>tenuis</i>	1	1	6	27	<b>49</b>	20	–	104
<i>latus</i>	–	–	1	16	80	<b>57</b>	4	158
<i>kryptostomus</i>	–	–	2	7	<b>27</b>	21	7	64

Species	Blind-side Pectoral-fin Rays						N
	5	6	7	8	9	10	
<i>novaezeelandiae</i>	–	1	1	28	<b>60</b>	25	115
<i>tenuis</i>	1	–	<b>25</b>	66	13	1	106
<i>latus</i>	–	1	12	59	<b>36</b>	3	111
<i>kryptostomus</i>	–	–	<b>8</b>	35	20	1	64

Species	Ocular-side Pelvic-fin Rays		
	5	6	N
<i>novaezeelandiae</i>	6	131	137
<i>tenuis</i>	1	110	111
<i>latus</i>	2	147	149
<i>kryptostomus</i>	–	74	74

Species	Blind-side Pelvic-fin Rays				N
	2	3	4	5	
<i>novaezeelandiae</i>	–	2	135	–	137
<i>tenuis</i>	1	–	103	–	104
<i>latus</i>	–	4	139	4	147
<i>kryptostomus</i>	–	2	71	–	73

Species	Dorsal-fin Rays													
	83	84	85	86	87	88	89	90	91	92	93	94	95	96
<i>novaezeelandiae</i>	–	–	–	–	–	–	–	–	–	–	1	3	5	7
<i>tenuis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>latus</i>	1	2	1	8	6	10	16	7	16	20	8	16	13	7
<i>kryptostomus</i>	–	–	–	1	–	3	8	3	8	14	11	12	10	2

Species	Dorsal-fin Rays (continued)													
	97	98	99	100	101	102	103	104	105	106	107	108	109	110
<i>novaezeelandiae</i>	5	7	7	12	15	13	20	16	3	7	2	4	2	2
<i>tenuis</i>	–	1	3	3	10	17	10	21	21	11	18	7	6	1
<i>latus</i>	14	7	3	–	–	–	–	–	–	–	–	–	–	–
<i>kryptostomus</i>	3	–	–	–	–	–	–	–	–	–	–	–	–	–

Species	Dorsal-fin Rays (continued)			N
	112	116		
<i>novaezeelandiae</i>	–	–		131
<i>tenuis</i>	1	1		131
<i>latus</i>	–	–		155
<i>kryptostomus</i>	–	–		75

Species	Anal-fin Rays															
	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	
<i>novaezeelandiae</i>	–	–	–	–	–	–	–	–	–	2	3	5	9	9	10	
<i>tenuis</i>	–	–	–	–	–	–	–	–	–	–	–	1	3	3	5	
<i>latus</i>	1	–	2	9	13	16	26	30	19	11	13	7	4	3	–	
<i>kryptostomus</i>	–	–	–	1	–	–	–	–	6	14	11	14	16	8	3	

Species	Anal-fin Rays (continued)									N
	66	67	68	69	70	71	72	73		
<i>novaezeelandiae</i>	18	23	25	11	6	6	–	2		129
<i>tenuis</i>	8	19	16	21	19	9	7	–		111
<i>latus</i>	–	–	–	–	–	–	–	–		154
<i>kryptostomus</i>	1	1	–	–	–	–	–	–		75

Species	Scales Eye-Jaw									N
	1	2	3	4	5	6	7	8	9	
<i>novaezeelandiae</i>	–	2	3	11	36	<b>28</b>	7	4	2	93
<i>tenuis</i>	–	–	2	18	54	14	<b>5</b>	1	–	94
<i>latus</i>	3	50	<b>63</b>	2	–	–	–	–	–	118
<i>kryptostomus</i>	–	–	1	21	<b>36</b>	2	–	–	–	60

Species	Lateral-line scales													
	64	65	66	67	68	69	70	71	72	73	74	75	76	77
<i>novaezeelandiae</i>	–	–	–	–	–	–	–	–	–	–	–	–	1	–
<i>tenuis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>latus</i>	1	–	9	7	6	6	4	8	7	10	9	8	7	3
<i>kryptostomus</i>	1	–	–	2	1	2	1	4	5	4	5	4	6	5

Species	Lateral-line scales (continued)													
	78	79	80	81	82	83	84	85	86	87	88	89	90	91
<i>novaezeelandiae</i>	–	–	–	2	–	2	1	5	4	3	2	1	5	<b>4</b>
<i>tenuis</i>	–	–	–	–	1	1	1	1	–	1	7	10	4	4
<i>latus</i>	5	8	2	5	<b>3</b>	4	–	–	–	1	–	–	–	–
<i>kryptostomus</i>	<b>8</b>	2	1	1	1	–	–	–	–	–	–	–	–	–

Species	Lateral-line scales (continued)													
	92	93	94	95	96	97	98	99	100	101	102	103	104	
<i>novaezeelandiae</i>	9	3	6	5	3	3	3	3	4	1	–	1	–	
<i>tenuis</i>	10	8	5	1	5	<b>11</b>	8	5	1	2	–	1	1	
<i>latus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	
<i>kryptostomus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	

Species	Lateral-line scales (continued)					N
	105	106	107	108		
<i>novaezeelandiae</i>	1	2	1	1	76	
<i>tenuis</i>	1	–	–	–	90	
<i>latus</i>	–	–	–	–	113	
<i>kryptostomus</i>	–	–	–	–	53	

Species	Interorbital Scales							N
	0	1	2	3	4	5	6	
<i>novaezeelandiae</i>	–	3	12	68	<b>9</b>	2	1	95
<i>tenuis</i>	–	1	17	<b>72</b>	7	1	–	98
<i>latus</i>	2	<b>80</b>	36	–	–	–	–	118
<i>kryptostomus</i>	–	–	15	<b>43</b>	5	–	–	63

Species	Head Scales Mid-Eye to Dorsal Margin									
	5	6	7	8	9	10	11	12	13	N
<i>novaezeelandiae</i>	–	2	1	2	17	<b>37</b>	10	11	2	82
<i>tenuis</i>	–	–	1	15	<b>27</b>	24	3	3	–	73
<i>latus</i>	2	2	23	41	<b>22</b>	4	–	–	–	94
<i>kryptostomus</i>	–	–	3	<b>12</b>	27	14	3	–	–	59

Species	Filaments on Ventral Margin of Ocular-side Lower Jaw										N
	0	1	2	3	4	5	6	7	8		
<i>novaezeelandiae</i>	1	2	16	17	27	14	4	–	2	83	
<i>tenuis</i>	6	20	30	23	12	2	–	–	–	93	
<i>latus</i>	120	–	1	–	–	–	–	–	–	121	
<i>kryptostomus</i>	5	25	12	11	9	1	–	–	–	63	

Species	Gillrakers on Upper Limb of First Gill Arch							N
	1	2	3	4	5	6		
<i>novaezeelandiae</i>	2	10	70	45	8	2	137	
<i>tenuis</i>	–	19	42	39	2	–	102	
<i>latus</i>	–	11	119	71	3	–	204	
<i>kryptostomus</i>	–	–	–	12	46	6	64	

Species	Gillrakers on Lower Limb of First Gill Arch												N
	5	6	7	8	9	10	11	12	13	14	15	16	
<i>novaezeelandiae</i>	–	–	1	4	5	12	27	38	31	14	5	1	138
<i>tenuis</i>	2	–	6	21	25	32	12	4	–	–	–	–	102
<i>latus</i>	–	3	11	39	83	52	13	3	–	–	–	–	204
<i>kryptostomus</i>	–	–	–	–	–	3	15	26	17	3	–	–	64

Species	Total Number of Gillrakers on First Gill Arch													N
	8	9	10	11	12	13	14	15	16	17	18	19	20	
<i>novaezeelandiae</i>	–	–	4	4	5	8	24	28	27	18	11	7	2	138
<i>tenuis</i>	1	1	10	18	24	17	18	9	3	1	–	–	–	102
<i>latus</i>	1	4	9	36	56	57	27	8	4	–	–	–	–	202
<i>kryptostomus</i>	–	–	–	–	–	–	1	8	12	19	22	1	1	64

**Description** (based on Günther (1862), Norman (1926, 1934), James (1972), Guibord (2003), and current study). Frequency data for meristic features of the four species of *Peltorhamphus* appear in Table 1; morphometric data for the four species are summarized in Table 2. Body ovate to elongate (Figs. 4A–D, 7–8, 11, 17, 18, 21–22, 25–26); greatest body depth usually anterior to, sometimes almost at, body midpoint; caudal peduncle relatively broad and very short. Head wide, with broadly rounded to bluntly pointed snout ending in conspicuous, flat, fleshy, ventrally directed rostral hook. Rostral hook expanded posteriorly as membranous flap (rostral hood) nearly, or sometimes completely, concealing mouth on ocular side (Figs. 4–5).

Nasal organs nearly symmetrical in position on either side of head, each with inhalant and exhalant nares (Figs. 5A–C); olfactory laminae few, parallel to one another and to main axis of body, without central rachis. Eyes dextral, moderate in size; with anterior margin of upper eye nearly equal in position to anterior margin of lower eye; eyes almost contiguous to separated by narrow to wide interorbital space (Figs. 5A–C).

Pupillary operculum (Fig. 2B) present (sometimes only weakly developed) or absent. Mouth small, inconspicuous on ocular side (Figs. 5A–C); jaws curved, especially on blind side. Ocular-side lower lip without fringe of labial papillae. Blind-side dentary and premaxilla with two distinct series of small, slender, pointed teeth; ocular-side dentary and premaxilla toothless. Inner anteroventral margin of fleshy skinfold on ocular-side lower jaw of three species with 1–8 (usually 1–5) small, pointed, fleshy, finger-like filaments (Fig. 3A); fourth species without filaments (Fig. 3B). Vomer and palatines without teeth. Blind-side palatine lying beneath ectopterygoid bone, without posterior bony projection (*Peltorhamphus* among Rhombosoleids lacks this bony projection). Lower pharyngeals rather narrow, their inner edges scarcely angular, approximated anteriorly; lower pharyngeals scarcely expanded posteriorly; each with several series of pointed teeth. Gill openings narrow; gill membranes broadly united to each other ventrally, but not connected to isthmus. Gillrakers present on upper and lower branches of first gill arch; moderate in number (8–20); small, conical. Dorsal-fin origin far forward reaching to tip of rostral hook;

anterior dorsal-fin rays partly free from membrane; remainder of dorsal-fin rays and all, or nearly all, anal-fin rays branched. Anal-fin origin just posterior to anus, without spine; anal-fin rays similar to dorsal-fin rays in middle and posterior parts of dorsal fin. Blind sides of dorsal- and anal-fin rays without scales (three species); one species with one or two series of small ctenoid scales extending over basal one-third to nearly entire lengths of rays (Fig. 2C). Dorsal and anal fins on eyed side with low scaly sheath covering basal parts of fins. Pectoral radials absent, pectoral-fin rays inserted on hypocoracoid. Both pectoral fins well developed; ocular-side fin larger and longer than blind-side counterpart, with second dorsal-most ray conspicuously prolonged and filamentous in both sexes (Figs. 4A–D); ocular-side pectoral-fin rays 5–11, usually 8–11; blind-side pectoral-fin rays 5–10, usually 7–10. Pelvic fins asymmetrical in size and position. Ocular-side pelvic fin with 6, widely spaced rays; its origin far forward on isthmus extending to the urohyal; posteriorly, ocular-side pelvic fin with broad membranous connection to first anal-fin ray. Blind-side pelvic fin noticeably shorter than ocular-side counterpart, short-based with usually 4 (rarely 2, 3, or 5), narrowly spaced rays; not connected to anal fin or ocular-side pelvic fin; its origin located usually at point equal to space between bases of fifth and sixth ocular-side pelvic-fin rays. Scales small; those on ocular side transforming ctenoid (Roberts 1993); scales on blind side transforming ctenoid or cycloid. Lateral line equally developed on both sides of body; straight with slight curve above pectoral fin; supratemporal branch poorly developed. Scales in lateral line 64–108.

**TABLE 2.** Comparisons of ranges and mean values for 19 morphometric features (in % SL or % HL) for specimens of four species of *Peltorhamphus*. Abbreviations defined in Methods and Materials.

SPECIES	RANGE	MEAN	N
<b>BD/SL</b>			
<i>P. latus</i>	39.7–50.1	44.1	69
<i>P. kryptostomus</i>	42.5–50.4	46.7	34
<i>P. novaezeelandiae</i>	33.2–48.3	42.4	87
<i>P. tenuis</i>	31.2–42.3	36.3	78
<b>TKL/SL</b>			
<i>P. latus</i>	64.8–83.8	72.5	68
<i>P. kryptostomus</i>	65.3–76.2	71.8	34
<i>P. novaezeelandiae</i>	70.1–81.6	74.5	87
<i>P. tenuis</i>	70.1–86.1	75.6	72
<b>HL/SL</b>			
<i>P. latus</i>	22.9–30.1	27.7	68
<i>P. kryptostomus</i>	26.1–32.5	28.4	34
<i>P. novaezeelandiae</i>	22.2–30.8	25.6	87
<i>P. tenuis</i>	20.9–27.9	24.7	78
<b>HW/SL</b>			
<i>P. latus</i>	29.8–49.5	40.4	68
<i>P. kryptostomus</i>	34.2–49.3	44.2	34
<i>P. novaezeelandiae</i>	32.0–47.4	39.5	87
<i>P. tenuis</i>	24.2–38.7	29.6	78
<b>POL/SL</b>			
<i>P. latus</i>	11.3–15.5	13.3	68
<i>P. kryptostomus</i>	12.9–16.3	14.4	34
<i>P. novaezeelandiae</i>	11.7–16.1	13.7	87
<i>P. tenuis</i>	10.8–14.1	12.3	78

<b>UHL/SL</b>			
<i>P. latus</i>	15.0–28.5	22.7	51
<i>P. kryptostomus</i>	22.0–26.4	24.7	34
<i>P. novaezeelandiae</i>	18.3–25.9	22.4	85
<i>P. tenuis</i>	16.0–23.5	19.8	72
<b>LHL/SL</b>			
<i>P. latus</i>	11.2–17.3	14.1	51
<i>P. kryptostomus</i>	11.5–18.8	15.1	34
<i>P. novaezeelandiae</i>	9.0–16.0	12.6	85
<i>P. tenuis</i>	7.6–14.3	11.2	72
<b>OSP/SL</b>			
<i>P. latus</i>	19.9–45.0	30.3	65
<i>P. kryptostomus</i>	15.0–35.0	28.8	34
<i>P. novaezeelandiae</i>	13.1–37.0	27.4	83
<i>P. tenuis</i>	26.6–56.4	39.4	73
<b>CFL/SL</b>			
<i>P. latus</i>	19.1–26.6	23.1	66
<i>P. kryptostomus</i>	17.6–32.2	22.0	34
<i>P. novaezeelandiae</i>	14.8–26.1	19.8	84
<i>P. tenuis</i>	16.2–26.2	20.5	74
<b>CPD/SL</b>			
<i>P. latus</i>	8.8–13.1	10.7	51
<i>P. kryptostomus</i>	9.5–11.9	10.7	34
<i>P. novaezeelandiae</i>	8.6–11.1	9.5	85
<i>P. tenuis</i>	6.9–10.2	8.7	71
<b>HW/HL</b>			
<i>P. latus</i>	1.0–2.2	1.46	68
<i>P. kryptostomus</i>	1.2–1.8	1.56	34
<i>P. novaezeelandiae</i>	1.2–1.8	1.55	87
<i>P. tenuis</i>	0.9–1.7	1.20	78
<b>POL/HL</b>			
<i>P. latus</i>	43.4–62.3	47.9	68
<i>P. kryptostomus</i>	46.5–56.2	50.5	34
<i>P. novaezeelandiae</i>	47.0–59.5	53.4	87
<i>P. tenuis</i>	44.0–57.7	49.8	78
<b>SNL/HL</b>			
<i>P. latus</i>	24.1–44.3	30.9	68
<i>P. kryptostomus</i>	27.8–33.6	30.9	34
<i>P. novaezeelandiae</i>	24.3–40.3	30.6	87
<i>P. tenuis</i>	29.8–39.9	34.8	78

<b>ED/HL</b>			
<i>P. latus</i>	17.7–27.3	21.9	68
<i>P. kryptostomus</i>	13.5–23.3	18.6	34
<i>P. novaezeelandiae</i>	12.2–21.6	16.5	87
<i>P. tenuis</i>	12.0–20.2	15.2	78
<b>IO/HL</b>			
<i>P. latus</i>	3.1–7.9	5.4	68
<i>P. kryptostomus</i>	5.6–11.2	8.8	34
<i>P. novaezeelandiae</i>	5.3–16.6	10.8	87
<i>P. tenuis</i>	7.5–13.2	10.2	78
<b>EUM/HL</b>			
<i>P. latus</i>	6.0–11.7	9.0	68
<i>P. kryptostomus</i>	9.3–18.4	14.9	34
<i>P. novaezeelandiae</i>	7.4–26.7	16.7	87
<i>P. tenuis</i>	9.7–19.2	15.1	77
<b>DHW/HL</b>			
<i>P. latus</i>	23.1–42.0	31.8	68
<i>P. kryptostomus</i>	25.0–43.4	34.3	34
<i>P. novaezeelandiae</i>	22.0–57.9	38.7	85
<i>P. tenuis</i>	24.5–46.4	35.0	78
<b>UJL/HL</b>			
<i>P. latus</i>	22.5–30.1	25.8	68
<i>P. kryptostomus</i>	24.1–33.3	28.9	34
<i>P. novaezeelandiae</i>	21.2–38.2	30.4	87
<i>P. tenuis</i>	22.1–42.9	27.0	78
<b>RHL/HL</b>			
<i>P. latus</i>	12.4–31.0	22.8	68
<i>P. kryptostomus</i>	14.2–30.3	21.4	34
<i>P. novaezeelandiae</i>	18.7–35.7	26.4	87
<i>P. tenuis</i>	21.3–37.6	29.1	76

Intestine elongate; no pyloric caecae. Genital papilla small, located on ocular side of body about three scale rows dorsal to body midline between end of pelvic fin and beginning of anal fin. Anus located on blind side of body, slightly off body midline, bordered medially by blind-side pelvic fin.

Supracranial dorsal-fin proximal pterygiophores 21–31, usually 23–30; usually with 2–4 dorsal-fin proximal pterygiophores inserted into first interneural space (examples of each visible in Fig. 6). Total vertebrae 35–43; abdominal vertebrae with parapophyses not united, usually 10 (3 vertebrae without and 7 with haemal spines; Fig. 6), rarely 9 (3 + 6) or 11 (3 + 8). Caudal vertebrae 26–33. Dorsal-fin rays 83–116. Anal-fin rays 51–73. Anal-fin proximal pterygiophores inserted anterior to first haemal spine 6–12, usually 8–11. Caudal-fin rays 18, rarely 17, 19 or 20.

*Colour.* Background colour of ocular side usually light- to dark-brown, greenish-gray, or gray with variable darker markings of small ocelli, irregular dark blotches of various sizes, series of faint longitudinal lines, or with small, irregular clusters of darker melanophores scattered over the body surface; some species with longitudinal series of white blotches along dorsal and ventral contours of body; sometimes with up to three conspicuous



black blotches on lateral line. Blind side usually white, or sometimes sooty gray featuring dense clusters of small melanophores. Ocular sides of dorsal and anal fins uniformly pigmented, or with a series of a dark ray alternating with several lighter-coloured rays.

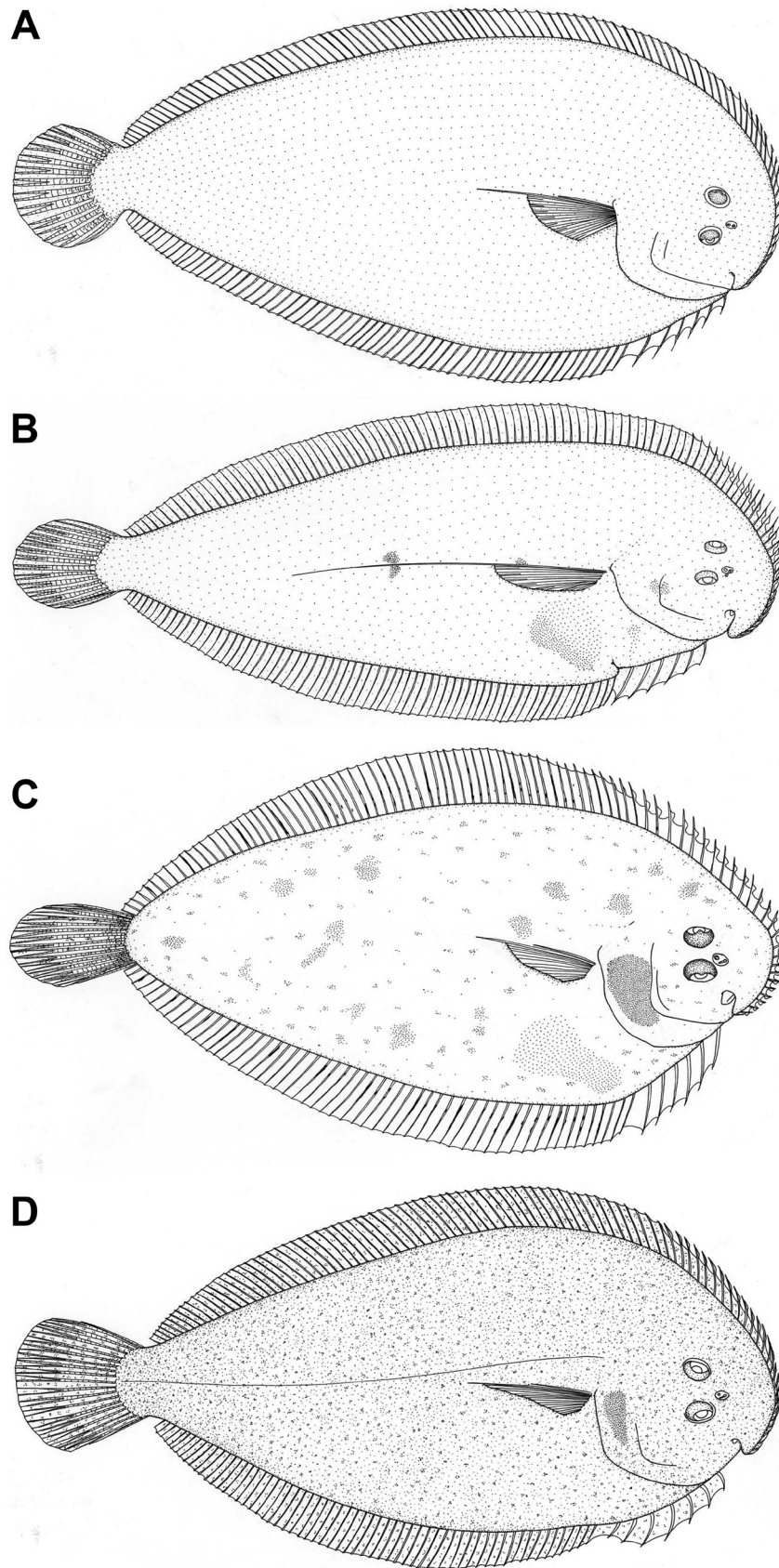
**Remarks.** Günther (1862:460) described *Peltorhamphus* as a monotypic genus of the family Pleuronectidae, which at the time included all known species of flatfishes. He distinguished this new genus from other ‘pleuronectid’ flatfishes by the combination of: eyes on right side of head; a small mouth with small teeth developed only on blind-side jaws; dilated, flat snout ending in a rostral hook; eyes moderate in size; both pectoral fins present and well developed; dorsal-fin origin commencing on foremost part of snout; dorsal- and anal-fin rays branched and without scales; two pelvic fins present, the ocular-side pelvic fin connected to anal fin and blind-side pelvic fin much smaller than its counterpart. He placed this genus near *Rhombosolea* Günther, 1862 noting that it differed from *Rhombosolea* primarily in having two pelvic fins (vs. one in *Rhombosolea*) and in the more advanced position of the dorsal-fin origin on the snout. Günther (1862:460) described a single species, *Peltorhamphus novaezeelandiae*, based on 12 syntypes, all except one, collected in New Zealand waters. As noted above, syntype BMNH 1848.3.18.216, one of the smaller specimens (122.6 mm SL), was presumably collected at Norfolk Island, but capture location for this specimen is erroneous (more comments in Distribution section of generic description below). No figures or illustrations accompanied this description. Macleay (1882) provided a brief redescription of the genus and also listed it as from Norfolk Island following Günther (1862). Waite (1911) included a detailed black and white drawing of a specimen of the type species (Fig. 7).

In his review and classification of fishes in the pleuronectid subfamily Rhombosoleinae, Norman (1926) recognized Günther’s *Peltorhamphus* as one of the more specialized genera within the subfamily and considered it to have close relationship to *Ammotretis* and *Colistium*. He mentioned that specialized rhombosoleid genera, such as *Peltorhamphus*, *Ammotretis* and *Colistium* exhibit a general resemblance to members of the Soleidae. In particular, he noted similarities in general shape of the body and head, particularly the preorbital region; the nearly symmetrical nasal organs; strongly curved blind-side jaws; absence of teeth on ocular-side jaws; small eyes; and extension of the dorsal fin to the anterior end of the snout. Norman further observed that other morphological features of these rhombosoleids, such as development of membranous folds on blind sides of the vertical fin rays and modification of many scales on the blind side of the head to form filamentous processes, were also similar to those found in Soleidae. He emphasized that it was likely that these features resulted from convergent evolution in the members of these two families and were not indicative of close relationship.

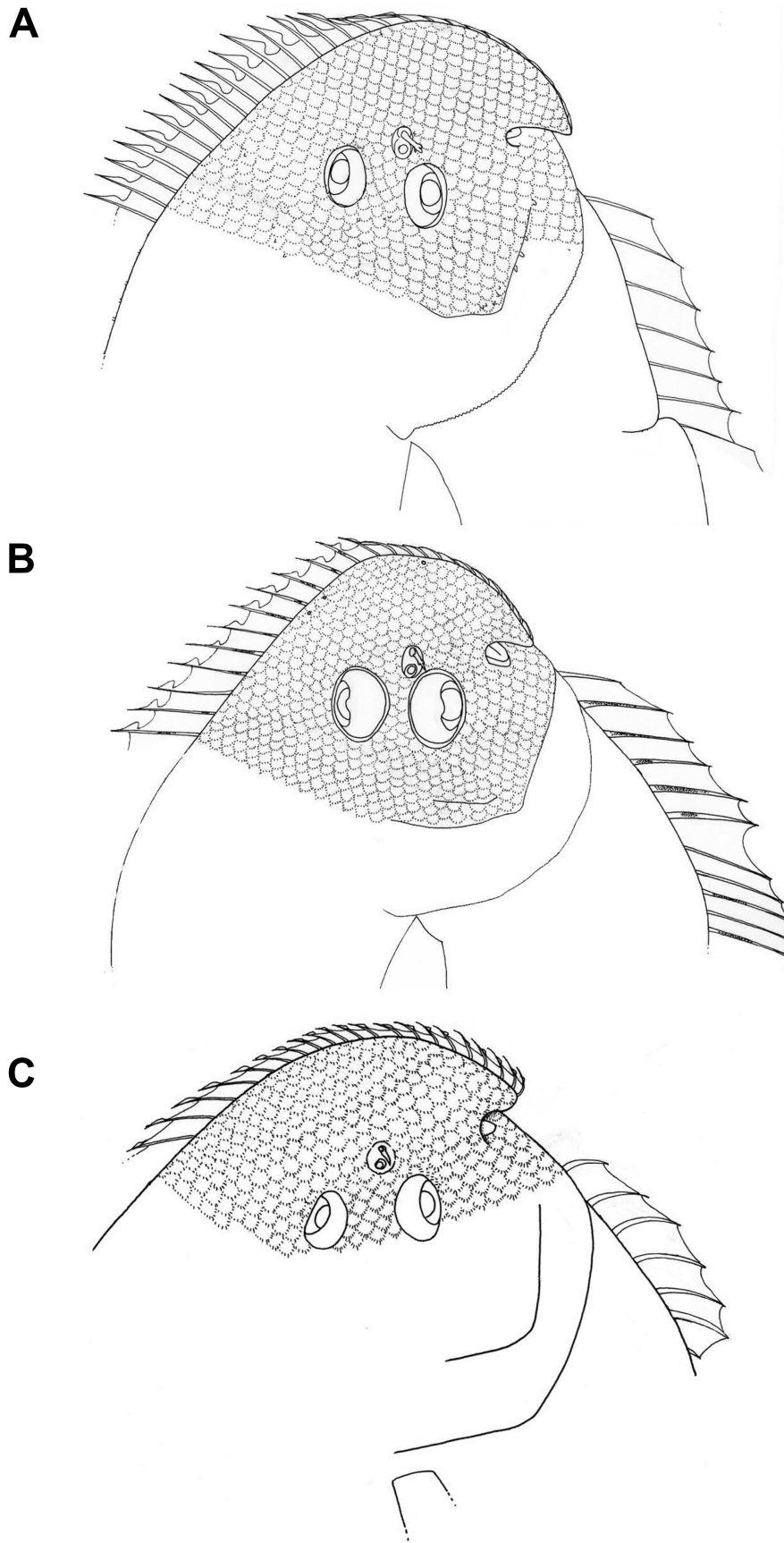
Norman (1934) followed conclusions in his earlier study (Norman 1926) in which he considered *Peltorhamphus* to be closely related to *Ammotretis* and *Colistium*, noting that *Peltorhamphus* is readily distinguished from these other rhombosoleid genera by the distinctive shape and degree of development of the membranous flap on the rostral hook which, when viewed from the ocular surface, completely, or nearly completely, obscures the mouth (vs. rostral flap not obscuring mouth in these other genera), and by the presence of an elongate second ray in the ocular-side pectoral fin (vs. non-elongate second ray in ocular-side pectoral fin). He further distinguished *Peltorhamphus* from *Colistium* by the absence (vs. presence in *Colistium*) of a fringe of labial papillae on the ocular-side lips. Norman (1934) also designated a “holotype” (= lectotype in present terminology) for *P. novaezeelandiae*, with significant consequences for the concept of the type species of this genus (see Remarks section under account of *P. novaezeelandiae*).

Following Norman’s (1934) monograph on the Heterosomata (= Pleuronectiformes in current nomenclature), no studies challenged the monotypic status of *Peltorhamphus* until James (1972) conducted a comprehensive revision of the genus. That study examined 800+ specimens, 11 of which were the syntypes of *P. novaezeelandiae*. Based on these results, James concluded that *Peltorhamphus* was not monotypic, but rather comprised three species: *P. novaezeelandiae* Günther, the largest species reaching to about 550 mm TL, and two smaller, previously undescribed species, *P. latus* and *P. tenuis*, which reach maximum sizes to about 200 mm TL.

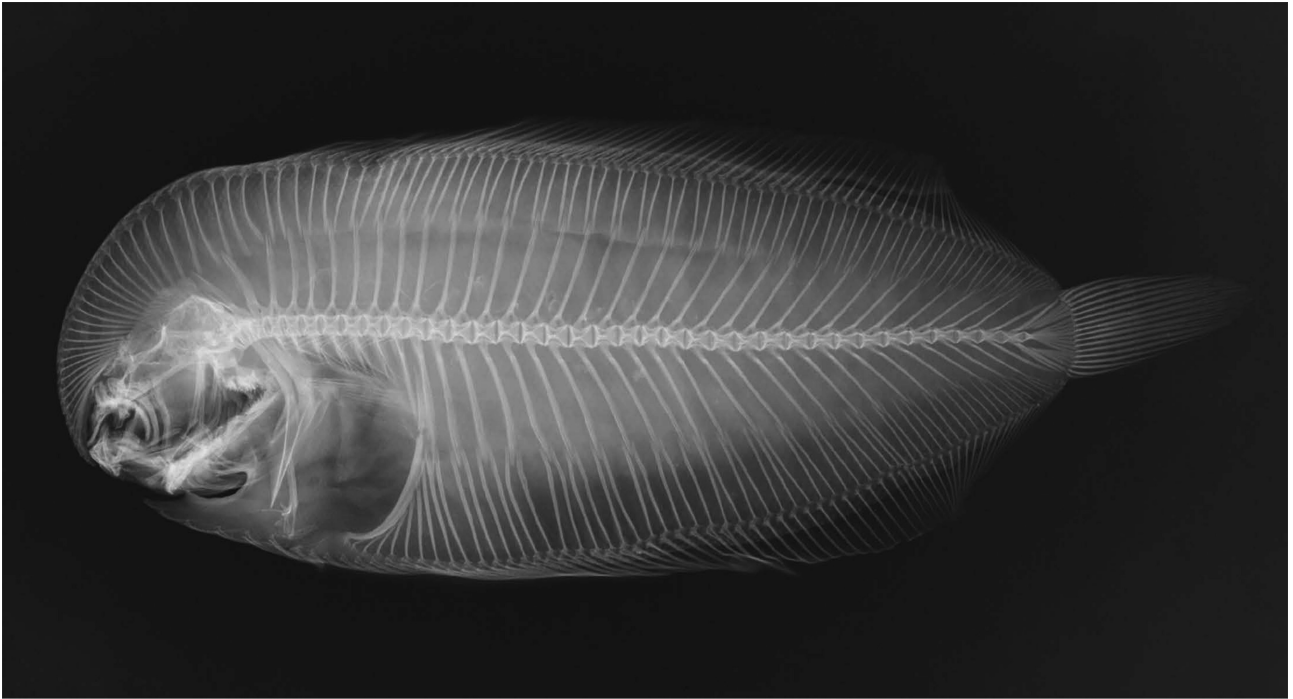
Based on morphological information of these three species, James expanded the generic concept of *Peltorhamphus*. He also briefly discussed relationships of *Peltorhamphus* among Rhombosoleinae genera, and considered that characters previously identified by Norman (1934) as diagnostic for distinguishing *Peltorhamphus* from *Colistium* and *Ammotretis* were of sufficient importance to continue recognizing *Peltorhamphus* as distinct. James noted that members of *Peltorhamphus* are restricted to marine and estuarine waters of New Zealand, and the Chatham Islands (with one species having also been reported (once) from Norfolk Island). James (1972) also reviewed the type status and identification of specimens included in the original syntype series of *P. novaezeelandiae*. These findings are discussed below in the account for *P. novaezeelandiae*.



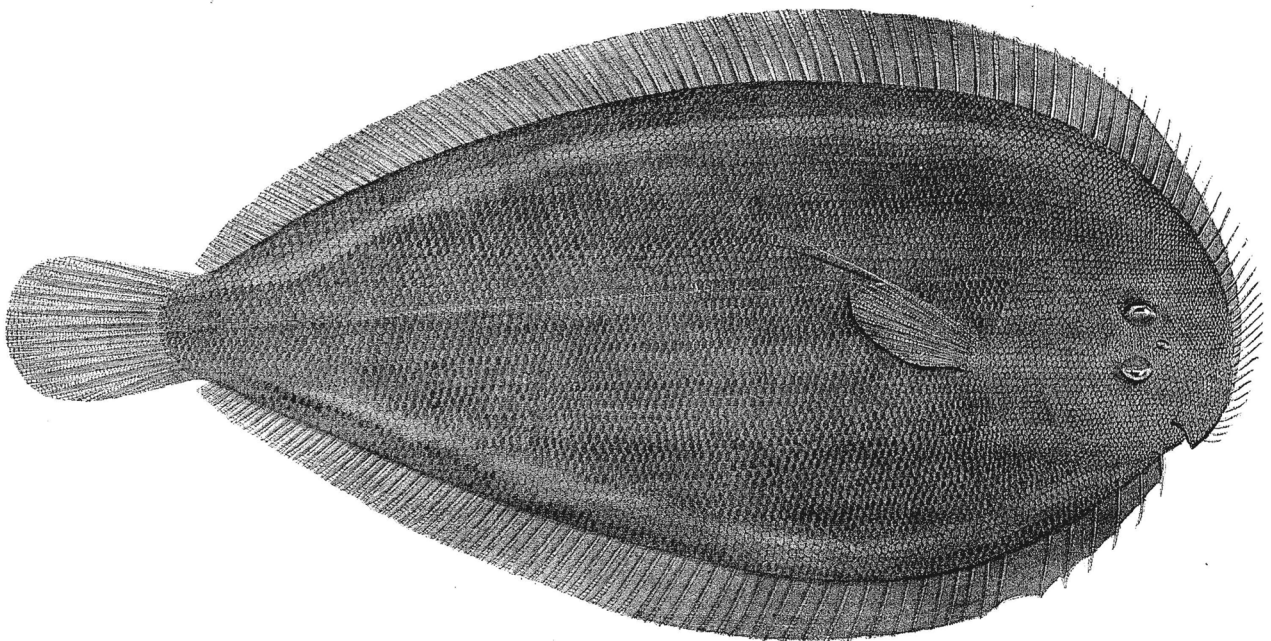
**FIGURE 4.** General body and head shapes, and relative lengths of elongate ocular-side second pectoral-fin rays of *Peltorhamphus*. **A.** *P. novaezeelandiae* (drawn from NMNZ P.032937, 277 mm SL). **B.** *P. tenuis* (drawn from NMNZ P.005421, 124.9 mm SL). **C.** *P. latus* (drawn from NMNZ P.041941, 129.0 mm SL). **D.** *P. kryptostomus* **n. sp.** (drawn from NMNZ P.046429, 132.0 mm SL, paratype). Drawn by: M. Freeborne.



**FIGURE 5.** Differences in anterior head shapes, relative sizes of eyes and interorbital distances, and rostral hooks of *Peltorhamphus*. **A.** *P. tenuis* (drawn from NMNZ P.005421, 122 mm SL). **B.** *P. latus* (drawn from NMNZ P.041941, 129 mm SL). **C.** *P. kryptostomus* **n. sp.** (drawn from NMNZ P.046429, 132.0 mm SL). Drawn by: M. Freeborne.



**FIGURE 6.** *Peltorhamphus novaezeelandiae* lectotype radiograph (BMNH 1848.3.18.-, 245 mm SL); collected at an unknown location, New Zealand. Prepared by: S. Raredon.



[*Edgar R. Waite, del.*

**FIGURE 7.** Adult *Peltorhamphus novaezeelandiae* originally Plate XLII in Waite (1911). Specimen approximately 375 mm SL and 438 mm TL.

Sakamoto (1984), in a phenetic classification of species of the family Pleuronectidae, including the Rhombosoleids, recognized *Peltorhamphus* as a valid genus in the subfamily Rhombosoleinae. He provided descriptive osteology for two of the three species then recognized, and discussed relationships of this genus among pleuronectid flatfishes based on this classification.

Guibord (2003) conducted a morphological study using a cladistic approach wherein she defined *Peltorhamphus*

as a monophyletic genus, sister taxon to *Rhombosolea*, within the Rhombosoleidae based on four apomorphies and six homoplasies. The apomorphies defining *Peltorhamphus* include 23 or more supracranial pterygiophores (versus fewer in related taxa), a membranous rostral hood covering the ocular-side jaws, an elongate second ocular-side pectoral-fin ray, and lack of a posterior bony projection on the blind-side palatine bone beneath the ectopterygoid bone (*Peltorhamphus* among Rhombosoleids lacks this bony projection). Guibord (2003) also identified six homoplasies of *Peltorhamphus* including absence of a sensory canal in the blind-side preopercle; presence of a large, round cartilage between the basioccipital and the prootic; absence of a sensory canal on the blind-side parietal; presence of scales on most of the ocular-side pectoral fin; ocular-side maxilla with labial portion shorter than rostral portion; and presence of conspicuous neuromasts on the blind side.

**Distribution.** Endemic to New Zealand, including the Chatham Islands. In the original description of *Peltorhamphus*, Günther (1862) listed one syntype of *P. novaezeelandiae* as having been collected at Norfolk Island. No registration numbers were reported for any syntypes, nor were there any illustrations accompanying the original description of this genus. To date, this record (now registered as BMNH 1848.3.18.216; 122.6 mm SL) is the only one of this genus purportedly from Norfolk Island. All early reports (Günther 1862; Hutton 1872; Macleay 1882; Waite 1906, 1910, 1916; Norman 1926, 1934; Chabanaud 1939) of this species from Norfolk Island, as well as later studies (Manikiam 1969; James 1972; Eschmeyer *et al.* 1998b; Munroe 2015b) citing these earlier studies, are based on this syntype of *P. novaezeelandiae*.

Whitley (1968) questioned the validity of the Norfolk Island record, but didn't provide any further discussion. In an attempt to shed some light on this question, correspondence with James Maclaine, Senior Curator, Fish Section, Natural History Museum, provided critical information (email pers. comm. 06/08/2020) regarding this syntype. The specimen had been received by Richardson and presented to the NHM, but Richardson, himself, did not actually collect this fish. Maclaine could not find any information at the NHM regarding where and how the specimen had been collected. Although the label on the jar indicates Norfolk Island as the collection locality, the register indicates that BMNH 1848.3.18.216 actually is the registration number for a specimen of *Trigla*, whereabouts currently unknown. The registration number, BMNH 1848.3.18.216, is now retained for the syntype of *Peltorhamphus novaezeelandiae*. A check of the register also revealed that no flatfish in the BMNH collection were from Norfolk Island. Thus, it appears that the Norfolk Island location reported for this syntype is a labelling mistake that likely occurred when this specimen was registered at the BMNH.

Since all the other syntypes of *P. novaezeelandiae* originate from New Zealand waters, it is likely that this specimen also was collected in New Zealand. In light of this new information, the genus *Peltorhamphus* (Günther 1862; Norman 1926, 1934; Chabanaud 1939; James 1972; Eschmeyer *et al.* 1998b; Munroe 2015b) as well as the species *P. novaezeelandiae* (Hutton 1872; Macleay 1882; Waite 1906, 1910, 1916; Norman 1926, 1934; Chabanaud 1939; Manikiam 1969) or *P. latus* (James 1972; Francis 1993; Munroe 2015b) should be removed from lists of fish species known from Norfolk Island.

## Species Accounts

### ***Peltorhamphus novaezeelandiae* Günther, 1862**

New Zealand Sole; Common Sole

Figs. 1A–B, 2A–B, 3A, 4A, 6–8, 9A–J, 10A–E, 11, 12A, 13A, 14A, 15A–C, 16A–D; Tables 1–7

### ***Peltorhamphus novaezeelandiae* Günther, 1862**

Günther 1862:461 (in part; syntype series at least 12 specimens including at least 10 specimens of *P. latus* James, 1972; Norfolk Island record erroneous, and based on misidentified specimen of *P. latus*; description; counts, measurements, colour description; New Zealand).

Hutton 1872:52 (in part; redescription based on Günther 1862; Norfolk Island record erroneous, and based on misidentified specimen of *P. latus* following Günther, 1862; listed, catalogue of New Zealand fishes; counts, measurements; colour description; black & white line drawing; Wellington Harbour, New Zealand).

Macleay 1882:134 (in part; Norfolk Island record erroneous, and based on misidentified specimen of *P. latus* following Günther, 1862; brief redescription with counts, colour, following Günther, 1862).

Sherrin 1886:22, 304 (brief redescription; listed, handbook of New Zealand fishes).

Hutton 1890:283 (listed, catalogue of New Zealand fishes).

Gill 1893:121 (listed, New Zealand, after Hutton 1890).

- Hutton 1904:48 (listed, faunal index of New Zealand fishes).
- Waite 1906:200 (in part; Norfolk Island record erroneous, and based on misidentified specimen of *P. latus* following Günther, 1862; comparison with other flatfishes).
- Waite 1907:27 (listed, checklist of fishes of New Zealand).
- Waite 1910:381 (in part; Norfolk Island record erroneous, and based on misidentified specimen of *P. latus*).
- Waite 1911:213 (synonymy; redescription with limited counts and measurements; colour description; black & white drawing; in key; New Zealand, including Chatham Islands).
- Waite 1912:321 (listed, addendum to checklist of fishes of New Zealand).
- Waite 1916:454 (in part; Norfolk Island record erroneous, and based on misidentified specimen of *P. latus* following Günther, 1862; listed, New Zealand).
- Norman 1926:276 (in part; redescription based on 19 specimens, including 11 syntypes, 10 of which are *P. latus* James 1972; incorrectly listed for Norfolk Island based on erroneous record and misidentified specimen of *P. latus*; synonymy; counts, measurements, colour description; New Zealand, Chatham Islands).
- Phillipps 1927a:12 (listed, checklist of New Zealand fishes).
- Phillipps 1927b:29 (listed, bibliography of New Zealand fishes; synonymy).
- Young 1929:143 (listed, Chatham Islands, New Zealand).
- Norman 1934:427 (in part; paralectotypes are *P. latus* James 1972; incorrectly listed for Norfolk Island based on erroneous record and misidentified specimen of *P. latus*; redescription based on 19 specimens, including original syntypes; designated holotype [= lectotype in contemporary designation of types]; counts, measurements, black & white line drawing, colour description; size to about 450 mm SL; New Zealand, including Chatham Islands).
- Chabanaud 1939:763 (in part; incorrectly listed for Norfolk Island based on erroneous record, and misidentified specimen of *P. latus*; listed, world catalogue of flatfishes; New Zealand, Chatham Islands).
- Chabanaud 1949:10 (osteology).
- Graham 1953:206 (in part; may include more than one species; distinguishing features; Otago, South Island, New Zealand).
- Graham 1956:206 (in part; may include more than one species; distinguishing features; Otago, South Island, New Zealand).
- Whitley 1956:405 (listed, checklist of New Zealand fishes).
- Parrott 1960:115 (brief redescription, diagnosis; black & white illustration; common in New Zealand waters).
- Doogue & Moreland 1961:218 (in part; may include more than one species; brief redescription, diagnosis; distribution North and South islands, New Zealand).
- Doogue & Moreland 1964:218 (in part; may include more than one species; brief redescription, diagnosis; distribution North and South islands, New Zealand).
- Powell 1966:242 (brief diagnosis; black & white illustration).
- Heath & Moreland 1967:32 (distinguishing characters; colour illustration).
- Whitley 1968:49 (in part; follows Günther; listed, checklist of fishes of New Zealand; Norfolk Island record questioned).
- Manikiam 1969:126 (in part, includes more than one species; Norfolk Island record based on erroneous record, and misidentified specimen of *P. latus*; common names; in key; distribution around New Zealand including Chatham Islands; diagnostic features; line drawing).
- James 1972:345 (redescription; counts, measurements, black & white illustration; in key; size information; diagnosis; synonymy; endemic throughout New Zealand waters, including Chatham Islands).
- Francis 1979:69 (listed, off Kaikoura, South Island, New Zealand).
- Roper 1979:136 (in part; may include data from *Peltorhamphus* n. sp. Munroe; Blueskin Bay, South Island; distribution; difficulty distinguishing *P. novaezeelandiae* juveniles from those of *P. latus* and *P. tenuis*; separated from congeners by meristic and morphometric characters; size to 500 mm; ontogenetic series of juveniles figured).
- Nicholson 1979:136 (listed, checklist of fishes of Cavalli Islands, Northland, North Island, New Zealand).
- Ayling & Cox 1982:312 (brief redescription including counts, colour; black & white line drawing; diagnosed from other New Zealand pleuronectiforms; New Zealand, most commonly around South Island).
- Doogue & Moreland 1982:227 (brief redescription, diagnosis; distribution North and South islands, New Zealand).
- Sakamoto 1984:95 (morphology; osteology; valid species; placement in phenetic classification of Pleuronectidae).
- Paulin & Stewart 1985:57 (New Zealand endemic; widespread in coastal waters).
- Paul 1986:141 (brief redescription; colour photograph, black & white illustration; distinguished from congeners; widespread around New Zealand, more abundant in southern parts of range).
- Paulin *et al.* 1989:240, 265 (in key; listed, Pleuronectidae; New Zealand).
- Roberts 1991:19 (listed, Chatham Islands, New Zealand).
- Armitage *et al.* 1994:110 (brief redescription; colour photograph, line drawing; endemic to New Zealand).
- Colman 1994:34 (brief redescription, colour photograph; member of Pleuronectidae; recognized taxonomic confusion identifying juveniles and diagnosing juveniles and adults of congeners; New Zealand, more common around South Island).
- Francis 1996:69 (brief redescription; *in situ* colour photograph).
- Paulin 1996:13 (brief diagnostic features; colour description; size; black & white illustration; distribution).
- Paul & Heath 1997 (no pagination; species account 89) (brief redescription; colour photograph).
- Eschmeyer *et al.* 1998b:1203 (valid species in *Peltorhamphus*: Rhombosoleinae; list of syntypes; New Zealand; recognized Norfolk Island record based on misidentified specimen of *P. latus*).

Eschmeyer 1998b:2433 (valid species in *Peltorhamphus*: Rhombosoleinae).  
 Paulin 1998:19 (brief redescription with black & white illustration; diagnosis).  
 Paul 2000:141 (brief redescription; colour photograph, black & white illustration).  
 Paulin *et al.* 2001:240, 265 (in key; listed in Pleuronectidae; New Zealand).  
 Guibord 2003:202 (osteology; morphology; systematic relationships; member of Rhombosoleidae; unresolved relationships with other species of *Peltorhamphus*).  
 Evseenko 2004:20 (after Günther) (in part; syntype series includes at least 10 specimens of *P. latus*; incorrectly listed for Norfolk Island based on erroneous collection location and misidentified specimen of *P. latus*; valid species in Rhombosoleinae: Pleuronectidae; 12 syntypes listed with catalogue numbers; New Zealand).  
 Hirt-Chabbert 2006:120 (brief redescription; colour photographs; brief diagnosis).  
 Roberts *et al.* 2009:536 (listed, checklist of New Zealand Chordata).  
 Voronina 2009:945 (description of structure of lateral-line scales).  
 McMillan *et al.* 2011:277 (diagnostic features; colour photo; endemic to New Zealand, more common around South Island).  
 Francis 2012:247 (brief redescription; diagnosed from congeners and other New Zealand flatfishes; *in situ* colour photograph).  
 Campbell *et al.* 2014:180 (whole mitochondrial genome sequences to examine phylogenetic affinities within Pleuronectiformes).  
 Wang *et al.* 2014:53 (complete mitogenome and comparison with other flatfish genomes).  
 Roberts *et al.* 2015:S177 (listed, checklist of fishes of New Zealand; endemic; types listed; type locality New Zealand).  
 Munroe 2015b:1696 (species redescription, including colour photograph; diagnostic features; in key; endemic to New Zealand, including Chatham Islands).  
 Roberts *et al.* 2018:126 (listed, online checklist of New Zealand fishes; endemic; types listed; type locality New Zealand).  
 McMillan *et al.* 2019:250 (brief redescription with colour photo; diagnosed from congeners; New Zealand endemic; widespread, more common around South Island).

**Diagnosis.** *Peltorhamphus novaezeelandiae* is distinguished from congeners by the following combination of characters: its maximum size (reaching 550 mm TL vs.  $\leq 200$  mm TL in congeners); relatively deep body with greatest depth located well anterior to body midpoint, and with noticeable posterior taper beyond this point; broad, distinctively rounded anterior profile of head (Figs. 1, 4A, 5A, 6–8, 10–11); relatively short, filamentous, second ocular-side pectoral-fin ray usually much shorter than greatest body depth; a combination of meristic features, including 37–39 (usually 37–38) total vertebrae, 93–110 dorsal- and 60–73 anal-fin rays, 76–108 (usually 85–100) lateral-line pores, 23–29 (usually 25–28) supracranial pterygiophores, 10–20 (usually 13–19) gillrakers on first gill arch, 6–13 scales (usually 9–12) between mid-eye and dorsal margin of head, and 2–9 scales (usually 4–6) between anteroventral margin of lower (non-migrated) eye and dorsal margin of rostral hood above mouth; relatively small gillrakers on upper limb of first gill arch not reaching dorsalmost gillrakers on lower limb; in lacking scales on blind sides of dorsal- and anal-fin rays (cf. Fig. 2C); in possessing 1–8 (usually 2–5) fleshy, finger-like filaments on inner anteroventral margin of fleshy skinfold on ocular-side lower jaw (Fig. 3A); smaller eye; wider IO space that increases with growth (Figs. 9H, 10); relatively wide dorsal head width; relatively narrow caudal peduncle; uniform ocular-side background colouration without longitudinal lines or ocelli (Figs. 8, 11), but sometimes with up to three dark blotches along lateral line, and/or with series of white to purplish spots along dorsal and ventral contours of body (Fig. 11); sometimes with dusky (not black) pigment on entire inner lining of ocular-side opercle; and with dusky pigment on only part of roof of mouth.

**Lectotype (Figs. 1A–B, 6):** BMNH 1848.3.18.- (245 mm SL); locality not specified, New Zealand; designated by Norman (1934).

**Description.** Meristic data summarized in Table 1. Values for lectotype in bold here and in Table 1. Supracranial pterygiophores **24**, range 23–29, usually 25–28 (121 of 131 individuals). Pterygiophores inserted into first interneural space **2**, usually 3 (97 of 131 individuals). Pterygiophores inserted anterior to first haemal spine **9**, range 7–12, usually 9–11 (119 of 127 individuals). Dorsal-fin rays **103**, range 93–110. Anal-fin rays **67**, range 60–73. Caudal-fin rays **18**, range 17–19, usually 18 (128 of 131 individuals). Ocular-side pectoral-fin rays **10**, range 8–11, usually 9–11 (114 of 115 individuals); blind-side pectoral-fin rays **9**, range 6–10, usually 8–10 (113 of 115 individuals). Ocular-side pelvic-fin rays **6**, usually 6 (131 of 137 individuals); blind-side pelvic-fin rays **4**, usually 4 (135 of 137 individuals). Abdominal vertebrae **3+7**, usually 3+7 (124 of 132 individuals). Caudal vertebrae **27**, range 27–29 (132 individuals). Total vertebrae **37**, range 37–39, usually 37–38 (115 of 132 individuals). Fleshy, finger-like filaments (Fig. 3B) on inner anteroventral margin of fleshy skinfold on ocular-side lower jaw **5**, range 1–8, usually 2–5 (74 of 83 individuals). Gillrakers on upper limb of first gill arch **4**, range 1–6, usually 3–4 (115 of 137 individuals); gillrakers on lower limb of first gill arch **12**, range 7–16, usually 10–14 (122 of 138 individuals). Total gillrakers on first arch **17**, range 10–20, usually 13–19 (123 of 138 individuals). Interorbital scales varying ontogenetically, lectotype with **4**, adults usually with 3 scales (68 of 95 individuals); smaller juveniles (15 of 95 individuals counted) with only 1–2 scales in interorbital region. Scales in

diagonal row between anteroventral margin of lower eye and dorsal margin of mouth opening **6**, range 2–9, usually 4–6 (75 of 93 individuals) in adults; juveniles usually with only 2 or 3 scales in EUM space. Scales between mid-dorsal margin of dorsal eye and dorsal margin of head **10**, range 6–13, usually 9–12 (75 of 82 individuals). Lateral-line pores **91**, range 76–108, usually 85–100 (63 of 76 individuals).

**TABLE 3.** Size distribution (in mm SL) and comparisons of male and female lengths within a species for 598 specimens representing four species of *Peltorhamphus*.

Size	<i>novaezeelandiae</i>		<i>tenuis</i>		<i>latus</i>		<i>kryptostomus</i>	
	Male	Female	Male	Female	Male	Female	Male	Female
21–30	–	–	–	–	–	–	–	–
31–40	–	–	–	–	1	–	–	1
41–50	1	2	–	–	3	8	–	1
51–60	–	–	1	1	6	11	1	3
61–70	1	3	3	5	14	16	–	–
71–80	3	7	9	10	17	18	1	2
81–90	–	5	3	4	13	21	3	4
91–100	3	4	6	2	14	18	7	10
101–110	2	5	17	5	10	15	3	3
111–120	3	–	1	7	8	19	1	3
121–130	–	1	11	15	2	13	1	3
131–140	4	2	3	7	–	3	2	5
141–150	3	–	1	8	–	1	–	2
151–160	2	2	2	5	–	–	–	–
161–170	6	2	–	1	–	–	–	–
171–180	2	11	–	–	–	–	–	–
181–190	2	9	–	–	–	–	–	–
191–200	5	5	–	–	–	–	–	–
201–210	10	3	–	–	–	–	–	–
211–220	6	11	–	–	–	–	–	–
221–230	5	7	–	–	–	–	–	–
231–240	4	1	–	–	–	–	–	–
241–250	5	7	–	–	–	–	–	–
250+	8	22	–	–	–	–	–	–
N	75	109	57	70	88	143	19	37

Morphometric data summarized in Table 3, compared with that of other species in Table 2, discussed in further detail in the Morphometric variation section below, and plotted for select features in Figs. 9A–J. Body oval to moderately elongate (Fig. 8), laterally compressed; trunk length moderate (TKL 70.1–81.6% of SL,  $\bar{X}$  = 74.4%); greatest body depth (BD 33.2–48.3% of SL,  $\bar{X}$  = 42.2%) varying ontogenetically with larger fish having deeper bodies (Fig. 9A); greatest body depth in anterior one-third of body, usually at point about equal with anal-fin ray 10, and with gradual taper posteriorly and gradual rounded slope anteriorly from this point. Caudal peduncle short, relatively narrow (CPD 8.6–10.8% of SL,  $\bar{X}$  = 9.5%). Head large, broadly rounded anteriorly (Figs. 1, 4A, 6–8, 10E, 11), without noticeable blunt point on anteriormost profile; anterior dorsal profile steeply convex to a point about equal with vertical through anterior margin of lower eye; ventral margin of head steeply angled ventrally to its posterior margin. Head relatively short (HL 22.2–30.8% of SL,  $\bar{X}$  = 25.6%); proportionally larger in smaller individuals (Fig. 9B); HL shorter than head width (HW 32.0–44.7% of SL,  $\bar{X}$  = 39.1%); growth in HW over SL slightly positive in fish to about 275 mm SL and decreasing in larger fish (Fig. 9C); HW/HL 1.21–1.85 ( $\bar{X}$  = 1.53). Head width dorsal to upper eye (DHW 22.0–57.9% of HL,  $\bar{X}$  = 37.8%) broad (Fig. 8), increasing proportionally with fish size (Figs. 9E, 10); no secondary scales on head scales above dorsal eye. Snout moderately long (SNL 24.3–40.3% of HL,  $\bar{X}$  = 30.6%); growth in



SNL isometric relative to HL in fish > 20 mm HL (Fig. 9F); snout broadly rounded, covered with ctenoid and cycloid scales; greatest SNL either at horizontal slightly anterior to dorsal eye, or on horizontal between eyes; 10–12 rows of scales between anterior margin of eyes and anterior profile of snout. Ocular side of snout with conspicuous rostral flap whose dorsoposterior margin nearly surrounds and almost hides entire mouth, except for posteriormost end of jaws (Figs. 4A, 8); rostral flap also with relatively long, fleshy rostral hook (RHL 18.7–35.7% of HL,  $\bar{X}$  = 26.1%) with its posterior tip extending ventrally to, or slightly beyond, mouth opening in adults, and not usually reaching posterior margin of mouth opening in smaller fish. Ventroposterior section of rostral flap also with vertical, notch-shaped opening usually resembling a question mark, exposing only posteriormost tips of jaws ventrally (Figs. 8, 10). Two ocular-side nostrils situated just anterior to IO space, slightly closer to ventral eye than to dorsal eye (Fig. 5A). Anterior ocular-side nostril, a short round tube with elongate flap on ventroposterior margin, situated on snout at vertical through posterior mouth opening. Posterior ocular-side nostril a rounded slit without flaps on margin. Blind-side nostrils located dorsal to blind-side upper jaw at point about equal to one-third to one-half of its length. Anterior blind-side nostril a short, round, slightly elevated tube with small delicate flap on anterior margin. Posterior blind-side nostril a slightly larger, round opening with delicate membrane around entire margin. Eyes relatively small (ED 12.2–21.6% of HL,  $\bar{X}$  = 16.5%); ED decreasing proportionally with increasing fish size (Fig. 9G), larger individuals having proportionally smaller ED/HL ratios; eyes elliptical, usually with anterior margins of eyes nearly equal in position, or sometimes with anterior margin of upper eye slightly in advance of anterior margin of lower eye; eyes usually with pupillary operculum (Fig. 2B), better developed in juveniles. Interorbital width (IO) varying ontogenetically (Figs. 9H, 10); smaller juveniles with eyes nearly contiguous (Figs. 9H, 10) but separated by narrow IO space (ca. 5% of HL and usually IO much smaller than eye diameter); both width of IO space (Fig. 9H) and number of scales in IO space increasing in juveniles larger than ca. 18 mm HL and continuing to increase in subadult fish; adults with eyes widely separated by IO space 12–16.6% of HL.



**FIGURE 8.** *Peltorhamphus novaezeelandiae* (NMNZ P.049689, 335 mm SL) freshly frozen and thawed, adult female; off Golden Bay, Nelson, South Island, New Zealand. Photo: C. Struthers.

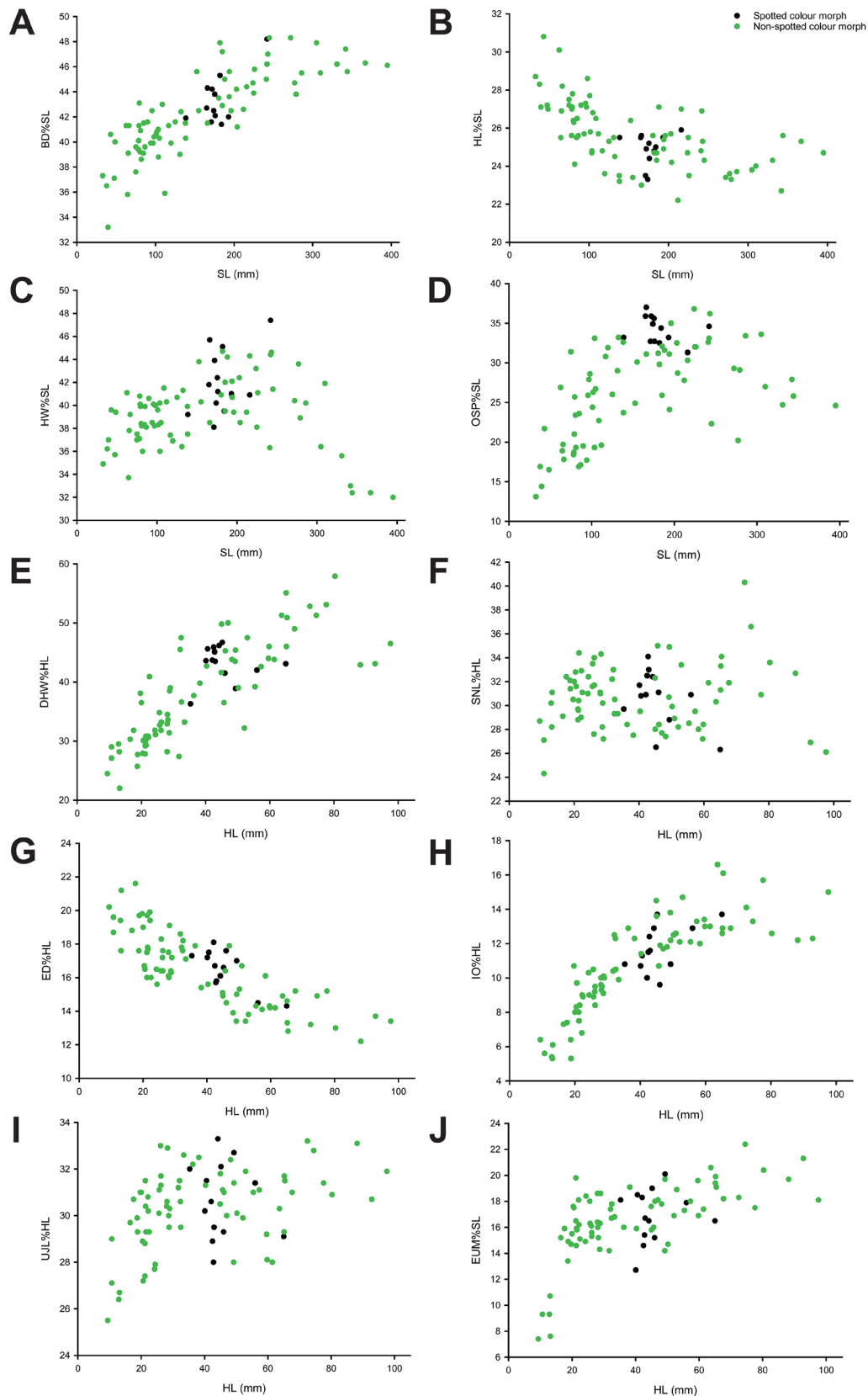
Mouth relatively large (UJL 21.2–38.2% of HL,  $\bar{X}$  = 30.3%), UJL (Fig. 9I) proportionally smaller in individuals of ca. 7 to 15 mm HL; larger individuals without distinct pattern of allometric growth in UJL; jaws asymmetrically developed towards blind side; all but posterior margin of jaws on ocular side nearly completely concealed by rostral flap; jaws on blind side straighter, only slightly decurved posteriorly. Diagonal distance between upper mouth and ventral rim of lower eye (EUM) increasing proportionally in size ontogenetically (Fig. 9J); EUM in smallest individuals (9.4 to ca. 18 mm HL) 11% or less of HL; EUM distance wider (13–27% of HL,  $\bar{X}$  = 16.6%) in fish with HL values from ca. 16–94 mm (Fig. 9J). Mouth opening on ocular side small, usually shaped like a question mark (Figs. 8, 10); opening usually anterior to vertical through anterior nostril. Ocular-side lower lip without labial papillae. Teeth present only on blind-side jaws; slender, villiform, in 2–4 irregular rows; teeth in outer rows, especially anteriorly, slightly

larger than teeth in inner rows and those located more posteriorly. Fleshy skinfold on inner anteroventral margin of ocular-side lower jaw with 1–8 (usually 2–5; rarely 1, 6, or 8) finger-like filaments (Fig. 3B). Postorbital head length (POL 11.7–16.1% of SL,  $\bar{X}$  = 13.7%) moderately long, about equal to 36–37% of HW. Upper head lobe (UHL 18.3–25.9% of SL,  $\bar{X}$  = 22.3%) much wider than Lower head lobe (LHL 9.0–16.0% of SL,  $\bar{X}$  = 12.6%).

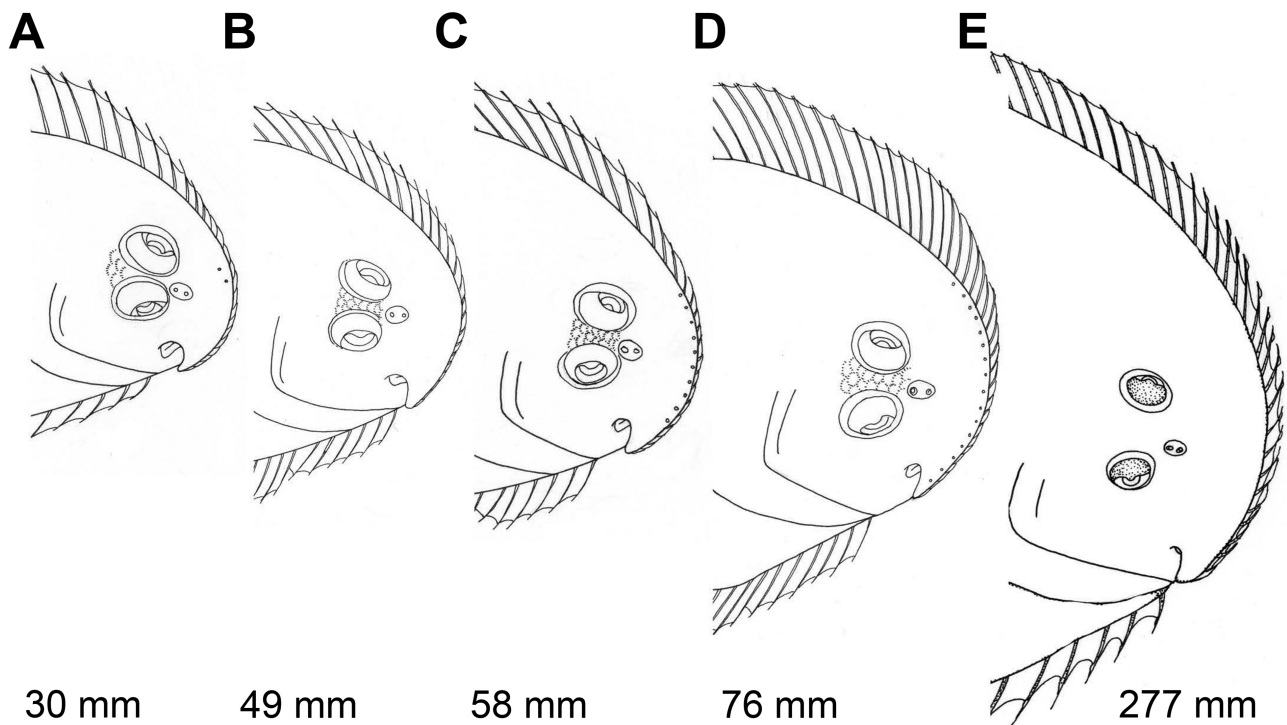
Blind and ocular sides of head and body with superficial neuromasts occurring singly or with several arranged in series; neuromasts varying in size, shape of their lappets, and location (Roper (1981) and Livingston (1987a) provide more detailed information on structure and arrangement of neuromasts in *P. novaezeelandiae*). Superficial neuromasts present on both sides of body along and above lateral line. Individual variation occurs in number and arrangement of superficial neuromasts, but four types recognized according to size, shape of lappets, and location (Roper 1981). Neuromasts on blind side of head most conspicuous as large organs with thick, fleshy lappets curling over, leaving only narrow slit above sensory epithelium; medium-sized neuromasts on ocular side of head with fleshy lappets and exposed sensory epithelium. Ocular and blind sides of head and body also with small, less conspicuous neuromasts; those on ocular side of head with short, stubby lappets and exposed epithelium; those on blind side of body small, with elongate, flaccid lappets and exposed epithelium. Most conspicuous and consistent arrangement of larger neuromasts on blind side of head, usually in three, more or less parallel longitudinal rows dorsal to horizontal through nostrils, with another series just posterior to jaws. Dorsalmost row of neuromasts, close to body margin, beginning on snout and extending posteriorly to about midpoint of head; middle longitudinal row of neuromasts beginning anteriorly on snout and extending posteriorly nearly to three-fourths of head length; ventralmost longitudinal row with fewer, more closely spaced neuromasts than in other rows, in shallow groove beginning just posterior to nostrils and extending posteriorly to about midpoint of head. Another series of prominent neuromasts in curved row following contour of jaws; ventralmost neuromasts in this series located just ventral to posterior margin of jaws, with remaining neuromasts in this series more or less following anterodorsal curvature of jaws nearly to their distal tips. Several prominent free neuromasts also on blind side of head dorsoposterior to neuromast series behind jaws, with several other neuromasts also submarginally along ventral areas on opercle and lower jaw.

Gillrakers not toothed, on both limbs of arches on ocular and blind sides (Fig. 12A); occasional specimens also with small gillraker in junction between upper and lower limbs of first arch. Gillrakers on upper limb of first blind-side arch fleshier, more flimsy, and triangular with wide base and narrow pointed tips; gillrakers on upper limb relatively small (usually < one-half length of gillrakers on lower limb), lengths subequal to distance between their bases, and not reaching ventrally (Fig. 12A) to level of second dorsalmost gillraker on lower limb of same arch (excluding gillraker at angle, if present). Lower limb gillrakers of first blind-side arch much longer and more robust than those on upper limb (Fig. 12A), except ventralmost 2–4 gillrakers which are usually much smaller and more rounded than others on lower limb.

Dorsal-fin origin at, or near, tip of rostral hook, located well ventral to visible part of mouth opening. Anteriormost dorsal-fin rays, from first to approximately 20<sup>th</sup> to 25<sup>th</sup> ray, with distinct, cup-shaped, fleshy membrane approximately at their midpoints and with distal halves curved, filamentous, and without connecting membrane; remainder of rays connected by membrane at approximately three-fourths of length of each ray and without cup-shaped, fleshy membrane at their midpoints. Anal-fin rays connected by membrane nearly at distal tips of rays. No scales on blind sides of dorsal- and anal-fin rays. Caudal fin broadly rounded, relatively short (CFL 14.8–26.1% of SL,  $\bar{X}$  = 19.9%) compared with that of congeners. Caudal fin covered proximally on both sides with scales, with scales extending distally on rays to about three-fourths of their lengths. Both pectoral fins well developed; ocular-side pectoral fin with elongate second ray extending slightly posterior to vertical through body midpoint; length of second ocular-side ray (OSP 13.1–36.8% of SL,  $\bar{X}$  = 26.1%) increasing ontogenetically to about 250 mm SL (Fig. 9D); OSP usually much shorter than greatest body depth (length of second ocular-side ray in BD = 1.2–1.4) and  $\geq$  HL, except fish < 80 mm SL with length of second ocular-side ray < HL. Blind-side pectoral fin shorter than ocular-side fin (BSP 8.2–21.5% of SL,  $\bar{X}$  = 10.4%), with rays spaced much closer together than those of ocular-side fin, and without elongate rays. Pelvic fins well developed, unequal in position, surrounding anus, not connected to each other. Ocular-side fin origin nearly at tip of isthmus; blind-side fin with base of first ray positioned opposite space between fifth and sixth ocular-side fin rays, or equal to base of sixth ocular-side ray. Ocular-side rays widely separated, with distal tips free from membrane; first and second rays (noticeably) shorter than others; posteriormost ocular-side pelvic-fin ray with broad, membranous connection to first anal-fin ray. Blind-side pelvic fin much shorter, rays spaced more closely together than those of ocular-side fin, and thickening posteriorly; first blind-side ray notably shorter, and fourth ray longer, than others; blind-side pelvic fin without membranous connection to anal fin, but fourth ray connected by membrane from its base to approximately mid-length to body in region just anterior to anus.



**FIGURE 9.** Selected morphometric features for 86 specimens of two colour morphs of *Peltorhamphus novaezeelandiae* with size range from 42.9 to 395 mm SL. **A–D.** Body depth (BD), Head length (HL), Head width (HW), and Ocular-side pectoral fin (OSP) expressed as percent of SL versus SL (in mm), respectively. **E–J.** Dorsal head width (DHW), Snout length (SNL), Eye diameter (ED), Interorbital width (IO), Upper jaw length (UJL), and Eye to upper mouth distance (EUM) expressed as percent of HL versus HL (in mm), respectively.



**FIGURE 10.** Ontogenetic increase in Interorbital width (IO) illustrated for five specimens of *Peltorhamphus novaezeelandiae* 30–284 mm SL. Specimens A–D drawn from NMNZ P.046446; Specimen E drawn from NMNZ P.032937. Drawn by: M. Freeborne.

Ocular-side scales transforming ctenoid in both juveniles and adults; blind-side scales vary ontogenetically and sexually dimorphic in adult fish. Juveniles (both sexes, and usually smaller than ca. 80 mm SL) with weakly ctenoid scales on blind side; blind side of adults (both sexes) usually with cycloid scales, or with scales with only weakly denticulate posterior margins. Adult females with cycloid scales on both blind-side preopercle and subopercle; adult males with weakly ctenoid scales on blind-side preopercle and subopercle. Juveniles (both sexes, and smaller than ca. 80 mm SL) with ctenoid scales on blind-side opercle.

Anus on blind side, slightly off body midline, bordered medially by blind-side pelvic fin.

Lateral line straight, except for slight rise anteriorly above pectoral fin; posteriorly, lateral-line pores on both sides extending to distal tip of middle caudal-fin ray.

**Morphometric variation.** Detailed examination of variation in 10 morphometric features of 74 *P. novaezeelandiae*, 32.7–395 mm SL, revealed that allometric growth was readily apparent in most features examined (Figs. 9A–J). Body depth (BD; Fig. 9A) values showed significant variation with a range of 33.2–48.3% of SL, and with positive allometric growth throughout the size range studied. These values reflect the noticeable deepening of the body with growth. The smallest (32.7–ca. 50 mm SL) usually had BD measurements < 38% of their SL, whereas fish from 50 to ca. 180 mm SL had BD values between 38–45% of SL. For fish > ca. 180 mm SL, although growth in BD continued to increase proportionally with increasing fish size, rate of growth in BD (41–48% of SL) was not as dramatic (significant) as that for smaller individuals. Changes in BD measurements appeared to be levelling off in these largest individuals measured.

Head length (HL; Fig. 9B), expressed as % of SL, had less total variation (about 9%) than that for BD (16%), and showed negative allometric growth increasing proportionally with fish size. The smallest individuals (< 105 mm HL) had proportionally larger heads (HL usually 27–31% of SL) compared with HL values (22.9–27.0%) for fish > 105 mm HL. Head width values (HW; Fig. 9C) ranged from 32.0–47.4% of SL over the size range examined, which reflected considerable variation (range of ca. 15% of SL) in this feature. Head width showed a positive trend of increase with increasing fish size until ca. 250 mm SL. For larger fish, many of the HW measurements were proportionally less than those of fish smaller than 250 mm SL.

Length of the elongate ray of the ocular-side pectoral fin (OSP; Fig. 9D) had positive growth for fish of 32.7–ca. 250 mm SL. For larger fish (260–395 mm SL), OSP values varied from 20–38% of SL, but no clear trend of increasing

OSP length with increasing fish size was evident. Given the fragility of this ray, and difficulty determining whether the tip of the ray is intact or broken, lack of positive allometry in the largest specimens cannot be discounted.

Of the other six morphometric features of the head (Fig. 9E–J), all but snout length (SNL; Fig. 9F) showed allometric growth. Changes in dorsal head width (DHW; Fig. 9E) and interorbital width (IO; Fig. 9H) both showed strong positive allometry throughout the size range measured. Width of the head region dorsal to the eyes varied considerably, with a span of 32% measured between the smallest to the largest fish, as did variation in IO measurements (16% between smallest and largest fish). Data for eye to upper mouth measurements (EUM; Fig. 9J) showed that this region also undergoes positive allometric growth with increasing fish size. Eye to upper mouth values (range 7.6–22.4% of HL) varied about 14% between the smallest and largest fish, with fastest rate of change occurring in the smallest fish (to about 20 mm HL); EUM measurements continued to increase, but at a slower rate, throughout the range of sizes measured. Increases in DHW, IO and EUM with increasing fish size reflects broadening of head width as fish grow larger, and these changes in HW are most evident in the region dorsal to the eyes and in the interorbital area (Figs. 10A–E).

For the size range 32.7–395 mm SL, fish all had SNL values between 24.3–40.3% of HL (SNL; Fig. 9F). Although SNL measurements varied about 16% between the smallest and largest individuals, no clear trends of increasing or decreasing growth in SNL relative to increasing HL were evident. Lower eye diameter (ED; Fig. 9G) varied about 9% between the smallest and largest specimens measured (total range 12.2–21.6% of HL). Eye diameter measurements showed clear negative allometry with increasing size, indicating that larger fish have a proportionally smaller eye relative to HL. Upper jaw length (UJL; Fig. 9I) ranged about 7% between smaller and larger fish (total range 26.4–33.3% of HL). Upper jaw length measurements were positively allometric for fish of 9.4–ca. 25.0 mm HL, whereas for fish measuring 26.0–97.6 mm in HL, no clear pattern of allometry was evident.

*Colour in life.* (Based on freshly thawed specimens: NMNZ P.049582, NMNZ P.049685, NMNZ P.046989, NMNZ P.049686, NMNZ P.049687 and NMNZ P.049688; *in situ* photographs in Francis (2012:247) and on the iNaturalist.org website for Austral-New Zealand fishes ([https://www.inaturalist.org/taxa/55408-Peltorhamphus-novaezeelandiae/browse\\_photos](https://www.inaturalist.org/taxa/55408-Peltorhamphus-novaezeelandiae/browse_photos)).

Background colour of ocular side of head and body variable, somewhat influenced by substratum occupied by fish, ranging from uniformly medium-brown, grayish-green or green with some scales (irregularly positioned on body) darker than others; ventroposterior region of ocular-side opercle with slightly darker pigment compared with that on rest of body; some specimens also with 2–3 conspicuous, darkly pigmented blotches along lateral line, blotches irregular in shape and slightly larger than eye diameter. Individual scales on head and body with numerous, small melanophores, especially concentrated posteriorly, outlining posterior scale margin and ctenii; scales also with horizontal line of black pigment, or with irregular, spherical or elliptical blotch of dark pigment on central region of exposed areas of scales. Posterior one-third of scales also with some iridescent pigment. Medial regions of scales not as darkly pigmented as posterior margins. Anteromedial portion of each scale also with dense concentration of melanophores.

Some freshly collected specimens taken off South Canterbury and others photographed *in situ* from Wellington Harbour and Okiwi Bay feature a series of gray to grayish-blue or white, rounded to irregular, pigmented spots arranged in series along dorsal and ventral contours of their bodies (Fig. 11). Most (10 of 13) specimens examined from off South Canterbury were immature females and three were males. These spots—usually 5–9 in number—run from the head above the eye and continue along the dorsum, nearly evenly spaced, to just before the vertical through the posterior end of the dorsal fin. Along the ventral contour of the body are 5–7, smaller, sometimes more diffuse (less conspicuous), whitish or grayish-blue spots. The largest of these are about 3 scale rows wide and about 3 scales high. After fixation, the South Canterbury specimens had lost some of their grayish-blue pigmentation of the spots, which subsequently have turned dark brown or dull blackish. After just over one year in preservative, these spots have nearly completely faded and are scarcely noticeable in some specimens.

Distal, submarginal area of anterior snout with several, nearly evenly spaced, small, pigmented circles surrounding sensory pores along nearly the entire perimeter of snout, these circles more prominent in small juveniles. Ocular-side nostrils not conspicuously pigmented, but with slightly lighter colour than that on remainder of snout. Pupil of eye black; iris iridescent silvery. Tips of jaws white. Exterior of mouth and lips slightly pinkish. Roof of mouth white, without dark pigment. Inner opercular lining on ocular side white with small, sooty to sooty-black patch on posterodorsal region. Isthmus white on both sides.

Blind side of head and body generally uniformly white, sometimes with patches of dusky to sooty-gray scales varying in size from small blotches to large patches, which sometimes cover as much as one-third of blind side of body. Region around snout, mouth and operculum white with pinkish overtones. Blind-side inner opercular lining

whitish, or with small sooty patch dorsally. Filaments on inner anteroventral margin of fleshy skinfold on ocular-side lower jaw, and fleshy tags on ventral margin of ocular-side opercle, bright white. Small patches of scales on caudal region a darker, sooty gray.



**FIGURE 11.** *Peltorhamphus novaezeelandiae* (NMNZ P.061016) freshly frozen, thawed; collected off the Canterbury region, South Island, New Zealand, featuring purplish and off-white pigmented spots along dorsal and ventral contours of body. Photo: C. Struthers.

Fin rays and membranes in middle to posterior of dorsal and anal fins with uniform lighter pigment; anterior one-third of dorsal-fin membrane light sooty gray, but darker than that in remainder of fin. Anteriormost 30 or so rays with proximal halves black and distal halves white, including filamentous tips of these rays. Some specimens with a series, beginning in anterior one-third and continuing through posterior half of fin, of a single darker ray alternating with up to three lighter rays. Approximately 20 anteriormost dorsal-fin rays white with fleshy, tubular membrane and filamentous tips free from membranes. Successive rays becoming increasingly darker posteriorly, but all with white tips. Anal fin with sooty-coloured membrane throughout its length, with darker streaking on rays. Blind sides of dorsal and anal fins white. Ocular side of caudal fin with similar colouration to that on ocular side of body, except outer margins of fin whitish. Distal tips of caudal-fin rays darker. Blind side of caudal fin off-white; caudal-fin membrane sooty gray, with numerous small melanophores.

Ocular-side pectoral fin with same general background colouration as that on ocular side of body; some specimens with distinct whitish blotch at base of ocular-side pectoral fin. Non-elongate rays of ocular-side pectoral fin darker distally. Underside of fin white without melanophores; slightly yellowish in axil region. First and second dorsalmost rays of ocular-side pectoral fin blackish on their proximal halves and white distally; third ray white on proximal half, darker distally; rays 4–6 with black streaks. Remainder of rays streaked black in stark contrast to uniformly, more lightly pigmented (sooty) fin membrane. First four rays of ocular-side pelvic fin with tubular, cup-shaped membrane and filamentous white tips; remainder of rays with dark streaks. Blind-side pectoral and pelvic fins uniformly white.

*Colour of preserved specimens.* Ocular-side background colour greenish-brown, sandy-coloured, or brownish-grey; some specimens with up to three large, irregular, conspicuous dark blotches on lateral line, blotches usually 2–4 scales wide and 2–3 long. Blind side of body uniformly whitish overall with many specimens also featuring numerous, minute melanophores that in some specimens form dense concentrations rendering nearly all of the blind side of body sooty-gray. Inner lining of ocular-side opercle white, except posterodorsal region black or dusky; blind-side opercular lining white, except for dusky to darker sooty-gray on its ventroposterior regions; roof of mouth without black pigment.

Dorsal- and anal-fin rays either uniformly pigmented throughout length of fin, or sometimes with series of one

to several darkly streaked rays alternating with 4–10 lightly pigmented rays throughout and continuing posteriorly to about 20<sup>th</sup> ray from posterior ends of both fins. Caudal-fin rays pigmented throughout their lengths; membranes between rays translucent. Scale-covered region of ocular-side caudal fin with same colour as that on body. Ocular-side pectoral fin with some pigment on rays; membranes between rays translucent. Ocular-side pelvic fin with first and sometimes second rays whitish; remaining rays darker with connecting membranes translucent. Blind sides of dorsal and anal fins whitish; blind side of caudal fin yellowish-white; blind-side pectoral fin yellowish-white; blind-side pelvic fin white. Peritoneum off-white to grayish, without dark pigment. Ocular side of membrane of elongate ovaries in mature and maturing females with few to many, small, dark melanophores. Blind-side pigmentation of elongate ovary grayish to yellowish and sometimes with numerous small melanophores.

**TABLE 4.** Summary of depth of capture information (m) presented as numbers of individuals and percent of total individuals within a species for 1394 specimens representing four species of *Peltorhamphus*.

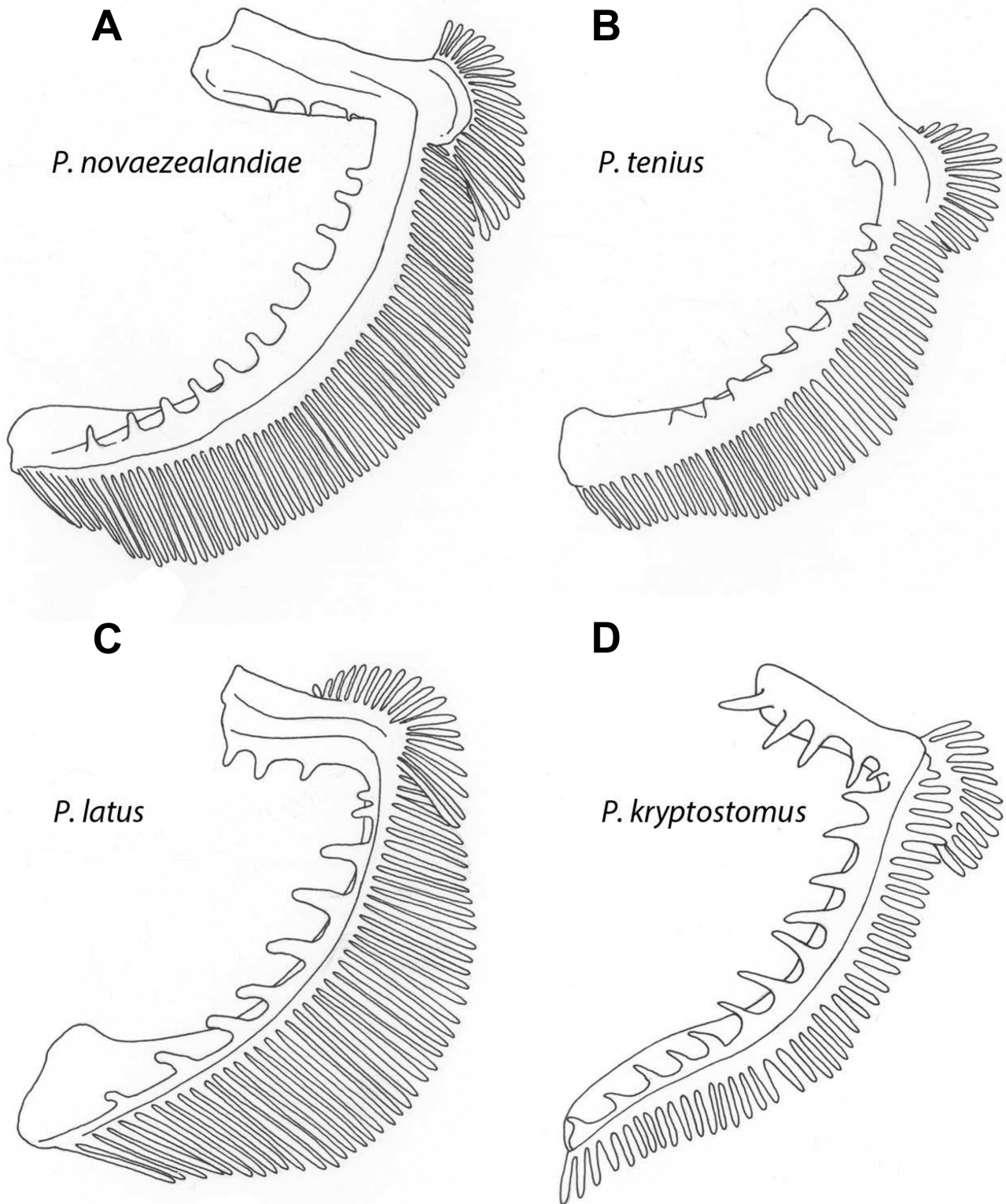
Number	Depth (m)									N
	0.5–5	6–10	11–20	21–30	31–40	41–50	51–62	126	274	
<i>P. novaezeelandiae</i>	46	73	278	117	33	13	11	1	1	573
<i>P. latus</i>	65	140	265	63	52	0	1	0	0	586
<i>P. tenuis</i>	2	44	92	13	2	1	0	0	0	154
<i>P. kryptostomus</i>	8	0	70	2	1	0	0	0	0	81

% of total for species	Depth (m)									%
	0.5–5	6–10	11–20	21–30	31–40	41–50	51–62	126	274	
<i>P. novaezeelandiae</i>	8.0	12.7	48.5	20.4	5.8	2.3	1.9	0.2	0.2	100
<i>P. latus</i>	11.1	23.9	45.3	10.6	8.9	0.0	0.2	0.0	0.0	100
<i>P. tenuis</i>	1.3	28.6	59.7	8.4	1.3	0.6	0.0	0.0	0.0	99.9
<i>P. kryptostomus</i>	9.9	0.0	86.4	2.5	1.6	0.0	0.0	0.0	0.0	100

**Size, longevity, and maturity.** *Peltorhamphus novaezeelandiae* is the largest species in the genus, attaining a maximum size of ca. 550 mm TL and approximately 510–525 mm SL (James 1972; Paul 1986, 2000; Munroe 2015b). It is considered a relatively fast-growing species (Beentjes 2003; Beentjes & MacGibbon 2013; Mockett 2013; New Zealand Ministry for Primary Industries 2017) with fastest growth occurring during the first two years. Based on James (1969), Stevens *et al.* (2004) and Mockett (2013), New Zealand Sole are relatively short-lived, attaining an estimated maximum age of 7–10+ years. Maximum age of 6+ years was estimated for *P. novaezeelandiae* by James (1969) through readings of whole otoliths (290 specimens >180 mm TL), and 7+ years were estimated based on thin-sectioned otoliths of specimens measuring 440–500 mm TL taken off Greymouth, West Coast of South Island by Stevens *et al.* (2004). Stevens *et al.* (2004) also noted that New Zealand Sole grow to 550 mm TL and estimated that fish of this size were likely to be 10+ years in age. James (1969) noted that attempts to age New Zealand Sole using whole otoliths were largely unsuccessful, and Stevens *et al.* (2004) reported that although some success was achieved when using thin sections of otoliths, estimating reliable ages of these fish was still difficult. Webb (1972) provided annual estimates of lengths-at-age for different year-classes (sexes combined) based on a small number of tag returns as follows: Age I, 120–130 mm TL; Age II, 210–220 mm TL; and Age III, 300–310 mm TL. Length-weight relationships for New Zealand Sole ranging in size from 200 mm to 480 mm TL, collected off the West Coast of South Island, were provided by Stevenson (2004, 2006) and MacGibbon & Stevenson (2013).

A total of 188 specimens was examined for size and sex information. Of these, sex could not be determined for four individuals, including three smaller specimens measuring 32.7–39.5 mm SL and one larger specimen measuring 104.8 mm SL. Of 184 specimens (Table 4), 75 were males measuring 42.9–344 mm SL, and 109 were females measuring 48.4–395 mm SL. Based on these data for fish up to 395 mm SL, male *P. novaezeelandiae* attain nearly similar maximum sizes as those of females. Stevenson (2004) also reported similar sizes for males and females of this species captured off the West Coast of South Island. Mockett (2013) reported that for *P. novaezeelandiae* taken off Otago and Southland, males were smaller than females in both length and weight. Fish in her study in size classes >400 mm were exclusively females, while fish < 250 mm in length were exclusively males.



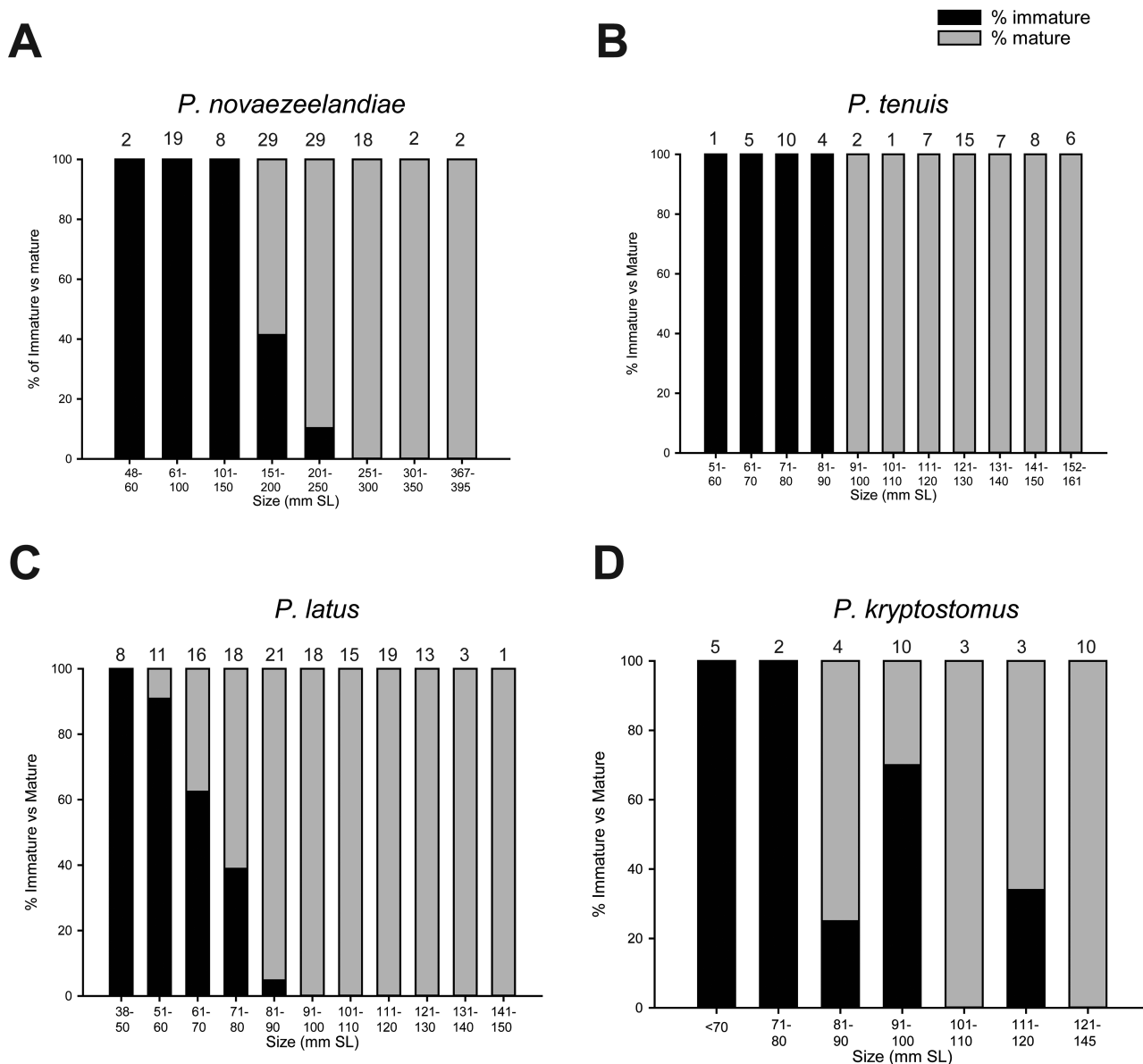
**FIGURE 12.** Differences in size and shape of gillrakers on the first gill arch of *Peltorhamphus*. **A.** *P. novaezealandiae* (drawn from NMNZ P.009457, 196 mm SL). **B.** *P. tenuis* (drawn from NMNZ P.005421, 124.9 mm SL). **C.** *P. latus* (drawn from NMNZ P.041941, 129.0 mm SL). **D.** *P. kryptostomus* **n. sp.** (drawn from NMNZ P.044384, 108.2 mm SL). Drawn by: M. Freeborne.

Graham (1956) reported a sex ratio of 1.5 males to 1.0 females, and James (1969) found a sex ratio of 1.67 males to 1.0 females. Mockett (2013) noted that for the population off Otago, the sex ratio was 1.8 females to 1.0 males, while that off Southland was 1.75 males to 1.0 females.

Based on 109 females (164–395 mm SL) examined in this study (Fig. 13A), 65 (59.6%) were mature with elongate



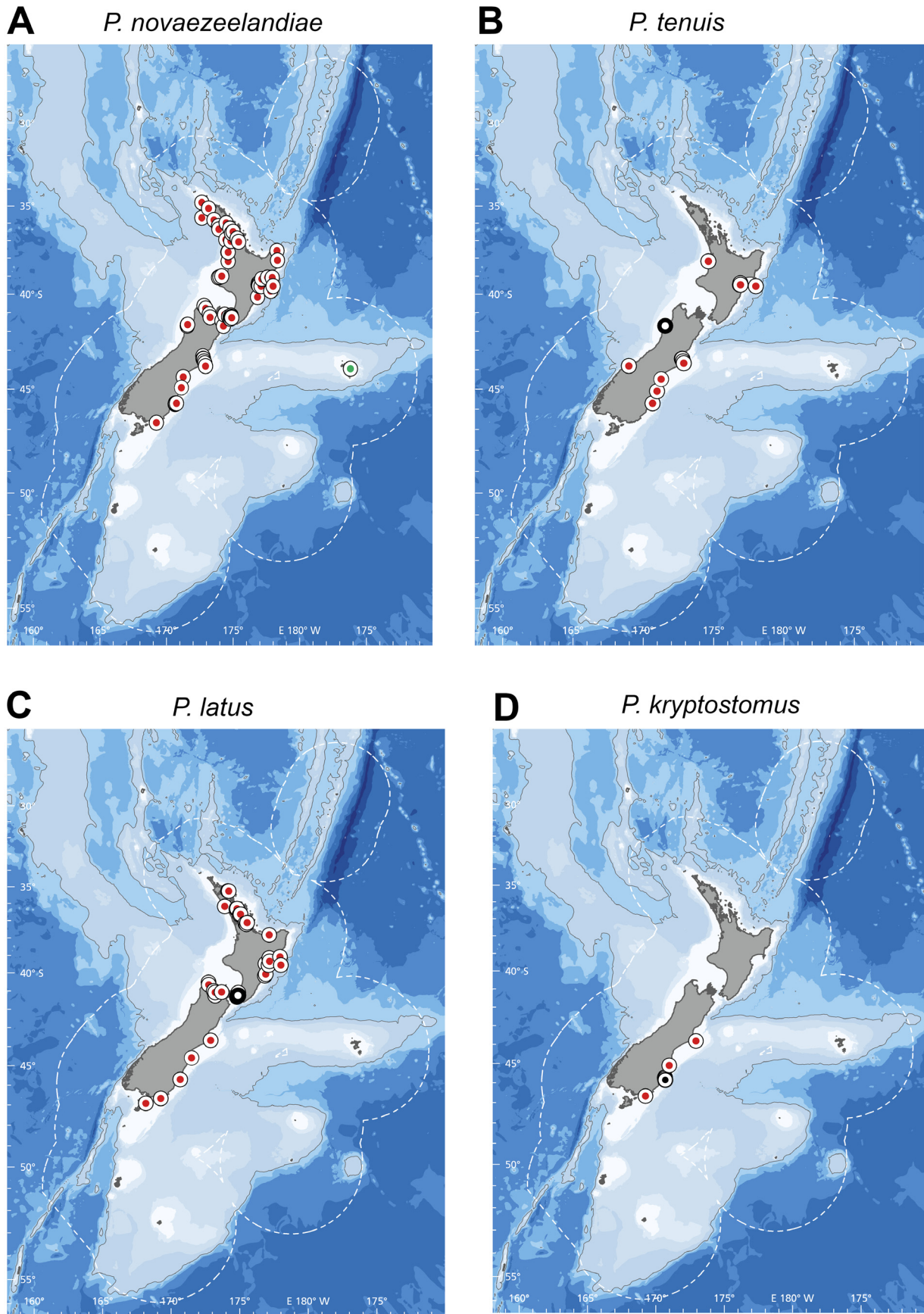
ovaries, or had elongate ovaries with developing ova that were obvious and visible to the naked eye. The smallest females with elongate gonads measured 164 and 166 mm SL; however, 100% maturity usually does not occur until about 178 mm SL, as all but two females 178 mm SL or larger were mature. According to Webb (1973a), fish of 178 mm SL correspond to lengths reached at the end of their second year.



**FIGURE 13.** Size (mm SL) and maturity stage for females of *Peltorhamphus*. **A.** *P. novaezeelandiae*. **B.** *P. tenuis*. **C.** *P. latus*. **D.** *P. kryptostomus* n. sp. Number at top of each column corresponds to number of females within each size range.

Of females examined (Fig. 13A), 44 (48.9–216 mm SL) were immature with ovaries not elongate or only slightly elongate. All females smaller than 164 mm SL were immature; 9 of 22 (nearly 41%) of 160–190 mm SL were also immature. The two largest immature females measured 193 and 216 mm SL, and were the only females >190 mm SL assessed as immature.

Size at maturity noted herein is similar to that reported for *P. novaezeelandiae* in other studies. Graham (1939) recorded size of the smallest female (supposedly this species) with developing ova as ca. 6.25 inches TL (ca. 159 mm), and the smallest fish (9.5 inches) he examined with mature eggs measured 241 mm TL. Webb (1973a) reported that both sexes reached sexual maturity at ca. 220 mm TL, and Munroe (2015b) reported sexual maturity starting around 160 mm SL. Thomson & Anderton (1921) reported a female of ca. 140 mm (sic 5¼ in) as their smallest ripe fish, but given the small size, it seems more likely that this was one of the other smaller species of *Peltorhamphus* (undescribed at the time).



**FIGURE 14.** Geographic distributions of *Peltorhamphus*. **A.** *P. novaezeelandiae*. **B.** *P. tenuis*. **C.** *P. latus*. **D.** *P. kryptostomus* **n. sp.** Black circles in **B**, **C**, and **D** represent collection sites for the holotypes of *P. tenuis*, *P. latus* and *P. kryptostomus* **n. sp.**, respectively. Prepared by: J. Barker.

**Distribution.** *Peltorhamphus novaezeelandiae* is endemic to New Zealand waters (Fig. 14A) where it is widespread from Northland to Southland (James 1972; Paulin & Stewart 1985; Armitage *et al.* 1994; Paulin 1998; Anderson *et al.* 1998; Paul 2000; Munroe 2015b; New Zealand Ministry for Primary Industries 2017, New Zealand Seafood Industry Council 2018; McMillan *et al.* 2019; see additional references in Appendix 1). It has also been reported from the Chatham Islands (Waite 1911; Young 1929; Norman 1934; Chabanaud 1939; Manikiam 1969; James 1972; Roberts 1991; Munroe 2015b). Of lots examined in the present study, the northernmost was taken off Northland (34°48.00'S), North Island; the southernmost was from off Southland, east of Bluff (46°50.55'S). New Zealand Sole have not been reported from the Auckland or Campbell islands (Parrott 1958). Although this species has widespread distribution around New Zealand, its abundance and occurrence varies locally, most likely depending upon suitable habitat.

Earlier reports (Günther 1862; Hutton 1872; Macleay 1882; Waite 1906, 1910, 1916; Norman 1926, 1934; Chabanaud 1939) of this species from Norfolk Island, as well as later studies (Manikiam 1969; Eschmeyer *et al.* 1998b) citing these, are based on a syntype of *P. novaezeelandiae* (BMNH 1848.3.18.216; 122.6 mm SL), which is actually a specimen of *P. latus* that had been misidentified (James 1972; Munroe 2015b; Roberts *et al.* 2018; Remarks section under *P. latus* species account, this study). Whitley (1968) questioned validity of the Norfolk Island record, and, to date no voucher specimens document this species at Norfolk Island. Thus, *P. novaezeelandiae* should be removed from lists of fishes from this area.

**TABLE 5.** Summary of morphometric information for the Lectotype and 86 non-type specimens of *Peltorhamphus novaezeelandiae*. Measurements 1–12 expressed as % of Standard Length; measurements 14–23 expressed as % of Head Length. Abbreviations defined in text.

Character	Lectotype	All Specimens including Lectotype				
		Min	Max	Mean	Stdev	N
SL (mm)	245	32.7	395.0	159.82	82.274	87
1. BD	48.3	33.2	48.3	42.36	3.165	87
2. OSP	22.3	13.1	37.0	27.36	6.175	83
3. BSP	11.2	8.2	21.5	10.41	1.543	87
4. HL	24.3	22.2	30.8	25.57	1.642	87
5. HW	41.4	32.0	47.4	39.54	3.064	87
6. POL	13.9	11.7	16.1	13.65	0.951	87
7. DHW	10.7	6.8	14.0	9.78	1.700	85
8. UHL	22.5	18.3	25.9	22.38	1.608	85
9. LHL	12.7	9.0	16.0	12.64	1.473	85
10. TKL	75.9	70.1	81.6	74.53	2.238	85
11. CFL	18.2	14.8	26.1	19.82	1.853	84
12. CPD	8.8	8.6	11.1	9.53	0.508	85
13. HW/HL	1.70	1.21	1.85	1.55	0.151	87
14. POL	57.0	47.0	59.5	53.42	2.661	87
15. SNL	27.2	24.3	40.3	30.65	2.599	87
16. ED	14.3	12.2	21.6	16.48	2.065	87
17. IO	13.4	5.3	16.6	10.75	2.647	87
18. EUM	19.6	7.4	26.7	16.67	3.025	87
19. DHW	44.0	22.0	57.9	38.67	8.220	85
20. UJL	29.2	21.2	38.2	30.39	2.086	87
21. RHL	27.5	18.7	35.7	26.35	2.946	87
22. UHL	92.4	63.8	105.9	88.17	9.779	85
23. LHL	52.2	35.3	62.7	49.60	5.821	85

Several studies (Waite 1911; Norman 1926, 1934; Young 1929; Chabanaud 1939; Manikiam 1969; James 1972; Roberts 1991; Munroe 2015b) have included the Chatham Islands in the distribution they reported for *P. novaezeelandiae*.

Interestingly, the only study among those listed that actually captured specimens of this species is that of Waite (1911:213). All subsequent records from the Chatham Islands appear to be based on Waite (1911); Station data (Station 70) reported in Waite (1909) for this record indicates a fine sand substratum located at 16–25 fathoms (29.3–45.7 m) in Hanson Bay, Chatham Islands. Both substratum and depth range are typical of those where this species has been captured elsewhere. No specimens from the Government trawling expedition verifying this capture appear to have survived. Waite (1909:49) reported that nearly all trawl-caught specimens of the expedition had washed overboard during a storm. Other specimens that were brought back to the Canterbury Museum were subsequently lost due to prolonged absence of curatorial staff after Waite's return to Sydney (A. Stewart, pers. comm.). Despite this, the species description provided by Waite (1911) agrees with that of *P. novaezeelandiae*. That no other records of this species from the Chatham Islands are known may reflect a paucity of sampling due to the remoteness of the Chathams, lack of sampling in suitable habitat at this location, or due to the expense of getting to this location and bringing specimens back to the mainland (A. Stewart, pers. comm.). More information is needed regarding the status of this species at the Chatham Islands.

New Zealand Sole are reportedly taken more commonly around South Island (James 1972; Ayling & Cox 1982; Paul 1986, 2000; Armitage *et al.* 1994; Colman 1994; Beentjes 2003; Stevenson 2004; McMillan *et al.* 2011, 2019; Morrison *et al.* 2014a). Of specimens examined in this study, 76 lots were collected off North Island compared with 80 lots from off South Island. Nicholson (1979) included this species in his checklist of fishes from the Cavalli Islands, and one lot from the present study was taken at 90 Mile Beach (34°48'S) north of Auckland. Crossland (1981) noted that *P. novaezeelandiae* is only rarely observed in Hauraki Gulf, whereas Paul (1986, 2000) reported it as abundant in Hawke Bay. Paul *et al.* (1983) recorded this species generally in low abundance along the west coast of North Island. Tong & Elder (1968) captured this species in only < 10% of 141 trawls in the Bay of Plenty.

Around South Island, New Zealand Sole are sufficiently abundant to be fished in Tasman Bay (Stevenson 2004; Morrison *et al.* 2014a), and off the West Coast (Beentjes 2003; Stevenson 2004). In inshore trawl surveys (Stevenson 2004, 2006; MacGibbon & Stevenson 2013) along the West Coast of South Island, New Zealand Sole occur in relatively low abundances. It is known from off the east coast of South Island at Pegasus Bay (Stevenson 2004), Canterbury Bight (Beentjes 2003), off Otago, and along the Southland coast (Graham 1938, 1953; Stevenson 2004; Mockett 2013; Morrison *et al.* 2014a). Anderson *et al.* (1998) indicated a few captures of this species off the southern coast of Southland. The southernmost lot examined in the present study was that of four specimens taken off the southeastern coast of Southland off The Caitlins, between Waikawa Harbour and Chaslands Mistake (46°40.55'S). Mockett (2013) also reported captures of this species in this region off Southland at about 46°40'S.

**Habitat and bathymetric distribution.** *Peltorhamphus novaezeelandiae* is found primarily on sand and mud bottoms in estuarine (Parrott 1960; Webb 1972, 1973a; Ryan 1974; McMillan *et al.* 2011, 2019; Francis 2012; Beentjes & MacGibbon 2013) and coastal marine waters to moderate depths (ca. 65 m) on the inner continental shelf (Anderson *et al.* 1998; Beentjes *et al.* 2002; Francis *et al.* 2002; Kendrick & Francis 2002; Stevenson 2004, 2006; McMillan *et al.* 2011, 2019; Beentjes & MacGibbon 2013; Munroe 2015b). Capture depth information, available for 573 museum specimens examined in the present study (Table 5), revealed that this species has been taken from 0.5 m to 274 m. Most of the fish (547 = 95.5%) were taken in 40 m or less; another 24 specimens (4.2%) were taken between 41 and 62 m; and a single individual each was collected at 126 m and 274 m. James (1972) reported a similar depth distribution from 2.0 to 124 m, with greatest abundance between 5.0 and 40 m. Anderson *et al.* (1998) also noted the majority of captures of this species in less than 100 m. Francis *et al.* (2002), based on analysis of presence/absence data compiled from analysis of 19,232 trawls, classified this species as a member of the inshore demersal assemblage with a depth preference of ca. 20 m. Off the West Coast of South Island, several studies (Stevenson 2004, 2006; MacGibbon & Stevenson 2013) report depth ranges of 24–65 m.

Different life-history stages of *P. novaezeelandiae* appear to occupy different habitats (Roper & Jillett 1981). Little information is available regarding habitats occupied by newly settled and the smallest ( $\leq 20$  mm SL) benthic juveniles because information on these size classes has seldom been collected. Some information was summarized by Hurst *et al.* (2000). For these smallest sizes, the difficulty of distinguishing early juvenile stages of *P. novaezeelandiae* from those of co-occurring species has contributed uncertainty to the reliability of any information. Doogue & Moreland (1982) reported that juvenile *P. novaezeelandiae* can often be seen fleeing from the water's edge as one approaches, and that juveniles of this species are also often stranded in tide pools during low tides. Other researchers have not reported *P. novaezeelandiae* in these shallow habitats. Prior to description of *P. latus* (James 1972), all small specimens of *Peltorhamphus* were identified as *P. novaezeelandiae* (maybe also including those of Webb 1972, 1973a, 1973b).

However, both juvenile and adult *P. latus* co-occur throughout the range of *P. novaezeelandiae*, and both adults and juveniles of *P. latus* are common and abundant in estuaries (James 1972; Roper 1979; Healy 1980; Roper & Jillett 1981; Lowe 2013; Morrison *et al.* 2002, 2014b; this study). Roper (1979) and Roper & Jillett (1981) reported that juvenile *P. novaezeelandiae* occur sympatrically in the shallow waters of Blueskin Bay with juveniles of *P. latus* and *P. tenuis*. More recently (Munroe 2015b; this study, see below), problems identifying young stages of species of *Peltorhamphus* from the southeastern region of South Island have compounded as juveniles and adults of a fourth species, *P. kryptostomus* n. sp., were also found to co-occur with juvenile *P. novaezeelandiae* and juvenile and adult *P. latus*. Morphological similarities among these species, and their sympatric occurrence in these shallow-water systems, complicate identifications of at least three of the four species, especially so for newly settled and the smallest of benthic juveniles. Phenotypic similarity and ecological overlap requires further study on the biology and habitat use by early life-history stages of these smaller fishes.

**TABLE 6.** Summary of size versus depth of capture for 303 specimens of *Peltorhamphus novaezeelandiae*.

Size (mm SL)	Depth (m)									N
	0.5–5.0	6–10	11–20	21–30	31–40	41–50	51–62	126	274	
24–50	4	0	4	0	0	0	0	0	0	8
51–100	16	7	8	2	1	0	0	0	0	34
101–150	2	3	18	3	1	3	2	0	0	32
151–200	2	8	58	25	1	6	4	1	1	106
201–250	0	9	37	16	9	3	5	0	0	79
251–300	2	3	5	15	7	0	0	0	0	32
301–395	1	0	3	5	2	1	0	0	0	12
N	27	30	133	66	21	13	11	1	1	303
%	8.9	9.9	43.9	21.8	6.9	4.3	3.6	0.3	0.3	

The smallest (24.0–50.0 mm SL) juvenile *P. novaezeelandiae* examined in this study (Table 6) were collected between 0.5 and 18 m, most between 0.5 and 14 m in open bays or coastal areas. None of these were captured in estuarine inlets. One of these was taken at 18 m, the deepest record for this size range.

Whether small juveniles of *P. novaezeelandiae*, especially those 25–50 mm SL, are estuarine dependent is debatable, partly due to problems with questionable identifications in some previous studies. Some have reported that juveniles in this size range, at least seasonally, inhabit nursery areas located in shallow waters of bays and inshore coastal areas, and to a lesser extent, also in estuaries (Parrott 1960; Webb 1972, 1973a; Kilner & Akroyd 1978; Roper 1979; Healy 1980; Roper & Jillett 1981; Paul 1986, 2000; Hurst *et al.* 2000; Morrison *et al.* 2002; McMillan *et al.* 2011; Francis 2012; Beentjes & MacGibbon 2013). However, one example where data, purportedly for juvenile *P. novaezeelandiae*, may have been confounded with that for juvenile and adult *P. latus* is Webb's studies (1972, 1973a), who published prior to, or at the same time as, the description of *P. latus*. He reported that juvenile *P. novaezeelandiae* used the Avon–Heathcote estuary as a nursery, but his material also included some, or possibly all juveniles of *P. latus*, since that species is common and abundant in this estuary.

Not all estuaries serve as nurseries for New Zealand Sole (Hurst *et al.* 2000). Several studies published after description of *P. latus*, such as Kilner & Akroyd (1978), Healy (1980), Eldon & Kelly (1985), and Jellyman *et al.* (1997), did not capture juvenile *P. novaezeelandiae* in some estuaries sampled. Kilner & Akroyd (1978) reported only infrequent captures and low abundance of juveniles in the Ahuriri Estuary, Napier. In the Otago region, Roper (1979) and Roper & Jillett (1981) rarely captured juvenile *P. novaezeelandiae* in the estuaries or inlets sampled, but identified many juvenile *P. novaezeelandiae* (N = 393, 5.0–49 mm TL) collected from shallow, coastal waters of Blueskin Bay. Healy (1980) reported that in Pauatahanui Inlet, which has a sandy bottom and waters with low turbidity, juvenile *P. novaezeelandiae* were common, whereas in the adjoining Porirua Inlet, where the bottom is muddy, waters more turbid, and pollution greater (A. Stewart, pers. comm.), this species was apparently absent as none were collected there during the entire sampling period.

Contrasting results reported in previous studies about importance and use of estuaries by early settled *P. novaezeelandiae* led Beentjes (2003) to conclude that, perhaps, recruitment to estuarine areas by juvenile *P. novaezeelandiae* was variable and area dependent. However, data from Francis *et al.* (2011), who conducted extensive,

summer-time, beach seine surveys in estuaries on both North and South islands, challenged this idea. They captured only 6 juveniles that they identified as *P. novaezeelandiae* in 6 of 69 estuaries sampled. From these data, Francis *et al.* (2011) concluded that juvenile *P. novaezeelandiae* apparently do not recruit to estuaries or inlets. This was reiterated by Morrison *et al.* (2014a), who, citing results of Francis *et al.* (2011), further noted that only occasional juvenile *P. novaezeelandiae* have been found in estuaries and harbours, but that juveniles (no sizes stated) were caught elsewhere with adults. Based on these two points, Morrison *et al.* (2014a) suggested that the earliest accounts of juvenile *P. novaezeelandiae* in estuaries may have resulted from confusion identifying juveniles of *P. latus*, which are very abundant in these habitats. Conflicting results reported in recent studies on whether or not recruitment of newly settled and early juvenile *P. novaezeelandiae* occur in estuaries or estuarine inlets needs further investigation.

Larger juvenile (51.0–100 mm SL), subadult (101–150 mm SL), and adult *P. novaezeelandiae* inhabit the substrata of open coastal bays on the inner continental shelf (Anderton 1907; Graham 1938, 1953, 1956, 1963; Moreland 1963; James 1972; Webb 1972, 1973a; Roper 1979; Roper & Jillett 1981; Paul *et al.* 1983; Paul 1986, 2000; Beentjes *et al.* 2002; McMillan *et al.* 2011, 2019; Beentjes & MacGibbon 2013). Adult *P. novaezeelandiae* have also been reported in estuaries (Webb 1972, 1973a; Healy 1980; Beentjes & MacGibbon 2013). Webb (1972, 1973a) reported that during winter, mature adults move out of the estuary into coastal waters to spawn (as do adults of *P. latus*, see below). Beentjes & MacGibbon (2013) estimated that *P. novaezeelandiae* reside in sheltered estuaries until about 2–3 years of age after which they move to deeper waters.

Along the Otago coast, Roper (1979) and Roper & Jillett (1981) collected juvenile *P. novaezeelandiae* more frequently in coastal waters, with larger fish in deeper waters. Based on specimens in this study (Table 6), larger juveniles (51.0–100 mm SL) were found in relatively shallow waters of bays and on the open coast. Of 34 fish in this size range, 16 were collected between 0.5 and 5.0 m; 15 were taken between 6–20 m; and three (78.4, 78.6, and 74.8) were taken at 14, 28 and 35 m, respectively. Of 32 fish measuring 101–150 mm SL, five were collected between 1.5 and 9.0 m, 22 were taken between 11–35 m, and five were collected between 41 and 62 m. The deepest capture for fish of this size range is that of two individuals (101.7, 103.7 mm SL) collected at 62 m.

Based on museum collection records, subadult and adult *P. novaezeelandiae* >151 mm SL are usually collected on sandy substrata, mostly between 11 and 50 m (Table 6), although a small number were occasionally taken much shallower (1–3 m) and much deeper (126 m, 274 m). Twelve fish measuring >300 mm SL were not the deepest occurring examined in this study, all but one were collected between 14–46 m, including the largest specimen examined (395 mm SL), which was collected at 18 m. An exceptional shallow depth of a large fish was that of an individual measuring 310 mm SL collected in 3 m. The deepest depths for *P. novaezeelandiae* are those of a single fish (185 mm SL) taken at 126 m and another (182 mm SL) collected at 274 m.

Capture depths for specimens examined herein are consistent with those reported for adult *P. novaezeelandiae* in other studies (Anderton 1907; James 1972; Paul 1986, 2000; Beentjes *et al.* 2002; Stevenson 2004, 2006; McMillan *et al.* 2011, 2019; MacGibbon & Stevenson 2013). Anderton (1907) reported seasonal movements of this species into deeper waters noting that large numbers of New Zealand Sole were trawled in 5–6 fms (9–11 m) during June–July. By late July–early August females had moved to deeper waters 13–18 fms (22–33 m). Beentjes *et al.* (2002) considered *P. novaezeelandiae* as a member of the demersal fish fauna inhabiting the inner continental shelf during both summer and winter. They reported that during summer, *P. novaezeelandiae* occupy a mean depth of approximately 28 m (range 21–41 m), whereas in winter, they moved slightly deeper to about 40 m (range 40–41 m).

**Trophic biology.** *Peltorhamphus novaezeelandiae* is primarily a nocturnal predator (Sherrin 1886; Graham 1956; Livingston 1987a, 1987b; Francis 1996, 2012) consuming a diverse variety of benthic infaunal and epifaunal invertebrates, including small crustaceans (cumaceans, crabs, shrimps, amphipods and isopods), polychaetes, anemones, brittle stars and molluscs (Thomson 1892; Anderton 1907; Thomson & Anderton 1921; Graham 1953, 1956; Parrott 1960; Moreland 1963; Webb 1973b; Paul 1986, 2000; Livingston 1987a, 1987b; Francis 1996, 2012; Mockett 2013). Occasionally, small fishes are also taken (Graham 1956).

Diet composition varies regionally. In Otago Harbour (Thomson & Anderton 1921), large quantities of the galatheid crustacean, *Munida gregaria*, as well as brittle starfishes (Ophiuroidea) were consumed. Whereas in the Avon–Heathcote estuary (Webb 1973b), *P. novaezeelandiae* fed principally on crustaceans. In Wellington Harbour, diets included over 18 different prey categories, including mostly sedentary benthic invertebrates, dominated by polychaetes, crustaceans and ophiuroids (Livingston 1987a). Mockett (2013), using stomach content data and stable isotope analysis, found that diets differed for fish taken off Otago compared with those from off Southland. Overall, *P. novaezeelandiae* examined in her study had consumed primarily amphipods, followed by annelids, decapods,

and a smaller number also had squid beaks in their intestines. Mockett concluded that *P. novaezeelandiae* feeds at a trophic level including prey that are benthic deposit feeders, benthic suspension feeders, and those that are secondary consumers.

*Peltorhamphus novaezeelandiae* have an extensive external taste bud system and additional free neuromasts on the blind side of the head and on the anteriormost dorsal- and pelvic-fin rays that facilitate non-visual prey location (Livingston 1987a). In aquaria, adult New Zealand Sole were observed to sweep across the sediment touching different locations with their fin rays in search of prey (Livingston 1987a). Once located, the fish ingested both prey and sand in which it was buried. This behavior suggested that fin ray contact and sensors on the blind side of the head were used for prey location immediately prior to ingestion.

**Reproductive biology.** New Zealand Sole spawn over a protracted season, usually during winter through spring (Anderton 1907; Thomson & Anderton 1921; Phillipps 1921; Graham 1956; Robertson 1973; Roper & Jillett 1981; Ayling & Cox 1982; Paul 1986, 2000; Dolphin 1997; Paulin 1998; Beentjes & MacGibbon 2013). Peak spawning likely varies regionally dependent upon local environmental conditions (Colman 1994). Several North Island studies report peak spawning activity occurring in August–September (Anderton 1907; Thomson & Anderton 1921; Phillipps 1921; Graham 1956; Robertson 1973; Ayling & Cox 1982; Francis 1996, 2012; Dolphin 1997; Parsons 1999). Phillipps (1921) reported spawning in September for fish taken off Napier. At South Island localities, spawning occurs from autumn to spring, with peak spawning during winter between July and October (Anderton 1907; Thomson & Anderton 1921; Graham 1956; Robertson 1973; Ayling & Cox 1982; Dolphin 1997; Parsons 1999).

*Peltorhamphus novaezeelandiae* is a batch-spawner (Thomson & Anderton 1921; Webb 1973a), with estimates of fecundity (unsure if estimates are those of batch or annual fecundity) ranging as high as 1.0–1.5 million eggs in fish approximately 450 mm TL (Graham 1956). Spawning likely occurs at night (Thomson & Anderton 1921) in shallow coastal waters outside of estuaries (Anderton 1907; Webb 1972, 1973a). Paul (1986, 2000) noted that larvae and juveniles occur close inshore, and Roper & Jillett (1981) reported that larvae were common in coastal waters off the Otago coast. Webb (1972, 1973a) reported that adults used the Avon–Heathcote estuary for feeding and that mature fish moved outside of the estuary during winter to spawn in coastal waters. Beentjes & MacGibbon (2013) also reported an inshore-offshore spawning migration during winter. Ages at which this species spawns are unknown, but have been estimated as likely at 2–3 years of age (Beentjes & MacGibbon 2013).

Eggs and early life-history stages of *P. novaezeelandiae* have been described and illustrated in several studies (Anderton 1907; Thomson 1913; Thomson & Anderton 1921; Webb 1973a; Robertson 1973, 1975; Frentzos 1980; Healy 1980; Dolphin 1997). Robertson (1973) emphasized that eggs of *P. novaezeelandiae* and *P. tenuis* are very similar and difficult to distinguish and that ripe adults of both species occur in the same season. Similarly, Frentzos (1980) noted that early larvae of *P. novaezeelandiae* and *P. latus* are difficult to identify and these also co-occur in ichthyoplankton samples in Wellington Harbour. Because of this, it is likely that some earlier studies confused or misidentified eggs and larvae, and caution should be used when evaluating data from these.

**Utilization and commercial importance.** *Peltorhamphus novaezeelandiae* is a highly desirable food fish with a long history of commercial exploitation (Hector 1872, 1884, 1886; Thomson 1877, 1878, 1879; Sherrin 1886; Anderton 1907; Prince 1916; Phillipps 1921; Phillipps & Hodgkinson 1922; Graham 1938, 1953, 1956, 1963; Parrott 1960; Ayling & Cox 1982; Paul 1986, 2000; Armitage *et al.* 1994; Colman 1994; Paulin 1996, 1998; Paul & Heath 1997; Banks *et al.* 2007; McMillan *et al.* 2011; New Zealand Ministry for Primary Industries 2017, New Zealand Seafood Industry Council 2018). It is the most abundant and commercially important flatfish in New Zealand waters (Ayling & Cox 1982; Beentjes 2003). It has excellent food qualities (Powell 1993; Paulin 1998); adults are consumed as fillets, smaller individuals are prepared as whole fish (Doogue & Moreland 1961, 1964, 1982; Ayling & Cox 1982; Paul 1986, 2000; New Zealand Seafood Industry Council 2018).

This species has (Sherrin 1886) and continues to be caught primarily by trawling (New Zealand Ministry for Primary Industries 2017), and to a lesser extent with set nets (Beentjes 2003) or by Danish seine fleets around South Island (New Zealand Ministry for Primary Industries 2017). It sometimes appears in catches of recreational fishers (Paul 1986, 2000). New Zealand Sole in commercial catches range in size from 150–640 mm TL, with the bulk of the catches consisting of fish measuring 250 to 500 mm TL (Stevenson 2004; Beentjes & Manning 2010; Beentjes & MacGibbon 2013; New Zealand Seafood Industry Council 2018). Most commercial fishing for this species occurs in 10–30 m, and not usually deeper than 50 m. *Peltorhamphus novaezeelandiae* is landed year-round (Armitage *et al.* 1994; Colman 1994; Banks *et al.* 2007), although Beentjes & Stevenson (2000) and Beentjes *et al.* (2002) noted that catch rates are higher in summer than winter.

Although flatfish landings from New Zealand waters are largely reported as the total catch for all flatfish species combined, in some areas, New Zealand Sole occur in sufficient abundance to constitute a minor component of fisheries in the Quota Management System (Beentjes *et al.* 2002; Beentjes 2003; Beentjes & MacGibbon 2013; New Zealand Ministry for Primary Industries 2017). The main areas they are commercially targeted are the inshore trawl fisheries off the West Coast of South Island, off Otago, off Southland, and in Canterbury Bight and Pegasus Bay (Graham 1953, 1956, 1963; Beentjes & Stevenson 2000; Beentjes *et al.* 2002; Beentjes 2003; New Zealand Ministry for Primary Industries 2017). It is most abundant, and the main target, of inshore trawl fisheries off Otago and the Canterbury Bight (Beentjes & Stevenson 2000; Beentjes 2003).

Information on flatfish landings from 1983–84 to 2015–16 (New Zealand Ministry for Primary Industries 2017) indicated that annual landings ranged from ca. 2700 t in 1986–87 to peak values of ca. 5160 t in 1983–84 and 5086 t in 1992–93. In other years, flatfish landings averaged between 3000 and 4000 t/yr until 2009–10. From 2010–11 to 2015–16, landings had declined to less than 3000 t/yr (range 2464–2861 t/yr). In years where annual catch data were reported for individual species, such as 1990–91 to 2013–14, New Zealand Sole constituted 14.4–44.5% of total flatfish landings for the southeast region of South Island (New Zealand Ministry for Primary Industries 2017). No apparent trends in annual catches are evident in these data.

Beentjes (2003) noted that although flatfish catches in New Zealand fisheries did not appear to be declining, it was difficult to gauge effects of current exploitation on populations of individual species. He noted that although combined data from annual landings suggested that flatfish stocks may appear to be stable, these combined data do not provide adequate information to evaluate fishing stress on populations of individual species. He recommended that more species-specific data be collected to better monitor populations of the individual species, and emphasized that only when such data became available would it then be possible to monitor changes in populations in order to better manage exploitation rates of individual species, including those for *P. novaezeelandiae*.

**Etymology.** The name “*novaezeelandiae*” is the Latinized form for New Zealand, in reference to the capture location of this species.

**TABLE 7.** Summary of meristic information reported for specimens purportedly of *Peltorhamphus novaezeelandiae* Günther, 1862. Counts reported by Günther (1862) are not those of the Lectotype, and may be those for a specimen of *P. latus* James, 1972 (see text for more detail). Counts from Norman (1934) include those for specimens of both *P. novaezeelandiae* and *P. latus*. NA = not available.

Character	Günther 1862 ?	Norman 1934 Mixture of species	James 1972 Lectotype	James 1972 All specimens including Lectotype	Munroe 2015b All specimens including Lectotype	This study Lectotype	This study All specimens including Lectotype
Dorsal-fin rays	92	94–104	102	94–112	94–112	103	93–110
Anal-fin rays	57	60–70	67	60–73	60–73	67	60–73
Caudal-fin rays	NA	16–18	NA	18	18	18	17–19
Vertebrae	NA	36	37	36–39	37–39	37	37–39
Ocular-side pelvic-fin rays	6	6	NA	6	6	6	5–6
Blind-side pelvic-fin rays	5	4–5	NA	4	4	4	3–4
Lateral-line scales	78	75–85	85	80–102	80–102	91	76–108
Gill rakers on lower arch	NA	8–15	13	9–15	9–15	12	7–16
Ocular-side pectoral-fin rays	11	10–11	NA	10–11	10–11	10	8–11
Blind-side pectoral-fin rays	7	7	NA	8–10	8–10	9	6–10

**Remarks.** Günther’s (1862:461) original description of *Peltorhamphus novaezeelandiae* is based on at least 12 syntype specimens. No registration numbers were reported for any of the specimens in the original description, nor were



there any illustrations of this species. Günther considered all but the largest individual (11 inches = 279.4 mm) to be juveniles or half-grown. Apparent from the descriptive part is that information from some, if not all, of the syntype specimens was included in Günther's description. A single count is provided (Table 7) for each of seven meristic features. Of the syntypes examined in the present study, none have counts that match those reported by Günther (see below). It is not known which, if any, syntypes he used. What can be ascertained is that the counts he reported were not those from the largest syntype (= lectotype) (compare counts for lectotype by three different investigators; Table 7). Norman (1926, 1934) did not list individual counts from the lectotype in either of his studies. However, ranges he provided for most meristic features encompass counts reported for the lectotype by James (1972), Munroe (2015b), and this study, indicating data for the lectotype were likely included in his ranges. Because Norman (1926, 1934) considered Günther's concept of *P. novaezeelandiae* as representing one species, he likely regarded differences in data of the largest versus small specimens as intraspecific variation.

Counts for several features reported by Günther are different from those of the lectotype as reported by James (1972) and this study (Table 7). Differences were found in dorsal-fin rays (92 in Günther's study vs. 102 and 103 in James (1972) and this study); anal-fin rays (57 in Günther vs. 67 and 67, respectively); and lateral-line scales (78 in Günther vs. 85 and 91, respectively; Table 7). Counts for dorsal- and anal-fin rays reported by Günther are, in fact, lower than the lower limits of ranges reported by both James (1972) and this study (N = 200+ specimens, both studies combined). In fact, Günther's counts of dorsal- (92) and anal-fin rays (57), and lateral-line scales (78) are more similar, but not identical (Munroe, unpubl. data), to those of the two syntypes later re-identified as *P. latus* by James (1972) and this study.

Other early works (Hutton 1872; Macleay 1882; Waite 1911) that relied on Günther's (1862) description are also potentially compromised because their accounts could have been based on two and possibly as many as four different species. Studies by Hutton (1872) and Macleay (1882) include counts for dorsal- and anal-fin rays and lateral-line scales that are lower, and for some counts, even beyond the ranges of those reported for *P. novaezeelandiae* by James (1972), Munroe (2015b), and the present study. Waite's study (1911) likely included only *P. novaezeelandiae* because counts of dorsal- and anal-fin rays, vertebrae and lateral-line scales listed for a single individual are within respective ranges reported for *P. novaezeelandiae* in James (1972), Munroe (2015b), and the present study. Although Hutton's (1872) text descriptions likely feature two or more species, illustrations accompanying that redescription, and the line drawing in Waite (1911, Fig. 7), are of *P. novaezeelandiae*.

Two major systematic works on Rhombosoleid flatfishes that also adopted the species concept for *P. novaezeelandiae* proposed by Günther appear in Norman (1926, 1934). Norman (1926) examined 19 specimens that he identified as *P. novaezeelandiae*, including "the types," but which were not listed with registration numbers nor were sizes specified. Norman noted colour differences between smaller and the largest specimen in his study, but in agreement with Günther, attributed these to ontogenetic changes.

The later account of *P. novaezeelandiae* in his monograph on the flatfishes (Norman 1934) was based on many (if not all) of the same 19 specimens included in his earlier study (Norman 1926), as well as a few other specimens. Norman listed a 'holotype' (290 mm TL) with the registration number BMNH 1848.3.18.- (Fig. 1). This specimen is the largest of Günther's syntypes. However, Norman did not provide any individual counts for this specimen, or an illustration or photograph. In addition to this 'holotype,' Norman also listed 10 'paratypes,' without catalogue numbers, but with sizes for some individuals and size ranges for lots containing multiple specimens.

Norman's selection of a 'holotype' constituted designation of a lectotype according to Article 74.5 of the International Code of Zoological Nomenclature (1999), and it restricted the species concept of *P. novaezeelandiae*. Accordingly, the remaining syntypes referred to by Norman (1934) as 'paratypes' became paralectotypes (ICZN Article 74.1.3).

The lectotype (BMNH 1848.3.18.-; Figs. 1A–B, 6), as designated by Norman, is the largest (290 mm TL; 245 mm SL) specimen of the original syntype series of Günther (1862). It has different meristic features from those of the other syntypes of *P. novaezeelandiae*. This distinction is important because at least 10 of 11 of the other, smaller, syntypes of *P. novaezeelandiae* are not this species, but are *Peltorhamphus latus* James, 1972, a species with lower meristic values than those of *P. novaezeelandiae* (see below). Identity of the 12<sup>th</sup> syntype (ZMB 5002) is unknown because this specimen could not be located at ZMB (P. Bartsch, Museum für Naturkunde, Berlin, pers. comm. 02/22/2017). However, Günther (1862) listed this syntype as "half-grown," as were all of the other syntypes currently identified as *P. latus*, and it is likely also this species. Photographs of the ocular and blind sides (Figs. 1A–B), as well as a radiograph (Fig. 6) are the first published of the lectotype of *P. novaezeelandiae*.

In 1972, James conducted the first detailed revision of the genus *Peltorhamphus* wherein he examined over 800 specimens revealing three species: *P. novaezeelandiae* and two undescribed ones. He noted that of earlier studies reporting systematic information on *P. novaezeelandiae*, only those by Graham (1956) and Manikiam (1969) suggested more than one species was present among material being identified as that species. James reported summaries of meristic information (dorsal-fin rays, anal-fin rays, and vertebrae), as well as summaries of other meristic features (gillrakers, lateral-line scales) and morphometric information from 160 specimens. His account included meristic features of the lectotype of *P. novaezeelandiae*, where he followed Norman's (1934) reference to this specimen as the "holotype."

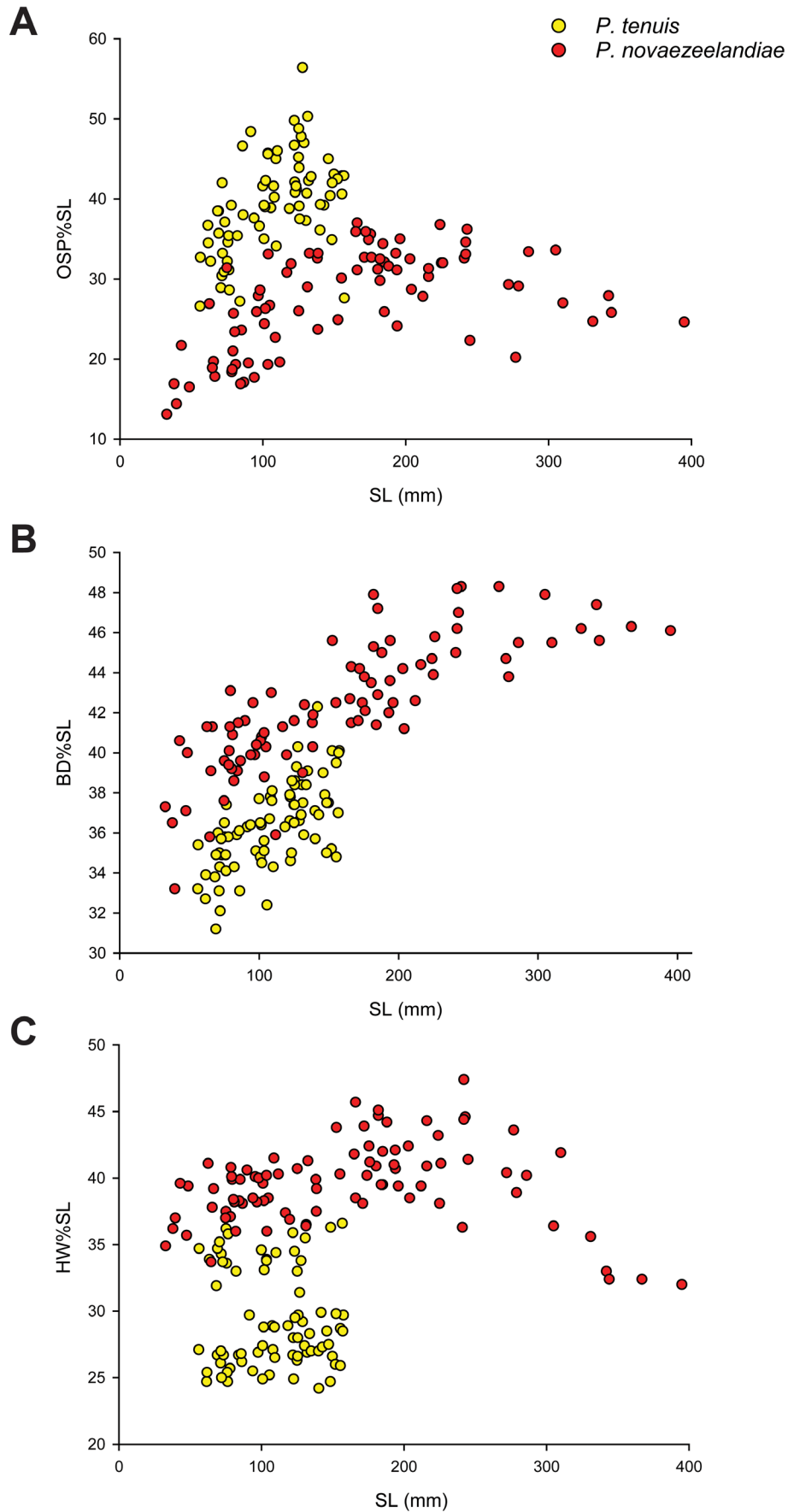
All works after James (1972) reporting meristic, morphometric or other diagnostic information for *P. novaezeelandiae* have employed the species concept for *P. novaezeelandiae* of James, including Ayling & Cox (1982), Doogue & Mooreland (1982), Paulin & Stewart (1985), Paul (1986, 2000), Paulin *et al.* (1989, 2001), Armitage *et al.* (1994), Francis (1996, 2012), Paul & Heath (1997), Hirt-Chabbert (2006), McMillan *et al.* (2011, 2019), and Munroe (2015b). Information in the most recent account (Munroe 2015b) has been incorporated and expanded upon in the detailed species account above.

The present study represents the most comprehensive summary of meristic and morphometric information for *P. novaezeelandiae*; a complete list of characters and data is presented in Table 1. The absence of frequency distribution information in earlier studies precludes making detailed comparisons between those and this study. Previous studies (James 1972; Munroe 2015b) reporting meristic information for an extensive series of specimens of *P. novaezeelandiae* presented only ranges and means for meristic data. Comparisons of range values for seven of 10 meristic features reported in common between James' (1972) study and this study reveal nearly identical results. Only for counts of lateral-line scales and counts of upper and lower limb gillrakers are the ranges reported herein slightly broader than those listed in James' study. Differences between studies are small and relatively few individuals are represented by outlier values, so these values are considered negligible. Ranges for six morphometric characters also varied slightly between the two studies, but again these differences are small and also assessed as negligible.

Overall, specimens of *P. novaezeelandiae* examined in this study exhibit considerable homogeneity in meristic, morphometric, qualitative, and pigmentation features. No noticeable differences were evident among specimens collected from different areas off North and South islands with exception of specimens recently collected in the South Canterbury region, South Island. These specimens, mostly immature females, have a distinctive pigmentation pattern of a series of grayish-blue spots arranged along dorsal and ventral contours of the ocular side of the body (detailed above in colour description). No previous accounts of this species (Günther 1862; Norman 1926, 1934; James 1972; Munroe 2015b) noted this colour. Other than this difference in pigmentation, these specimens had identical meristic features to those recorded for other specimens. Also, these specimens had nearly identical morphological values (no more than 1.5% difference in any of 18 characters measured) revealed by the large overlap in these features (Figs. 9A–J). Based on the nearly complete overlap in meristic and morphometric features, these were confidently identified as *P. novaezeelandiae*. A distinctive spotted pattern in the ocular-side pigmentation is also evident in a variety of other specimens of *P. novaezeelandiae* photographed *in situ* at several different regions. Spotting does not appear unique to specimens from specific regions, those caught on specific substrata, or only in immature females, but on a variety of individuals of both sexes from different locations, and may be a common colour pattern, best evident in live or freshly caught specimens.

Two studies (Sakamoto 1984; Guibord 2003), based on morphological characters, have included *P. novaezeelandiae* in their classifications of Rhombosoleid flatfishes. Sakamoto detailed osteological features of *P. novaezeelandiae* and *P. latus* and concluded that these two species, together with *P. tenuis*, constitute the genus *Peltorhamphus*. Guibord (2003) in a phylogenetic analysis of intrarelationships among species of the Rhombosoleidae detailed osteological information for *P. novaezeelandiae*, *P. latus* and *P. tenuis*. Based on this analysis, Guibord agreed with James (1972), recognizing these three as valid species in *Peltorhamphus*. However, Guibord was unable to resolve intrarelationships between *P. novaezeelandiae* and its congeners.

**Comparisons.** *Peltorhamphus novaezeelandiae* is the largest species in the genus (Table 4), reaching sizes of ca. 550–600 mm TL, with individuals of 300–400 mm SL commonly captured. Other species in this genus generally do not exceed 170 mm SL and about 200 mm TL (James 1972; Munroe 2015b; Table 4, this study), so size alone distinguishes the largest individuals (> 175 mm SL) of *P. novaezeelandiae* from congeners.



**FIGURE 15.** Selected morphometric features (as % of SL) plotted against SL (in mm) for *Peltorhamphus novaezeelandiae* and *P. tenuis*. **A.** Ocular-side pectoral-fin ray (OSP). **B.** Body depth (BD). **C.** Head width (HW).

Values of most meristic features for *P. novaezeelandiae* and *P. tenuis* overlap (Table 1), including numbers of dorsal- and anal-fin rays and lateral-line scale counts. However, they differ in counts of total vertebrae with *P. novaezeelandiae* usually with 37–38 (infrequently 39) compared with 40–42 (rarely 39) in *P. tenuis*. *Peltorhamphus novaezeelandiae* also has more gillrakers on the lower limb of the first gill arch (7–16, usually 10–14) compared with that in *P. tenuis* (5–12, usually 8–11), and more total gillrakers on this gill arch (10–20, usually 14–18 vs. 8–17, usually 10–15 in *P. tenuis*; Table 1). All sizes of *P. novaezeelandiae* lack scales on the blind sides of their dorsal- and anal-fin rays, whereas larger juveniles and adult *P. tenuis* have a series of small scales on the blind sides of their dorsal- and anal-fin rays (Fig. 2C). Individuals of *P. novaezeelandiae* also lack accessory scales overlying primary scales on the posterodorsal region of the head and dorsal region of the anterior body, whereas many larger *P. tenuis* have such accessory scales.

*Peltorhamphus novaezeelandiae* differs distinctively from *P. tenuis* in having a much shorter ocular-side second pectoral-fin ray (Fig. 15A). Differences in length of this elongate pectoral fin relative to the body depth is easily seen in adults and larger juveniles of these species, especially when the ray is intact. In *P. novaezeelandiae*, this fin ray is much shorter than the greatest body depth at all sizes (Figs. 3A, 7–8), whereas in adult and larger juvenile (>80 mm SL) *P. tenuis*, the elongate ray is usually longer than the greatest body depth (Figs. 3B, 17–18). In even some of the smallest *P. tenuis*, this ray still equals the greatest body depth.

*Peltorhamphus novaezeelandiae* also differs in body shape (deeper and more oval or elliptical with rounded anterior profile of the head) compared with the slender, more elongate body and narrower, more pointed head of *P. tenuis* (Figs. 4A–4B and comparisons of Fig. 8 with Figs. 17–18). These differences in BD (Fig. 15B) are reflected in measurements of greatest body depth (BD 33.2–48.3% of SL,  $\bar{X}$  = 42.2% in *P. novaezeelandiae* vs. BD 31.2–42.3% of SL,  $\bar{X}$  = 36.3% in *P. tenuis*, Table 2), but also in the position of greatest body depth. In *P. novaezeelandiae*, this is located well anterior to the body midpoint; posterior to this point body depth tapers fairly rapidly. By contrast, in *P. tenuis*, greatest body depth occurs over a much broader region both anterior and posterior to the body midpoint, and beyond this region, the posterior taper of the body is more moderate than is that in *P. novaezeelandiae*. *Peltorhamphus novaezeelandiae* usually also has a much wider head than does *P. tenuis* (Fig. 15C). However, when HW is expressed as a ratio of HL these differences are not as apparent (HW/HL 1.2–1.8 ( $\bar{X}$  = 1.53) in *P. novaezeelandiae* vs. 0.9–1.7 ( $\bar{X}$  = 1.20) in *P. tenuis*). Other morphometric features have more overlap and are presented in Table 2.

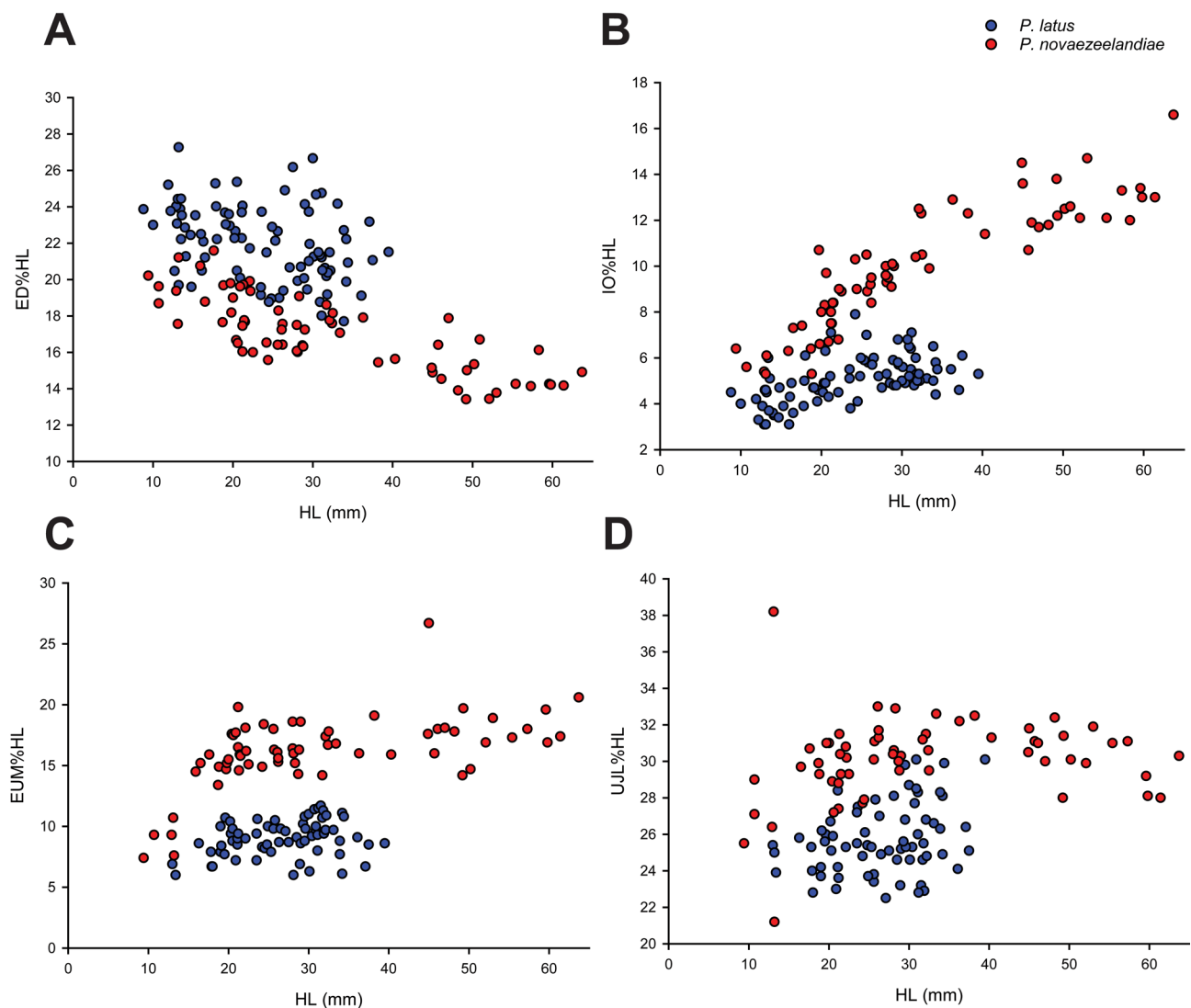
The colour pattern of *P. novaezeelandiae* differs from that of *P. tenuis* (compare Figs. 8 and 11 with Figs. 17–18). In *P. novaezeelandiae*, the ocular-side background colour is more or less uniformly greenish- to grayish-brown sometimes with up to three conspicuous darker-brown blotches along the lateral line and sometimes with a series of whitish spots along dorsal and ventral contours of the body (Fig. 11), and lacks any distinct series of longitudinal markings on the ocular-side scales. Ocular-side pigmentation of *P. tenuis* consists of a darker-brown background colouration overlain by a conspicuous longitudinal series of small, parallel dark markings on the scales, and specimens may also have up to three darker-brown blotches along the lateral line (Fig. 18C).

In addition to its larger size (Table 4), *P. novaezeelandiae* is further distinguished from both *P. latus* and *P. kryptostomus* **n. sp.** by its higher counts of dorsal-fin rays, anal-fin rays, and lateral-line scales (Table 1). *Peltorhamphus novaezeelandiae* can also be distinguished from *P. latus* and *P. kryptostomus* **n. sp.** in lacking black pigment over the entire inner lining of the ocular-side opercle and on the entire roof of mouth, whereas these are black in the other species. *Peltorhamphus novaezeelandiae* also has short, triangular-shaped, gillrakers on the first gill arch, with gillrakers on the upper limb of the first blind-side arch noticeably shorter and rounder than those on the lower limb and not overlapping gillrakers on the lower limb. In *P. latus* and *P. kryptostomus* **n. sp.**, these are longer and more pointed (compare Figs. 12A with 12C and 12D), especially those of *P. kryptostomus* **n. sp.**, which has the lowermost gillraker overlapping the uppermost gillraker(s) on the lower limb. *Peltorhamphus novaezeelandiae* also differs from *P. latus* and *P. kryptostomus* **n. sp.** in having cycloid or weakly ctenoid scales on the blind side of the body (vs. more strongly ctenoid in *P. latus* and *P. kryptostomus* **n. sp.**), and in having cycloid scales on the blind-side pre- and subopercles (vs. ctenoid scales on blind-side pre- and subopercles in *P. kryptostomus* **n. sp.**).

*Peltorhamphus novaezeelandiae* differs further from *P. latus* in possessing several fleshy, finger-like filaments on the inner anteroventral margin of the fleshy skinfold on the ocular-side lower jaw (vs. no filaments on inner anteroventral margin of fleshy skinfold on ocular-side lower jaw of *P. latus*; compare Fig. 3A with 3B). These species differ in several meristic features. *Peltorhamphus novaezeelandiae* has more scales in a diagonal row between the anteroventral margin of the lower (non-migrated) eye and dorsal margin of the rostral flap above the mouth (2–9,

usually 4–6) than does *P. latus* (1–4 scales, usually 2–3); more scales between mid-region of upper eye and dorsal margin of the head (6–13, usually 9–12 vs. 5–10, usually 7–9 scales, in *P. latus*), and adult *P. novaezeelandiae* have more scales in the interorbital space (usually 2–4) than that (0–2 scales) found in *P. latus* (Table 1). *Peltorhamphus novaezeelandiae* has more (76–108, usually 85–100) lateral-line scales compared with that (64–83, usually 66–79) found in *P. latus*. Counts for total vertebrae are different between those of *P. novaezeelandiae* (37–38 total vertebrae) and that of *P. latus* (36–37 total vertebrae). These two species also differ in total gillraker count on the first gill arch (Table 1); *P. novaezeelandiae* has 10–20, but usually 14–19 gillrakers vs. *P. latus* with 8–16, usually 10–15.

*Peltorhamphus novaezeelandiae* has a smaller eye (Fig. 16A), and a broader interorbital width (Fig. 16B) compared with those features in *P. latus*; differences in IO width are especially evident in fish >28 mm HL. The EUM distance (diagonal distance between ventral rim of lower eye at mid-eye and dorsalmost margin of rostral hook) in all but the smallest *P. novaezeelandiae* (Fig. 16C) is much larger in *P. novaezeelandiae* than that of *P. latus*. This difference is especially evident in fish of 15 mm HL or larger. *Peltorhamphus novaezeelandiae* usually has a longer jaw length (UJL) than that of *P. latus* of corresponding sizes (Fig. 16D).



**FIGURE 16.** Selected morphometric features of the head (as % of HL) plotted against HL (in mm) for *Peltorhamphus novaezeelandiae* and *P. latus*. **A.** Eye diameter (ED). **B.** Interorbital width (IO). **C.** Eye to upper mouth distance (EUM). **D.** Upper jaw length (UJL).

Other qualitative differences between these species are head shape, where *P. novaezeelandiae* is more broadly rounded and lacks a distinct point vs. *P. latus* with distinct blunt point. *Peltorhamphus novaezeelandiae* also has cycloid scales on the blind side of its body, whereas *P. latus* has ctenoid scales on its blind side.

*Peltorhamphus novaezeelandiae* differs further from *P. kryptostomus* n. sp. in having more supracranial

pterygiophores (23–29, usually 25–28 vs. 21–26, usually 23–24 in *P. kryptostomus* n. sp.), higher, nearly non-overlapping, counts for dorsal-fin rays (Table 1), and *P. novaezeelandiae* has fewer gillrakers on the upper limb of the first gill arch (1–6, usually 3–4 vs. 4–6, usually 4–5, in *P. kryptostomus* n. sp.). *Peltorhamphus novaezeelandiae* has a smaller, less conspicuous pupillary operculum, and has cycloid scales on the blind side of the body, whereas *P. kryptostomus* n. sp. has a more conspicuous pupillary operculum and ctenoid scales on its blind side.

### ***Peltorhamphus tenuis* James, 1972**

Slender Sole

Figs. 2A, 2C, 3A, 4B, 5A, 12B, 13B, 14B, 15A–C, 17, 18A–B, 19A–J, 20A–C; Tables 1–4, 8–9



**FIGURE 17.** *Peltorhamphus tenuis* holotype, preserved (NMNZ P.005138, 155.3 mm SL); collected off Westport, South Island, New Zealand. Photo: C. Struthers.

### ***Peltorhamphus tenuis* James, 1972**

James 1972:353 (description with counts, measurements, colour description; black & white illustration; diagnosed from congeners by meristic and morphometric features and electrophoretic information; bathymetric distribution 9–38 m; less abundant than congeners; endemic in New Zealand waters; likely more abundant off South Island).

Roper 1979:136 (Blueskin Bay, South Island; distribution; distinguished from *P. novaezeelandiae* and *P. latus* by meristic and morphometric features; to 190 mm SL; figures of juveniles at various sizes).

Ayling & Cox 1982:308 (brief mention; smaller species; distinguished from congeners by higher vertebral counts).

Sakamoto 1984:95 (morphology; osteology; valid species).

Paulin & Stewart 1985:57 (endemic; widespread in coastal waters; 0–20 m).

Paul 1986:141 (less common species compared with congeners; brief comments on identification).

Paulin *et al.* 1989:240 (in key; partial meristic features; distinguished from congeners; listed, Pleuronectidae; New Zealand).

Hardy 1990:14 (listed, type catalog of fishes in National Museum of New Zealand).

Colman 1994:34 (likely confused with juveniles of *P. novaezeelandiae*).

Eschmeyer *et al.* 1998b:1663 (valid species in *Peltorhamphus*; New Zealand type locality; list of type specimens).

Eschmeyer 1998b:2433 (valid species in *Peltorhamphus*: Rhombosoleinae: Pleuronectidae).

Paul 2000:141 (less common species compared with congeners; brief comments on identification; black & white illustration).

Paulin *et al.* 2001:240 (in key; partial meristic features; distinguished from congeners; listed in Pleuronectidae; New Zealand).

Guibord 2003:202 (osteology; morphology; unresolved relationships among congeners).

Evseenko 2004:20 (valid species in Rhombosoleinae; holotype information; western South Pacific).

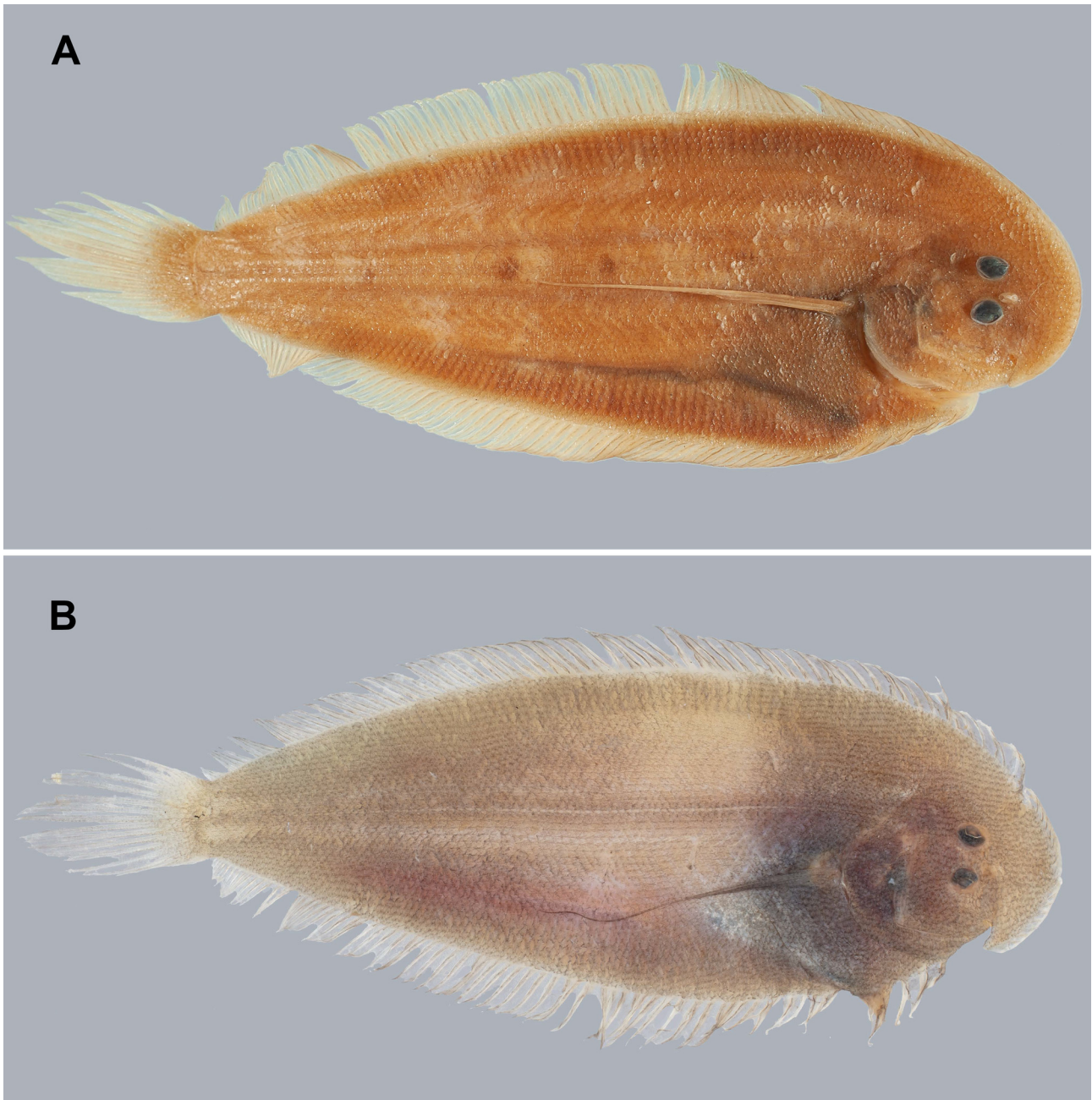
Roberts *et al.* 2009:536 (listed, checklist of New Zealand Chordata).

McMillan *et al.* 2011:277 (briefly mentioned; size < 200 mm TL; distinguished from congeners).

Roberts *et al.* 2015:S178 (listed, checklist of fishes of New Zealand; type locality New Zealand).

Munroe 2015b:1697 (species account, including black & white line drawing; size; diagnostic features; in key; endemic in New Zealand waters).

Roberts *et al.* 2018:12 (listed, online checklist of fishes of New Zealand; holotype listed; type locality New Zealand).  
McMillan *et al.* 2019:249 (brief mention; size <200 mm TL; distinguished from *P. latus* and *P. novaezeelandiae*, respectively).



**FIGURE 18.** *Peltorhamphus tenuis* collected off New Zealand. **A.** NMNZ P.005421, 124.9 mm SL, off Napier Beach, Hawke Bay, North Island; preserved. **B.** NMNZ P.061008, 117.4 mm SL, off South Canterbury, South Island; freshly frozen, thawed. Photos: C. Struthers.

**Diagnosis.** *Peltorhamphus tenuis* is distinguished from congeners by the following combination of characters: its elongate body (greatest depth more evenly distributed over its length and with more gradual posterior taper beyond this point); long, filamentous second ocular-side pectoral-fin ray longer than, or equal to greatest body depth; relatively narrow head; presence of scales on blind sides of dorsal- and anal-fin rays (at sizes  $\geq 70$  mm SL; Fig. 2C); its higher and mostly non-overlapping meristic values, including  $\geq 40$  total vertebrae, 98–116 dorsal-fin rays, 62–72 anal-fin rays, 82–106 lateral-line pores, 25–31 supracranial pterygiophores, usually 10–15 gillrakers on first gill arch; usually 8–10 scales between mid-eye and dorsal margin of head; usually 4–6 scales between anteroventral margin of lower (non-migrated) eye and dorsal margin of rostral hood above mouth; relatively small, thin gillrakers on upper limb of first gill arch not reaching dorsalmost gillrakers on lower limb; presence of 1–5 fleshy, finger-like filaments on

inner anteroventral margin of fleshy skinfold on ocular-side lower jaw (Fig. 3A); relatively wide IO space; ocular-side colour pattern with several faint longitudinal lines and sometimes with up to three dark blotches along lateral line; dorsal- and anal-fin rays uniformly pigmented; inner lining of ocular-side opercle dusky (not black); roof of mouth unpigmented; and morphometric features including shorter postorbital length, narrower upper and lower head lobes, narrower caudal peduncle, smaller ratio of HW/HL, longer snout, and smaller eye (Table 2).

**Holotype (Fig. 17):** NMNZ P.005138 (155 mm SL); off Westport, Westland, South Island (41°43'S, 171°34'E); 12–20 m; collected 18 Dec 1969.

**Description.** Meristic data summarized in Table 1. Values for holotype in bold here and in Table 1. Supracranial pterygiophores **27**, range 25–31, usually 26–29 (126 of 136 individuals). Pterygiophores inserted into first interneural space **3**, range 2–4, usually 3 (115 of 136 individuals). Pterygiophores inserted anterior to first haemal spine **10**, range 8–11, usually 9–10 (91 of 107 individuals). Dorsal-fin rays **105**, range 98–116, usually 101–107. Anal-fin rays **70**, range 62–72, usually 66–72. Caudal-fin rays **18**, usually 18 (131 of 136 individuals). Ocular-side pectoral-fin rays **9**, range 5–10, usually 8–10 (96 of 104 individuals); blind-side pectoral-fin rays **7**, range 5–10, usually 7–8 (91 of 106 individuals). Ocular-side pelvic-fin rays **6**, usually 6 (110 of 111); blind-side pelvic-fin rays **4**, usually 4 (103 of 104 individuals). Abdominal vertebrae **10**, usually 10 (126 of 132 individuals with 3 + 7 arrangement); caudal vertebrae **32**, range 29–33, usually 30–32 (114 of 132 individuals); total vertebrae **42**, range 39–43, usually 40–42 (135 of 138 individuals). Finger-like filaments on inner anteroventral margin of fleshy skinfold on ocular-side lower jaw **1**, range 0–5, usually with 1–4 (87 of 93 individuals). Gillrakers on upper limb of first arch on blind side **3**, usually 2–4 (100 of 102 individuals); gillrakers on lower limb of first arch on blind side **9**, usually 8–11 (96 of 102 individuals); total gillrakers on first arch **12**, range 8–17, usually 10–15 (96 of 102 individuals). Interorbital scales **3**, range 1–5, usually 2–4 (96 of 98 individuals). Scales in diagonal row between anteroventral margin of non-migrated eye and dorsal margin of mouth opening **7**, usually 4–6 (86 of 94 individuals). Head scales from mid-eye to dorsal margin of head **9**, range 7–12, usually 8–10 (66 of 73 individuals). Lateral-line pores **97**, range 82–105, usually 88–99 (85 of 90 individuals).

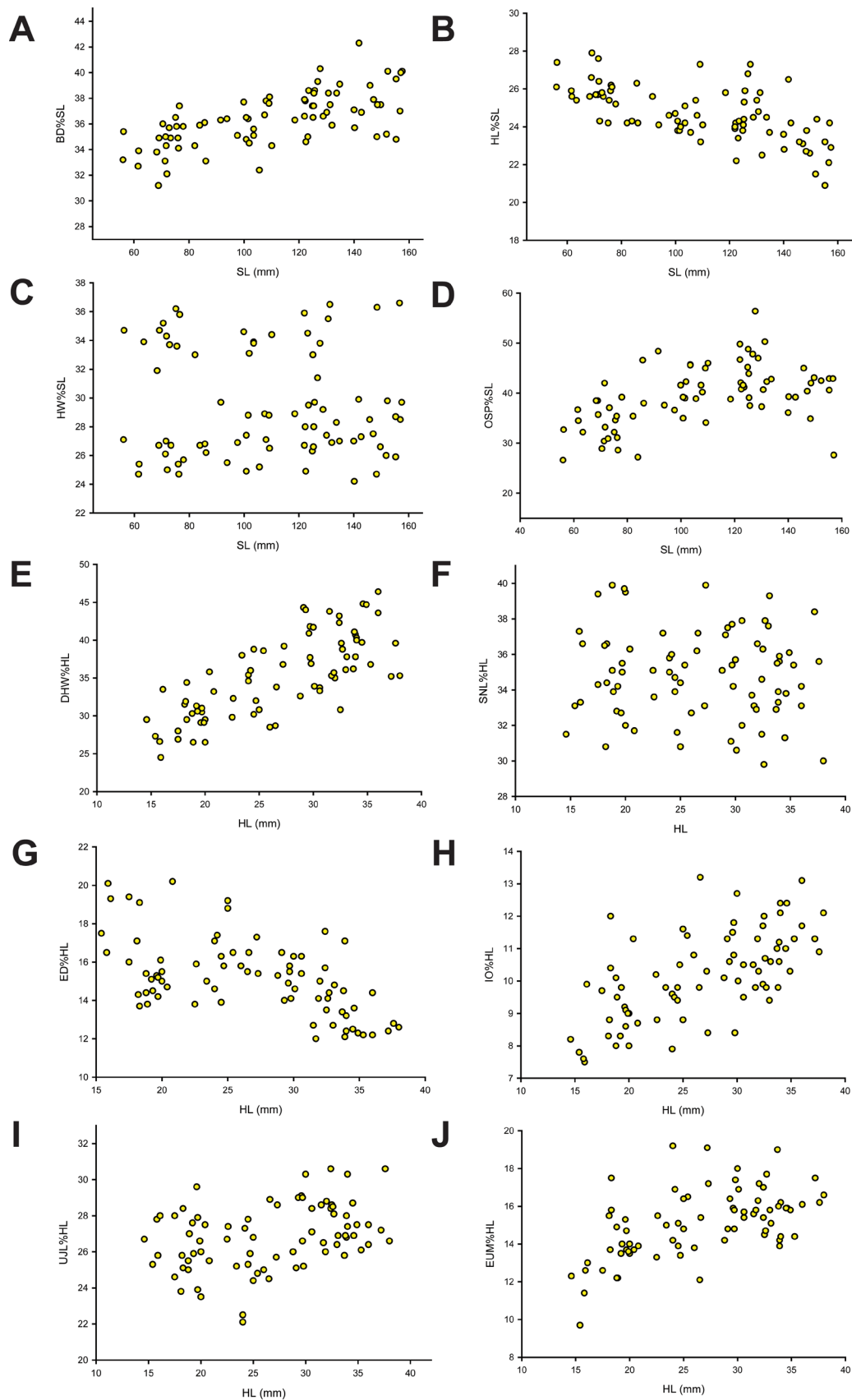
Morphometric data summarized in Table 8, compared with that of other species in Table 2, discussed in further detail in the Morphometric variation section below, and plotted for selected features in Figure 19A–J. Body relatively elongate (Figs. 4B, 17–18, 19A), with long trunk (TKL 70.1–86.1% of SL,  $\bar{X} = 75.6\%$ ); laterally compressed; greatest body depth (31.2–42.3% of SL,  $\bar{X} = 36.3\%$ ) increasing proportionally with fish size (Fig. 19A); greatest depth located posterior to anus at point between verticals at anal-fin ray 5 and ray near body midpoint, BD gradually tapering anteriorly and posteriorly to this point. Some females with slightly greater BD than that of males of comparable size. Caudal peduncle short, narrow (CPD 6.9–10.2% of SL,  $\bar{X} = 8.7\%$ ). Head relatively short (HL 20.9–27.9% of SL,  $\bar{X} = 24.7\%$ ), proportionally larger in smaller individuals (Fig. 19B); head relatively narrow (HW 24.2–38.7% of SL,  $\bar{X} = 29.6\%$ ), HW/SL isometric (Fig. 19C); HW/HL 0.9–1.7 ( $\bar{X} = 1.20$ ). Dorsal profile of head rising steeply to point about equal with vertical just posterior to posterior margin of eyes; ventral margin of head with steep decurvature anteriorly, followed posteriorly by more gradual ventral decline to point about equal with posterior margin of preopercle; anterior profile rounded, or with blunt point about equal with horizontal between eyes. Head width dorsal to upper eye (Fig. 19E) moderately wide (DHW 24.5–46.4% of HL,  $\bar{X} = 35.0\%$ ), about equal to 2.5 times eye diameter; DHW increasing proportionally with fish size (Fig. 19E). Head region between eye and dorsal body margin with ctenoid scales, many also with smaller, secondary scales covering about one-third length of exposed medial region of these primary scales. Snout long (SNL 29.8–39.9% of HL,  $\bar{X} = 34.8\%$ ), growth in SNL isometric relative to fish size (Fig. 19F); snout bluntly pointed to rounded, greatest length at horizontal between eyes; about 7–8 small ctenoid scales between anterior margin of eyes and anterior profile of snout. Ocular side of snout with conspicuous rostral flap with dorsoposterior margin nearly, or sometimes completely, surrounding mouth and nearly hiding entire mouth, except for posteriormost end of jaws; rostral flap also with long, fleshy, rostral hook (RHL 21.3–37.6% of HL,  $\bar{X} = 29.1\%$ ) with posterior tip extending posteroventrally well beyond vertical at posterior margin of mouth opening. Ventroposterior section of rostral flap also with vertical, notch-shaped opening resembling a question mark, exposing only posteriormost tips of jaws ventrally. Blind side of rostral hook with ctenoid scales. Two ocular-side nostrils in anterior interorbital space, asymmetrically positioned closer to dorsal margin of lower eye (illustrated in Fig. 5A). Anterior ocular-side nostril a small opening surrounded by fleshy membrane extending posteriorly into relatively long flap, wide at its base and with long fleshy tip on its posterior rim. When depressed posteriorly, anterior nostril tip reaching posterior margin of nasal capsule. Ocular-side posterior nostril a larger, round opening surrounded by low fleshy membrane extending posteriorly as a flap.



Two blind-side nostrils; not conspicuous, and with short, fleshy nares. Posterior blind-side nostril a small opening with thin, translucent membrane, located just anterior to vertical through mid-jaw region; anterior blind-side nostril over anterior one-third of jaw. Eyes relatively small (ED 12.0–20.2% of HL,  $\bar{X}$  = 15.2%); ED/HL decreasing proportionally with increasing HL (Fig. 19G), larger individuals with proportionally smaller ED/HL ratios compared to those of smaller individuals; eyes subspherical, with length slightly longer than width; not contiguous; with anterior margin of upper eye nearly equal in position to, or slightly in advance of, anterior margin of lower eye; without pupillary operculum. Interorbital width (IO 7.5–13.2% of HL,  $\bar{X}$  = 10.2%) moderately narrow (IO < eye diameter), increasing proportionally relative to increasing HL (Fig. 19H). Mouth relatively small (UJL 22.1–42.9% of HL,  $\bar{X}$  = 27.0%), UJL/HL proportionally isometric relative to increasing HL (Fig. 19I); jaws asymmetrically developed towards blind side; ocular-side jaws scarcely obvious, all but posterior margin of jaws nearly completely concealed by rostral flap. Diagonal distance between anteroventral margin of lower (non-migrated) eye and dorsal margin of rostral flap above mouth (EUM) 9.7–19.2% of HL ( $\bar{X}$  = 15.1%); EUM increasing proportionally with increasing HL (Fig. 19J). Mouth opening on ocular side small, shaped like question mark; mouth opening located at vertical through posterior ocular-side nostril. Ocular-side lower lip without labial papillae. Ocular-side jaws without teeth. Blind-side jaws slightly angled posteroventrally and with 2–4 irregular rows of slender, villiform teeth covering entire lengths of blind-side jaws. Fleshy skinfold on inner anteroventral margin of ocular-side lower jaw with 1–5 fleshy, finger-like filaments (Fig. 3A). Postorbital head length (POL 10.8–14.1% of SL,  $\bar{X}$  = 12.3%) relatively long, about equal to 36–45% of HW. Upper head lobe (UHL 16.0–23.5% of SL,  $\bar{X}$  = 19.8%) relatively narrow, but noticeably wider than Lower head lobe (LHL 7.6–14.3% of SL,  $\bar{X}$  = 11.2%).

**TABLE 8.** Summary of morphometric information for the Holotype, 13 paratypes, and 64 non-type specimens of *Peltorhamphus tenuis*. Characters 1–12 expressed as % of SL; characters 14–23 expressed as % of HL. Abbreviations defined in text.

Character	Holotype	All specimens including Holotype				
		Min	Max	Mean	Stdev	N
SL (mm)	155.3	56.0	157.5	108.90	30.166	78
1. BD	39.5	31.2	42.3	36.34	2.109	78
2. OSP	42.9	26.6	56.4	39.45	5.973	73
3. BSP	8.4	6.0	12.2	9.31	1.087	78
4. HL	23.2	20.9	27.9	24.67	1.439	78
5. HW	28.7	24.2	38.7	29.57	3.895	78
6. POL	11.7	10.8	14.1	12.28	0.834	78
7. DHW	10.1	6.3	12.2	8.61	1.191	78
8. UHL	21.4	16.0	23.5	19.84	1.286	72
9. LHL	11.3	7.6	14.3	11.15	1.357	72
10. TKL	79.1	70.1	86.1	75.64	2.319	72
11. CFL	20.2	16.2	26.2	20.54	1.827	74
12. CPD	9.6	6.9	10.2	8.66	0.693	71
13. HW/HL	1.2	0.9	1.7	1.20	0.159	78
14. POL	50.3	44.0	57.7	49.82	2.258	78
15. SNL	33.1	29.8	39.9	34.84	2.481	78
16. ED	14.4	12.0	20.2	15.24	2.009	78
17. IO	11.7	7.5	13.2	10.16	1.356	78
18. EUM	16.1	9.7	19.2	15.11	1.792	77
19. DHW	43.6	24.5	46.4	35.04	5.339	78
20. UJL	27.5	22.1	42.9	27.03	2.542	78
21. RHL	33.3	21.3	37.6	29.07	2.988	76
22. UHL	92.5	65.7	98.1	80.62	6.734	72
23. LHL	48.9	32.0	54.4	45.17	4.939	72



**FIGURE 19.** Selected morphometric features for 77 specimens of *Peltorhamphus tenuis* 56.0–158 mm SL. **A–D.** Body depth (BD), Head length (HL), Head width (HW), and Ocular-side pectoral fin (OSP) expressed as percent of SL versus SL (in mm), respectively. **E–J.** Dorsal head width (DHW), Snout length (SNL), Eye diameter (ED), Interorbital width (IO), Upper jaw length (UJL), and Eye to upper mouth distance (EUM) expressed as percent of HL versus HL (in mm), respectively.

Superficial neuromasts on blind side of head inconspicuous, but with lappets and consistently arranged in three, more or less parallel, longitudinal rows dorsal to horizontal through nostrils, and with another series located just posterior to jaws. Dorsalmost row of neuromasts, located close to dorsal body margin, beginning dorsoanteriorly on snout and ending posteriorly at about midpoint of head; middle longitudinal row of neuromasts beginning anteriorly on snout above jaws, and extending posteriorly on preopercle to nearly three-fourths of head length; ventralmost longitudinal row curved and with fewer, more closely spaced neuromasts located in shallow groove beginning just posterior to nostrils and extending to about midpoint of head. Another series of 4–8 conspicuous neuromasts in curved row following contour of jaws; ventralmost neuromasts in this series located just ventral to posterior margin of jaws, with remaining neuromasts more or less following ventral curvature of jaws nearly to their distal tip. Several prominent free neuromasts also on blind side of head situated dorsoposteriorly to neuromast series located behind jaws, submarginally along ventral margin of opercle, and also on ventral portion of lower jaw.

Gillrakers not toothed, present on both limbs of arches on ocular and blind sides. Gillrakers on upper limb of first blind-side arch relatively short, wide-spaced, and nearly triangular (Fig. 12B); gillrakers on upper limb of anterior arch only slightly smaller than those on dorsal region of lower arch. Gillrakers on dorsal region of lower limb of anterior arch slightly longer than those on ventral region. No gillrakers in angle between upper and lower limbs of first gill arch. Gillrakers on lower limb of first blind-side arch small, bluntly pointed, and widely spaced; those on upper limb fewer and smaller.

Dorsal-fin origin at distal tip of rostral hook, located ventral to visible part of mouth opening. Anteriormost dorsal-fin rays, from first to approximately 20<sup>th</sup> ray, with distinct, cup-shaped, fleshy membrane approximately at their midpoints and with distal halves curved, filamentous, and noticeably free from connecting membrane; nearly all rays on dorsal head region with distinct fleshy flap near distal tips; remainder of fin rays connected by membrane at approximately three-fourths length of each ray and without cup-shaped, fleshy membrane at their midpoints. Dorsal-fin rays, from region above posterior head to posterior end of fin, about equal in length. Anal-fin rays connected by membrane nearly to distal tips. Blind sides of dorsal- and anal-fin rays in larger specimens (> ca. 70 mm SL) with row of small, mostly cycloid scales on basal half of rays anteriorly (Fig. 2C), while rays in middle and posterior region of fin with scale rows extending to two-thirds to four-fifths of lengths of the rays. Caudal fin pointed, moderately long (CFL 16.2–26.2% of SL,  $\bar{X} = 20.5\%$ ) compared with that of congeners. Proximal regions on both sides of caudal fin, both rays and connecting membrane, covered with scales from base to ca. one-fourth or less of fin length; beyond this point only rays with ctenoid scales for nearly entire length. Both pectoral fins well-developed; ocular-side fin with conspicuously elongate second ray extending posteriorly well beyond vertical through body midpoint; second ray (OSP 26.6–56.4% of SL,  $\bar{X} = 39.4\%$ ) long, OSP increasing proportionally in length with increasing fish length (Fig. 19D); OSP longer than greatest body depth in specimens smaller than about 130 mm SL, about equal to body depth in larger specimens; OSP > HL at all sizes. Successive rays in ocular-side pectoral fin decreasing in size ventrally. Second ocular-side pectoral-fin ray covered with small scales for nearly three-fourths of its length; other ocular-side pectoral-fin rays covered with scales only to < one-half of their lengths; base of ocular-side pectoral fin scaly. Blind-side pectoral fin noticeably shorter (BSP 6.0–12.2% of SL,  $\bar{X} = 9.3\%$ ) than ocular-side fin, with rays spaced much closer together than those of ocular-side fin; central rays of blind-side fin longer than remaining rays, but none elongate; base of fin with small patch of scales, scales not extending onto rays. Pelvic fins well developed; unequal in position; surrounding anus; not connected to each other. Rays of ocular-side fin more robust than those of blind-side fin. Origin of ocular-side fin nearly at tip of isthmus, rays widely separated from each other, with distal tips free from membrane; first and second pelvic-fin rays noticeably shorter than others; posteriormost ray with broad, membranous connection to anal fin. Blind-side pelvic fin much shorter, its rays spaced more closely together than those of ocular-side fin. Base of first blind-side ray located at point equal to space between fifth and sixth ocular-side rays, or sometimes more posterior and equal with base of sixth ocular-side ray. First blind-side pelvic-fin ray notably shorter and fourth notably longer than others. Rays of blind-side fin progressively increasing in thickness posteriorly; rays 3–4 with small patch of scales on their bases. Blind-side pelvic fin without membranous connection to anal fin, but fourth ray, from its base to approximately its mid-length, with membranous connection to body just anterior to anus.

Ocular-side scales transforming ctenoid in adults and juveniles of both sexes. Scales on blind side of body sexually dimorphic. Scales on midbody region of blind side of males weakly ctenoid; those of females mostly cycloid. Dorsal region of blind side of head anterior to opercle with ctenoid scales in both sexes. Scales above and behind jaws weakly ctenoid or denticulated, without obvious ctenii in both sexes. Scales on preopercle cycloid to

weakly ctenoid in both sexes. Males with weakly ctenoid scales and females with mostly cycloid or weakly ctenoid scales on subopercle.

Anus on blind side, slightly off body midline, bordered medially by blind-side pelvic fin.

Lateral line straight, except for slight rise anteriorly above pectoral fin; posteriorly, lateral-line pores on both sides extending to distal tip of middle caudal-fin ray.

**Morphometric variation.** Detailed examination of variation in 10 morphometric features on 78 *P. tenuis*, 56.0–158 mm SL, revealed allometric growth in most features examined (Figs. 19A–J). Body depth (BD; Fig. 19A) ranged from 31.2% to 42.3% of SL, with positive allometry. The range in BD measurements (11% between smallest and largest fish) reflects a slight deepening of the body relative to SL as fish grow.

Head length (HL; Fig. 19B), expressed as % of SL (total range 21.5–27.9% of SL), had less variation (range 6.5% of SL) than did BD measurements. A slightly negative trend in allometric growth with increasing fish size (Fig. 19B) was evident, but both small and large fish had nearly equal values for HL indicating that this negative trend was not strong. Head width values (HW; Fig. 19C) ranged between 24.7% and 36.6% of SL, without any allometric trends, but separation of data into two groups was evident. Further analyses of these data indicated that both males and females were included in each of the two groups and it is unclear what, if any, factors resulted in this separation. Based on all measurements, variation in HW as a proportion of SL is fairly constant over the size range of fish measured.

Length of the elongate ray in the ocular-side pectoral fin (OSP; Fig. 19D) varied widely with values ranging between 26.6% and 50.3% of SL. Positive allometric growth of this ray was more evident in small- to medium-sized fish, but growth appeared to level off, becoming more isometric among the largest specimens measured. Differences in OSP measurements between the smallest versus medium-sized (to ca. 130 mm SL) fish likely reflects a pattern of allometric growth. For larger fish, however, although growth in length of the OSP appeared to slow, this may not necessarily reflect an isometric growth pattern. The elongate, attenuated ray in large individuals is fragile and difficult to determine whether broken or not, and OSP values in the larger fish may merely reflect a greater frequency of broken rays resulting in an apparent isometric pattern.

Of six other morphometric features of the head (Figs. 19E–J) measured, all, except for SNL and UJL, showed allometric growth with increase in head length. Changes in dorsal head width (DHW; Fig. 19E) and interorbital width (IO; Fig. 19H) both showed positive allometry throughout the size range. Dorsal head width values ranged from 24.5% to 46.4% of HL, and growth in head width increased proportionally relative to growth in head length. For IO width, measurements were 7.5–13.2% of HL, and the small range in variation (6%) reflects that the eyes at all sizes are separated only by a relatively narrow space. Values for eye to upper mouth distance (EUM; Fig. 19J) varied about 9% between the smallest and largest fish (total range 9.7–19.2% of HL), and positive allometric growth with increasing size was evident.

Of the size range measured (56.0 mm to 158 mm SL), snout length values (SNL; Fig. 19F) of all *P. tenuis* ranged between 29.8% and 39.9% of HL. Although SNL measurements varied about 10% between smallest and largest individuals, no clear trends of increasing or decreasing growth in SNL proportionate with increasing HL were evident. Measurements of lower eye diameter (ED; Fig. 19G) varied about 8% between the smallest and largest specimens (12.0–20.2% of HL), with clear negative allometry with increasing fish size. Values for upper jaw length (UJL; Fig. 19I, excluding outlier) ranged about ca. 21% between smaller and larger fish (22.1–42.9% of HL), and no clear trend of allometric growth was evident.

*Colour, based on photographs of freshly thawed and recently collected fish* (Fig. 18B; NMNZ P.061088). Ocular-side background uniformly light- to dark-brown with numerous darker scales arranged more or less in faint longitudinal rows from head to caudal peduncle. Darker scales on head and body with small, dark, roughly circular, markings on their outer margins encircling lighter interiors. Ocular side also with some scattered larger and darker dull blotches. Body region overlying abdominal cavity darker brown to sooty black. Lateral line sometimes darker black compared to body colour.

Dorsal- and anal-fin rays with dark pigment on basal one-half to three-fourths of their lengths and with whitish pigment on distal one-fourth of rays. Rays in anterior half of dorsal and anal fins darker than rays in posterior halves. Ocular side of caudal fin medium brown on scaly base; distal regions of fin with darker pigment on rays compared with that on membrane between rays. Colour of proximal half of ocular-side pectoral fin similar to that on body; distal half of fin, except elongate second ray, lighter in colour compared with that of proximal half. Elongate second ray darker brown to black on distal half.

*Colour of preserved fish* (Figs. 17–18A; NMNZ P.005138; NMNZ P.005421). Ocular side of head and body uniformly medium brown with posterior scale margins distinctly outlined in black and enclosing or nearly enclosing lighter pigmented areas on interior of scales; some larger fish (> 60 mm SL; both sexes) with up to three, large, irregular dark blotches along lateral line, and also with several smaller dark, irregular blotches on body; some specimens also with faint pattern of several to many, more or less, faint longitudinal lines. Anterior blotch on lateral line somewhat more diffuse, elliptical, about 4 scale rows wide. Posterior blotch darker and more conspicuous, about 4 scale rows wide and extending 2 scales above and 2 scales below lateral line. Blind side uniformly white. Eyes bluish-black. Ocular sides of dorsal and anal fins and connecting membranes either with similar colouration to that on ocular side of body, or with fin rays with obvious dark streaks and membranes darker with dense concentrations of small melanophores. Older specimens with yellowish-brown pigment along lengths of dorsal- and anal-fin rays, and with several series of 2–3 darker rays alternating with 3–4 lighter rays. Blind sides of dorsal and anal fins whitish, except occasionally some rays with small melanophores coalesced into sooty black pigment patch, otherwise blind sides of these fins not conspicuously pigmented. Ocular side of caudal fin yellowish-brown in region covered by scales, and light brown distally (about two-thirds length of fin). Ocular-side pectoral fin darker on posterior half including most of length of elongate second ray. Distal tip of elongate ray darker than basal region. No dark streak at anterior base of pectoral fin. Ocular-side pelvic fin with first ray whitish; others with dark streaks on rays and lighter pigment on membrane; blind sides of ocular-side pelvic-fin rays whitish. Blind-side pelvic fin without pigment on distal three-fourths; sometimes basal one-fourth of fin with reddish-brown pigment. Large mature females with elongate ovary on ocular side covered by darkly pigmented membrane visible through body wall for nearly entire length of ovary. Smaller mature females with unpigmented membrane covering both sides of ovaries. Pigmented membrane covering ovary not as visible through abdominal wall on blind side of largest females. Inner lining of ocular-side opercle sometimes dusky (but definitely not black), especially dorsoposteriorly; inner opercular lining on blind side unpigmented; roof of mouth unpigmented. Gill filaments yellowish-white.

**Size and maturity.** *Peltorhamphus tenuis* reaches a maximum of ca. 161 mm SL and 191 mm TL (James 1972; Table 4, this study). Of 127 fish examined, males (N = 57; 56.0–157 mm SL) and females (N = 70; 56.2–161 mm SL) reach similar maximum sizes (Table 4). Of the 66 females for which maturity stage was determined (Fig. 13B), 20, ranging from 56.2 mm to 85.7 mm SL are immature, while 46 (93.0–161 mm SL) are mature. Based on these 66 females, 100% sexual maturity is reached by ca. 93 mm SL.

**Distribution** (Fig. 14B). *Peltorhamphus tenuis* is endemic to New Zealand waters (James 1972; Paul *et al.* 1983; Munroe 2015b). Based on museum records, this species ranges from north of Taranaki Bight off Albatross Point (38°11.00'S) North Island, to Blueskin Bay, Otago (45°43'S) South Island (Fig. 14B). James (1972), Paul *et al.* (1983), Paul (1986, 2000) and Munroe (2015b) considered this to be an uncommon, widespread species, with localized distribution, perhaps on specific substrata. James (1972) commented that this species is probably present around most of New Zealand, although it is markedly less abundant than either *P. novaezeelandiae* or *P. latus*.

Based on James (1972) and Anderson *et al.* (1998), *P. tenuis* is more common in the southern parts of its range. James (1972) had only eight specimens from two locations off North Island versus 107 specimens collected at three sites off South Island. Most, if not all, captures of this species reported in Anderson *et al.* (1998) were made at South Island locations. Data associated with museum lots reported herein also support the conclusion of greater frequency and greater abundance off South Island. Six lots (31 specimens) were from off North Island, 15 lots (146 specimens) were from off South Island (Material examined).

*Peltorhamphus tenuis* has been collected from relatively few locations off North Island (Fig. 14B), with Hawke Bay (James 1972) and off Taranaki Bight representing the northernmost localities and Wellington Harbour (Livingston 1987a) the southernmost. It has also been reported from off the west coast of North Island (Paul *et al.* 1983).

Off South Island, *P. tenuis* is known from several locations off both coasts (Fig. 14B). Along the West Coast, this species is known (James 1972; Munroe 2015b) from several sites off Westport (41°43'S) south to off Haast Beach (43°49'S). Although not recorded from the Fiordland region (Anderson *et al.* 1998), Cooper *et al.* (1990) recorded *P. tenuis* from stomach contents of Crested Penguins (*Eudyptes pachyrhynchus*) collected in Jackson Bay and Martins Bay, south of Haast Beach. Although possible that *P. tenuis* may occur farther south along this coast than present records indicate, it seems unlikely as the continental shelf off Fiordland is extremely narrow, and the prevailing westerly winds and heavy swell that occur there would dislodge any soft sediments from benthic habitats that are necessary to support *P. tenuis* (A. Stewart, pers. comm.). A more likely possibility is that these penguins ventured farther north than Jackson Bay and Martins Bay in their foraging activities.

Along the east coast of South Island, *P. tenuis* has been reported from Pegasus Bay, north of Christchurch, south to Blueskin Bay, just north of Dunedin (James 1972; Beentjes *et al.* 2002; Munroe 2015b). Of interest is that in most locations where this species has been collected, it appears to occur in similar abundance. Lots containing 10–15 specimens are known from widely separated areas from Hawke Bay (east coast North Island), off Westport (West Coast South Island), and from Blueskin Bay (east coast South Island). The largest number of specimens reported from any one location was during a one-year period in Blueskin Bay with 68 reported by Roper & Jillett (1981), with a peak density (N = 33) in austral summer.

**Habitat and bathymetric distribution.** *Peltorhamphus tenuis* occurs in subtidal coastal waters on sandy or sandy-mud bottoms (Roper & Jillett 1981; Colman 1994) in 5–47 m (James 1972; Table 5, this study). Based on Roper & Jillett (1981), and information gleaned from specimens examined in this study (Table 9), small juveniles are captured at depths similar to those where adults are found. Although juvenile *P. tenuis* are known to inhabit shallow water, they do not occur in shallow-water inlets (Roper & Jillett 1981), perhaps reflecting an avoidance for areas with soft, silty substrates. Intensive sampling in estuarine environments at other locations (Healy 1980; Morrison *et al.* 2002, 2014a; Francis *et al.* 2005, 2011; Lowe 2013) also have not reported *P. tenuis*, in contrast to *P. novaezeelandiae* and *P. latus*.

**TABLE 9.** Summary of size versus depth of capture for 88 specimens of *Peltorhamphus tenuis*.

Size (mm SL)	Depth (m)						N
	1–5	6–10	11–20	21–30	33	43	
< 60	–	–	2	2	–	–	4
61–70	–	1	–	–	2	–	3
71–80	–	2	4	–	–	–	6
81–90	–	3	3	–	–	–	6
91–100	–	–	3	–	–	1	4
101–110	–	–	8	–	–	–	8
111–120	–	–	7	–	–	–	7
121–130	2	4	15	–	–	–	21
131–140	–	2	8	–	–	–	10
141–150	–	1	6	3	–	–	10
151–160	–	–	7	1	–	–	8
161	0	1	–	–	–	–	1
N	2	14	63	6	2	1	88
%	3.2	8.1	80.6	3.2	3.2	1.6	

*Peltorhamphus tenuis* has most often been collected in relatively shallow, coastal waters. James (1972) reported a depth range of 9–38 m for specimens he examined, and Paul *et al.* (1983) extended this range slightly to 40 m, based on one specimen collected off the west coast of North Island. Anderson *et al.* (1998) also noted that this species is caught in relatively shallow waters of less than 70 m. One lot (NMNZ P.006016), consisting of one specimen (93.8 mm SL) collected in 39–47 m off Waikato, North Island, possibly represents the deepest known documented capture for this species (Table 9). The shallowest depth record is approximately 5 m (Roper & Jillett 1981). Of 154 specimens with depth of capture information (Table 5), two were captured between 0.5–5.0 m, 44 of 154 (28.6%) were taken in depths of 6–10 m, 92 of 154 (59.7%) were collected between 11–20 m, 13 of 154 (8.4%) were taken between 21–30 m. Only three specimens were taken deeper than 30 m. One lot was reported to have been collected with a beach seine. Although no depth data were recorded for this specimen, it likely occurred in waters shallower than 5 m. A summary of size versus depth of capture for 88 individuals (Table 9) reveals that small and larger fish are taken at similar depths, mostly in < 20 m.

**Trophic biology.** Little is known of the feeding ecology of this species. However, based on jaw morphology and mouth size, prey consumed is probably similar to that of its congeners: small epibenthic and infaunal invertebrates (crustaceans, molluscs, and polychaetes).

**Reproductive biology.** Paul (1986, 2000) suggested that *P. tenuis* is probably a winter spawner. Based on five gravid females examined in the present study, it may have a protracted spawning season, or different populations

may have different spawning seasons based on their location. Two gravid females taken off Westport were collected in December; one gravid female each were taken off Canterbury and Otago in October; and one gravid female was taken off Canterbury in April.

Robertson (1973) described eggs stripped from a gravid female collected in July in Blueskin Bay. Robertson (1975) also noted both spatial and temporal overlaps in occurrence and spawning season between those of *P. tenuis* and *P. novaezeelandiae*. He found many similarities between the eggs of *P. tenuis* and those of *P. novaezeelandiae*, rendering it nearly impossible to differentiate eggs taken in field collections. Paul (1986) noted that larvae and juveniles are found close to shore, but are sparsely distributed.

**Etymology.** The name “*tenuis*” is from the Latin, “*tenuis*” meaning narrow, in reference to the relatively narrow body depth of this species.

**Remarks.** *Peltorhamphus tenuis* is the most distinctive species in the genus, and since its description, no confusion has been evident concerning its systematic status. It is one of three species in the genus possessing small, fleshy, finger-like filaments on the inner anteroventral margin of the fleshy skinfold on the ocular-side lower jaw (Fig. 3A); these are evident even on the two smallest specimens (28 mm SL) examined. *Peltorhamphus tenuis* is readily identified by a number of distinctive morphological features. It has a slender body compared with that of congeners (Figs. 4A–D); it has the highest (and non-overlapping) vertebral counts in the genus (Table 1); it is the only species with scales on the blind sides of dorsal- and anal-fin rays (Fig. 2C); and, it has the longest second ocular-side pectoral-fin ray, equal to or longer than, the greatest body depth (Table 2). This last feature is evident in even the smallest specimens of *P. tenuis* examined (28 mm SL).

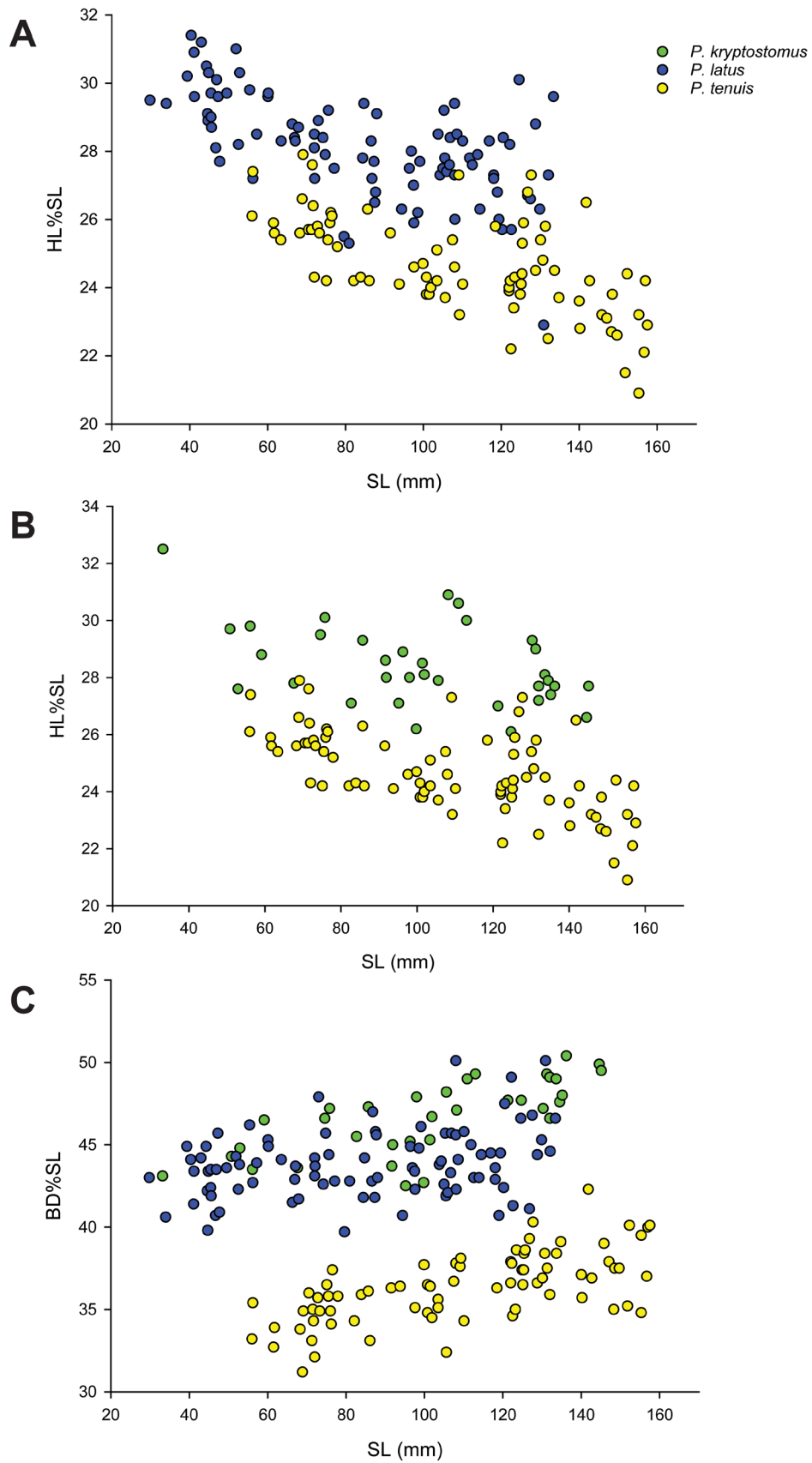
**Comparisons.** Characters distinguishing *P. tenuis* from *P. novaezeelandiae* were discussed under the comparisons section for *P. novaezeelandiae* above. Further comparisons of meristic and morphometric features among all four species are given in Tables 1 and 2.

*Peltorhamphus tenuis* is distinguished from *P. latus* by several characters including: its higher and non-overlapping values for total vertebrae (39–43 vs. 35–38 in *P. latus*); its higher and minimally overlapping counts for other meristic features (98–116 vs. 83–99 dorsal-fin rays; 62–72 vs. 51–64 anal-fin rays; 82–105 vs. 64–83 lateral-line scales; and 3–8 vs. 1–4 scales between anteroventral margin of lower eye and dorsal margin of mouth opening; Table 1); in having several finger-like filaments on its lower jaw vs. absent in *P. latus* (Figs. 3A–3B); and in individuals  $\geq 70$  mm SL, *P. tenuis* has scales on blind sides of its dorsal- and anal-fin rays (Fig. 2C), whereas scales are absent in all sizes of *P. latus*. The gillrakers of *P. tenuis* are shorter and less robust than those of *P. latus* (compare Figs. 12B and 12C); and *P. tenuis* has cycloid or weakly ctenoid scales on the blind side of the body (vs. *P. latus* with more strongly ctenoid scales on its blind side).

*Peltorhamphus tenuis* is further distinguished from *P. latus* by its more elongate body (Fig. 20C) with greatest depth more evenly distributed over its length (refer to Fig. 4B) and with more gradual posterior taper, compared with that of *P. latus* (Fig. 4C), which has its greatest depth anterior to the body midpoint and has a more rapid posterior taper. *Peltorhamphus tenuis* has a more rounded head profile (vs. anterior profile with blunt point in *P. latus*), and in *P. tenuis*, the second ocular-side pectoral-fin ray is either longer than, or equal to, body depth, while that of *P. latus* is shorter than body depth (compare Fig. 4B with Fig. 4C); and *P. tenuis* usually also has a shorter head length compared with that of *P. latus* (Fig. 20A).

These species also differ in several aspects of colouration: the ocular side of *P. tenuis* features several longitudinal lines (sometimes faint) on the scales, and lacks incomplete ocelli. This differs markedly from that of *P. latus*, which has a more uniform background colour pattern lacking longitudinal streaks on the scales, and often has numerous circular or semi-circular rings resembling incomplete ocelli. The dorsal and anal fins in *P. tenuis* are usually uniformly pigmented, whereas those of *P. latus* feature a conspicuous pattern of a single, darkly streaked ray alternating with 4–8 lightly pigmented rays (compare Figs. 17–18 with 21–22). *Peltorhamphus tenuis* has a dusky (not black) inner lining on the ocular-side opercle, and the roof of the mouth is unpigmented (vs. inner lining of ocular-side opercle and entire roof of mouth black in *P. latus*).

*Peltorhamphus tenuis* is readily distinguished from *P. kryptostomus* n. sp. by numerous differences including several meristic features (Table 1), such as more total vertebrae (39–43 vs. 36–38), more dorsal-fin rays (98–116 vs. 86–97), more lateral-line scales (82–106 vs. 64–82), fewer gillrakers on the lower limb of the first gill arch (5–12 vs. 10–14), and more supracranial pterygiophores (25–31, usually 26–29 vs. 21–26, usually  $\leq 25$ ). *Peltorhamphus tenuis* has cycloid or weakly ctenoid scales on the blind side of the body compared with the more strongly ctenoid scales on the blind side of *P. kryptostomus* n. sp.



**FIGURE 20.** Selected morphometric features of *Peltorhamphus tenuis* compared with those of *P. latus*, and *P. kryptostomus* n. sp. **A.** Head length (HL) as percent of SL vs. SL (in mm) for *P. tenuis* and *P. latus*. **B.** Head length (HL) as percent of SL vs. SL (in mm) for *P. tenuis* and *P. kryptostomus* n. sp. **C.** Body depth (BD) as percent of SL vs. SL (in mm) for *P. tenuis*, *P. latus*, and *P. kryptostomus* n. sp.



Conspicuous differences in morphometric features between these two species are that *P. tenuis* has a narrower, elongate body (BD 31.2–42.3% of SL,  $\bar{X}$  = 36.3%) compared to that (BD 42.5–50.4% of SL,  $\bar{X}$  = 46.7%) of *P. kryptostomus* n. sp. (Fig. 20C). *Peltorhamphus tenuis* also has a much longer second ocular-side pectoral-fin ray (usually  $\geq$  body depth vs. second ocular-side pectoral-fin ray much shorter than body depth in *P. kryptostomus* n. sp.). *Peltorhamphus tenuis* usually also has a shorter head (HL 20.9–27.9% of SL,  $\bar{X}$  = 24.7%) compared with that of *P. kryptostomus* n. sp. (HL 26.1–32.5% of SL,  $\bar{X}$  = 28.4%) (Fig. 20B; Table 2). Other morphometric differences (i.e., HW; SNL; RHL; etc.) between these species are apparent in Table 2.

*Peltorhamphus tenuis* differs from *P. kryptostomus* n. sp. in its ocular-side colour pattern; uniform often with a faint series of dark longitudinal lines (vs. no longitudinal lines in *P. kryptostomus* n. sp.; compare Figs. 17–18 with Figs. 25–26). *Peltorhamphus tenuis* has a dusky inner opercular lining and the roof of the mouth is unpigmented (vs. roof of mouth and ocular-side inner opercular lining black in *P. kryptostomus* n. sp.).

Qualitative differences between these species include presence (vs. absence in *P. kryptostomus* n. sp.) of scales on blind sides of dorsal- and anal-fin rays (best developed in specimens > 70 mm SL); absence (vs. presence in *P. kryptostomus* n. sp.) of a pupillary operculum; and by differences in size, robustness and position of gillrakers on the upper limb of the first gill arch (compare Figs. 12B and 12D).

### ***Peltorhamphus latus* James, 1972**

Speckled Sole

Figs. 2B, 3B, 4C, 5B, 12C, 13C, 14C, 16A–D, 20A–B, 21, 22A–B, 23A–J, 24A–D, 28A; Tables 1–4, 10–11



**FIGURE 21.** *Peltorhamphus latus* holotype (NMNZ P.005139), preserved, Wellington Harbour, North Island, New Zealand. Photo: C. Struthers.

### ***Peltorhamphus novaezeelandiae* (not of Günther).**

Günther 1862:461 (in part; 10 of 12 syntypes of *P. novaezeelandiae* are *P. latus*; meristic and morphometric information; New Zealand; Norfolk Island record erroneous).

Krefft 1871:82 (Norfolk Island record erroneous, based on misidentified specimen of *P. latus*).

Hutton 1872:52 (in part; record from Norfolk Island erroneous, based on misidentified specimen of *P. latus*).

Waite 1910:381 (listed, after Günther (1862); Norfolk Island record erroneous).

Norman 1926:276 (in part; 10 of 12 syntypes of *P. novaezeelandiae* examined are *P. latus*; Norfolk Island record erroneous).

Norman 1934:427 (in part; 10 of 12 syntypes of *P. novaezeelandiae* are *P. latus*; Norfolk Island record erroneous, based on misidentified specimen of *P. latus*).

Chabanaud 1939:17 (in part; Norfolk Island record based on misidentified specimen of *P. latus*).

Whitley 1968:49 (questioned Norfolk Island record for *P. novaezeelandiae*).

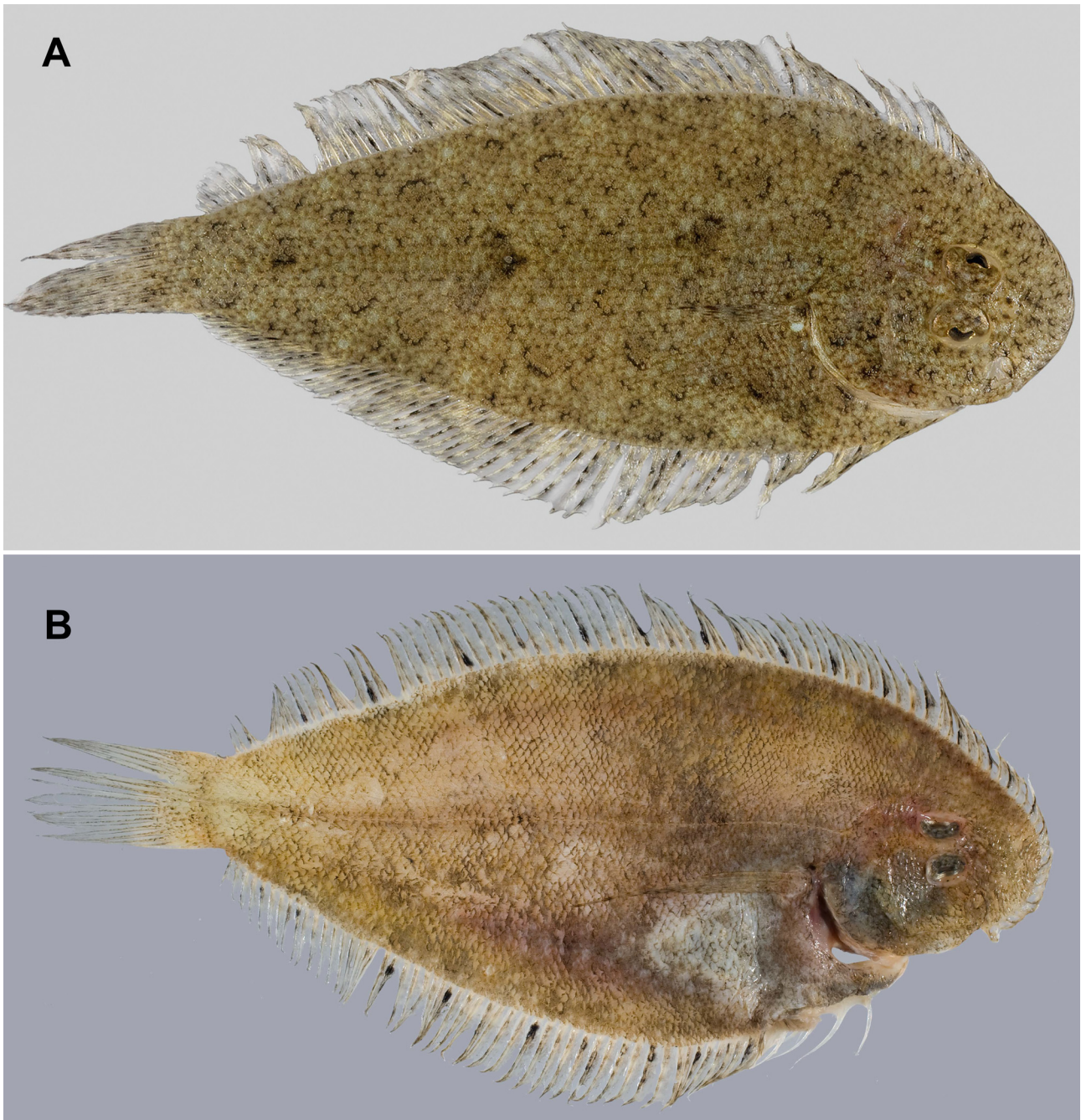
Manikiam 1969:126 (in part; Norfolk Island record based on misidentified specimen of *P. latus*).

### ***Peltorhamphus latus* James, 1972**

- James 1972:354 (in part; two paratypes re-identified as *Peltorhamphus* n. sp. Munroe 2015b); (original description; photograph; size and depth information; morphometric variation; New Zealand, Norfolk Island erroneous).
- Roper 1979:136 (in part; may include data from *Peltorhamphus* n. sp. Munroe 2015b; Blueskin Bay, South Island; distinguished from *P. novaezeelandiae* and *P. tenuis*; to 180 mm TL; figures of juveniles of various sizes and adult).
- Frentzos 1980:150 (meristic features of adults; Wellington Harbour).
- Ayling & Cox 1982:308 (brief mention of morphology, small size; distinguished from congeners).
- Sakamoto 1984:95 (morphology; osteology; valid species; placement in phenetic classification of Pleuronectidae).
- Paulin & Stewart 1985:57 (endemic in New Zealand waters; widespread, coastal species; 10–50 m).
- Paul 1986:141 (listed; small species to 150 mm SL; possible confusion with juvenile *P. novaezeelandiae*; distinguished from congeners).
- Paulin *et al.* 1989:240 (in key; listed, Pleuronectidae; distinguished from congeners).
- Hardy 1990:14 (listed, type catalog of fishes, National Museum of New Zealand).
- Francis 1993:168 (in checklist of fishes; listed, Norfolk Island based on erroneous record; New Zealand).
- Armitage *et al.* 1994:111 (brief mention; size to 200 mm TL; possible confusion with juvenile *P. novaezeelandiae*).
- Colman 1994:34 (brief mention; small size; likely confused with juvenile *P. novaezeelandiae*).
- Eschmeyer *et al.* 1998a:881 (valid species in *Peltorhamphus*; New Zealand type locality; list of type specimens).
- Eschmeyer 1998b:2433 (valid species in *Peltorhamphus*: Rhombosoleinae: Pleuronectidae; New Zealand, Norfolk Island record erroneous).
- Paul 2000:141 (listed; black & white illustration; small species to 150 mm SL; possible confusion with juvenile *P. novaezeelandiae*; distinguished from congeners).
- Paulin *et al.* 2001:240 (in key; partial meristic features; distinguished from congeners; listed in Pleuronectidae; New Zealand).
- Guibord 2003:202 (osteology; morphology; systematic relationships among members of Rhombosoleidae; unresolved relationships with congeners).
- Evseenko 2004:20 (valid species in Rhombosoleinae; holotype information; western South Pacific).
- Roberts *et al.* 2009:536 (listed, checklist of New Zealand Chordata).
- McMillan *et al.* 2011:277 (brief mention; size < 200 mm TL; distinguished from congeners).
- Francis 2012:246 (brief colour description; *in situ* colour photograph; distinguished from other New Zealand flatfishes).
- Roberts *et al.* 2015:S177 (listed, checklist of fishes of New Zealand; types listed; type locality New Zealand; New Zealand; Norfolk Island record erroneous).
- Munroe 2015b:1695 (species account, colour photograph; diagnostic features; in key; New Zealand; Norfolk Island record erroneous).
- Roberts *et al.* 2018:126 (listed, online checklist of fishes of New Zealand; types listed; two species in type series; type locality New Zealand; New Zealand; Norfolk Island record erroneous).
- McMillan *et al.* 2019:249 (colour photo; diagnostic features; size to 180 mm TL; distinguished from congeners; New Zealand endemic; widespread distribution; demersal; 1–60 m).

**Diagnosis.** *Peltorhamphus latus* is distinguished from congeners by the combination of: a deep body, with greatest depth anterior to midpoint and with moderate posterior taper; anterior profile of snout bluntly pointed; short, filamentous, second ocular-side pectoral-fin ray shorter than body depth; no fleshy, finger-like filaments on inner anteroventral margin of fleshy skinfold on ocular-side lower jaw; scales absent on blind sides of dorsal- and anal-fin rays; relatively large eyes with well-developed pupillary operculum and separated by narrow interorbital space (usually < eye diameter) with 0–2 (usually 1–2) interorbital scales; distance between anteroventral margin of lower (non-migrated) eye and dorsal margin of rostral flap above mouth narrow with usually only 2–3 scales in diagonal row between these structures; low meristic values (35–38 total vertebrae, 83–99 dorsal-fin rays, 51–64 anal-fin rays, 64–87 lateral-line pores, 23–29 supracranial pterygiophores, 8–16 gillrakers on first arch); relatively large, robust gillrakers on upper limb of first gill arch not reaching dorsalmost gillrakers on lower limb (Fig. 12C, cf. Figs. 12A–B, D); ctenoid scales on blind side of body, cycloid scales on blind-side preopercle and subopercle; relatively wide caudal peduncle; ocular-side background colouration light to dark brown with greenish highlights, sometimes with pigmented scales arranged in semi-circular pattern resembling incomplete ocelli, and with up to three conspicuous, irregular, black blotches on lateral line; dorsal and anal fins of both sexes with conspicuous pattern of a single, darkly streaked ray alternating with 4–8 lightly pigmented rays (Figs. 21–22); whitish spot at base of ocular-side pectoral fin; and with inner lining of ocular-side opercle and entire roof of mouth black.

**Holotype (Fig. 21):** NMNZ P.005139 (104.3 mm SL); Wellington Harbour, North Island (41°15.00'S, 174°52.50'E); 20 m; collected 10 Feb 1970.



**FIGURE 22.** *Peltorhamphus latus*. **A.** NMNZ P.048368, 36.2 mm SL, Hokianga Harbour; fresh specimen. **B.** NMNZ P.046428, 119.4 mm SL, off Southland, South Island; freshly frozen, thawed. Photos: C. Struthers.

**Description.** Meristic data summarized in Table 1. Values for holotype listed first and in bold here and in Table 1. Supracranial pterygiophores **28**, range 23–29, usually 25–27 (118 of 152 individuals). Pterygiophores inserted into first interneural space **3**, range 2–4, usually 2 (93 of 155 individuals) or 3 (59 of 155 individuals). Pterygiophores inserted anterior to first haemal spine **10**, range 8–11, usually 8–10 (143 of 149 individuals). Dorsal-fin rays **96**, range 83–99. Anal-fin rays **60**, range 51–64. Caudal-fin rays **18**, range 17–20; usually 18 (149 of 159 individuals). Ocular-side pectoral-fin rays **10**, range 7–11, usually 9–10 (137 of 158 individuals). Blind-side pectoral-fin rays **9**, range 6–10, usually 8–9 (95 of 111 individuals). Ocular-side pelvic-fin rays **6**, range 5–6, usually 6 (147 of 149 individuals). Blind-side pelvic-fin rays **4**, range 3–5, usually 4 (139 of 147 individuals). Abdominal vertebrae **10**, range 9–11, usually 10 (154 individuals with 3+7 arrangement); rarely with 3+6 or 3+8 arrangements (1 and 2 individuals, respectively). Caudal vertebrae **27**, range 26–28; usually 27 (112 of 158 individuals). Total vertebrae **37**, range 35–38; usually 36–38 (156 of 157 individuals); rarely 35 (1 individual). Finger-like filaments on inner anteroventral margin of fleshy

skinfold on ocular-side lower jaw **0** (121 of 122 individuals without filaments; one individual with 2 filaments). Gillrakers on upper limb of first arch on blind side **3**, range 2–5, usually 3–4 (190 of 204 individuals). Gillrakers on lower limb of first arch on blind side **9**, range 6–12, usually 8–10 (174 of 204 individuals). Total gillrakers on first arch on blind side **12**, range 8–16, usually 11–14 (176 of 202 individuals). Interorbital scales **1**, range 0–2, usually 1 (80 of 118 individuals), less frequently 2 (36 of 118 individuals). Scales in diagonal row between anteroventral margin of lower eye and dorsal margin of mouth opening **3**, range 1–4, usually 2–3 (113 of 118 individuals). Scales between mid-dorsal margin of dorsal eye and dorsal margin of head **9**, range 5–10, usually 7–9 (86 of 94 individuals). Lateral-line pores **82**, range 64–87, usually 66–83 (108 of 113 individuals).

**TABLE 10.** Summary of morphometric information for the Holotype, 17 paratypes, and 51 non-type specimens of *Peltorhamphus latus* (21 additional specimens measured for IO). Characters 1–12 expressed as % of SL; characters 14–23 expressed as % of HL. Abbreviations defined in text.

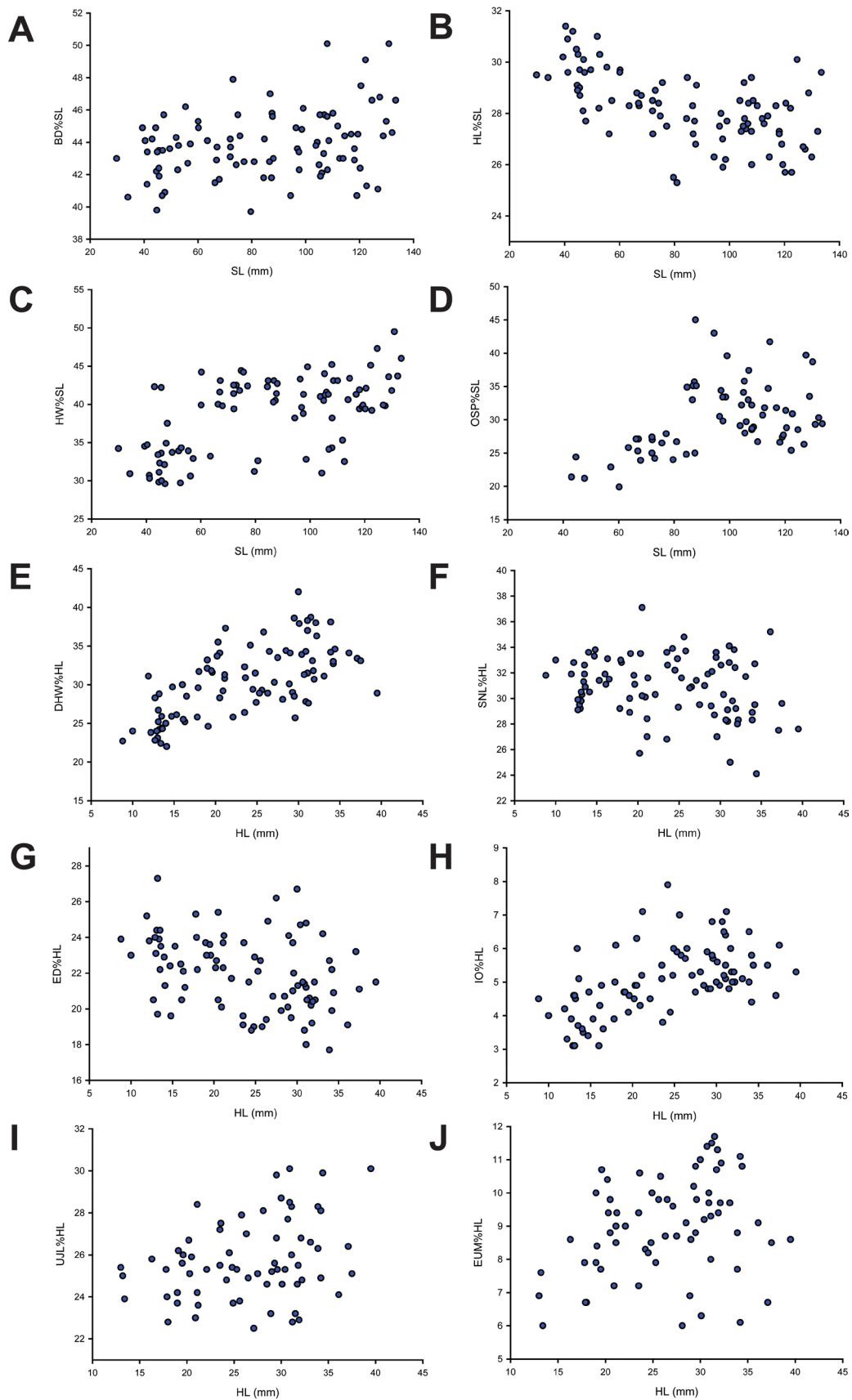
Character	Holotype	All specimens including Holotype				
		Min	Max	Mean	Stdev	N
SL (mm)	104.3	44.6	133.4	96.76	22.780	69
<b>1. BD</b>	44.0	39.7	50.1	44.05	2.150	69
<b>2. OSP</b>	32.2	19.9	45.0	30.28	5.224	65
<b>3. BSP</b>	11.7	9.5	14.8	12.52	1.138	68
<b>4. HL</b>	27.3	22.9	30.1	27.70	1.267	68
<b>5. HW</b>	31.0	29.8	49.5	40.39	4.058	68
<b>6. POL</b>	13.4	11.3	15.5	13.27	0.874	68
<b>7. DHW</b>	9.4	6.7	10.6	8.8	0.942	68
<b>8. UHL</b>	22.3	15.0	28.5	22.70	1.884	51
<b>9. LHL</b>	14.6	11.2	17.3	14.07	1.320	51
<b>10. TKL</b>	75.7	64.8	83.8	72.52	2.551	68
<b>11. CFL</b>	25.5	19.1	26.6	23.13	1.626	66
<b>12. CPD</b>	10.9	8.8	13.1	10.66	0.777	51
<b>13. HW/HL</b>	1.1	1.0	2.2	1.46	0.160	68
<b>14. POL</b>	49.1	43.4	62.3	47.95	2.792	68
<b>15. SNL</b>	31.9	24.1	44.3	30.92	3.044	68
<b>16. ED</b>	20.7	17.7	27.3	21.88	2.151	68
<b>17. IO</b>	4.9	3.1	7.9	5.03	0.992	90
<b>18. EUM</b>	9.1	6.0	11.7	9.02	1.419	68
<b>19. DHW</b>	34.4	23.1	42.0	31.85	4.004	68
<b>20. UJL</b>	24.6	22.5	30.1	25.78	1.876	68
<b>21. RHL</b>	20.0	12.4	31.0	22.78	2.894	68
<b>22. UHL</b>	81.8	53.1	113.0	82.4	7.829	51
<b>23. LHL</b>	53.3	41.1	65.0	51.0	4.841	51

Morphometric data summarized in Table 10, compared with that of other species in Table 2, discussed in further detail in the Morphometric variation section below, and plotted for select features in Figs. 23A–J. Body wide, oval (Figs. 4C, 21–22), with relatively short trunk (TKL 64.8–83.8% of SL,  $\bar{X}$  = 72.5%); laterally compressed; greatest depth (BD 39.7–50.1% of SL,  $\bar{X}$  = 44.1%) varying ontogenetically with larger fish having deeper bodies than smaller fish (Fig. 23A); greatest body depth in anterior one-third usually at, or anterior to, vertical through base of pectoral fin, and with moderate posterior taper and rather steep taper anteriorly beyond this point. Caudal peduncle short, relatively wide (CPD 8.8–13.1% of SL,  $\bar{X}$  = 10.7%). Head large, wide; with blunt point on anterior profile equal with horizontal between eyes (Figs. 21–22); dorsal profile of head and anterior body smoothly convex to point about equal with vertical through base of ocular-side pectoral fin, followed by gradual posterior taper; ventral margin of head convex, steeply angled nearly to posterior margin of opercle. Head length (HL 22.9–30.1% of SL,  $\bar{X}$  = 27.7%) proportionally larger

in smaller individuals (Fig. 23B); HL shorter than head width (HW 29.8–49.5% of SL,  $\bar{X}$  = 40.4%); HW increasing proportionally relative to increasing SL (Fig. 23C); HW/HL 1.0–2.2 ( $\bar{X}$  = 1.46). Head width dorsal to upper eye (DHW 23.1–42.0% of HL,  $\bar{X}$  = 31.8%) relatively narrow; DHW increasing proportionally with increasing fish size (Fig. 23E); no secondary scales on scales above dorsal eye, nor on scales on head dorsoposterior to dorsal eye. Snout moderately long (SNL 24.1–44.3 of HL,  $\bar{X}$  = 30.9%); growth in SNL isometric to slightly negative relative to increasing fish size (Fig. 23F); snout bluntly pointed, and covered with strong ctenoid scales; its greatest length at horizontal between eyes; about 10 scales between anterior margin of eyes and anterior profile of snout. Ocular side of snout with conspicuous rostral flap whose dorsoposterior margin nearly surrounds and hides entire mouth, except for posteriormost end of jaws (Figs. 21–22); rostral flap with moderately long, fleshy, rostral hook (RHL 12.4–31.0% of HL,  $\bar{X}$  = 22.8%) anteriorly; anterior end of rostral hook at tip of lower jaw, posterior end of rostral hook extending ventrally to point between verticals through anterior and posterior ocular-side nostrils. Ventroposterior section of rostral flap also with vertical, notch-shaped opening resembling a question mark, exposing only posteriormost tips of jaws ventrally (Figs. 21–22). Two ocular-side nostrils in anterior interorbital space, asymmetrically placed closer to dorsal margin of lower eye (Fig. 5B). Anterior ocular-side nostril a vertical slit surrounded by fleshy membrane extending posteriorly as long flap, wide proximally and with long fleshy tip distally on its posterior rim. When depressed posteriorly, anterior nostril tip reaching posterior margin of posterior nostril. Ocular-side posterior nostril a larger round opening surrounded by low fleshy membrane extending posteriorly as a flap. Ocular-side nostrils slightly larger in adult males than those in adult females. Blind-side nostrils not conspicuous, and with short, white, fleshy nares. Posterior nostril located just anterior to midpoint of jaw; anterior nostril over anterior one-third of jaw. Eyes large (ED 17.7–27.3% of HL,  $\bar{X}$  = 21.9%), ED/HL ratios decreasing proportionally with increasing fish size (Fig. 23G); eyes elliptical, not contiguous, but nearly touching, especially in smaller fish; usually with anterior margin of upper eye nearly equal in position to, or slightly in advance of, anterior margin of lower eye; eyes with conspicuous, well-developed pupillary operculum (Fig. 2B). Interorbital width narrow at all sizes (IO 3.1–7.9% of HL,  $\bar{X}$  = 5.0%), increasing slightly relative to increasing fish size (Fig. 23H); IO narrower than ED, and with only 1–2 scales in IO space between midpoints of eyes. Mouth small (UJL 22.5–30.1% of HL,  $\bar{X}$  = 25.8%), UJL increasing slightly with increasing fish size; jaws asymmetrically developed towards blind side; all but posterior margin of jaws on ocular side nearly completely concealed by rostral flap; jaws on blind side straighter, only slightly decurved posteriorly. Diagonal distance between anteroventral margin of lower (non-migrated) eye and dorsal margin of rostral flap above mouth narrow at all life stages (EUM 6.0–11.7% of HL,  $\bar{X}$  = 9.0%), EUM increasing slightly with increasing fish size (Fig. 23J). Mouth opening on ocular side small, shaped like a question mark, at vertical through anterior margin of lower eye. Ocular-side lower lip without labial papillae. Teeth present only on blind-side jaws, slender, villiform, in 2–4 irregular rows; those in anteriormost rows slightly larger than teeth in posterior rows. Fleshy skinfold on inner anteroventral margin of ocular-side lower jaw without fleshy, finger-like filaments (Fig. 3B). Postorbital head length (POL 11.3–15.5% of SL,  $\bar{X}$  = 13.3%) about 31–38% of HW. Upper head lobe (UHL 15.0–28.5% of SL,  $\bar{X}$  = 22.7%) much wider than Lower head lobe (LHL 11.2–17.3% of SL,  $\bar{X}$  = 14.1%).

Superficial neuromasts on blind side of head conspicuous, consistently arranged usually in three, more or less parallel longitudinal rows dorsal to horizontal through nostrils, and with another series just posterior to jaws. Dorsalmost row of neuromasts close to body margin beginning on snout and extending posteriorly to about midpoint of head; middle longitudinal row of neuromasts beginning on anterior snout and extending posteriorly nearly to three-fourths of head length; ventralmost longitudinal row with fewer, more closely spaced neuromasts than in other rows, located in shallow groove beginning just posterior to nostrils and extending posteriorly to about midpoint of head. Another series of prominent neuromasts in curved row following contour of jaws; ventralmost neuromasts in this series located just ventral to posterior margin of jaws, with remaining neuromasts in this series more or less following anteroventral curvature of jaws nearly to distal tip of jaws. Several prominent free neuromasts also on blind side of head situated dorsal and posterior to neuromast series located behind jaws, and also submarginally along ventral opercle and on ventral portion of lower jaw.

Gillrakers not toothed, present on both limbs of gill arches on ocular and blind sides. Gillrakers on upper limb of first arch on blind side robust, similar to those on lower limb (Fig. 12C). Upper gillrakers relatively long, not reaching ventrally to dorsalmost gillraker on lower limb; gillrakers bluntly pointed, conical. Lower arch gillrakers 6–12 (usually 7–11); slightly longer than those on upper limb (Fig. 12C), except ventralmost 2–4 on lower limb usually much smaller and more rounded than others on lower limb.



**FIGURE 23.** Selected morphometric features for 91 specimens of *Peltorhamphus latus* 43.0–133.4 mm SL. **A–D.** Body depth (BD), Head length (HL), Head width (HW), and Ocular-side pectoral fin (OSP) expressed as percent of SL versus SL (in mm), respectively. **E–J.** Dorsal head width (DHW), Snout length (SNL), Eye diameter (ED), Interorbital width (IO), Upper jaw length (UJL), and Eye to upper mouth distance (EUM) expressed as percent of HL versus HL (in mm), respectively.

Dorsal-fin origin at, or near tip of rostral hook, located ventral to visible part of mouth opening. Antermost dorsal-fin rays, from first to approximately 20<sup>th</sup> ray, with distinct cup-shaped, fleshy membrane approximately at their midpoints and with their distal halves curved, filamentous, and noticeably free from connecting membrane; remainder of dorsal-fin rays connected by membrane between rays at approximately three-fourths length of each fin and without cup-shaped, fleshy membrane at their midpoints. Anal-fin rays connected by membrane nearly at distal tips of rays. No scales on blind sides of dorsal- or anal-fin rays. Caudal fin slightly pointed, relatively long (CFL 19.1–26.6% of SL,  $\bar{X}$  = 23.1%). Ocular side of fin with scales covering fin rays and membrane for proximal one-half or less, scales extending distally on rays to about three-fourths of their lengths; blind side of fin with scales on basal one-fourth and with scales extending distally on rays to about one-half to one-third their lengths. Both pectoral fins well developed; ocular-side fin with elongate, filamentous, second ray extending posteriorly to about vertical through body midpoint; length of elongate ray (OSP 19.9–45.0% of SL,  $\bar{X}$  = 30.3%) increasing proportionally with increasing fish size (Fig. 23D); OSP shorter than greatest body depth and  $\geq$  HL. Blind-side pectoral fin (BSP 9.5–14.8% of SL,  $\bar{X}$  = 12.5%) noticeably shorter than ocular-side fin, with rays spaced much closer together, and without elongate rays. Pelvic fins well developed; unequal in position; surrounding anus; not connected to each other. Origin of ocular-side fin nearly at tip of isthmus; base of first blind-side ray located at point equal to space between fifth and sixth ocular-side pelvic-fin rays, or equal with base of sixth ocular-side ray. Ocular-side rays widely separated from each other and with distal tips free from membrane; first and second rays noticeably shorter than others; posteriormost ocular-side ray with thick, membranous connection to first anal-fin ray. Blind-side pelvic fin much shorter; rays spaced more closely together than those in ocular-side fin, thickening posteriorly; first blind-side ray notably shorter, and fourth ray longer, than others; fin without membranous connection to anal fin, but fourth ray, from its base to approximately middle of ray, with thick membranous connection to body region near anus.

Ocular-side scales transforming ctenoid in both adults and juveniles of both sexes. Blind-side scales sexually dimorphic, males with strong transforming ctenoid scales and females with weakly ctenoid to mostly cycloid scales. Scales on blind side of rostral hook ctenoid dorsally, and cycloid medially. Blind-side preopercle and subopercle with cycloid scales.

Anus on blind side, slightly off body midline, bordered medially by blind-side pelvic fin.

Lateral line straight, except for slight rise anteriorly above pectoral fin; posteriorly, lateral-line pores on both sides of body extending onto nearly three-fourths of length of middle caudal-fin ray.

**Morphometric variation.** Detailed examination of variation in 10 morphometric features based on 91 *P. latus*, 29.8–133.4 mm SL, revealed that allometric growth was apparent in most features (Figs. 23A–J). Body depth (BD; Fig. 23A) ranged between 39.7% and 50.1% of SL, most individuals with BD 41–47% of SL; largest BD values occurring in the largest individuals (> 120 mm SL). Body depth measurements showed a small, positive, allometric growth pattern throughout the size range measured. The small range in variation for BD measurements (only ca. 10%) reflects the relatively deep body of this species at all sizes with little change in overall shape with size.

Head length (HL 25.3–31.4% of SL; Fig. 23B) had less variation (about 6%) than that noted for BD, and showed a slightly negative trend in allometric growth with increasing fish size. Smaller individuals generally had proportionally larger head lengths compared with those of medium-sized individuals and had values comparable with those of the largest fish. Head width (HW 29.6–49.5% of SL; Fig. 23C) had considerable variation (nearly 20%), and showed a continuous positive trend in allometric growth throughout the size range examined (29.8 to 133.4 mm SL).

Length of the elongate ray in the ocular-side pectoral fin (OSP; Fig. 23D) has a trend of continuous positive growth throughout the size range measured. Considerable variation (ca. 25% difference between smallest and largest) was observed, as well as variation in measurements of OSP in larger individuals that may have had this fin tip broken. Again, this is sometimes difficult to detect, and may have resulted in an underestimate of OSP lengths in some larger individuals.

Of six other morphometric features of the head measured (Figs. 23E–J), four showed distinct allometric growth. Dorsal head width (DHW; Fig. 23E) values ranged between 22.0% and 42.0% of HL and showed distinct positive allometry throughout the entire size range. Dorsal head width is one region on the head that varied considerably (span of 20% measured between smallest and largest individuals), representing significant changes in head width in the region dorsal to the eyes. Interorbital width (IO; Fig. 23H), ranging between 3.1% and 7.9% of HL, also had a pattern of positive allometric growth over the size range examined. However, the range (ca. 5%) was relatively small and reflected that the eyes in this species are close together at all sizes. A slight, positive allometry in measurements of eye to upper mouth measurements (EUM; Fig. 23J) across the size range might also be evident, but this trend is not distinct. Values

for EUM ranged between 6.0% and 11.7% of HL, with both smaller and some larger fish having EUM values of about 6.0% of HL.

Growth in snout length appears to be isometric (SNL; Fig. 23F). All *P. latus* measured (29.8 mm to 133.4 mm SL) had snout lengths between 24.1% and 37.1% of HL. Although SNL values varied about 13% between smallest and largest, no clear trends of increasing or decreasing growth relative to HL were evident. Measurements of lower eye diameter (ED; Fig. 23G) varied about 10%, but no distinct trend in proportionate growth of eye size with increasing fish length was discernible. Values for upper jaw length (UJL; Fig. 23I) ranged about 8% between smaller and larger individuals. Despite these rather small differences, a slight, but continuous increase is evident in the proportion of jaw size relative to head length.

*Colour based on fresh specimen* (NMNZ P.048368; Fig. 22A), *freshly thawed specimen* (NMNZ P.046428; Fig. 22B), and *from fish photographed in situ*. Photos available on iNaturalist.org website for Austral-New Zealand fishes [https://www.inaturalist.org/taxa/570840-Peltorhamphus-latus/browse\\_photos](https://www.inaturalist.org/taxa/570840-Peltorhamphus-latus/browse_photos)). Ocular-side background light to dark brown with greenish highlights (background colour somewhat dependent on substratum occupied by fish), and with up to three conspicuous, irregular, black blotches on lateral line. Ocular side also with numerous scales with black posterior borders scattered irregularly over entire surface. Many of the darkly pigmented scales occur singly, others clustered in groups of 2–5 scales of irregular size and position; some specimens with pigmented scales arranged in semi-circular pattern resembling incomplete ocelli. Specimens with blotches on lateral line with first blotch usually located on body above middle to posterior section of pectoral fin; second blotch, usually darkest, on lateral line just posterior to body midpoint; and third blotch (often smallest of three) situated just anterior to caudal peduncle. Blotches usually 2–4 scales wide and 2–3 scales long. Some specimens also with 2–3 rows of smaller, dark, irregular blotches arranged in longitudinal series along dorsal and ventral margins of body, and some also with darker blotches on lateral line. Some specimens photographed *in situ* from Wellington Harbour and several other locations around North Island with series of rounded to irregular, white spots along dorsal and ventral contours of their bodies. Dorsal row of spots usually beginning anteriorly on head above dorsal eye and continuing along dorsum, nearly evenly spaced, and ending just before vertical through posterior end of dorsal fin. Ventral contour of body with smaller series of white spots, sometimes more diffuse, beginning near anal-fin origin and continuing to caudal peduncle. Head just posterior to eyes with area of diffuse pigment slightly darker than anterior head. Eyes blackish-blue. Rim of mouth on ocular side outlined in darker brown compared to anterior head region. Outer posterior surface of ocular-side opercle somewhat dusky to brownish-black due to dark inner opercular lining showing through to outer surface. Inner lining of ocular-side opercle and entire roof of mouth black. Inner lining of blind-side opercle whitish. Blind side of body uniformly white or yellowish-white, but without peppercorn pigmentation. Dorsal and anal fins of both sexes lightly pigmented and with conspicuous series of a single, darkly streaked ray alternating with 4–8 lightly pigmented rays (i.e., those with either no streaking, or only with a portion of ray streaked). Some exceptional specimens with many streaked rays separated by only 1–2 unpigmented rays. Ocular side of caudal fin with similar pigmentation as that on body, especially basally where scales occur, and with multiple black dashes on distal regions of rays. Ocular-side pectoral-fin rays with some light-brown pigment on proximal half of fin and with either darker brown-black smudge of pigment, or patch of whitish pigment, on fleshy base of fin, and with dark spot at junction near opercle; distal half of ocular-side pectoral fin with several rays streaked with black. Ocular-side pelvic fin with first ray lightly pigmented; second and third rays darker and streaked; fourth ray lightly pigmented; fifth ray darker; and, sixth ray lightly pigmented. Blind side of ocular-side pelvic fin unpigmented. Blind sides of dorsal, anal, and caudal fins without obvious pigment, or sometimes blind side of caudal fin white (same as colour of blind side of body). Blind-side pectoral fin white. Blind-side pelvic fin unpigmented.

*Colour of preserved specimens* (Fig. 21; NMNZ P.005139). Ocular-side background yellowish-brown or brownish-grey to straw-coloured usually with up to three larger, irregular, conspicuous dark blotches on lateral line. First blotch on lateral line usually above pectoral fin; second blotch, usually darkest, on lateral line just posterior to body midpoint; third blotch situated just anterior to caudal peduncle. Blotches usually 2–4 scales wide and 2–3 scales long. Some specimens also with 2–3 rows of smaller, dark, irregular blotches arranged in longitudinal series along dorsal and ventral margins of body and on lateral line. Ocular side of body also with several to numerous scales with darkly pigmented posterior borders scattered irregularly over entire surface. Many of these darkly pigmented scales occur singly, others in small groups of 2–5 scales of irregular size and position; some specimens with pigmented scales arranged in semi-circle pattern resembling incomplete ocelli. Head just posterior to eyes with area of diffuse pigment slightly darker than anterior region of head. Eyes blackish-blue. Rim of mouth on ocular side outlined in darker brown compared to anterior head region. Outer posterior surface of ocular-side opercle dusky brownish-black due to dark inner opercular lining



showing through to outer surface. Inner lining of ocular-side opercle and entire roof of mouth black. Inner lining of blind-side opercle whitish. Blind side of body uniformly white or yellowish-white, but without peppercorn pigmentation. Pigmentation of all fins of preserved fish (both sexes) the same as, or similar to, the fresh colour.

**Size and maturity.** *Peltorhamphus latus* is the smallest species in the genus, reaching a maximum size of about 150 mm SL and 177 mm TL (James 1972; Roper 1979; Roper & Jillett 1981; Paul 1986, 2000; Munroe 2015b; Table 4, this study). Studies including information about *P. latus* collected from nearshore areas outside of estuaries or harbours (e.g., Roper & Jillett 1981; Armitage *et al.* 1994; McMillan *et al.* 2011) report maximum sizes from 170–200 mm TL. Studies concentrating on estuarine fishes (e.g., Healy 1980; Roper & Jillett 1981; Morrison *et al.* 2002; Lowe 2013; Morrison *et al.* 2014a), where the majority of *P. latus* taken are juveniles and subadults (see below), report maximum sizes of only 130 mm TL or smaller for this species.

A total of 942 *P. latus*, 12.0–144.0 mm SL, were examined and standard length was measured for 427. Most of these specimens are 60–130 mm SL. The largest is a female of 144.0 mm SL (Table 4; Fig. 13C). All three fish in the next smallest size class (131–140 mm SL) are also females.

Size and sex information for a subset of 233 fish was examined in greater detail (Table 4), including 88 males, 143 females, and 2 immature individuals (25.2 and 25.5 mm SL) for which sex could not be determined macroscopically. Ovaries of female *P. latus* are clearly identifiable in individuals as small as 41.2 mm SL. Smaller than this size, it is difficult to distinguish ovaries from testes macroscopically. Most fish in the smallest size group were listed as immature, sex undetermined, and were not included in summaries of size-sex information presented in Table 4. Males ranged in size from 38.1 to 126.8 mm SL, females from 41.2 to 144.0 mm SL. Based on these data, females attain slightly larger maximum sizes (to at least 144.0 mm SL) compared with those attained by males (to 126.8 mm SL).

A size-maturity schedule (Fig. 13C) compiled for 143 females of 41.2 mm to 144.0 mm SL confirms that female *P. latus* mature at relatively small sizes, with some maturing as small as 60 mm SL. However, 100% maturity in females is not attained until fish are about 85 mm SL. Of females examined, 36 of 143, from 41.2–84.4 mm SL, were immature, with little elongation of the ovaries. Mature females (N = 107), measuring 60.1–144.0 mm SL, had elongate ovaries extending to at least two-thirds of the body length. Among the smallest (38–60 mm SL) females examined, 18 of 19 are immature. Only one of these (60.1 mm SL) is presumed mature by its elongate ovary; however, no evidence of ripening ova was apparent in this specimen. Among 16 females in the next size group (61–70 mm SL), six were mature, including one female of 62.0 mm SL, the smallest gravid female observed for this species, as well as for any others in this genus. Over the next two larger size intervals (71–80 mm SL and 81–90 mm SL), ratios of mature/immature females continued to increase from 61.1% to 95.2%. In 21 females in the 81–90 mm SL size range, all but one are mature. All 89 of the largest females (> 85 mm SL) are mature with elongate and/or gravid ovaries.

**Distribution** (Fig. 14C). *Peltorhamphus latus* has a discontinuous, but widespread, distribution throughout inshore and coastal waters of New Zealand (James 1972; Paul *et al.* 1983; Anderson *et al.* 1998; Morrison *et al.* 2002; Francis *et al.* 2011; Francis 2012; Lowe 2013; Morrison *et al.* 2014a, 2014b; Munroe 2015b), with the exception of the erroneous reports of the Norfolk Island specimen detailed above. Thus far, this species has not been recorded from the Chatham Islands (James 1972; Roberts 1991; Anderson *et al.* 1998). Paul *et al.* (1983) regarded *P. latus* as a common species in inshore waters, with small to moderate numbers taken in Tasman Bay and Golden Bay, and outside of Kawhia Harbour and Manakau Harbour. Crossland (1981) reported the species as abundant in Hauraki Gulf. Captures of *P. latus* off the main islands of New Zealand (Fig. 14C) range from the Bay of Plenty (39°05.55'S) to Southland, east of Bluff (46°40.55'S). One lot (NMNZ P.007315) also documents this species from off Stewart Island at 46°55'S, 168°09'E.

James (1972) reported that *P. latus* is as abundant around North Island as it is around South Island. Museum specimens examined in the present study included 65 lots taken around North Island, and 14 lots around South Island. James observed that although *P. latus* has a discontinuous distribution, it is probably present around the entire New Zealand coastline wherever suitable habitat occurs. Comprehensive surveys, such as that by Francis *et al.* (2011), which sampled many estuaries on both main islands, also document this species over a broad geographical area.

**Habitat and bathymetric distribution.** *Peltorhamphus latus* has been collected on a variety of substrata, including subtidal and intertidal mud and sand flats, rocky substrata, channel banks of inlets, and in seagrass meadows located in estuaries, harbours, bays, and nearshore coastal waters (James 1972; Roper & Jillett 1981; Healy 1980; Paul *et al.* 1983; Morrison *et al.* 2002; Francis *et al.* 2005, 2011; Lowe 2013; Morrison *et al.* 2014b; Munroe 2015b).

James (1972) noted that this species is abundant in shallow waters, particularly harbours and bays. Roper (1979) reported that *P. latus* was the only one of three species of *Peltorhamphus* that entered Otago Harbour, Papanui Inlet,

and Hooper's Inlet on South Island. Similar results were also reported in Roper & Jillett (1981) from the Otago region. They found juvenile *P. latus* concentrated in finite nursery areas in inlets or shallow coastal waters, whereas adults were common only in shallow waters of Blueskin Bay where they co-occurred with juvenile *P. novaezeelandiae* and juvenile *P. tenuis*. In the Pauatahanui-Porirua Inlets, Healy (1980) reported that *P. latus* was a widely distributed, resident species on sandy, muddy and rocky substrata. Both juveniles and adults (50–130 mm SL) were collected in these inlets year-round, with fewer individuals appearing in winter collections.

Several studies of estuarine fishes conducted around New Zealand detail local distribution, abundance and habitat usage of *P. latus*. Morrison *et al.* (2002) studied diurnal and tidal variation of fishes occurring on a mud flat in Manukau Harbour, North Island, where they found that *P. latus* was common with 1248 individuals taken. Other findings in that study were that more *P. latus* were collected at low versus high tide, and more of them were caught at night versus daytime. Most *P. latus* were captured when they were concentrated in deep channels immediately adjacent to the tideline, fewer were taken on open mud flats. Francis *et al.* (2005) reported that *P. latus* was the fourth most frequently caught species and the fifth most abundant species captured by beach seines in 25 estuaries sampled around northern North Island. In an expanded study, Francis *et al.* (2011) sampled 69 of 443 estuaries spanning some 1500 km. Their results also indicated that *P. latus* was a common inshore species inhabiting estuaries and harbours of both North and South islands. They captured 5,024 individuals, mostly juveniles, in 50% of the 63 estuaries, and in 83% of 69 harbours sampled, and ranked this species as one of the top two most frequently occurring demersal fishes. Lowe (2013) reported on local distribution, abundance and habitat use of *P. latus* in estuaries and harbours around northern New Zealand. She also found they occurred in a wide variety of habitats, including intertidal sand and mud flats, intertidal seagrass beds, and to a lesser degree in subtidal seagrass beds or on subtidal flats. *Peltorhamphus latus* was also found on banks and in channel habitats, especially in muddy habitats, within harbours. In areas sampled by Lowe (2013), *P. latus* was a dominant component of the fish assemblage where it ranked among the 12 most abundant species.

Lowe (2013) observed that no specimens of *P. latus* were taken in mangrove habitats she sampled. With abundance of soft, muddy substrata in mangrove habitats, it is surprising that *P. latus* were not found there, probably indicating that other environmental parameters influence the distribution of *P. latus* in this habitat. Both Lowe (2013) and Morrison *et al.* (2014b) found *P. latus* in seagrass meadows on both islands. This species occurs commonly enough in seagrass meadows that Morrison *et al.* (2014b) considered *P. latus* to have a more cosmopolitan distribution in these habitats than do some of the other fishes typically found in seagrass meadows.

A number of studies report seasonal movements by *P. latus* out of estuarine habitats. In the Pauatahanui-Porirua inlets, Healy (1980) reported that both juvenile and adults (50–130 mm) were collected year-round, but that fewer individuals appeared in winter collections. In the Otago region, Roper & Jillett (1981) also found that juveniles were common in the inlets, with peak abundance during warmer months (November–March). Small numbers caught there during winter likely indicated that the juveniles had moved out of these shallow inlets. More recently, Lowe (2013), too, remarked that *P. latus* moved out of the estuaries in fall, where, most likely, adults moved to offshore waters during winter to spawn, while juveniles were located outside the estuaries.

James (1972) reported that *P. latus* inhabits a bathymetric range between 1.0 and 55 m, but appeared most abundantly in less than 25 m, particularly in harbours and bays. This is supported by other studies, such as that by Anderson *et al.* (1998) who also collected the majority of *P. latus* in relatively shallow waters (ca.  $\leq$  30 m). In a trawl survey conducted in inshore waters off the West Coast of South Island, MacGibbon & Stevenson (2013:113) collected this species at only one station located in 33 m. No information on size of fish at different depths were provided in these studies.

Depth of occurrence information (0.5–55 m) summarized for 586 museum specimens examined in the present study confirms that *P. latus* is a shallow-water species (Table 5). Of these, 470 (= 80.2%) were in 20 m or less, 63 (10.8%) were between 21–30 m, and only 52 (8.9%) were collected between 31–40 m. The deepest recorded museum specimen is for one individual captured at 55 m (cited in James 1972).

This depth information can be broken down as follows (Table 5); 65 (11.1%) were in 0.5–5.0 m; 140 (23.9%) between 6–10 m; 265 (45.2%) between 11–20 m; 63 (10.8%) between 21–30 m; and 52 (8.9%) from 31–40 m; and only one individual (0.2% of total) collected at 55 m.

When this depth information is examined in greater detail (Table 11), adults and juveniles appear to have different depth preferences. Size versus depth of capture revealed that the majority (101 of 165, 61.2%) of the smallest specimens (almost entirely juveniles 12.0–60.0 mm SL) were captured in 0.5–10.0 m both inside and outside of

estuaries (see below). Another 62 specimens, (ca. 37.6%) were collected at intermediate depths (11–20 m), and only two specimens (42.7 and 60 mm SL) were collected deeper than 20 m (at 23 and 35 m, respectively).

**TABLE 11.** Summary of size (mm SL) versus depth of capture for 436 specimens of *Peltorhamphus latus*.

Size (mm SL)	Depth (m)						N
	0.5–5.0	6–10	11–20	21–30	31–40	55	
11–20	4	–	10	–	–	–	14
21–30	3	–	12	–	–	–	15
31–40	8	–	12	1	–	–	21
41–50	11	10	18	1	–	–	40
51–60	12	54	6	–	1	–	73
61–70	9	32	13	–	–	–	54
71–80	11	18	10	1	–	–	40
81–90	4	9	12	–	3	–	28
91–100	1	10	9	23	9	–	52
101–110	1	–	13	14	11	–	39
111–120	–	–	6	23	8	1	38
121–130	–	8	8	–	2	–	18
131–140	–	–	2	–	–	–	2
141–150	–	–	2	–	–	–	2
N	64	141	133	63	34	1	436
%	14.7	32.3	30.5	14.4	7.8	0.2	

Of 174 medium-sized specimens (61.0–100.0 mm SL), representing a mixture of subadults and adults, 94 (54.3%) were collected at depths shallower than 10.0 m, 44 (25.3%) were captured between 11 and 20 m, and 24 (13.8%) were taken between 21–30 m. Only 12 (6.9%) individuals in this medium-size class were collected deeper (31–40 m).

For the 99 largest-sized museum specimens (101.0–144.0 mm SL), only 9 (9.1%) were taken in shallow water (2.0–7.5 m), whereas 31 (31.3%) were taken between 11.0–20 m, 37 (37.4%) in 21–30 m, and 21 (21.2%) were collected between 31–40 m. Only a single large specimen collected at 55 m was taken in waters deeper than 40 m.

In the inlets and open waters off Otago, Roper & Jillett (1981) also observed juveniles have a wide bathymetric distribution from the shallow inlets (0.5 m) to open waters of Blueskin Bay. By contrast, adults were found only in the open waters of Blueskin Bay. Differences in spatial distributions of juveniles and adults suggested the life stages of *P. latus* have different depth preferences. Other studies (Francis *et al.* 2005, 2011; Morrison *et al.* 2002; Lowe 2013) conducted in estuaries or harbours also report that *P. latus* taken were juveniles, and that adults were uncommon.

A synthesis of capture locations (inside versus outside of estuaries and harbours) for the 94 largest (103.8–144.0 mm SL) museum specimens also supports these findings. Only 26 of 94 individuals (27.7%) were taken inside estuaries or harbours. These included the largest specimen (144.0 mm SL), which was collected at 12 m inside Wellington Harbour. The majority (68 of 94 = 72.3%) of the largest *P. latus* were collected in coastal waters located beyond estuaries or harbours. Likewise, data for 154 smaller (12.0–99.9 mm SL) museum specimens also indicate that this size group occupies both inshore (estuaries, harbours) and offshore habitats in nearly equal abundance. Of these, 74 (48.1%) were taken at inshore locations, 80 (52.0%) were collected outside of estuaries or harbours. Even amongst the 13 smallest fish examined (< 26 mm SL), the numbers taken inshore (6) nearly equalled those taken offshore (7). The size ranges for fish from these locations were comparable: 17.0–25.5 mm SL for inshore fish vs. 12.0–25.9 mm SL for fish captured outside of estuaries or harbours. This suggests that recruitment of *P. latus* likely occurs both within estuaries and harbours as well as in nearshore areas outside of estuaries and harbours.

**Trophic biology.** Lowe (2013) and Morrison *et al.* (2014b) examined diet composition of *P. latus* 20–120 mm TL. *Peltorhamphus latus* (20–99 mm TL) has a non-specialized diet comprising a variety of prey items (N = 16–26 prey items/size class). However, based on biomass estimates of stomach contents, the most important items, particularly for fish 20–99 mm TL, were cumaceans (43% of total biomass of prey consumed), followed by bivalve molluscs (22% of total biomass). For *P. latus* on sandy substrata, mussels were also an important item in the diets.

Diet composition varies ontogenetically with that of the smallest size class dominated by cumaceans and other zooplankton. As fish size increases, diet composition expands to include a spectrum of benthic prey: polychaetes, nematodes, bivalves/bivalve siphons, cumaceans, and infaunal amphipods. The largest fish (80–99 mm TL) examined by Lowe (2013) consumed mostly crustaceans (Pericarids) and molluscs; for the largest (100–120 mm TL) examined by Morrison *et al.* (2014b), decapod crustaceans constituted an important component of their diets.

**Reproductive biology.** Although *P. latus* is common and abundant in inlets, estuaries and harbour environments, adults are more commonly found in deeper, nearshore coastal waters outside of the inlets and estuaries and it is there where spawning likely occurs (Healy 1980; Roper & Jillett 1981; Lowe 2013). Healy (1980) reported catching both juvenile and adult (50–130 mm TL) *P. latus* inside the Pauatahanui-Porirua inlets, but few females had mature ovaries, were in running-ripe condition, or had spent ovaries, indicating that spawning didn't occur within these inlets. He commented that *P. latus* were abundant in coastal waters just outside the harbour, and it was in these nearshore waters where spawning occurred. Lowe (2013) noted that *P. latus* occurred in much lower abundance in Manukau Harbour during winter, also suggesting that they may move out during autumn to overwinter offshore and spawn. In Otago Harbour and Blueskin Bay on South Island, Roper & Jillett (1981) reported that adult *P. latus* were not taken in inlets or in Otago Harbour, but only in Blueskin Bay. Based on distribution of adults, they concluded spawning likely occurred in Blueskin Bay. Data from museum records also support this conclusion: near Wellington Harbour, 37 of 53 (69.8%) gravid females were captured in coastal waters outside of the harbour, and although 16 of 53 (30.2%) of the gravid females were taken inside the harbour, all were captured in deeper waters (11–16 m). None of the 53 gravid females were taken in shallower areas or inlets.

Although some information is available on early life-history stages, additional work is needed that relies on accurate identifications. Crossland (1981) and Keith (1998) noted that eggs of *P. latus* have not been described. And, several authors (Frentzos 1980; Crossland 1981; Keith 1998) observed that larvae of *P. latus* are indistinguishable from those of *P. novaezeelandiae* until they have developed a full complement of dorsal- and anal-fin rays, although Crossland (1982) used pigmentation to identify small (at least to 4.2 mm TL) larval *P. latus*. Also unknown is how to distinguish early life stages of *P. latus* from those of *P. kryptostomus* n. sp., which occurs sympatrically with *P. latus* in the Otago region of southeastern South Island.

Larvae purportedly of *P. latus* were described by Roper (1979) from specimens collected off the Otago region. However, it is uncertain if larvae of *P. kryptostomus* n. sp. were not also present in these samples. Other studies describing larvae or pre-juveniles of *P. latus* (Frentzos 1980; Crossland 1981; Keith 1998) were based on samples collected from Wellington Harbour or the Hauraki Gulf, where *P. kryptostomus* n. sp. does not occur. Frentzos (1980) described and published photos of late-state larvae (8.3–11.1 mm TL) collected in ichthyoplankton samples from Wellington Harbour. He reported that the prejuvenile stages of *P. latus* were more abundant than those of *P. novaezeelandiae*. Keith (1998) also described two larvae from Wellington Harbour and provided a colour photograph of the largest larva (11.0 mm TL). Crossland (1981) described and figured two different-sized larvae of *P. latus* that were collected in Hauraki Gulf.

Based on larval occurrences in plankton samples, or on settlement periods for juveniles, at least in some parts of its range, *P. latus* likely spawn in early winter through spring. Roper (1986), for example, recorded larvae in samples taken in Whangateau estuary, North Island, during April and June–February, with peak occurrence of larvae in October. In Hauraki Gulf, northern New Zealand (Crossland 1981, 1982), the spawning season can extend from at least October to February (spring–summer). During a two-year study in this region, larval *P. latus* were collected in abundance over a protracted season from October–February (spring–summer), with highest densities in November in one year, and densities more evenly distributed over this time period in the second year. Limited data available from 39 gravid females examined in museum collections also may confirm a spring spawning season for *P. latus* in the Hauraki Gulf: 35/39 gravid females from the Gulf were collected in November. Two other gravid females were taken in Hawke Bay in October, and two others from Wellington Harbour were collected in December and May. Roper & Jillett (1981) reported that larvae were commonly taken in Otago Harbour, South Island, from late winter to early spring or early summer, and that juveniles settle out of the plankton during spring.

**Etymology.** The name “*latus*” is from the Latin, “*latus*” meaning wide, in reference to the relatively deep body of this species.

**Remarks.** James (1972) concluded that, in contrast to earlier investigators, besides *P. novaezeelandiae*, two additional undescribed species of this genus were also present in New Zealand waters. Of 11 original syntypes of *P. novaezeelandiae* that James examined, he found that 10 syntypes were individuals of a smaller, undescribed species, which he went on to describe as *P. latus*. He did not examine Günther's 12<sup>th</sup> syntype. Given this specimen was of similar size, it seems possible that this was also *P. latus*.

In the description of *P. latus*, James designated 19 paratypes. Two of these (NMNZ P.005147; BMNH 1970.12.15.2), both collected in Blueskin Bay, are re-identified herein as *P. kryptostomus* **n. sp.** Although many meristic and morphometric features of these two specimens overlap those of *P. latus*, they possess several features diagnostic for *P. kryptostomus* **n. sp.**, including presence of finger-like filaments on inner anteroventral margin of the fleshy skinfold on ocular-side lower jaw, more supracranial pterygiophores, number of scales in interorbital region and scales between anteroventral margin of lower eye and dorsal margin of rostral flap above mouth, and numbers of total gillrakers, which distinguish them from *P. latus* (see Comparisons section for *P. kryptostomus* **n. sp.**).

*Peltorhamphus latus* is known only from New Zealand waters, with the noted exception of the erroneous Norfolk Island specimen. Based on this information presented herein, no specimens of *Peltorhamphus latus*, or for that matter, any species of *Peltorhamphus*, are known from Norfolk Island.

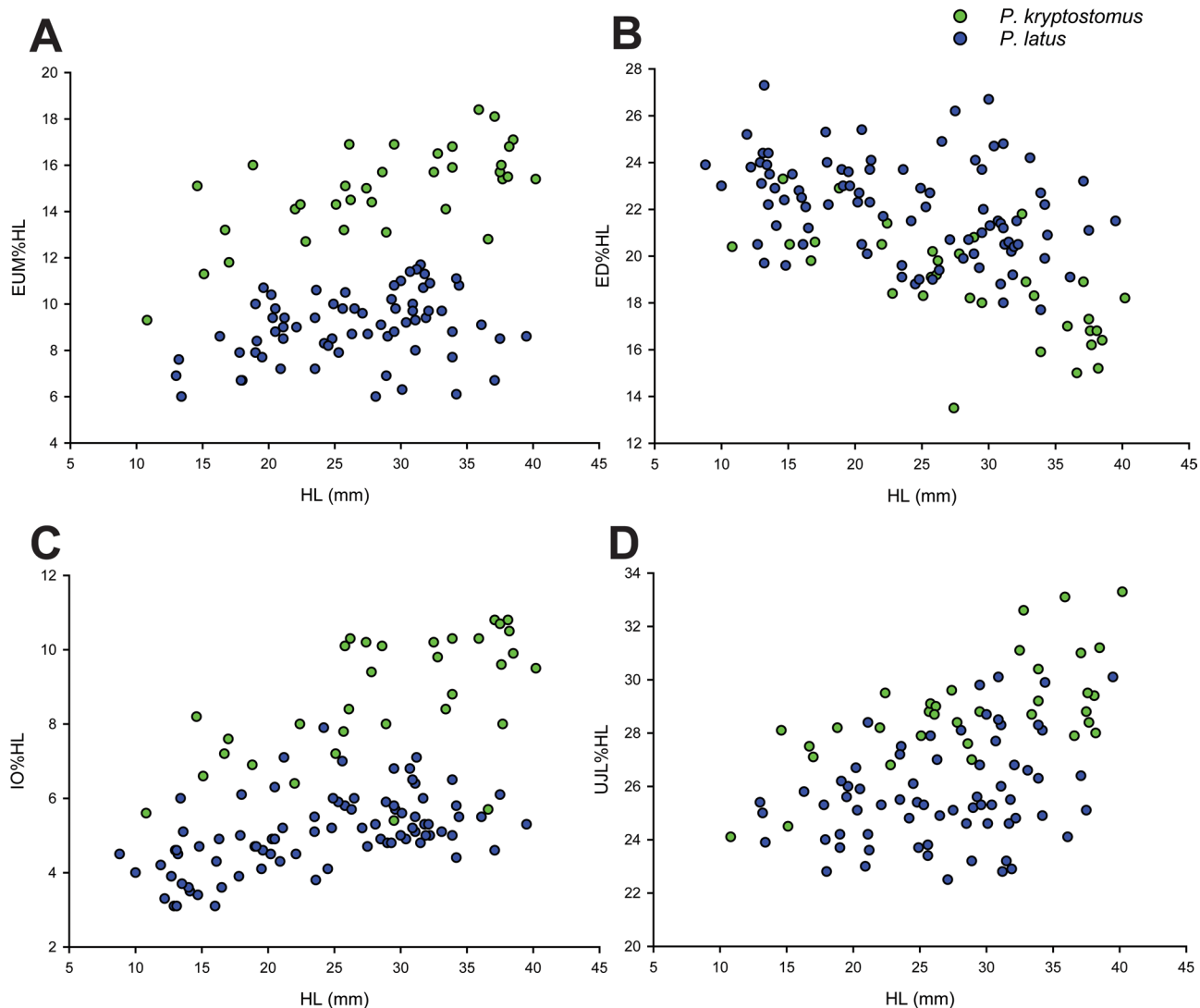
**Comparisons.** *Peltorhamphus latus* is distinguished from its congeners in that it is the only species in the genus lacking fleshy, finger-like filaments on the inner anteroventral margin of the fleshy skinfold on the ocular-side lower jaw (vs. filaments present in *P. novaezeelandiae*, *P. tenuis* and *P. kryptostomus* **n. sp.**). Further differences between *P. latus* and *P. novaezeelandiae* and *P. tenuis* were discussed in the comparisons section in each of these species accounts.

Of the other three species in the genus, *P. latus* is morphologically most similar to *P. kryptostomus* **n. sp.** in that both reach similar maximum sizes and have lower meristic values compared with those of *P. novaezeelandiae* and *P. tenuis*. Both species also have similar body shapes with their greatest body depth located anterior to the body midpoint and with more rapid posterior tapering beyond this point as compared to the more elongate shape in the other two species, especially that of *P. tenuis*.

Despite similarities in size and body shape, *P. latus* is readily distinguished from *P. kryptostomus* **n. sp.** in meristic and morphometric features (compare meristic values in Table 1 and morphometric values in Table 2 and Fig. 24), as well as differences in pigmentation. Features useful for separating the two species include: lack of finger-like filaments on inner anteroventral margin of the fleshy skinfold of the ocular-side lower jaw in *P. latus* vs. usually 1–4 filaments on inner anteroventral margin of the fleshy skinfold on ocular-side lower jaw in *P. kryptostomus* **n. sp.** (differences illustrated in Figs. 3A and 3B); in having only 2–3 scales in the EUM space (vs. 4–5 scales in EUM space in *P. kryptostomus* **n. sp.**); the ventralmost gillraker on upper branch of first gill arch not overlapping the dorsalmost gillraker on the lower branch (vs. ventralmost gillraker on upper branch of first gill arch overlapping dorsalmost gillraker of lower branch in *P. kryptostomus* **n. sp.**; compare Fig. 12C with Fig. 12D); and in having more supracranial pterygiophores (23–29, usually 25–28 in *P. latus* vs. 21–26, usually 23–24, in *P. kryptostomus* **n. sp.**). *Peltorhamphus latus* also has fewer (8–16, usually 11–14) total gillrakers on the first gill arch, whereas *P. kryptostomus* **n. sp.** has 14–20, but usually 15–18, total gillrakers.

The most distinctive morphometric difference between *P. latus* and *P. kryptostomus* **n. sp.** is in the EUM (Fig. 24A). *Peltorhamphus latus* at all sizes have a shorter EUM (6.0–11.7% of HL,  $\overline{X}$  = 9.0%) compared with that of *P. kryptostomus* **n. sp.** (9.3–18.4% of HL,  $\overline{X}$  = 14.9%). Other morphometric differences are that *P. latus* usually also has a slightly larger eye (Fig. 24B; Table 2). For *P. latus*, ED is 17.7–27.3% of HL ( $\overline{X}$  = 21.9%), compared with that (ED is 13.5–23.3% of HL,  $\overline{X}$  = 18.6%) in *P. kryptostomus* **n. sp.** The width of the interorbital region (Fig. 24C) is usually narrower (IO 3.1–7.9% in HL,  $\overline{X}$  = 5.4% in *P. latus* vs. IO 5.6–11.2% of HL,  $\overline{X}$  = 8.8% in *P. kryptostomus* **n. sp.**). *Peltorhamphus latus* usually has a smaller UJL compared with that of *P. kryptostomus* **n. sp.** (Fig. 24D), though greater overlap is evident than that of other morphometric features.

Other differences are that *P. latus* has cycloid scales on the blind-side preopercle and posterodorsal region of the blind-side opercle, whereas *P. kryptostomus* **n. sp.** has ctenoid scales in both areas. *Peltorhamphus latus* also features a pigmentation pattern consisting of a series of a single, darkly streaked ray alternating with 4–8 lighter rays throughout the lengths of both dorsal and anal fins. In contrast, many specimens of *P. kryptostomus* **n. sp.** have uniformly pigmented dorsal and anal fins. Where specimens of *P. kryptostomus* **n. sp.** have darkly-streaked rays in the dorsal and anal fins, these are fewer in number and not as regularly spaced as are those in *P. latus*.



**FIGURE 24.** Comparisons of selected morphometric features of *Peltorhamphus latus* and *P. kryptostomus* **n. sp.** as percent of HL versus HL (in mm). **A.** Eye to upper mouth distance (EUM). **B.** Eye diameter (ED). **C.** Interorbital width (IO). **D.** Upper jaw length (UJL).

***Peltorhamphus kryptostomus* new species**

New Zealand Gray Sole

Figs. 2A–B, 3A, 4D, 5C, 12D, 13D, 14D, 20A & C, 24A–D, 25, 26A–C, 27A–J, 28B; Tables 1–4, 12–13

***Peltorhamphus latus* (not of James 1972).**

James 1972:354 (in part; two paratypes of *P. latus*, collected from Blueskin Bay, Otago, South Island, herein re-identified as *P. kryptostomus*).

Roper & Jillett 1981:2 (in part? Blueskin Bay, Otago, South Island; larval and juvenile samples may contain mix of species including *P. kryptostomus*).

Boyd 2008:8 (in part? eggs, larvae from Otago Harbour may include those of *P. kryptostomus*).

***Peltorhamphus* sp. A.**

Roberts *et al.* 2015:S178 (listed, checklist fishes of New Zealand).

Munroe 2015b:1698 (species account including colour photograph; size; diagnostic features; in key; brief summaries of biology, distribution and habitat; New Zealand).

Roberts *et al.* 2018:127 (listed, online checklist of fishes of New Zealand).

McMillan *et al.* 2019:249–250 (brief mention; size < 200 mm TL; distinguished from *P. latus* and *P. novaezeelandiae*, respectively).



**FIGURE 25.** *Peltorhamphus kryptostomus* n. sp., holotype (NMNZ P.046433, 75.8 mm SL), freshly frozen, thawed; Aramoana Flats, Otago Harbour, South Island, New Zealand. Photo: C. Struthers.

**Diagnosis.** *Peltorhamphus kryptostomus* n. sp. is distinguished from congeners by the combination of: a deep body, with greatest depth anterior to midpoint and with moderately rapid posterior taper; anterior profile of snout smoothly rounded; second ocular-side pectoral-fin ray filamentous and shorter than greatest body depth; 1–5 conspicuous, finger-like filaments on inner anteroventral margin of fleshy skinfold on ocular-side lower jaw; absence of scales on blind sides of dorsal- and anal-fin rays; relatively large eyes with well-developed pupillary operculum; relatively narrow interorbital space (usually < diameter of lower eye) with 2–4 scales; usually with 4–6 scales in diagonal row between anteroventral margin of lower (non-migrated) eye and dorsal margin of rostral flap above mouth; gillrakers on first arch long, pointed, robust, with first and sometimes second raker on upper limb overlapping dorsalmost raker(s) on lower limb of first arch); relatively low meristic values (37–38 total vertebrae, 86–97 dorsal- and 59–67 anal-fin rays, 64–82 lateral-line pores, usually 23–24 supracranial pterygiophores, 14–20 total gillrakers on first gill arch, 4–6 on upper limb of first arch); relatively large and wide head; wide caudal peduncle; light-brown to light-gray ocular-side background colouration with numerous, minute, pinkish spots over entire surface, and with many scales on ocular side of head and body with black pigment on bases of ctenii; dorsal and anal fins in both sexes with either a pattern of a single darkly pigmented ray alternating with 4–8 lighter-pigmented rays, or with rays uniformly pigmented; and with black pigmentation on inner lining of ocular-side opercle and entire roof of mouth.

**Holotype (Fig. 25).** NMNZ P.046433; (75.8 mm SL, immature female); Otago Harbour, Aramoana Flats, 45°47.25'S, 170°41'E; 1 m; 05 Feb 2010.

**Paratypes** (measurements in mm SL in parentheses). NMNZ P.005412; (105.6); Canterbury, Akaroa, 43°50'S, 172°56'E; 30 Jun 1965.

NMNZ P.051867; (113.0); Canterbury, Akaroa, 43°50'S, 172°56'E; 30 Jun 1965.

NMNZ P.046453; (91.9); Otago, Oamaru Harbour, 45°06.35'S, 170°58.75'E; Jan 1965.

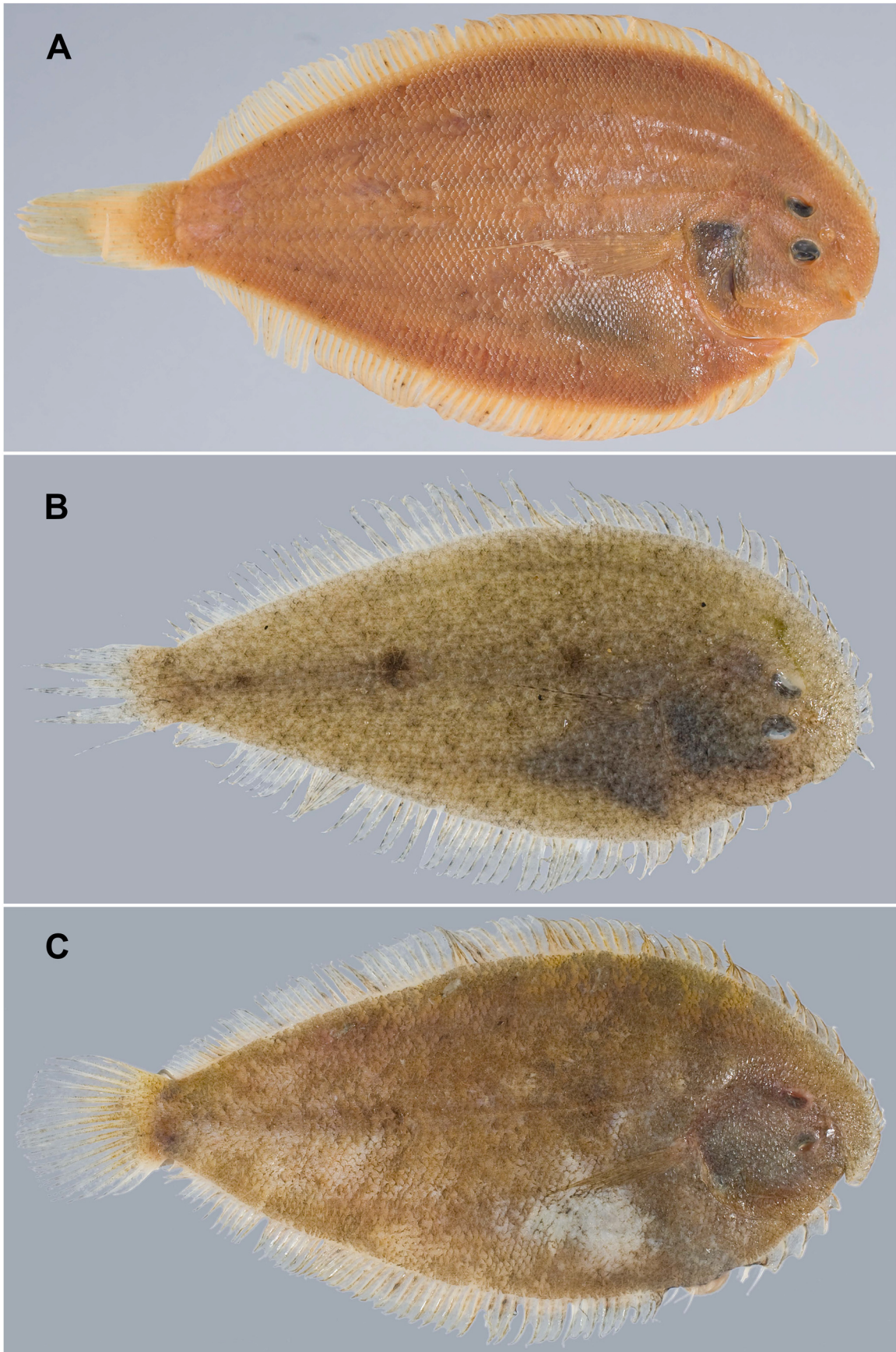
NMNZ P.004292; (101.9); Otago, Blueskin Bay, Otago Peninsula, 45°43.28'S, 170°40.33'E; 20–22 m; 09 May 1990.

MA125778 (formerly NMNZ P.046455); (74.6); Otago, Long Beach, Otago Peninsula, 45°45.18'S, 170°38.93'E; 2–5 m; 11 May 1990.

NMNZ P.046434; (59.1); Otago Harbour, Aramoana Flats, 45°47.25'S, 170°41'E; 05 Feb 2010.

NMNZ P.046436; (50.8); Otago Harbour, Aramoana Flats, 45°47.25'S, 170°41'E; 05 Feb 2010.

NMNZ P.046439; (33.2); Otago Harbour, Aramoana Flats, 45°47.25'S, 170°41'E; 05 Feb 2010.



**FIGURE 26.** *Peltorhamphus kryptostomus* n. sp. paratypes. **A.** NMNZ P.005412, 105.6 mm SL, Akaroa, Canterbury, South Island; preserved. **B.** USNM 427115 (formerly NMNZ P.046437), 56.1 mm SL, Otago Harbour, South Island; freshly frozen, thawed. **C.** NMNZ P.046439, 33.2 mm SL, Otago Harbour, South Island; freshly frozen, thawed. Photos: C. Struthers.



USNM 427115 (formerly NMNZ P.046437); (56.1); Otago Harbour, Aramoana Flats, 45°47.25'S, 170°41'E; 05 Feb 2010.

NMNZ P.046429; (132.0); Southland, between Waikawa Harbour and Chaslands Mistake, Caitlins, 46°40.55'S, 169°14.50'E; 40 m; 19 Mar 2010.

(See also **Non-type material** under **Material examined**.)

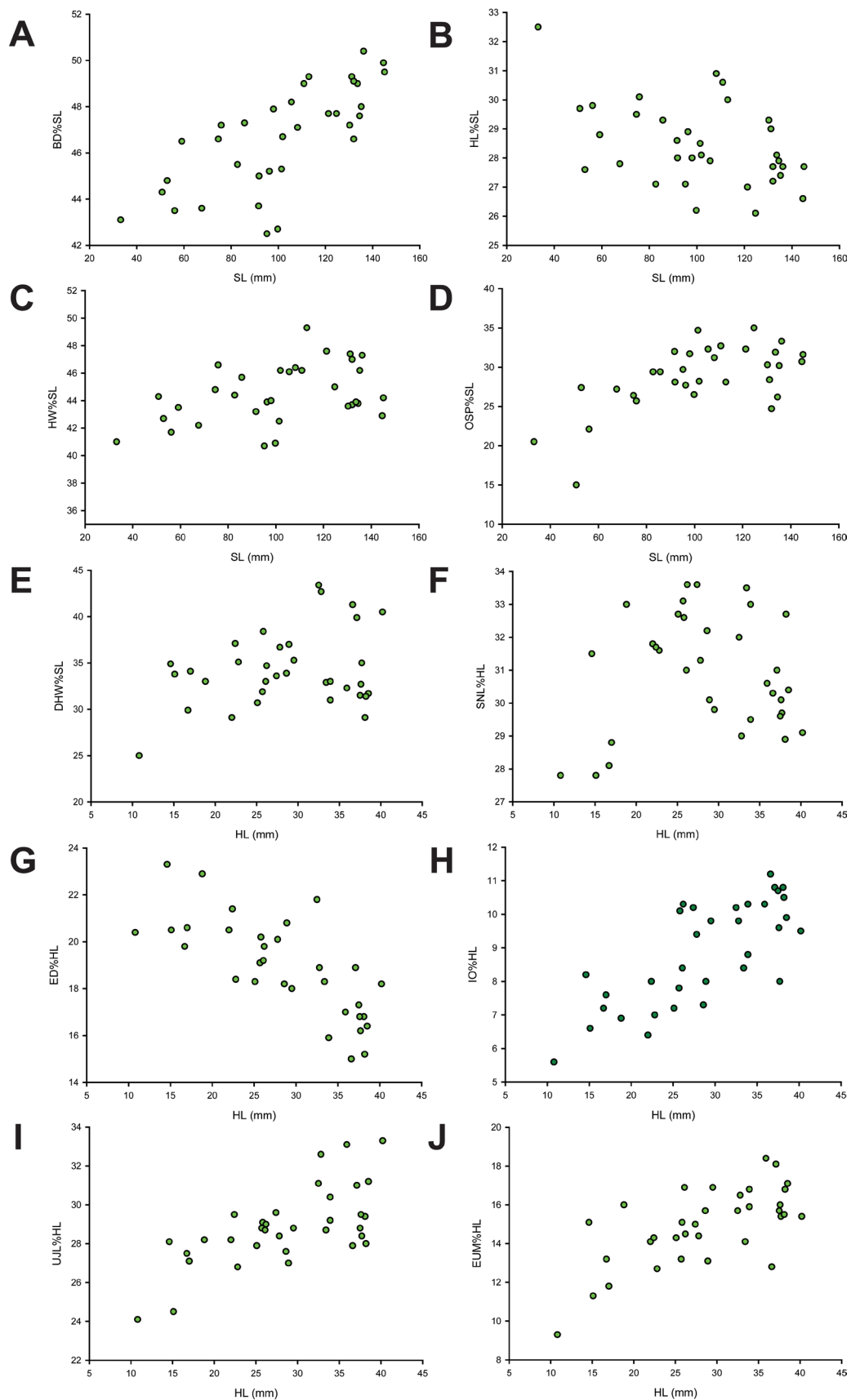
**Description.** Meristic data summarized in Table 1. Values for holotype listed first and in bold here and in Table 1. Supracranial pterygiophores **23**, range 21–26, usually 23–24 (60 of 74 individuals). Pterygiophores inserted into first interneural space **3**, range 1–3, usually 2–3 (73 of 74 individuals). Pterygiophores inserted anterior to first haemal spine **9**, range 6–11, usually 8–9 (55 of 74 individuals). Dorsal-fin rays **95**, range 86–97, usually 88–97 (74 of 75 individuals). Anal-fin rays **62**, range 59–67. Caudal-fin rays **18**, range 17–20, usually 18 (69 of 74 individuals). Ocular-side pectoral-fin rays **9**, range 7–11, usually 8–11 (62 of 64 individuals), rarely 7 (2 individuals). Blind-side pectoral-fin rays **7**, range 7–10, usually 8–9 (55 of 64 individuals). Ocular-side pelvic-fin rays **6** (74 of 74 individuals). Blind-side pelvic-fin rays **4**, range 3–4, usually 4 (71 of 73 individuals). Abdominal vertebrae **10**, range 9–11, usually 10 (71 of 75 individuals including holotype with 3+7 arrangement), rarely 9 (3 of 75 individuals with 3+6 abdominal vertebrae), or 11 (1 individual with 3+8 abdominal vertebrae). Caudal vertebrae **27**, range 26–29, usually 27–28 (73 of 75 individuals). Total vertebrae **37**, range 36–38, usually 37–38 (74 of 75 individuals), rarely 36 (1 individual). Finger-like filaments on inner anteroventral margin of fleshy skinfold on ocular-side lower jaw **3**, range 0–4, usually 1–4 (57 of 63 individuals), rarely with 5 filaments (1 of 63 individuals), or without filaments (5 of 63 individuals; but see remarks below). Gillrakers on upper limb of first arch on blind side **4**, range 4–6, usually 5 (46 of 64 individuals). Gillrakers on lower limb of first arch on blind side **11**, range 10–14, usually 11–13 (58 of 64 individuals), rarely 10 or 14 (3 individuals each). Total gillrakers on first arch on blind side **15**, range 14–20, usually 16–18 (53 of 64 individuals). Interorbital scales **3**, range 2–4, usually 3 (43 of 63 individuals). Scales in diagonal row between anteroventral margin of lower (non-migrated) eye and dorsal margin of rostral flap above mouth **5**, range 3–6, usually 4–5 (57 of 60 individuals). Scales between mid-dorsal margin of dorsal eye and dorsal margin of head **8**, range 7–11, usually 8–10 (53 of 59 individuals). Lateral-line pores **78**, range 64–82, usually 67–82 (52 of 53 individuals).

Morphometric data summarized in Table 12, compared with that of other species in Table 2, discussed in further detail in the Morphometric variation section below, and plotted for select features in Figs. 27A–J. Body oval (Figs. 25–26), laterally compressed; with relatively short trunk (TKL 65.3–76.2% of SL,  $\bar{X}$  = 71.8%); greatest body depth (BD 42.5–50.4% of SL,  $\bar{X}$  = 46.7%) varying ontogenetically, larger fish having proportionally deeper bodies than smaller fish (Fig. 27A); greatest body depth in anterior one-third of body, usually equal with vertical through anterior third of ocular-side pectoral fin, and with moderately rapid posterior taper beyond this point, and with rather steep taper anterior to this point. Caudal peduncle very short, relatively wide (CPD 9.5–11.9% of SL,  $\bar{X}$  = 10.7%). Head large, wide, rounded anteriorly or with blunt point on horizontal between eyes (Figs. 25–26); dorsal profile of head above horizontal between eyes steeply convex to point about equal with vertical at posterior border of eyes, then rising more gradually to point about equal with posterior margin of opercle. Head relatively short (HL 26.1–32.5% of SL,  $\bar{X}$  = 28.4%); proportionally smaller in smaller individuals (Fig. 27B); HL shorter than head width (HW 34.2–49.3% of SL,  $\bar{X}$  = 44.2%); HW increasing slightly with increasing fish size (Fig. 27C); HW/HL = 1.2–1.8,  $\bar{X}$  = 1.56. Head width dorsal to upper eye (DHW 25.0–43.4% of HL,  $\bar{X}$  = 34.3%) moderately wide (Figs. 25–26); DHW increasing slightly with increasing fish size (Fig. 27E); no secondary scales on primary scales above or just dorsoposterior to dorsal eye. Snout moderately long (SNL 27.8–33.6% of HL,  $\bar{X}$  = 30.9%); SNL growth isometric relative to increasing HL (Fig. 27F); snout broadly rounded, or with blunt point on anterior profile and covered with strong, ctenoid scales; greatest length of snout at horizontal between eyes; about 8–10 scales between anterior margin of eyes and profile of snout. Ocular side of snout with conspicuous rostral flap whose dorsoposterior margin nearly surrounds and nearly conceals entire mouth, except for posteriormost end of jaws; rostral flap anteriorly with short, fleshy rostral hook (RHL 14.2–30.3% of HL,  $\bar{X}$  = 21.4%) covering tip of jaws anteriorly, and with posterior end extending ventrally to point about at vertical through posterior nasal sac. Ventroposterior section of rostral flap also with an inverted U-shaped vertical opening, exposing only posteriormost tips of jaws ventrally. Two ocular-side nostrils anterior to interorbital space, asymmetrically placed closer to dorsal margin of lower eye (Fig. 5C). Anterior ocular-side nostril a short tube with terminal, relatively long, membranous leaf-like flap reaching posterior nostril when depressed posteriorly, and with fleshy membrane at its base. Ocular-side posterior nostril a nearly vertical slit surrounded by thin membrane. Two blind-side nostrils; not conspicuous. Anterior blind-side nostril, located above

anterior one-third of lower jaw, a short tube with delicate terminal flap; posterior blind-side nostril, located above midpoint of jaw, a horizontal slit surrounded by fleshy membrane. Eyes relatively large (ED 13.5–23.3% of HL,  $\bar{X}$  = 18.6%); ED decreasing proportionally with increasing fish size (Fig. 27G); eyes elliptical, not contiguous; usually with anterior margins of eyes nearly equal in position, or with anterior margin of upper eye slightly in advance of anterior margin of lower eye; with conspicuous, well-developed pupillary operculum (Fig. 2B) in both juveniles and adults. Interorbital width relatively narrow (IO 5.6–11.2% of HL,  $\bar{X}$  = 8.8%), ontogenetically variable (Fig. 27H) and increasing proportionally with increasing HL; IO usually < eye diameter at all sizes. Mouth moderate in size (UJL 24.1–33.3% of HL,  $\bar{X}$  = 28.9%); UJL increasing proportionally with increasing HL (Fig. 27I); jaws asymmetrically developed towards blind side; all but posterior margin of jaws on ocular side nearly completely concealed by rostral flap; blind-side jaws straighter, only slightly decurved posteriorly. Diagonal distance between anteroventral margin of lower (non-migrated) eye and dorsal margin of rostral flap above mouth (EUM 9.3–18.4% of HL,  $\bar{X}$  = 14.9%), relatively broad in all but the smallest individuals, increasing in size ontogenetically (Fig. 27J). Mouth opening on ocular side small, an inverted U-shape (Fig. 28B), opening at vertical through anterior base of ocular-side nostrils. Ocular-side lower lip smooth, without labial papillae. Teeth, present only on blind-side jaws, slender, villiform, in 2–4 irregular rows; teeth in anteriormost rows slightly larger than posterior teeth in same row. Fleshy skinfold on inner anteroventral margin of ocular-side lower jaw with 1–5 finger-like filaments (Fig. 3A). Postorbital length relatively long (POL 12.9–16.3% of SL,  $\bar{X}$  = 14.4%), about 33–38% of HW. Upper head lobe (UHL 22.0–26.4% of SL,  $\bar{X}$  = 24.7%) wider than lower head lobe (LHL 11.5–18.8% of SL,  $\bar{X}$  = 15.1%).

**TABLE 12.** Summary of morphometric information for the Holotype, 10 paratypes, and 23 non-type specimens of *Peltorhamphus kryptostomus* n. sp. Characters 1–12 expressed as % of SL; characters 14–23 expressed as % of HL. Abbreviations defined in text.

	Holotype	All specimens including Holotype				
		Min	Max	Mean	Stdev	N
SL (mm)	75.8	33.2	145.1	101.56	30.083	34
1. BD	47.2	42.5	50.4	46.67	2.224	34
2. OSP	25.7	15.0	35.0	28.77	4.185	32
3. BSP	10.2	8.4	14.9	11.81	1.292	34
4. HL	30.1	26.1	32.5	28.43	1.406	34
5. HW	46.6	34.2	49.3	44.20	2.743	34
6. POL	14.0	12.9	16.3	14.35	0.822	34
7. DHW	10.6	8.1	11.5	9.71	0.935	34
8. UHL	24.9	22.0	26.4	24.72	1.113	34
9. LHL	15.6	11.5	18.8	15.10	1.587	34
10. TKL	72.0	65.3	76.2	71.78	2.236	34
11. CFL	17.7	17.6	32.2	22.04	2.694	34
12. CPD	11.1	9.5	11.9	10.74	0.606	34
13. HW/HL	1.5	1.2	1.8	1.56	0.115	34
14. POL	46.5	46.5	56.2	50.51	2.232	34
15. SNL	31.6	27.8	33.6	30.93	1.740	34
16. ED	18.4	13.5	23.3	18.63	2.292	34
17. IO	7.0	5.6	11.2	8.84	1.526	34
18. EUM	12.7	9.3	18.4	14.89	1.986	34
19. DHW	35.1	25.0	43.4	34.28	4.039	34
20. UJL	26.8	24.1	33.3	28.86	2.003	34
21. RHL	30.3	14.2	30.3	21.43	3.572	34
22. UHL	82.9	67.6	95.7	87.18	5.939	34
23. LHL	51.8	43.3	64.7	53.16	5.486	34



**FIGURE 27.** Selected morphometric features for 34 specimens of *Peltorhamphus kryptostomus* n. sp. 33.2–145.1 mm SL. **A–D.** Body depth (BD), Head length (HL), Head width (HW), and Ocular-side pectoral fin (OSP) expressed as percent of SL versus SL (in mm), respectively. **E–J.** Dorsal head width (DHW), Snout length (SNL), Eye diameter (ED), Interorbital width (IO), Upper jaw length (UJL), and Eye to upper mouth distance (EUM) expressed as percent of HL versus HL (in mm), respectively.

Superficial neuromasts on blind side of head inconspicuous, but with visible lappets; neuromasts usually in consistent arrangement of three, more or less, parallel longitudinal rows dorsal to horizontal through nostrils, and with another series located just posterior to jaws. Dorsalmost row of neuromasts, located close to body margin, beginning on snout and extending posteriorly to about midpoint of head; middle longitudinal row of neuromasts beginning on anterior snout and extending posteriorly nearly to three-fourths of head length; ventralmost longitudinal row located in shallow groove beginning just posterior to nostrils and extending to about midpoint of head, with fewer, more closely spaced neuromasts than in other rows. Another series of neuromasts in curved row following contour of jaws; ventralmost neuromasts in this series located just ventral to posterior margin of jaws, with remaining neuromasts in this series more or less following ventral curvature of jaws nearly to distal tip of jaws. Several prominent free neuromasts on blind side of head situated dorsal and posterior to neuromast series located behind jaws, submarginally along ventral surface of opercle, and on ventral portion of lower jaw.

Gillrakers not toothed, present on both limbs of gill arches on ocular and blind sides. Gillrakers on upper limb of first blind-side gill arch robust and similar in shape and size to those on lower limb (Fig. 12D). Upper gillrakers on first blind-side arch long, cylindrical, with thickness uniform over most of their lengths; tips pointed, sometimes recurved; posteriormost gillraker of upper limb reaching ventrally to, or slightly beyond, dorsalmost gillraker on lower limb of same gill arch, or sometimes reaching tip of second dorsalmost gillraker on lower limb. Gillrakers on lower limb of first gill arch slightly longer than those on upper limb, except ventralmost 2–4 gillrakers on lower limb of first blind-side gill arch usually much smaller and more rounded than others on this limb. Posterior margin of operculum usually fringed with conspicuous, small, membranous flaps and short, thin, finger-like cirri.

Dorsal-fin origin at tip of rostral hook, located ventral to visible part of mouth opening. Anteriormost rays, from first to approximately 15<sup>th</sup> ray, with distinct cup-shaped, fleshy membrane approximately to their midpoints and with their distal halves curved, filamentous, and noticeably free from connecting membrane; remainder of rays connected with membrane at approximately three-fourths the length of each ray and without cup-shaped, fleshy membrane at their midpoints. Anal-fin rays connected by membrane nearly at their distal tips. No scales on blind sides of dorsal- and anal-fin rays. Caudal fin rectangular, moderately long (CFL 17.6–32.2% of SL,  $\bar{X}$  = 22.0%) compared with that of congeners; scales covering both sides of caudal fin proximally for one-fourth or less length of fin, and with scales extending distally on rays to about three-fourths of their lengths. Both pectoral fins well developed; ocular-side fin with conspicuous, elongate, second ray reaching just slightly posterior to vertical through body midpoint; length of second ray (OSP 15.0–35.0% of SL,  $\bar{X}$  = 28.8%) increasing proportionally with increasing SL (Fig. 27D); OSP shorter than greatest body depth in adults, but nearly equal to body depth in small juveniles; remaining rays gradually decreasing in length ventrally. Blind-side pectoral fin much shorter than ocular-side fin (BSP 8.4–14.9% of SL,  $\bar{X}$  = 11.8%), with rays spaced much closer together than those of ocular-side fin, and without elongate rays. Both pelvic fins well developed; unequal in position and size; surrounding anus; not connected to each other. Ocular-side pelvic fin on body midline with its origin nearly at anterior tip of isthmus. Base of first blind-side pelvic-fin ray located at point equal to space between fifth and sixth ocular-side rays, sometimes equal with base of sixth ocular-side ray. Ocular-side rays widely separated and with distal tips free from membrane; first and second rays noticeably shorter than others; rays of ocular-side pelvic fin more robust than those of blind-side fin; posteriormost ocular-side pelvic-fin ray with broad, membranous connection to first anal-fin ray. Blind-side pelvic fin much shorter and with rays spaced more closely together than those in ocular-side fin; first blind-side ray notably slender and short, rays 2–4 becoming progressively more robust, fourth ray longer than others; blind-side pelvic fin without membranous connection to anal fin, but fourth ray, from base to approximately middle of ray, with membranous connection to body region near anus.

Ocular and blind sides of head and body with transforming ctenoid scales with strong ctenii in adults and juveniles of both sexes. Blind-side preopercle and subopercle of adult males with strongly ctenoid scales; whereas, adult females with weakly ctenoid or cycloid scales on preopercle, and with ctenoid scales on subopercle.

Anus on blind side, slightly off body midline, bordered medially by blind-side pelvic fin.

Lateral line straight, except for slight elevation anteriorly above pectoral fin; posteriorly, lateral-line pores extending nearly to 4/5ths of length of ocular-side middle caudal-fin ray, and on blind side to proximal one-third of length of middle caudal-fin ray.

**Morphometric variation.** Detailed examination of variation in morphometric features based on 34 *P. kryptostomus*, 33.2–145.1 mm SL, revealed allometric growth evident in most features examined (Figs. 27A–J). Values for body depth measurements (BD; Fig. 27A) varied from 41.6% to 50.4% of SL, and showed positive allometric growth throughout the size range of fish examined. Differences in BD from smallest to largest individuals (ca. 13%) reflects continued deepening of the body with increasing size.

Head length (HL; Fig. 27B) measurements varied between 26.6% and 32.5% of SL and had less variation (ca. 7%) than did BD measurements. Head length showed slight negative allometry over the size range measured. Smallest fish (to ca. 60 mm SL) had HL values between 26.6–32.5% of SL, whereas fish >120 mm SL usually had HL values of 26–30% of SL. Smaller fish have proportionally larger heads relative to SL than do larger *P. kryptostomus*. Head width values (HW; Fig. 27C) were 41.1–49.3% of SL over the size range measured. Although the data showed slight, but continuous, positive allometric growth of HW over SL, the difference between the smallest and largest fish was only 9%, indicating that HW increases relatively slowly compared to increasing fish size.

Length of the elongate ray in the ocular-side pectoral fin (OSP; Fig. 27D) also shows continuous, positive allometric growth for fish 33.2–145.1 mm SL. For these, OSP values ranged from 14.4% to 35.0% of SL, representing considerable variation (21%) compared with that observed for other features.

Of six other morphometric features of the head measured (Figs. 27E–J), all but SNL displayed allometric growth. Dorsal head width (DHW; Fig. 27E) and interorbital width (IO; Fig. 27H) both showed positive allometry throughout the size ranges. Width of the head region dorsal to the eyes varied considerably, with 18% difference between the smallest and largest fish. Variation in IO measurements (5.6–11.2% of HL) was considerably less than that for DHW, but the proportionate growth of this feature steadily increased with increasing fish size. Data for eye to upper mouth values (EUM; Fig. 27J) revealed that this region of the head undergoes continuous, positive allometric growth with increasing fish size (total range 9.3–18.4% of HL), values varied about 9% between the smallest and largest fish. Continued positive increases in DHW, IO, and EUM values proportional to increasing fish size reflect broadening of head width with growth; this broadening is especially evident in the regions dorsal to, and between, the eyes.

Values for snout length (SNL; Fig. 27F) were 27.8–33.6% of SL and growth of this feature appears to be isometric, with no clear trends apparent in the plotted data. Measurements of lower eye diameter (ED; Fig. 27G) varied about 10%, with a negative trend in proportionate growth evident between smaller and larger fish. Values for upper jaw length (UJL; Fig. 27I) ranged about 9% between smaller and larger fish (24.1–33.3% of HL), and were positively allometric throughout the size range examined.

*Colour based on freshly thawed specimens* (NMNZ P.046433; USNM 427115; NMNZ P.046439). Background colouration of ocular side of head and body light brown to light gray (Figs. 25, 26B–C). Ocular side with numerous, minute, pinkish spots over entire surface. Base of ctenii at posterior border of many scales on ocular side of head and body black. Neuromasts outlined with black pigment. Scales on various areas of ocular side of head and body highlighted with faint patches of brassy-gold and pinkish pigment. Ocular side of body, from about one-third length of longest ocular-side pectoral-fin ray and continuing to caudal peduncle, with irregular arrangement of clusters consisting of 4–5 black scales semi-enclosing an inner, brighter, pinkish-brown area. Most of ocular side of caudal peduncle with three darkly pigmented areas. Ocular side also with three, conspicuous, larger, irregular, dark blotches along lateral line. Two anteriormost blotches with numerous, small pink spots and scattered white pigment; some specimens also with small pink spots associated with posteriormost blotch. Anteriormost dark blotch located on lateral line about equal with point at mid-length of elongate ocular-side pectoral-fin ray, second blotch just posterior to vertical through body midpoint, and posteriormost blotch located just anterior to caudal peduncle. Second blotch, largest of the three, vertically elongate, ranging from 1–3 scales in width along horizontal axis and extending vertically in length 3–4 scales both dorsally and ventrally from lateral line. Lateral-line pores in region of dark blotches also black. Region around and including axil of ocular-side pectoral fin with black pigment much darker than that on body. Anterodorsal region of head with lighter colouration compared with that on ventroposterior region. Anterior ocular-side nostril tubular with three distinct patches of black pigment along its length. Dorsal surface of eyes, cornea and pupillary operculum gray; pupil outlined with small band of reflective silvery pigment. Mouth margined with black pigment. Exposed portion of ocular-side jaws gray with black margin on vertical portion. Roof of mouth black. Ocular-side inner opercular lining black. Gill filaments dusky gray with central rachis black. Blind side of body uniformly white; some scales on head and body with whitish iridescent sheen. Outer surface of operculum whitish to silvery. Blind-side inner opercular lining without conspicuous pigment. Fleishy finger-like filaments on inner anteroventral margin of skinfold on lower jaw white, conspicuously contrasted against darker colour of lower jaw and operculum.

Ocular side of dorsal fin on head with fine black spots on both fin rays and membrane. Spots more densely concentrated on rays than on connecting membrane. Remainder of fin with series of a single darkly pigmented ray alternating with 1–6 lighter pigmented rays. Anteriormost 5–10 rays with small, white flap of tissue on distal tips;

some rays, beginning with those posteriorly on head and continuing caudally, with yellowish-orange pigment on entire (most cases) posterior side of rays. Anal fin with same colour pattern as that on dorsal fin, except for fewer darkly pigmented rays. Most posterior anal-fin rays yellowish, posteriormost rays entirely yellow with a cluster of dark melanophores on their tips. Ocular side of caudal fin with small, black spots along entire length of rays; very few spots on connecting membrane. Axil of ocular-side pectoral fin sometimes with small patch of black or blackish-brown pigment, rays with same general colour as that on adjacent body. Two dorsalmost rays with pinkish overtones and three small areas of black pigment along their lengths. Distal tips of rays black. Ocular-side pelvic fin with similar colouration as that on dorsal and anal fins, except first pelvic-fin ray yellowish-pink. Blind sides of dorsal and anal fins uniformly white; caudal fin mostly white, except for fine black spots on membrane. Blind-side pectoral fin white. Blind-side pelvic fin iridescent white, except anterolateral side of first ray pink.

**Colour of preserved specimens** (Fig. 26B; USNM 427115). Ocular-side background colouration uniformly greenish- or yellowish-brown to grey sometimes with up to three, large, irregular, dark blotches on lateral line, and with smaller dark blotches irregularly placed over ocular surface. Axil of ocular-side pectoral fin with small patch of black or blackish-brown pigment. Some anterior sensory pores ringed and clearly outlined with brown pigment. Inner lining of ocular-side opercle and roof of mouth black; inner lining of blind-side opercle without conspicuous pigment. Dorsal and anal fins with pattern of single, darkly streaked ray alternating with 4–6 lightly pigmented rays; this alternating pattern more prominent in anterior half of these fins. Blind side uniformly white or yellowish-white.

**Size and maturity.** *Peltorhamphus kryptostomus* reaches a maximum size of about 145 mm SL (Table 4). No sexual dimorphism in size was observed for 56 specimens for which size and sex information was obtained (Table 4). The largest specimen examined is a female 145.1 mm SL, the largest male 135.2 mm SL. Of 56 specimens, 19 are males (52.9–135.2 mm SL) and 37 are females (33.2–145.1 mm SL).

Of the females, 16 (33.2–113.4 mm SL), are immature (Fig. 13D). Seven immature females smaller than 80 mm SL show little, if any, elongation of their ovaries; nine females (75.8–113.4 mm SL) have partially elongate ovaries. Mature females (N = 21), i.e., those with elongate ovaries, are 85.7–145.1 mm SL. Females attain sexual maturity beginning at sizes between 85–100 mm SL; three of four females 80–90 mm SL, and three of 10 females 91–100 mm SL, are mature. Seven females in the latter size range, the largest 95.7 mm SL, have ovaries still undergoing posterior elongation and were assessed as immature. Of 16 females  $\geq$  101 mm SL, 15 are sexually mature, having fully elongate ovaries, including some with visible ova in various stages of development. The exceptional female in this group, of 113.4 mm SL, has only partially elongate ovaries. Based on these limited data, female *P. kryptostomus* begin to mature sexually at sizes as small as 86 mm SL. By sizes  $\geq$  101 mm SL, all, with rare exception, have reached sexual maturity.

**Etymology.** The name “*kryptostomus*” is derived from the Greek “*krypto*” meaning hidden and “*stomus*” meaning mouth, in reference to the mouth on the ocular side being mostly hidden by the broad rostral flap.

**Distribution** (Fig. 14D). *Peltorhamphus kryptostomus* is endemic to New Zealand waters, with a restricted distribution in nearshore coastal waters and bays along the southeast coast of South Island from off Akaroa (43°50'S) to off the Caitlins at 46°40.55'S, 169°14.50'E.

**Habitat and bathymetric distribution.** *Peltorhamphus kryptostomus* is a shallow-water species that occurs in 1.5–40 m (Table 5). The majority of specimens (70 of 81) examined in this study were caught between 11 m and 20 m; 8 of 81 were collected in 1.5–5.0 m, 2 of 81 were taken at 21 m; only 1 of the 81 was taken at 40 m.

Of 49 fish with size and depth information (Table 13), it appears that small fish occur in shallower waters than do larger fish. All eight fish smaller than 80 mm SL were collected at the shallowest depths (1.5–5.0 m). Fish larger than 81 mm SL were collected deeper in 11–40 m, the majority in 11–20 m. The 12 largest fish (121–145 mm SL) were captured between 11–40 m, with only three specimens (101–140 mm SL) collected deeper than 20 m.

**Biology.** Other than information summarized above, little else is known about the ecology of this species.

**Remarks.** James (1972) recognized three species, and only for specimens identified as a ‘population’ of *P. latus* from Blueskin Bay (mostly fish  $>$ 115 mm SL) was any significant variation in body proportions apparent. For this ‘population,’ James reported that body depth, snout length, and upper jaw length were relatively greater than comparable morphometric features noted for other populations of *P. latus*. Differences in eye size between the Blueskin Bay ‘population’ and others were also noted.

My examination of specimens from Blueskin Bay, including some of those previously identified by James as *P. latus* (including two paratypes), reveals that most, especially many of the larger specimens, are *P. kryptostomus*.

This species occurs sympatrically and sometimes syntopically in Blueskin Bay with *P. latus*. Since both species were included in James' samples from Blueskin Bay, morphometric comparisons between this 'population' and other populations of *P. latus* were compromised. The question then is, did the differences James observed in body depth, snout length, upper jaw length, and eye size for his Blueskin Bay 'population' of *P. latus* actually reflect differences between two sympatric congeners?

**TABLE 13.** Summary of size versus depth of capture for 49 specimens of *Peltorhamphus kryptostomus*.

Size (mm SL)	Depth (m)					N
	1.5–5	6–10	11–20	21	40	
33–50	2	0	0	0	0	2
51–60	4	0	0	0	0	4
61–70	0	0	0	0	0	0
71–80	2	0	0	0	0	2
81–90	0	0	6	0	0	6
91–100	0	0	15	0	0	15
101–110	0	0	3	2	0	5
111–120	0	0	3	0	0	3
121–130	0	0	4	0	0	4
131–140	0	0	6	0	1	7
141–145	0	0	1	0	0	1
N	8	0	38	2	1	49
%	16.3	0	77.6	4.1	2	

To address this question, 18 morphometric features of specimens of all sizes identified in this study as *P. kryptostomus* and *P. latus* were compared. Data were taken from specimens of each species collected throughout their respective geographic ranges, including *P. latus* from Blueskin Bay, and all morphometric values expressed as percent of SL or HL. Comparisons of morphometric features (summarized in Table 2) revealed large overlaps between these species in most characters examined. The four morphometric characters (BD, SNL, ED, UJL), specifically identified by James (1972) as being significantly different between the Blueskin Bay 'population' (= composite sample including two species) versus those of other populations of *P. latus*, were examined in greater detail to assess their value as diagnostic characters useful for separating the two species.

Among these features, ranges for BD measurements overlapped nearly completely between the two species (BD 42.5–50.4% of SL in *P. kryptostomus* vs. 39.7–50.1% in *P. latus*), with the mean value only slightly greater in *P. kryptostomus* ( $\bar{X}$  = 46.7% of SL) compared with that in *P. latus* ( $\bar{X}$  = 44.1%). Likewise, significant overlaps and only slight differences between these species were also observed in SNL (7.8–10.4% of SL,  $\bar{X}$  = 8.8% in *P. kryptostomus* vs. 6.8–10.2% of SL,  $\bar{X}$  = 8.5% in *P. latus*) and ED (3.8–6.6% of SL,  $\bar{X}$  = 5.2% for *P. kryptostomus* vs. 5.0–7.2% of SL,  $\bar{X}$  = 5.3% for *P. latus*). When ED was expressed as a ratio of HL, the smaller eye of *P. kryptostomus* (ED 13.5–23.3% of HL,  $\bar{X}$  = 18.6% vs. ED 17.7–27.3% of HL,  $\bar{X}$  = 21.9% in *P. latus*) became slightly more apparent (Fig. 24D). However, the large overlap rendered this feature ineffective as a diagnostic character for distinguishing these species. Measurements of UJL (Fig. 24D), although slightly larger in *P. kryptostomus* compared with those of *P. latus* (UJL 7.3–9.2% of SL,  $\bar{X}$  = 8.2% vs. 6.0–8.9% of SL,  $\bar{X}$  = 7.1% in *P. latus*), also overlapped between species, and was also determined ineffective as a good diagnostic character. Of four morphometric features James (1972) found to differ significantly between the purported Blueskin Bay 'population' versus that of other populations of *P. latus*, none provide sufficient separation to be usefully diagnostic.

The large degree of overlap observed in the present study (Table 2) among many of the other morphometric features of these two species reveals the overall similarity between *P. kryptostomus* and *P. latus* in body shapes. Based on their similarities, it is understandable why James, despite recognizing some differences between Blueskin Bay specimens and those from other areas, concluded these differences only represented population variation and not that of co-occurring species.

Despite these similarities, ample support for recognizing *P. kryptostomus* as a species distinct from *P. latus* includes two other morphometric features not examined by James (1972): IO width (Fig. 24B) and EUM distance (Fig. 24A).

The eyes of *P. kryptostomus* are more widely separated (IO space 5.6–11.2% of HL,  $\bar{X}$  = 8.8%) compared with the nearly contiguously positioned eyes of *P. latus* (IO 3.8–7.9% of HL,  $\bar{X}$  = 5.4%). *Peltorhamphus kryptostomus* also has a much larger separation between the anteroventral margin of the lower eye and the upper margin of the rostral flap above the mouth (EUM 9.3–18.4% of HL,  $\bar{X}$  = 14.9%) compared with the smaller EUM (6.0–11.7% of HL,  $\bar{X}$  = 9.0%) for *P. latus*. Other differences, including size and position of gillrakers on the first arch, scale counts in IO and EUM spaces, presence vs. absence of finger-like filaments on the inner anteroventral margin of the lower jaw, presence of ctenoid scales on the blind-side preopercle and posterodorsal region of the blind-side opercle in *P. kryptostomus* (vs. cycloid scales in both locations in *P. latus*) are suitable diagnostic features that distinguish these as distinct species. Further differences between these species are highlighted in the Comparisons section below.

Two lots, NMNZ P.005147 and BMNH 1970.12.15.2, each containing a single specimen from Blueskin Bay, Otago, South Island, are part of the paratype series of *P. latus* selected by James (1972). These two specimens are herein re-identified as *P. kryptostomus*, but are not designated as paratypes of *P. kryptostomus*.

As mentioned above, one character distinguishing *P. kryptostomus* and *P. latus* is the presence in *P. kryptostomus* (vs. absence in *P. latus*) of finger-like filaments on the inner skinfold of the anteroventral margin of the lower jaw. Although this feature is prominent in the majority of specimens examined, five of the 63 (8%) specimens of *P. kryptostomus* examined, lacked these finger-like filaments. This was thought to result from their condition and/or long-term preservation. These fish were collected and preserved in the 1970s, and some were also partially dissected for otolith extraction. Despite lacking obvious filaments, these specimens possessed other characters that distinguish them as *P. kryptostomus*. Uncompromised data from these specimens, other than that for the finger-like filaments, were included in tallies for *P. kryptostomus*.

**Comparisons.** Features that distinguish *P. kryptostomus* from its congeners were discussed in detail in the Comparisons sections for *P. novaezeelandiae*, *P. tenuis*, and *P. latus*, respectively. In addition to its smaller size and scale type on the blind side (discussed above), *P. kryptostomus* differs from *P. novaezeelandiae* by its lower and nearly non-overlapping counts of dorsal- and anal-fin rays, and counts for lateral-line scales (compare frequency distributions for respective meristic features for these species in Table 1). *Peltorhamphus kryptostomus* also has more gillrakers on the upper limb of the first gill arch (4–6, usually 4–5 vs. 1–6, usually 3–4, in *P. novaezeelandiae*). The gillrakers on the first arch of *P. kryptostomus* are long and pointed, and some overlap the uppermost gillraker(s) on the lower limb of the first arch, whereas in *P. novaezeelandiae* the gillrakers on the first arch are short, triangular-shaped and those on the upper limb are noticeably shorter and rounder and not overlapping those on the lower limb of the arch (compare Figs. 12A and 12D). *Peltorhamphus kryptostomus* also differs from *P. novaezeelandiae* in having fewer supracranial pterygiophores (21–26, usually 23–24 vs. 23–29, usually 25–28). *Peltorhamphus kryptostomus* can further be distinguished from *P. novaezeelandiae* in having black pigment on the entire inner lining of the ocular-side opercle and on the entire roof of the mouth, which is lacking in *P. novaezeelandiae*. It is further distinguished from *P. novaezeelandiae* by its larger, more conspicuous pupillary operculum, and, in adults, by its narrower interorbital width (usually IO < eye diameter compared with that of larger juveniles and adult *P. novaezeelandiae* whose IO is greater than the eye diameter).

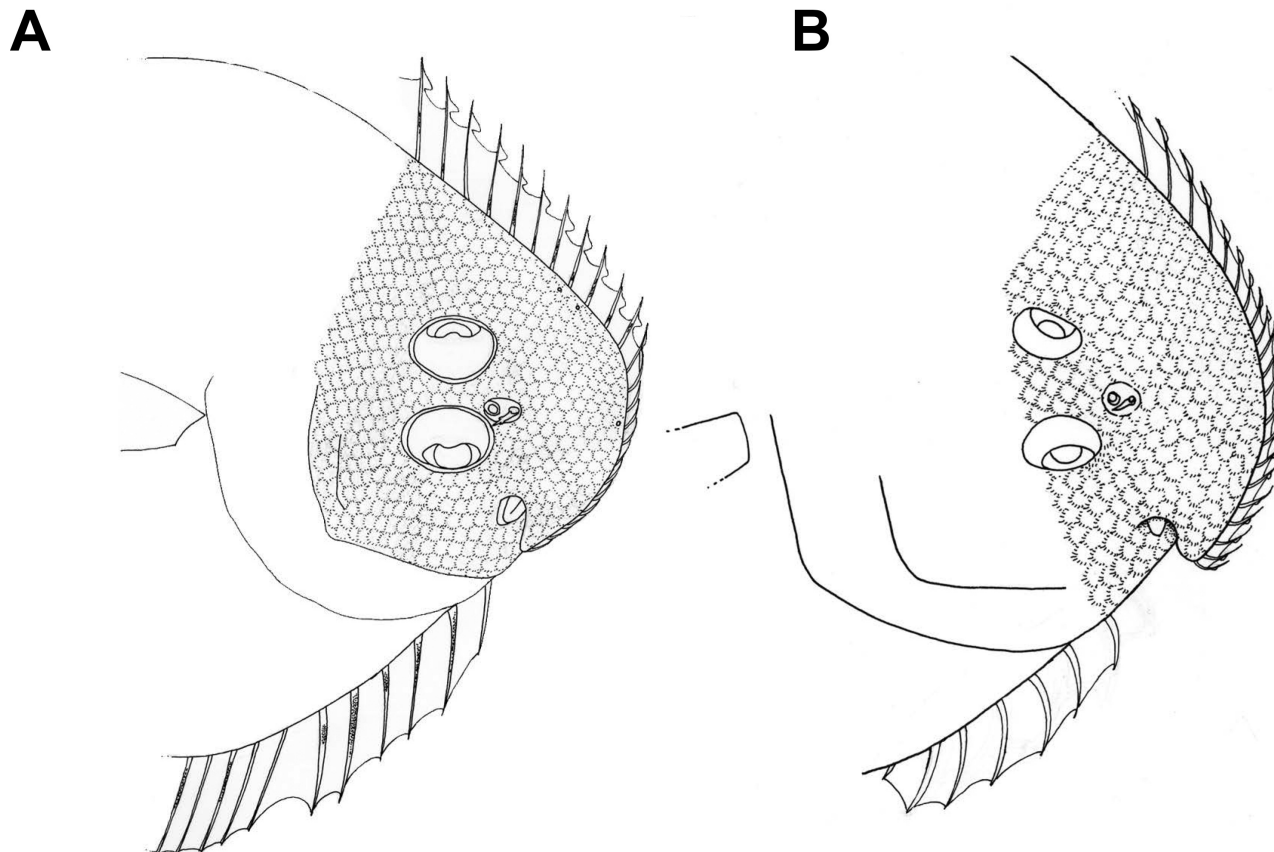
*Peltorhamphus kryptostomus* is readily distinguished from *P. tenuis* by differences in ocular-side colour patterns. *Peltorhamphus kryptostomus* has uniform colouration without longitudinal lines vs. *P. tenuis* often with faint series of longitudinal lines. Differences are also in pigmentation of the inner opercular lining and mouth; *P. kryptostomus* with roof of mouth and ocular-side inner opercular lining black vs. *P. tenuis* with dusky inner opercular lining and unpigmented roof of mouth. *Peltorhamphus kryptostomus* also differs from *P. tenuis* in having fewer total vertebrae (37–38 in *P. kryptostomus* vs. 40–43); fewer dorsal-fin rays (88–97 vs. 98–116); fewer lateral-line scales (64–82 vs. 82–105); more gillrakers on the lower limb of the first gill arch (10–14, usually 11–13 vs. 5–12, usually 8–11); and in having fewer supracranial pterygiophores (21–26, usually  $\leq 25$  vs. 25–31, usually 26–29).

These species also have conspicuous differences in morphometric features, with *P. kryptostomus* having a much deeper body (BD 42.5–50.4% of SL,  $\bar{X}$  = 46.7%) compared to the narrower, elongate body (BD 31.2–42.3% of SL,  $\bar{X}$  = 36.3%) of *P. tenuis* (Fig. 20C); *P. kryptostomus* has a much shorter second ocular-side pectoral-fin ray usually much shorter than the body depth versus a longer (usually  $\geq$  body depth) second ocular-side pectoral-fin ray in *P. tenuis*; *P. kryptostomus* also has a slightly longer head (HL 26.1–32.5% of SL,  $\bar{X}$  = 28.4% vs. HL 20.9–27.9% of SL,  $\bar{X}$  = 24.7%; Fig. 20B), and a wider caudal peduncle (CPD 9.5–11.9% of SL,  $\bar{X}$  = 10.7% vs. 6.9–10.2% of SL,  $\bar{X}$  = 8.7%). Other differences in morphometric features (HW; SNL; RHL; etc.) between these species appear in the summarized data presented in Table 2. Qualitative differences between these species include the absence (vs.



presence in *P. tenuis*) of scales on blind sides of the dorsal- and anal-fin rays (best developed in specimens > 70 mm SL); presence (vs. absence) of a pupillary operculum; and by differences in size, robustness and position of gillrakers on the upper limb of the first gill arch (compare Figs. 12D vs. 12B).

Of species in the genus, *P. kryptostomus* is most similar to *P. latus*: both reach similar maximum sizes (Table 4) and both feature similar lower meristic values compared with those of *P. novaezeelandiae* and *P. tenuis* (Table 1). Both species also have similar body shapes with their greatest body depths being located anterior to the body midpoint and with a more rapid posterior taper beyond this point (compare Figs. 21–22 with Figs. 25–26).



**FIGURE 28.** Differences between *Peltorhamphus latus* (A) and *P. kryptostomus* (B) in the ocular side of the head, including anterior head profiles, relative eye sizes, interorbital distances, and number of scales and distances along the diagonal between the anteroventral border of lower eye and upper margin of the mouth (EUM distance). Drawn by: M. Freeborne.

Despite similarities in size and body shapes, *P. kryptostomus* is distinguished from *P. latus* by differences in meristic and morphometric characters, including several features of the head (Figs. 28A–D), and in pigmentation. Features useful for separating the two species include the usual presence of 1–4 finger-like filaments on the inner anteroventral margin of the fleshy skinfold on the ocular-side lower jaw in *P. kryptostomus*, absent in *P. latus*; in usually having 4–5 scales between the anteroventral margin of the lower eye and dorsal margin of the mouth opening vs. 2–3 scales in this space in *P. latus* (compare Figs. 28A and 28B); in having the ventralmost gillraker on the upper branch of the first gill arch overlapping the dorsalmost gillraker of the lower branch of this arch vs. ventralmost gillraker on upper branch of first gill arch not overlapping dorsalmost gillraker of lower branch of this arch in *P. latus* (compare Figs. 12D vs. 12C); in having fewer supracranial pterygiophores (21–26, usually 23–24 vs. 23–29, usually 24–28, in *P. latus*); and more (14–20, but usually 15–18) total gillrakers compared with that of *P. latus* (8–16, usually 10–14). *Peltorhamphus kryptostomus* also has ctenoid scales on the blind-side preopercle and posterodorsal opercle, whereas *P. latus* has cycloid scales in both locations.

Morphometric features that distinguish these species include differences in EUM (Fig. 24A), ED (Fig. 24B), and IO width (Fig. 24C), illustrated in Figs. 28A–28B, and to a lesser degree by differences in UJL (Fig. 24D). The EUM distance (9.3–18.4% of HL,  $\bar{X}$  = 14.9%) is larger in *P. kryptostomus* compared with that (6.0–11.7% of HL,  $\bar{X}$  = 9.0%) of *P. latus* (Fig. 24A); and, *P. kryptostomus* also has a smaller eye (ED 13.5–23.3% of HL,  $\bar{X}$  = 18.6%; Fig. 24B) than does *P. latus* (17.7–27.3% of HL,  $\bar{X}$  = 21.9%). Interorbital width in *P. kryptostomus* (Fig. 24C) is

wider (IO 5.6–11.2% of HL,  $\overline{X}$  = 8.8%) compared with that (IO 3.1–7.9% in HL,  $\overline{X}$  = 5.0%) of *P. latus*. Usually, *P. kryptostomus* also has a larger UJL compared (Fig. 24D) with that of *P. latus*.

Most specimens of *P. kryptostomus* lack darkly streaked dorsal- and anal-fin rays altogether (vs. dorsal and anal fins of *P. latus* with conspicuous series of a single, darkly streaked ray alternating with multiple (4–8) lightly pigmented rays throughout the lengths of the dorsal and anal fins). When specimens of *P. kryptostomus* have darkly streaked fin rays, they are fewer in number and not as regularly spaced as are those in *P. latus*.

### Key to species of *Peltorhamphus*

- 1a Second ocular-side pectoral-fin ray elongate, longer than (in specimens  $\leq$  130 mm SL), or equal to (in specimens  $>$ 130 mm SL), maximum body depth; no pupillary operculum; specimens larger than about 70 mm SL with small, ctenoid scales on basal halves of blind sides of dorsal- and anal-fin rays (Fig. 2C); ocular-side colouration with series of faint longitudinal lines; usually 40–42 total vertebrae . . . . . *Peltorhamphus tenuis*
- 1b Second ocular-side pectoral-fin ray elongate, but usually noticeably shorter than maximum body depth; pupillary operculum present or absent; no scales on blind sides of dorsal- and anal-fin rays; ocular-side colouration without series of faint longitudinal lines; less than 40 total vertebrae . . . . . 2
- 2a Inner anteroventral margin of fleshy skinfold on ocular-side lower jaw without finger-like filaments (viewed from blind side, Fig. 3B); usually only 1–2 scales in diagonal row between anteroventral margin of lower eye and dorsal margin of mouth opening; eyes relatively large, diameter of lower eye greater than interorbital space, and greater than distance between anteroventral margin of lower eye and dorsal margin of rostral flap above mouth; interorbital space narrow, usually less than eye diameter and usually with only 1–2 scales . . . . . *Peltorhamphus latus*
- 2b Inner anteroventral margin of fleshy skinfold on ocular-side lower jaw with 1–5 fleshy, finger-like filaments (viewed from blind side, Fig. 3A); fish  $>$  40 mm SL with more than 2 (usually 4–5) scales in diagonal row between anteroventral margin of lower eye and dorsal margin of rostral flap above mouth (Fig. 2A); eyes relatively small, diameter of lower eye usually less than, or only equal to, interorbital space; diameter of lower eye usually less than distance between ventral margin of lower eye and dorsal margin of mouth opening; interorbital space wide, usually greater than eye diameter, and with 3 or more scales (in fish  $>$  40 mm SL). . . . . 3
- 3a Entire inner lining of ocular-side opercle and roof of mouth black; gillrakers on first arch of blind side long and robust (Fig. 12D), upper limb gillrakers equal in length to those on lower limb; posterior gillrakers on upper limb of first arch on blind side usually overlapping dorsalmost first or second gillrakers on lower limb; fish  $>$  ca. 80 mm SL with ctenoid scales on mid-body region of blind side and on blind-side preopercle and subopercle; pupillary operculum relatively large, conspicuous . . . . . *Peltorhamphus kryptostomus*
- 3b Inner lining of ocular-side opercle black only on dorsoposterior region (if at all); roof of mouth without black pigmentation; gillrakers on first arch of blind side relatively short, usually much shorter than gillrakers on lower limb, and thin (Fig. 12A); posterior gillrakers on upper limb of first arch on blind side not overlapping gillrakers on lower limb (Fig. 12A); fish  $>$  ca. 80 mm SL with cycloid scales on mid-body region of blind side and also on blind-side preopercle and subopercle; pupillary operculum relatively small, inconspicuous . . . . . *Peltorhamphus novaezeelandiae*

### Discussion

As presently conceived, Rhombosoleidae comprises a small family of flatfishes represented by eight (Campbell *et al.* 2019) or nine genera and about 22 species (Guibord 2003; Gomon 2008; Munroe 2005, 2012, 2015a). In nearly all earlier family-level classifications of the Pleuronectiformes (Regan 1910; Norman 1934; Sakamoto 1984; Ahlstrom *et al.* 1984) and also in more recent classifications (Eschmeyer 1990, 1998a, 1998c; Evseenko 2004; Van der Laan *et al.* 2014, Fricke *et al.* 2020), rhombosoleid flatfishes have been classified as a subfamily within an expanded family of dextral flounders, the Pleuronectidae. Jordan (1923) and Chabanaud (1946, 1949), among earlier authors, recognized the rhombosoleids as a distinct family within the Pleuronectiformes. Chabanaud (1939, 1946, 1949) disagreed with the classification of right-eye flounders proposed by Norman (1934). He (1946) argued for recognition of the autonomy of the Rhombosoleidae based on three important characters: asymmetry in the pelvic fins; absence of actinosts in the pectoral girdle; and, especially, the absence of a postcleithrum in *Peltorhamphus*. In his later classification, Chabanaud (1949) added another character, open haemal arches of the abdominal vertebrae, as evidence supporting his hypothesis of the autonomy of the Rhombosoleidae. Chabanaud (1946, 1949) commented that none of these characters are shared with members of the Pleuronectidae. Hensley & Ahlstrom (1984) discussed the history of classification of the subfamily Rhombosoleinae. In their synthesis of morphological features, they determined that the Rhombosoleinae was possibly monophyletic, but recommended further research to define this

group and determine its relationships with other flatfishes then classified in an expanded Pleuronectidae. Chapleau & Keast (1988) also recommended recognizing the Rhombosoleidae as a family distinct from the Pleuronectidae, whereas Chapleau (1993), who conducted the first cladistic analysis of the Pleuronectiformes based on morphological features, classified the rhombosoleid flatfishes as a monophyletic subfamily within his Clade IV, which did not include the Pleuronectinae. Chapleau also addressed issues concerning classification of flatfishes assigned to the different subfamilies of the more inclusive Pleuronectidae of previous authors, and recommended additional research to define the monophyly and inter-relationships of fishes in these subfamilies, including the Rhombosoleinae. Cooper & Chapleau (1998), following Chapleau & Keast (1988), recognized the former subfamily Pleuronectinae as the Pleuronectidae, a monophyletic lineage distinct from the Rhombosoleid flounders. Subsequent studies (Hoshino 2001; Chanet 2003; Guibord 2003; Nelson 2006; Gomon 2008; Munroe 2005, 2015a, 2015b; Nelson *et al.* 2016, Van der Laan 2020) also recommended elevating the subfamily Rhombosoleinae to familial rank, including several phylogenetic hypotheses based in whole or in part on molecular data (Betancur-R. *et al.* 2013; Betancur-R. *et al.* 2014; Betancur-R. & Orti 2014; Campbell *et al.* 2014; and Campbell *et al.* 2019, excluding *Oncopterus*). All of these studies also hypothesized the rhombosoleid flounders as a lineage distinct from that containing members of the former subfamily Pleuronectinae. Information contained within these latest morphological and molecular studies provides strong support for recognizing the Rhombosoleidae as a distinct family within the Pleuronectiformes.

The most diverse rhombosoleid fauna in the world occurs in marine and freshwater ecosystems of New Zealand, excluding marine habitats of the Kermadec Islands, represented by 12 species in five genera (Munroe 2012, 2015b). Of flatfishes inhabiting New Zealand waters (Munroe 2015b–f), the Rhombosoleidae is the predominant family, constituting a significant proportion of the taxonomic diversity of the flatfish fauna inhabiting this region (46.2% of ca. 26 species distributed among five family lineages within the Pleuronectiformes).

In this study a number of morphological synapomorphies and diagnostic features identified in the previous works of Günther (1862), Norman (1926, 1934), James (1972), Sakamoto (1984) and Guibord (2003), along with other features discussed herein, define and distinguish the genus *Peltorhamphus* from all other Rhombosoleid genera.

The study represents the most comprehensive systematic treatment of flatfishes of the genus *Peltorhamphus*. Data presented herein increases our knowledge concerning the diversity of species of *Peltorhamphus*. Previous systematic treatments of this genus (Günther 1862; Norman 1926, 1934) until the early 1970s, considered *Peltorhamphus* to be monotypic. In his 1972 revision of *Peltorhamphus*, James identified three species, *P. novaezeelandiae*, *P. latus* and *P. tenuis* that should be recognized. Amongst their specimens, an additional undescribed species, *P. kryptostomus*, discovered by Munroe (2015b) and formally described in the present study, brings to four the number of valid species that should be recognized in *Peltorhamphus*.

Species of *Peltorhamphus* are endemic to New Zealand waters. The single, extralimital record of one specimen at Norfolk Island is based on an individual with erroneous locality data. These four species are known only from shallow continental shelf waters of New Zealand.

Considerable morphological similarity among species of *Peltorhamphus* (James 1972; Munroe 2015b) contributed to confusion regarding the number of species in the genus, confusion which began with the first species, *P. novaezeelandiae*. Following James' (1972) revision of the genus, taxonomic uncertainty continued as some specimens identified as *P. latus* were subsequently re-identified and herein formally described and named *P. kryptostomus*. Recent discovery of this fourth species, along with re-identification of a relatively large number of misidentified specimens in fish collections of three of the four species within *Peltorhamphus*, necessitated taxonomic re-evaluation of all members of the genus. Diagnosis and description of the new species and redescription of its congeners, based on traditional and new characters developed in this study, hopefully will improve the accuracy of future identifications of specimens of this genus. More accurate identifications, in turn, will increase our knowledge regarding the taxonomy of species in *Peltorhamphus*, and also improve our knowledge of the ecology, distribution, and life histories.

Difficulties identifying specimens of *Peltorhamphus*, especially small juveniles, have been mentioned by a variety of authors (Roper 1979; Roper & Jillett 1981; Colman 1994; Armitage *et al.* 1994; Banks *et al.* 2007; Munroe 2015b). Many authors noted that these difficulties were due to overall morphological similarities, which are further compounded by the ecological co-occurrences of these species.

With redescription of three species and addition of a fourth species, some meristic and morphometric data of the present study were partitioned differently from that in James' (1972). This re-partitioning of data possibly may have reduced overlap compared with that observed in James' earlier study. However, as in James' study, large overlap in

meristic and morphometric features were still observed in specimens examined in the present study (Tables 1–2). Of 21 meristic features analyzed (Table 1), relatively few were found useful for diagnosing any of the four species. Only counts for total vertebrae clearly distinguished individuals of *P. tenuis* from their congeners. Total vertebrae for this species are  $\geq 40$ , the highest in the genus, and do not overlap with any of the other species (total vertebrae  $\leq 39$ ). Among the other three species, however, total vertebral counts, though showing some modal differences, overlapped sufficiently (Table 1), rendering this character ineffective for identifying species. Also of limited diagnostic value is the number of scales counted in a diagonal series from the middle anteroventral margin of the lower eye and the dorsalmost margin of the mouth (Scales Eye-Jaw; Table 1). For *P. latus*, this ranged between 1 and 4, with most having 3 or less scales, compared with counts of 3 to 9 (usually 4–6) in the other three species, except for small ( $< 40$  mm SL) *P. novaezeelandiae*, which had 1–4 scales. In *P. novaezeelandiae*, *P. tenuis*, and *P. kryptostomus*, this scale count is nearly completely overlapping. Another meristic feature, of limited diagnostic value, is the number of scales in the interorbital region (IO scales). For *P. latus*, these ranged from 0–2 (usually 1–2) compared with 2–4 (usually 2–3) in *P. kryptostomus*, 1–5 for *P. tenuis* and 1–6 (usually 2–4) for *P. novaezeelandiae*.

One trend evident in meristic data summarized in this study is that two species, *P. novaezeelandiae* and *P. tenuis*, usually have higher, and minimally overlapping counts of dorsal- and anal-fin rays, and lateral-line scales compared with respective counts in *P. latus* and *P. kryptostomus*. Based on each of these counts, two species pairs, a high count and a low count pair, can be recognized. Though useful to identify a specimen as a member of species pair, due to the large overlap between species in each species pair, these are of limited value for identifying a specimen to a species.

Overall similarities in morphology were also evident in analyses of 19 morphometric features measured (Table 2). The most significant difference in morphology is the large size (ca. 510 mm SL) attained by *P. novaezeelandiae*. None of the other species surpasses 160 mm SL, so size alone readily distinguishes larger *P. novaezeelandiae* from its congeners. Other than this, substantial overlap is evident in many morphometric features measured (Table 2), especially when small juveniles ( $\leq 30$  mm SL) are included in the analyses.

Allometry was evident in many morphometric features, and to detect patterns and compare these patterns across the four species, a subset of 10 features (BD, HL, HW, and OSP expressed as percent of SL; and SNL, ED, UJL, EUM, IO, and DHL expressed as percent of HL) were examined in greater detail. Six of eight features exhibited positive allometry; two negative allometric growth, relative to growth in HL or SL; and two displayed isometric growth within each species. Patterns of allometric growth for each of the 10 features were discussed in the Morphometric variation sections in the individual species accounts (compare data plots of measurements in Figs. 9, 19, 23, and 27).

Comparing morphometric features among the four species of *Peltorhamphus* revealed that not only was allometric growth evident in the same features across the four species, but direction of allometry was also nearly identical for almost all of these features (Figs. 9, 19, 23, and 27). Although some ontogenetic change was evident in most of the morphometric features examined, usually these were relatively small. The most significant changes observed for any of the species were the differences in the head between small juveniles and larger individuals of *P. novaezeelandiae* (Fig. 9; and changes in head shape in Fig. 10). Ontogenetic changes in this species include those in interorbital width, eye to upper mouth distance (EUM), and head width dorsal to upper eye.

Some morphometric features of larger juvenile and adult *P. novaezeelandiae* were distinctly different compared with similar measurements of other species (Figs. 15–16). When these measurements were compared among smaller juveniles of these species, the values nearly completely overlapped. Morphometric features of the greatest differences between species were identified earlier (Figs. 15–16, 20 and 24) and discussed in Comparisons sections of the individual accounts. Based on these observations, some morphometric characters of *Peltorhamphus* have utility as diagnostic features, but the overall morphological similarity of the four species, and ontogenetic changes in head shape of *P. novaezeelandiae* overlap the range of measurements of the other species. Thus, the value of morphometric features as diagnostic characters was found to be size dependent, and therefore of limited effectiveness in identifying all life stages of individual species.

Accurate identification, in addition to improving taxonomic knowledge of these species, is required to more precisely assess the ecology of these flatfishes, including better understanding of species' habitat requirements and for attaining more reliable estimates of occurrence and population abundance. In turn, improved identification increases our knowledge of the importance of these species in their biological communities and their contributions to commercial and recreational fisheries. Large species of rhombosoleid flatfishes are highly desirable food fishes,

frequently targeted by commercial, artisanal, and recreational fisheries of both New Zealand (Armitage *et al.* 1994; Banks *et al.* 2007; McMillan *et al.* 2011, 2019; Beentjes & MacGibbon 2013; Munroe 2015b; New Zealand Seafood Industry Council 2018) and southern Australia (Roughley 1961; Crawford 1984; Kailola & McNee 1993; Ferguson 2006, 2007; Gomon 2008; André *et al.* 2015). In fact, eight species of flatfishes commercially targeted and harvested in New Zealand waters by an inshore domestic trawl fleet (Colman 1994) or taken in seine operations are rhombosoleids. These fishes are a particularly important component in commercial landings from the Otago and Southland regions of New Zealand. Of New Zealand flatfishes with commercial importance, *P. novaezeelandiae* is the only species in the genus reaching sufficient size and abundance to contribute to regional commercial flatfish catches (James 1972; Armitage *et al.* 1994; Colman 1994; Paul 2000; Banks *et al.* 2007; New Zealand Ministry for Primary Industries 2017, New Zealand Seafood Industry Council 2018), none of the other *Peltorhamphus* grow large enough. However, these other species are likely ecologically important components of the benthic communities they inhabit.

This paper thoroughly reviews and evaluates previous literature dealing with the taxonomy of each species. Biological and ecological information associated with specimens consistently identified using diagnostic characters developed herein, and also from previous studies in which species identifications were deemed reliable, were also compiled, summarized, and discussed. This compilation serves as a useful data resource for those interested in researching the biology, ecology, fisheries and utilization of these flatfishes.

Difficulties with identifying and distinguishing the eggs, larvae, and the smallest juveniles of species of *Peltorhamphus* contribute uncertainties to the reliability of previous literature reporting early life-history ecological and distributional information. More work is still needed to develop reliable diagnostic characters to improve the accuracy of identifications of planktonic and early post-settlement stages for all four species. What we think we know of aspects of the biology, ecology, and demographics of these four species has been compromised by misidentifications, and highlights that our level of knowledge for these early life stages is actually quite poor. Only with accurate identifications can we begin to assemble the appropriate information to better understand and manage populations of these species.

The large number of misidentifications of juveniles in museum lots examined also handicaps the reliable information from many earlier publications that have utilized this material. The high frequency of misidentifications of early life-history stages of species of *Peltorhamphus* indicates that parameters such as geographic occurrences, bathymetric distributions, and general ecology of these smallest pre- and post-settlement size classes are not as well-known as we think they are. Accurate identifications of these early stages will be needed to obtain better estimates of recruitment patterns, abundance estimates of recruits, or locations and seasonal use of settlement habitats by recruits of the individual species. Correct identification of the specimens is the first and most critical step towards obtaining meaningful, accurate life history and distributional data to develop management plans for these species. For the commercially exploited *P. novaezeelandiae*, as well as for its congeners, accurate identifications of early life stages are paramount to properly address ecological and fisheries-related data gaps for these species. Understanding population demographics of individual species requires reliable information about location of settlement areas, determination of how species differ with respect to critical factors important for settlement and recruitment, and also where and when newly settled fish recruit to juvenile and adult segments of their populations. All of these life-history aspects hinge on accurate identifications, and all of these aspects (and more) are paramount to better understanding the life histories and population dynamics of these species.

Improved knowledge concerning species diversity within *Peltorhamphus* contributes to better understanding of the biodiversity of flatfishes occurring in waters surrounding New Zealand. Recognition of a fourth species of *Peltorhamphus* improves the accuracy of diversity assessments, not only within *Peltorhamphus* and Rhombosoleidae, but also regarding knowledge about the flatfish assemblage inhabiting New Zealand waters. Though not particularly diverse in terms of number of species, this assemblage of about 26 species of flatfishes (Munroe 2015b) represents five of the approximately 14 different family lineages within the Pleuronectiformes. The assemblage of New Zealand flatfishes includes both species of commercial importance and those with little to no commercial importance. Further assessments of the taxonomic status of at least 10 other New Zealand flatfish species is needed. Even for some better known and commercially important flatfish species inhabiting New Zealand waters, fundamental information on geographic and bathymetric distributions, morphological variation, population structure, and life-history aspects still remain poorly known. This is due, at least in part, to the taxonomic challenges associated with accurately identifying all life stages of these species. Given this present state of knowledge, clarification of the systematic

status and development of better diagnoses of species of New Zealand flatfishes continue to present challenges awaiting systematists and others interested in studying these interesting fishes.

## Material examined

Measurements of specimens appear in parentheses and are in mm SL, unless otherwise specified.

***Peltorhamphus novaezeelandiae*, 657 specimens (24.0–395). Meristic and morphometric data taken, 107 specimens (32.7–395). Lectotype:** BMNH 1848.3.18.-; (245); locality not specified, New Zealand. **North Island.** NMNZ P.006067; (185); N. Auckland off 90 Mile Beach, 34°48.00'S, 172°39.00'E; 126 m; 17 Jul 1969. NMNZ P.006068; 2(203–224); N. Auckland off Manganui Bluff, 35°42.00'S, 172°39.00'E; 62 m; 19 Jul 1969. NMNZ P.042765; 4(194–241); N. Auckland SE off Hokianga Harbour, 35°49'S, 173°34'E; 46 m; 19 Jul 1969. NMNZ P.006070; (185); N. Auckland off N. Kaipara, 36°21'S, 173°56'E; 52 m; 19 Jul 1969. NMNZ P.006071; 2(185–243); N. Auckland off N. Kaipara, 36°21'S, 173°56'E; 52 m; 19 Jul 1969. USNM 177043; (152.5); Auckland and vicinity; 04 Jan–01 Feb 1953. NMNZ P.033889; (188); Waikato off Raglan, 37°39.86'S, 174°36.5750'E; 50–52 m; 26 Oct 1996. NMNZ P.033890; (212); Waikato off Raglan, 37°39.86'S, 174°36.5750'E; 50–52 m; 26 Oct 1996. NMNZ P.006066; 3(101.7–166); Waikato off Raglan Head, 37°40'S, 174°38'E; 52 m; 16 Jul 1969. NMNZ P.006001; (182); Gisborne, Tokomaru Bay, 38°08'S, 178°20'E; 274 m; 16 Oct 1969. NMNZ P.006072; 4(119.7–155); Waikato, SW off Albatross Point, 38°11'S, 174°38'E; 39–47 m; 23 Jul 1969. NMNZ P.022749; (111.8); Taranaki, New Plymouth Power Station Inlet, 39°03'S, 174°01'E; 1986. NMNZ P.042771; 7(79.4–194); Hawke Bay SW of Mohaka River mouth, 39°10'S, 177°09'E; 9 m; 15 Apr 1970. NMNZ P.047961; 19(32.7–108.7); Wellington, Cameron Bay S. of Makara and W of Ohau Bay, 41°14.540'S, 174°39.947'E; 28 Jan 1996. NMNZ P.032937; (277); Wellington, Island Bay, 41°20'S, 174°47'E; 1–3 m; 12 Dec 1995. BMNH 1970.12.15.19–20; 2(66.4–75.0); Lyall Bay, Wellington, 41°20'S, 174°48'E; 2 m; 10 Mar 1970. **South Island.** NMNZ P.033552; (310); Nelson, Taupo Point, Abel Tasman, 40°47'S, 172°57'E; 1–5 m; 13 Dec 1993. USNM 410298; 2(74.8–131.2); off Waimangaroa N. of Westport, 41°38.42'S, 171°42.12'E; 28 m. NMNZ P.006116; 2(344–367); Westland off Cape Foulwind, 41°39'S, 171°35.5'E; 40 m; 20 Sep 1969. NMNZ P.042772; 6(225–286); Westland off Cape Foulwind, 41°39'S, 171°35.5'E; 40 m; 20 Sep 1969. NMNZ P.005150; 3(104.8–132.5); Westland off Westport, 41°43'S, 171°34'E; 12–20 m; 18 Dec 1969. NMNZ P.045189; (305); Canterbury, Inner Pegasus Bay N. of Woodend Beach, 43°18.89'S, 172°44.165'E; 13–15 m; 08 May 2007. NMNZ P.044380; 11(148–218); Canterbury, Pigeon Bay, Banks Peninsula, 43°41'S, 172°53'E; 18 m; 02 Sep 1969. NMNZ P.058689; 2(42.2–44.0); Canterbury, Pigeon Bay, Banks Peninsula, 43°41'S, 172°53'E; 18 m; 02 Sep 1969. NMNZ P.005423; (138.4); Canterbury off Akaroa, 43°50'S, 172°56'E; 30 Jun 1965. NMNZ P.061018; (242); south of Timaru, South Canterbury, 44°28.3'S, 171°16.633'E; 17 m; 22 May 2018. NMNZ P.061019; (138.6); south of Timaru, South Canterbury, 44°28.3'S, 171°16.633'E; 17 m; 22 May 2018. NMNZ P.061020; (165); south of Timaru, South Canterbury, 44°28.3'S, 171°16.633'E; 17 m; 22 May 2018. NMNZ P.061023; (182); south of Timaru, South Canterbury, 44°28.3'S, 171°16.633'E; 17 m; 22 May 2018. NMNZ P.061024; (166); south of Timaru, South Canterbury, 44°28.3'S, 171°16.633'E; 17 m; 22 May 2018. NMNZ P.061025; (216); south of Timaru, South Canterbury, 44°28.3'S, 171°16.633'E; 17 m; 22 May 2018. NMNZ P.061015; (175); south of Timaru, South Canterbury, 44°28.3'S, 171°16.633'E; 17 m; 22 May 2018. NMNZ P.061010; (172); off Wainono Lagoon, South Canterbury, 44°43'S, 171°18.217'E; 27.5 m; 22 May 2018. NMNZ P.061011; (171); off Wainono Lagoon, South Canterbury, 44°43'S, 171°18.217'E; 27.5 m; 22 May 2018. NMNZ P.061012; (193); off Wainono Lagoon, South Canterbury, 44°43'S, 171°18.217'E; 27.5 m; 22 May 2018. NMNZ P.061013; (184); off Wainono Lagoon, South Canterbury, 44°43'S, 171°18.217'E; 27.5 m; 22 May 2018. NMNZ P.061014; (174); off Wainono Lagoon, South Canterbury, 44°43'S, 171°18.217'E; 27.5 m; 22 May 2018. NMNZ P.061016; (176); off Wainono Lagoon, South Canterbury, 44°43'S, 171°18.217'E; 27.5 m; 22 May 2018. NMNZ P.005989; 2(342–395); Otago, Blueskin Bay, Otago Peninsula, 45°43'S, 170°40'E; 18 m; 16 Dec 1969. NMNZ P.005990; 7(205–257); Otago, Blueskin Bay, 45°43'S, 170°40'E; 18 m; 31 Oct 1969. NMNZ P.025035; (331); Otago, Blueskin Bay, Otago Peninsula, 45°43.28'S, 170°40.33'E; 20–22 m; 09 May 1990. NMNZ P.025183; (196); Otago, Blueskin Bay, Otago Peninsula, 45°43.28'S, 170°40.33'E; 20–22 m; 09 May 1990. NMNZ P.025161; 2(48.4–62.7); Otago, Long Beach, Otago Peninsula, 45°45.18'S, 170°38.93'E; 2–5 m; 11 May 1990. **Partial meristic data taken only, 75 specimens (24.0–261). North Island.** NMNZ P.004299; 4(102–173); N. Auckland, Waipu River, 36°00'S, 174°29'E; 18 Oct 1969. NMNZ P.006015; 3(87–94); N. Auckland N. of Kaipara, 36°10'S, 173°55'E; 3–18 m; Jul 1969. NMNZ P.044473; (91); N.

Auckland, "The Gap" S. end of Piha Beach, 36°57.655'S, 174°27.7417'E; 0–2 m; 11 Apr 2008. NMNZ P.028124; (101); Gisborne, Onepoto Bay, Hicks Bay, East Cape, 37°35.250'S, 178°18'E; 0–3 m; 04 May 1992. NMNZ P.018151; 3(24–62); Taranaki, Mangati Reef, New Plymouth, 39°01'S, 174°9'E; 0–1 m; 24 Jan 1986. NMNZ P.005148; (157); Hawke Bay SW of Mohaka River mouth, 39°10'S, 177°09'E; 9 m; 15 Apr 1970. NMNZ P.042768; 3(106–164); Hawke Bay off Napier, 39°24'S, 176°54'E; 9 m; 16 Apr 1970. NMNZ P.005422; 2(160–187); Hawke Bay, Napier Beach, 39°29'S, 176°55'E; 04 Dec 1964. NMNZ P.005995; (180); Hawke Bay N. of Cape Kidnappers, 39°34'S, 177°06'E; 31 m; Oct 1969. **South Island.** NMNZ P.049685; (196); Nelson NE of Ruataniwha Inlet, Golden Bay, 40°38.35'S, 172°49.47'E; 27 m; 29 Mar 2011. NMNZ P.049686; (218); Nelson NE of Ruataniwha Inlet, Golden Bay, 40°38.35'S, 172°49.47'E; 27 m; 29 Mar 2011. NMNZ P.049687; (261); Nelson NE of Ruataniwha Inlet, Golden Bay, 40°38.35'S, 172°49.47'E; 27 m; 29 Mar 2011. NMNZ P.049688; (260); Nelson NE of Ruataniwha Inlet, Golden Bay, 40°38.35'S, 172°49.47'E; 27 m; 29 Mar 2011. NMNZ P.051866; (137.7); Nelson, Tasman Bay, 41°05.34.50'S, 173°13.0350'E; 30–32 m; 21 Mar 1997. NMNZ P.010706; 2(75–85); N. Otago, 41°07'S, 174°22'E; Feb 1974. NMNZ P.005984; 8 specimens; Westland off Westport, 41°43'S, 171°34'E; 12–20 m; 18 Dec 1969. NMNZ P.009450; 6(193–203); Canterbury between New Brighton and Waimakariri River, 43°27'S, 172°45'E; 16 m; 20 Apr 1970. NMNZ P.009455; 10(148–195); Canterbury between New Brighton and Waimakariri River, 43°27'S, 172°45'E; 16 m; 20 Apr 1970. NMNZ P.009457; 7(196–207); Canterbury between New Brighton and Waimakariri River, 43°27'S, 172°45'E; 16 m; 20 Apr 1970. NMNZ P.009428; 10(148–207); Canterbury 16 miles NE of Lyttelton Harbour, 43°35'S, 172°50'E; 27 m; 23 Oct 1969. NMNZ P.005424; (130); Canterbury, off Akaroa, 43°50'S, 172°56'E; 30 Jun 1965. NMNZ P.005425; (157); Canterbury, off Akaroa, 43°50'S, 172°56'E; 30 Jun 1965. AMS I.14669, I.14673 and I.14676; 5(87–110); Blueskin Bay, 45°43'30"S, 170°35'00"E; 8 m; 29 Nov 1918. NMNZ P.025161; (75.3); Otago, Long Beach, Otago Peninsula, 45°45.18'S, 170°38.93'E; 2–5 m; 11 May 1990. **Morphometric data taken only, 9 specimens (217–287). North Island.** NMNZ P.005997; 5(217–287); Hawke Bay off Mahia Peninsula, 39°34'S, 178°00'E; 15–20 m; Oct 1969. NMNZ P.001243; (266); Wellington, York Bay, Wellington Harbour, 41°16'S, 174°54'E; 05 Mar 1953. **South Island.** NMNZ P.004294; (274); Westland off Westport, 41°39'S, 171°35'E; 30 m; 20 Sep 1969. NMNZ P.005151; 2(217–233); Canterbury, Pegasus Bay, 43°27'S, 172°47'E; 17 m. **Other material examined, 466 specimens (25.0–378). North Island.** NMNZ P.006069; (340); N. Auckland SE off Hokianga Harbour, 35°49'S, 173°34'E; 46 m; 19 Jul 1969. NMNZ P.042766; 2(160–178); N. Auckland SE off Hokianga Harbour, 35°49'S, 173°34'E; 46 m; 19 Jul 1969. NMNZ P.046444; (107.1); N. Auckland, SE off Hokianga Harbour, 35°49'S, 173°34'E; 46 m; 19 Jul 1969. NMNZ P.004298; (258); N. Auckland, Waipu River, 36°00'S, 174°29'E; 18 Oct 1969. NMNZ P.006002; 1 specimen; N. Auckland, Waipu River, 36°00'S, 174°29'E; 18 Oct 1969. NMNZ P.005153; (275); N. Auckland, Hauraki Gulf, 36°53'S, 175°18'E; 31 m; 10 Jul 1969. NMNZ P.005155; (169); N. Auckland, Hauraki Gulf, 36°35'S, 174°53'E; 22 m. NMNZ P.004333; 10(122–192); S. Auckland, Upper Firth of Thames, 37°05'S, 175°25'E; 4–22 m. NMNZ P.006013; 14 specimens; S. Auckland, Upper Firth of Thames, 37°05'S, 175°25'E; 4–22 m. USNM 176806; 2(202–208); Auckland and vicinity; 06 Jan–01 Feb 1953. NMNZ P.033890; 2(188–216); Waikato off Raglan, 37°39.86'S, 174°36.575'E; 50–52 m; 26 Oct 1996. NMNZ P.034226; (261); N. Taranaki off Oakura Beach, 39°04.967'S, 173°55.033'E; 40 m; 22 Jan 1996. NMNZ P.006000; 1 specimen; Hawke Bay, Hawke Bay, 39°05'S, 177°35'E; 22–24 m; 20 Jan 1970. NMNZ P.004297; 3(173–298); Hawke Bay, 39.05°S, 177°35'E; 22–24 m; 20 Jan 1970. NMNZ P.046446; 11(30.5–78.6); Bay of Plenty, Whangawehi, Mahia Peninsula, 39°05.55'S, 177°56.35'E; 14 m; 25 Jan 1996. NMNZ P.006117; 8(201–265); Hawke Bay SW of Mohaka River mouth, 39°10'S, 177°9'E; 9 m; 15 Apr 1970. NMNZ P.042770; 2 specimens; Hawke Bay SW of Mohaka River mouth, 39°10'S, 177°09'E; 9 m; 15 Apr 1970. NMNZ P.042767; 1 specimen; Hawke Bay off Napier, 39°24'S, 176°54'E; 9 m; 16 Apr 1970. NMNZ P.042769; 4(184–203 mm SL); Hawke Bay, off Napier, 39°24'S, 176°54'E; 9 m; 16 Apr 1970. NMNZ P.005152; 2 specimens; Hawke Bay off Napier, 39°24'S, 176°54'E; 9 m; 16 Apr 1970. NMNZ P.006118; 37(184–289); Hawke Bay off Napier, 39°24'S, 176°54'E; 9 m; 16 Apr 1970. NMNZ P.026836; (281); Hawke Bay, Reef off Hardinge Road, Napier, 39°28.65'S, 176°54'E; 3 m; 18 Dec 1990. NMNZ P.006080; 46(43–127); Hawke Bay, West shore, Napier, 39°29'S, 176°53'E. NMNZ P.046454; (60); Hawke Bay, West shore, Napier, 39°29'S, 176°53'E. NMNZ P.049582; (260); Hawke Bay off Awatoto, 39°32.928'S, 176°56.767'E; 16 Mar 2011. NMNZ P.005997; 4(201–215); Hawke Bay off Mahia Peninsula, 39°34'S, 178°00'E; 15–20 m; Oct 1969. NMNZ P.004293; 6(172–195); Hawke Bay off Mahia Peninsula, 39°34'S, 178°00'E; 15–20 m; Oct 1969. NMNZ P.006003; 17(216–290); SE Hawke Bay, 39°50'S, 177°05'E; 18–37 m; 10 Sep 1969. NMNZ P.004290; 2 specimens; SE Hawke Bay, 39°50'S, 177°50'E; 18–37 m; 10 Sep 1969. NMNZ P.046445; 8(44–83.8); Hawke Bay S. of Aramoana, 40°09.70'S, 176°50.30'E; 1–3 m; 19 Jan 1991. NMNZ P.032931; 2(60–62); Wellington, N. end of Plimmerton Beach, 41°10'S, 174°52'E; 0–1 m; 10 Dec 1995. NMNZ P.006009;

2(146–152); Wellington, Petone Beach, 41°14'S, 174°53'E; 11–13 m; 15 Dec 1969. NMNZ P.046440; (50.7); Wellington, Petone Beach, East end of wharf, 41°14'S, 174°53'E; 06 Sep 1964. NMNZ P.048085; (97); Wellington, Wellington Port, Aotea Quay, 41°15.95'S, 174°47.172'E; 23 Nov 2001. NMNZ P.037857; 1 specimen; Wellington Harbour, Petone, 41°15'S, 174°50'E; 4–11 m; 10 Feb 1970. NMNZ P.001243; (211); Wellington, York Bay, Wellington Harbour, 41°16'S, 174°54'E; 05 Mar 1953. NMNZ P.046442; (42.1); Wellington, York Bay, Wellington Harbour, 41°16'S, 174°54'E; Mar 1952. NMNZ P.00959; (171 mm TL); Wellington, Days Bay, Eastbourne, 41°17'S, 174°54'E; 19 Jan 1952. NMNZ P.005426; (94); Wellington, Days Bay, Eastbourne, Wellington, 41°17'S, 174°54'E; 23 Jun 1949. NMNZ P.005149; 3(73–95); Wellington, Lyall Bay, 41°20'S, 174°48'E; 10 Mar 1970. NMNZ P.006005; 15(64–162); Wellington, Lyall Bay, 41°20'S, 174°48'E; 10 Mar 1970. NMNZ P.048300; 16(62–140); Wellington, Lyall Bay, 41°20'S, 174°48'E; 23 Jan 1996. **South Island.** NMNZ P.049689; (335); Nelson NE of Ruataniwha Inlet, Golden Bay, 40°38.35'S, 172°49.47'E; 27 m; 29 Mar 2011. NMNZ P.048131; (44); Nelson Port, 41°15.60'S, 173°16.425'E; 17 Dec 2004. NMNZ P.053934; 3(48–54); Marlborough, Cloudy Bay, 41°26.35'S, 174°09.70'E; 27–28 m; 28 Jan 1979. NMNZ P.005154; 2 specimens; Westland off Westport, 41°39'S, 171°35'E; 30 m; 20 Sep 1969. NMNZ P.006116; 11 specimens; Westland off Cape Foulwind, 41°39'S, 171°35.50'E; 40 m; 20 Sep 1969. NMNZ P.004296; (184 mm TL); Westland off Westport, 41°43'S, 171°34'E; 12–20 m; 18 Dec 1969. BMNH 1970.12.15.18; (168); Westport, 41°43'S, 171°34'E; 12–20 m; 18 Dec 1969. NMNZ P.046447; (97.8); Marlborough, Second Gate Reef, Cape Campbell, 41°43.55'S, 174°16.35'E; 0–3 m; 15 Nov 1993. NMNZ P.045190; (293); Canterbury, Inner Pegasus Bay N. of Woodend Beach, 43°18.890'S, 172°44.1650'E; 13–15 m; 08 May 2007. NMNZ P.005151; (143); Canterbury, Pegasus Bay, 43°27'S, 172°47'E; 17 m. NMNZ P.009450; 6(193–203); Canterbury between New Brighton and Waimakariri River, 43°27'S, 172°45'E; 16 m; 20 Apr 1970. NMNZ P.009451; 10(165–195); Canterbury between New Brighton and Waimakariri River, 43°27'S, 172°45'E; 16 m; 20 Apr 1970. NMNZ P.009452; 7(185–202); Canterbury between New Brighton and Waimakariri River, 43°27'S, 172°45'E; 16 m; 20 Apr 1970. NMNZ P.009453; 9(172–200); Canterbury between New Brighton and Waimakariri River, 43°27'S, 172°45'E; 16 m; 20 Apr 1970. NMNZ P.009456; 6(158–183); Canterbury between New Brighton and Waimakariri River, 43°27'S, 172°45'E; 16 m; 20 Apr 1970. NMNZ P.009458; 9(168–190); Canterbury between New Brighton and Waimakariri River, 43°27'S, 172°45'E; 16 m; 20 Apr 1970. NMNZ P.009459; 7(187–203); Canterbury between New Brighton and Waimakariri River, 43°27'S, 172°45'E; 16 m; 20 Apr 1970. NMNZ P.009460; 10(132–199); Canterbury between New Brighton and Waimakariri River, 43°27'S, 172°45'E; 16 m; 20 Apr 1970. NMNZ P.005993; 45(212–242); Canterbury between New Brighton and Waimakariri River, 43°27'S, 172°45'E; 16 m; 20 Apr 1970. NMNZ P.009429; (300); Canterbury 16 miles NE of Lyttelton Harbour, 43°35'S, 172°50'E; 27 m; 23 Oct 1969. NMNZ P.006019; 39(203–305); Canterbury, 16 miles NE of Lyttelton Harbour, 43°35'S, 172°50'E; 27 m; 23 Oct 1969. NMNZ P.009427; 10(155–207); Canterbury, 16 miles NE of Lyttelton Harbour, 43°35'S, 172°50'E; 27 m; 23 Oct 1969. NMNZ P.044380; (218); Canterbury, Pigeon Bay, Banks Peninsula, 43°41'S, 172°53'E; 18 m; 02 Sep 1969. NMNZ P.006018; 2(122–207); Canterbury, Pigeon Bay, Banks Peninsula, 43°41'S, 172°53'E; 18 m; 02 Sep 1969. NMNZ P.044381; 16(134–190); Canterbury, Pigeon Bay, Banks Peninsula, 43°41'S, 172°53'E; 18 m; 02 Sep 1969. USNM 320592; 3(217–241); off Dunedin; 35 m; 1990. NMNZ P.004295; 4(219–241); Otago, Blueskin Bay/Otago Peninsula, 45°43'S, 170°40'E; 18 m; 16 Dec 1969. NMNZ P.005989; 5 specimens; Otago, Blueskin Bay/Otago Peninsula, 45°43'S, 170°40'E; 18 m; 16 Dec 1969. NMNZ P.005990; 3(147–203); Otago, Blueskin Bay, 45°43'S, 170°40'E; 18 m; 31 Oct 1969. NMNZ P.028778; (268); Otago, 11 miles N. of Tairoa Head and 5–13 miles off Karitane/Blueskin Bay, 45°43'S, 170°45'E; 18–35 m; 29 Oct 1990. NMNZ P.025035; 6(110–378); Otago, Blueskin Bay, Otago Peninsula, 45°43.28'S, 170°40.33'E; 20–22 m; 09 May 1990. AMS I.14678; (152); Cape Saunders, 45°52'S, 170°45'E; 27 m; 16 Dec 1918. NMNZ P.046427; (227); Southland between Waikawa Harbour and Chaslands Mistake, Caitlins, 46°40.55'S, 169°14.50'E; 40 m; 19 Mar 2010. NMNZ P.046430; (249); Southland between Waikawa Harbour and Chaslands Mistake, Caitlins, 46°40.55'S, 169°14.50'E; 40 m; 19 Mar 2010. NMNZ P.046431; (236); Southland between Waikawa Harbour and Chaslands Mistake, Caitlins, 46°40.55'S, 169°14.50'E; 40 m; 19 Mar 2010. NMNZ P.046432; (253); Southland between Waikawa Harbour and Chaslands Mistake, Caitlins, 46°40.55'S, 169°14.50'E; 40 m; 19 Mar 2010. **No Data.** NMNZ P.035218; (25); New Zealand.

***Peltorhamphus tenuis*, 167 specimens (25.0–161.0). Meristic and morphometric data taken, 78 specimens (56.0–157.5). Holotype:** NMNZ P.005138; (155.3); Westland, off Westport, 41°43'S, 171°34.00'E; 12–20 m; 18 Dec 1969. **Paratypes. North Island.** NMNZ P.005140; 2(122.3–128.8); Hawke Bay, off Napier, 39°24'S, 176°54'E; 9 m; 16 Apr 1970. BMNH 1970.12.15.15; (131.3); Hawke Bay, 39°24'S, 176°54'E; 9 m; 16 Apr 1970. **Paratypes. South Island.** NMNZ P.005141; 2(83.9–132.0); Westland, off Westport, 41°43'S, 171°34'E; 12–20 m;



18 Dec 1969. BMNH 1970.12.15.12-14; 3(75.5–156.7); Westland, off Westport, 41°43'S, 171°34.00'E; 12–20 m; 18 Dec 1969. NMNZ P.005142; 3(107.5–130.1); Canterbury, Pegasus Bay, 43°27'S, 172°47'E; 17 m; 20 Apr 1970. BMNH 1970.12.15.10-11; 2(99.9–130.7); Canterbury, Pegasus Bay, 43°27'S, 172°47'E; 17 m; 20 Apr 1970. **Non-type specimens. North Island.** NMNZ P.006016; (93.8); Waikato, SW off Albatross Point, 38°11'S, 174°38'E; 39–47 m; 23 Jul 1969. NMNZ P.005986; 3(126.8–141.8); Hawke Bay, off Napier, 39°24'S, 176°54'E; 9 m; 6 Apr 1970. NMNZ P.005421; 2(122.0–124.9); Hawke Bay, Napier Beach, 39°29'S, 176°55'E; 04 Dec 1964. NMNZ P.006081; 10(56.0–85.7); Hawke Bay, west shore, Napier, 39°29'S, 176°53'E. NMNZ P.005999; (123.5); Hawke Bay, off Mahia Peninsula, 39°34'S, 178°00'E; 15–20 m; Oct 1969. **South Island.** USNM 406765; 10(56.2–148.5); off Waimangaroa, N. of Westport, 41°38.70'S, 171°42.20'E; 28 m. NMNZ P.005985; 5(71.3–157.5); Westland, off Westport, 41°43'S, 171°34'E; 12–20 m; 18 Dec 1969. NMNZ P.044383; 5(72.0–155.3); Westland, off Westport, 41°43'S, 171°34'E; 12–20 m; 18 Dec 1969. NMNZ P.005994; 9(86.1–142.7); Canterbury, between New Brighton and Waimakariri River, 43°27'S, 172°45'E; 16 m; 20 Apr 1970. NMNZ P.006020; (147.1); Canterbury, 16 miles NE of Lyttelton Harbour, 43°35'S, 172°50'E; 27 m; 23 Oct 1969. NMNZ P.005316; 2(61.5–68.9); Westland, NW off Haast Beach, 43°49'S, 168°59'E; 33 m; 22 Nov 1970. NMNZ P.010633; (122.5); Otago, Oamaru Harbour, 45°06.35'S, 170°58.75'E; Jan 1965. AMS I.14677; (157); off Otago Heads, 45°45'S, 170°43'E; 27 m; 3 Dec 1918. NMNZ P.005991; 8(97.6–140.0); Otago, Blueskin Bay, 45°43'S, 170°40'E; 18 m; 31 Oct 1969. AMS I.27049–001; 5(70.5–82.1); Otago, Blueskin Bay; 8 m; 29 Nov 1918. **Meristic data taken only (including specimens with partial meristics), 60 specimens (25.0–157). North Island.** NMNZ P.006081; 2(55–90); Hawke Bay, west shore, Napier, 39°29'S, 176°53'E. **South Island.** NMNZ P.005985; 15(25.0–150); Westland, off Westport, 41°43'S, 171°34'E; 12–20 m; 18 Dec 1969. NMNZ P.044383; 14(56.0–81.7); Westland, off Westport, 41°43'S, 171°34'E; 12–20 m; 18 Dec 1969. NMNZ P.005994; 7(121.4–129.1); Canterbury, between New Brighton and Waimakariri River, 43°27'S, 172°45'E; 16 m; 20 Apr 1970. NMNZ P.006017; 9(113.5–157); Canterbury, Pigeon Bay, Banks Peninsula, 43°41'S, 172°53'E; 18 m; 02 Sep 1969. NMNZ P.061007; (114.3); S. of Timaru, South Canterbury, 44°28.3'S, 171°16.633'E; 17 m; 22 May 2018. NMNZ P.061008; (117.4); S. of Timaru, South Canterbury, 44°28.3'S, 171°16.633'E; 17 m; 22 May 2018. NMNZ P.061021; (111.8); S. of Timaru, South Canterbury, 44°28.3'S, 171°16.633'E; 17 m; 22 May 2018. NMNZ P.061022; (112.8); S. of Timaru, South Canterbury, 44°28.3'S, 171°16.633'E; 17 m; 22 May 2018. NMNZ P.005991; 4(129.9–143.3); Otago, Blueskin Bay, 45°43'S, 170°40'E; 18 m; 31 Oct 1969. AMS I.27049–001; 5(88.2–132.9); Otago, Blueskin Bay; 8 m; 29 Nov 1918. **Other material examined, 29 specimens (28.0–161). South Island.** USNM 406765; (28.0); off Waimangaroa, N. of Westport, 41°38.70'S, 171°42.20'E; 28 m. AMS I.27049–001; 12(76.0–81.8); Otago, Blueskin Bay; 8 m; 29 Nov 1918. AMS I.14666; AMS I.14667–68; AMS I.14670; I.14671–72; AMS I.14674–75; 16(67.0–161); Otago, Blueskin Bay, ca. 45°72'S, 170°59'E; 8 m; 29 Nov 1918.

***Peltorhamphus latus*, 942 specimens (12.0–144.0). Meristic and morphometric data taken, 67 specimens (44.6–133.4), including 17 type and 50 non-type specimens. Holotype:** NMNZ P.005139; (104.3); N. Island; Wellington Harbour, 41°15'S, 174°52.50'E; 20 m; 10 Feb 1970. **Paratypes. North Island.** NMNZ P.005143; 2(80.9–98.6); N. Auckland, N. of Kaipara Harbour entrance, 36°10'S, 173°55'E; 3–18 m; 15 May 1970. BMNH 1970.12.15.9; (87.3); Hawke Bay, 39°10'S, 177°08'E; 9 m; 15 Apr 1970. NMNZ P.005144; (108.0); Hawke Bay, E. off Tongio Bluff, 39°21'S, 177°11'E; 55 m; 15 Apr 1970. **Paratypes. South Island.** NMNZ P.005146; 3(79.6–111.9); Nelson, Tasman Bay, 41°00'S, 173°07'E; 25 m; 11 Jun 1970. BMNH 1970.12.15.3-5; 3(99.1–116.9); Nelson, Tasman Bay, 41°00'S, 173°07'E; 25 m; 11 Jun 1970. NMNZ P.005145; 4(44.6–112.6); Wellington Harbour, 41°15'S, 174°52.50'E; 20 m; 10 Feb 1970. BMNH 1970.12.15.7-8; 2(47.7–60.2); Wellington Harbour, 41°15'S, 174°52.50'E; 20 m; 10 Feb 1970. **Non-type specimens:** Erroneously listed for **Norfolk Island.** BMNH 1848.3.18.216; (paralectotype of *P. novaezeelandiae*; 122.6); locality not specified but likely New Zealand. BMNH 1845.3.18.131-135; 5(paralectotypes of *P. novaezeelandiae*; 67.1–77.1); New Zealand, locality not specified. BMNH 1853.2.14.21; (paralectotype of *P. novaezeelandiae*; 118.1); New Zealand, locality not specified. BMNH 1855.9.19.1236-1238; 3(paralectotypes of *P. novaezeelandiae*; 60.1–72.0); New Zealand, locality not specified. BMNH 1873.12.13.75 (113.9); New Zealand, locality not specified. **North Island.** NMNZ P.046004; (127.5); N. Auckland, 'Dab Patch', Hauraki Gulf, 36°40'S, 175°00'E; 04 Nov 1964. NMNZ P.005998; 5(87.7–129.9); Hawke Bay, off Mahia Peninsula, 39°34'S, 178°00'E; 15–20 m; Oct 1969. USNM 304935; 11(72.0–133.4); Wellington Harbour; 1987-1988. NMNZ P.046003; 11(66.3–108.6); Wellington, Petone Beach, 41°14'S, 174°53'E; 11–13 m; 15 Dec 1969. NMNZ P.005406; 4(86.8–132.1); Wellington, Shelly Bay, 41°18'S, 174°49'E; 16 m; 07 Sep 1964. NMNZ P.005416; (103.8);

Wellington, Eastbourne, N. of wharf, 41°17'S, 174°53'E; 12–16 m; 26 Feb 1964. **South Island.** NMNZ P.034100; 4(108.0–128.8); Nelson, Tasman Bay, 41°05.345'S, 173°13.035'E; 30–32 m; 21 Mar 1997. NMNZ P.046008; (97.5); Otago, Blueskin Bay, 45°43'S, 170°40'E; 18 m; 31 Oct 1969. NMNZ P.046428; (119.4); Southland, between Waikawa Harbour and Chaslans Mistake, Caitlins, 46°40.55'S, 169°14.50'E; 40 m; 19 Mar 2010. **Meristic data taken only, 148 specimens (12.0–138.0).** **North Island.** NMNZ P.002300; 2(35); N. Auckland, Bay of Islands, 35°15'S, 174°09'E; Jan 1957. NMNZ P.006122; 11(25–82); N. Auckland, Orokawa Bay, Bay of Islands, 35°15.40'S, 174°12.20'E; 3–7 m; 27 Nov 1971. NMNZ P.041941; 2(129); N. Auckland, Omaha Bay, 36°18.40'S, 174°48.37'E; 11 m; 13 Nov 1995. NMNZ P.003451; 4(33.8–52.7); N. Auckland, Whangateau Harbour, Leigh, 36°19'S, 174°46'E; 0–1 m; 23 Nov 1963. NMNZ P.003460; (63); N. Auckland, Whangateau Harbour, Leigh, 36°19'S, 174°46'E; 0–1 m; 23 Nov 1963. NMNZ P.046004; 9(64–130); N. Auckland, 'Dab Patch', Hauraki Gulf, 36°40'S, 175°00'E; 04 Nov 1964. NMNZ P.005397; 15(72.3–128.4); N. Auckland, 'Dab Patch', Hauraki Gulf, 36°40'S, 175°00'E; 04 Nov 1964. NMNZ P.005398; 13(104–140); N. Auckland, 'Dab Patch', Hauraki Gulf, 36°40'S, 175°00'E; 04 Nov 1964. NMNZ P.036755; 17(29.5–56.6); S. Auckland, Hook Point opposite Tern Island, Ohiwa Harbour, 37°50'S, 177°09.60'E; 0–1 m; 27 Apr 1999. NMNZ P.005987; 7(80–96); Hawke Bay, SW of Mohaka River mouth, 39°10'S, 177°09'E; 9 m; 15 Apr 1970. NMNZ P.005988; (121.5); Hawke Bay, E. off Tongio Bluff, 39°21'S, 177°11'E; 55 m; 15 Apr 1970. NMNZ P.026330; (25); Hawke Bay, Pauanui Point Reef, 40°04.70'S, 176°54.50'E; 0–3 m; 18 Jan 1991. NMNZ P.005417; 3(81.2–86.1); Wellington, Pauatahanui Inlet, 41°06'S, 174°54'E; 16 May 1962. NMNZ P.005411; (65.3); Wellington, Pauatahanui Inlet, 41°06'S, 174°54'E; 11 Apr 1962. NMNZ P.006010; 14(66.8–139.8); Wellington, Petone Beach, 41°14'S, 174°53'E; 11–13 m; 29 Aug 1969. NMNZ P.005415; 12(55.5–137.9); Wellington, Petone, 41°14'S, 174°53'E. NMNZ P.046003; 11(12–50); Wellington, Petone Beach, 41°14'S, 174°53'E; 11–13 m; 15 Dec 1969. NMNZ P.005402; 12(65.3–112.5); Wellington, between Petone and Somes Island; 41°14.55'S, 174°52'E; 16 m; 09 Dec 1964. NMNZ P.005409; 2(61–63); Wellington, Lowry Bay, 41°15'S, 174°55'E; 16 Apr 1962. NMNZ P.005416; (87.5); Wellington, Eastbourne, N. of wharf, 41°17'S, 174°53'E; 12–16 m; 26 Feb 1964. NMNZ P.005410; 2(52–73); Wellington, Kau Bay, 41°17'S, 174°49'E; 12 Nov 1964. NMNZ P.005414; (56); Wellington, Scorching Bay, 41°18'S, 174°50'E; 11 Apr 1962. **South Island.** NMNZ P.005329; 3(72.1–114.0); Marlborough, Golden Bay, 40°40'S, 172°45'E; 01 Jun 1966. NMNZ P.046449; 2(24.9–25.8); Canterbury, Pigeon Bay, Banks Peninsula, 43°41'S, 172°53'E; 18 m; 02 Sep 1969. **Stewart Island.** NMNZ P.007315; (42.7); N. side of Native Island; Paterson Inlet, 46°55'S, 168°09'E; 20–25 m; 06 Feb 1977. **Morphometric data taken only, 1. Paratype.** BMNH 1970.12.15.6; (96.4); Wellington Harbour, 41°15'S, 174°52.50'E; 20 m; 10 Feb 1970. **Other specimens examined, 726 (12.0–144.0).** **North Island.** NMNZ P.048368; (36.2); Hokianga Harbour (35°28.992'S, 173°22.948'E); 1 m; 15 Feb 2011. NMNZ P.041941; (129); N. Auckland, Omaha Bay, 36°18.40'S, 174°48.37'E; 11 m; 13 Nov 1995. NMNZ P.021944; 20(40–78); N. Auckland, Hauraki Gulf, 36°38'S, 175°04'E; 1981. NMNZ P.021954; 13(38–119); N. Auckland, Hauraki Gulf, 36°38'S, 175°04'E; 1981. NMNZ P.005396; 6(97.5–119.3); N. Auckland, 'Dab Patch', Hauraki Gulf, 36°40'S, 175°00'E; 04 Nov 1964. NMNZ P.005400; 50(33–118); N. Auckland, 'Dab Patch', Hauraki Gulf, 36°40'S, 175°00'E; 04 Nov 1964. NMNZ P.005420; 26(60–113); N. Auckland, 'Dab Patch', Hauraki Gulf, 36°40'S, 175°00'E; 33–37 m; 04 Nov 1964. NMNZ P.046004; 24(38.1–127.5); N. Auckland, 'Dab Patch', Hauraki Gulf, 36°40'S, 175°00'E; 04 Nov 1964. NMNZ P.005399; 50(64–130); N. Auckland; 'Dab Patch', Hauraki Gulf, 36°40'S, 175°00'E; 04 Nov 1964. BMNH 1935.3.14.217-226; 21(25.3–82.7); Hauraki Gulf. NMNZ P.005413; 2(75–77); S. Auckland; Firth of Thames, 37°08'S, 175°33'E; 19 Nov 1964. NMNZ P.006012; 20(79–125); S. Auckland; Upper Firth of Thames, 37°10'S, 175°25'E; 4–22 m; 02 Jul 1969. NMNZ P.005419; 18(31–77); S. Auckland, Thames River, 37°13'S, 175°30'E; 4 m; Nov 1964. NMNZ P.005996; 27(88–113); Hawke Bay, N. of Cape Kidnappers, 39°34'S, 177°06'E; 31 m; Oct 1969. NMNZ P.033632; (48.5); Bay of Plenty, Whangawehi, Mahia Peninsula, 39°05.55'S, 177°56.35'E; 14 m; 25 Jan 1996. NMNZ P.005418; (87.5); Wellington, Ration Point, Pauatahanui, 41°05.75'S, 174°54'E; 01 Mar 1964. NMNZ P.005401; 20(78–110); Wellington, Petone Beach, 41°14'S, 174°53'E; 19 May 1964. NMNZ P.005404; 17(69.8–122.3); Wellington, Petone Beach, 41°14'S, 174°53'E; 19 May 1964. NMNZ P.005405; 5(33–124); Wellington, Petone Beach, E. end of wharf, 41°14'S, 174°53'E; 06 Sep 1964. NMNZ P.005415; 12(55.5–137.9); Wellington, Petone, 41°14'S, 174°53'E. NMNZ P.006008; 40(12–50); Wellington, Petone Beach, 41°14'S, 174°53'E; 11–13 m; 15 Dec 1969. NMNZ P.006010; 11(61.6–105.5); Wellington, Petone Beach, 41°14'S, 174°53'E; 11–13 m; 29 Aug 1969. NMNZ P.046009; 44(61–144); Wellington, Petone Beach, 41°14'S, 174°53'E; 11–13 m; 29 Aug 1969. NMNZ P.046007; 34(12–50); Wellington; Petone Beach, 41°14'S, 174°53'E; 11–13 m; 15 Dec 1969. NMNZ P.005402; 8(41.2–56.9); Wellington, between Petone and Somes Island; 41°14.55'S, 174°52'E; 16 m; 09 Dec 1964. NMNZ P.005403; 6(68–113);

Wellington, off Petone, 41°15'S, 174°53'E; 03 Aug 1964. NMNZ P.006004; 128(40–124); Wellington Harbour, Petone, 41°15'S, 174°50'E; 4–11 m; 10 Feb 1970. NMNZ P.006011; 2(81–103); Wellington, Lowry Bay, 41°15'S, 174°55'E; 2 m; 28 Jul 1969. NMNZ P.044382; 2(104.8–111.9); Wellington, off Petone, 41°15'S, 174°53'E; 03 Aug 1964. NMNZ P.046005; (126); Wellington; Wellington Harbour, Petone, 41°15'S, 174°50'E; 4–11 m; 10 Feb 1970. NMNZ P.046100; (45); Wellington; Wellington Harbour, Petone, 41°15'S, 174°50'E; 4–11 m; 10 Feb 1970. NMNZ P.001099; 5(40–114); Wellington Harbour, York Bay, 41°16'S, 174°54'E; Mar 1952. NMNZ P.005394; 22(43–128); Wellington Harbour, off Days Bay Wharf, 41°17'S, 174°54'E; 26 Feb 1964. NMNZ P.005407; 6(44–112); Wellington, Shelly Bay, 41°18'S, 174°49'E; 12 Nov 1964. NMNZ P.005408; (82); Wellington, Shelly Bay, 41°18'S, 174°49'E; 04 May 1964. NMNZ P.006006; 3(62–92); Wellington, Lyall Bay, 41°20'S, 174°48'E; 0–1 m; 10 Mar 1970. NMNZ P.006007; (42); Wellington; Lyall Bay, 41°20'S, 174°48'E; 27 Oct 1970. **South Island.** NMNZ P.025291; (25); Nelson, Puponga, 40°32'S, 172°44'E; 12 Mar 1971. NMNZ P.006014; 28(93–120); Nelson, Tasman Bay, 41°00'S, 173°07'E; 25 m; 11 Jun 1970. NMNZ P.045551; 27(93–120); Nelson, Tasman Bay, 41°00'S, 173°07'E; 25 m; 11 Jun 1970. NMNZ P.005328; 6(24–53); Marlborough Sounds, Croiselles Harbour, 41°04'S, 173°41'E; 28 May 1966. NMNZ P.005395; 6(90–93); Nelson, Tasman Bay, 41°16'S, 173°13'E; Jul 1963. NMNZ P.030862; 3(17.0–19.6); Marlborough, Second Gate Reef, Cape Campbell, 41°43.55'S, 174°16.35'E; 0–3 m; 15 Nov 1993. BMNH 1876.2.12.21; 1 specimen; south side of Cook Strait. NMNZ P.061009; (101); S. of Timaru, South Canterbury, 44°28.300'S, 171°16.633'E; 17 m; 22 May 2018.

***Peltorhamphus kryptostomus*, 119 specimens (33.2–145.1). South Island.** Meristic and morphometric data taken, 31 (including 11 type specimens whose detailed collection information is listed above in species account) (33.2–145.1 mm SL). **Non-types:** NMNZ P.005147; (paratype of *P. latus*; 136.2); Otago, Blueskin Bay, 45°43'S, 170°40'E; 20 m; 31 Oct 1969. NMNZ P.046450; 10(82.7–135.2); Otago, Blueskin Bay, 45°43'S, 170°40'E; 18 m; 31 Oct 1969. NMNZ P.046452; 6(130.3–144.6); Otago, Blueskin Bay, 45°43'S, 170°40'E; 18 m; 31 Oct 1969. BMNH 1970.12.15.2; (paratype of *P. latus*; 145.1); Blueskin Bay, 45°43'S, 170°40'E; 20 m; 31 Oct 1969. NMNZ P.044384; (108.2); Otago, Blueskin Bay, Otago Peninsula, 45°43.28'S, 170°40.33'E; 20–22 m; 09 May 1990. NMNZ P.046438; (52.9); Otago Harbour, Aramoana Flats, 45°47.25'S, 170°41'E; 05 Feb 2010. **Meristic data taken only, 44 specimens (68.5–142).** NMNZ P.005992; 11(82.7–131.1); Otago, Blueskin Bay, 45°43'S, 170°40'E; 18 m; 31 Oct 1969. NMNZ P.046450; 15(68.5–136.2); Otago, Blueskin Bay, 45°43'S, 170°40'E; 18 m; 31 Oct 1969. NMNZ P.046452; 18(76.7–142); Otago, Blueskin Bay, 45°43'S, 170°40'E; 18 m; 31 Oct 1969. **Morphometric data taken only, 3 specimens (98.0–110.9).** NMNZ P.046451; 3(98.0–110.9); Otago, Blueskin Bay, 45°43'S, 170°40'E; 18 m; 31 Oct 1969. **Other Material examined, 41 specimens (56.6–131.1).** NMNZ P.005992; 23(82.7–131.1); Otago, Blueskin Bay, 45°43'S, 170°40'E; 18 m; 31 Oct 1969. NMNZ P.046451; 17(79.1–110.9); Otago, Blueskin Bay, 45°43'S, 170°40'E; 18 m; 31 Oct 1969. NMNZ P.046437; (56.6); Otago Harbour, Aramoana Flats, 45°47.25'S, 170°41'E; 1–2 m; 05 Feb 2010.

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**APPENDIX 1. Biological, ecological and fisheries references for *Peltorhamphus novaezeelandiae*, with annotated comments. Complete references listed in Literature cited section.**

- Hector 1872:117 (comments on qualities as food fish; line drawing).
- Hutton 1873:241 (belongs to group of New Zealand fishes with Pacific Island affinities).
- Hutton 1874:86 (belongs to group of New Zealand fishes with Pacific Island affinities).
- Thomson 1877:485 (seasonal landings in Otago region; comments on fishery practices for flounders and soles).
- Thomson 1878:326 (appearance in fish markets, Dunedin).
- Thomson 1879:382 (seasonal landings in Otago region; comments on fishery practices for flounders and soles).
- Sherrin 1886:22, 304 (some biological notes; occurrence in New Zealand markets).
- Thomson 1892:204, 213 (occurrence, Catlin's River and Waipapapa Point, New Zealand; diet includes crustaceans; weight to 2 pounds).
- Thomson 1906:551 (in part; may include more than one species; occurrence, Otago Harbour, South Island, New Zealand).
- Anderton 1907:481 (in part; may include more than one species; large numbers trawled in Blueskin Bay in 5–6 fathoms in June–July; diet includes cumaceans; females migrate to deeper water (13–18 fathoms) in late July; females ripe in August; description of eggs, larvae and juveniles; illustration of larva).
- Waite 1911:213 (New Zealand, including Chatham Islands; to about 415 mm TL; 9–50 fathoms).
- Thomson 1913:233 (abundant, east coast of New Zealand; spawning in laboratory; egg size and description).
- Prince 1916:125 (highly esteemed food fish).
- Phillipps 1921:122 (listed among edible fishes of New Zealand; seasonal appearance in Wellington markets; brief comments on spawning season and distribution).
- Thomson & Anderton 1921:88 (in part; may include more than one species; batch spawner; description of eggs, larvae and juveniles; diets include crabs, shrimp, amphipods, galatheid crabs, brittle starfish, small molluscs, polychaetes; Otago Harbour, South Island, New Zealand).
- Phillipps & Hodgkinson 1922:96 (included, edible fishes of New Zealand; small numbers in Auckland markets in summer; large quantities in March off Hokitika).
- Rendahl 1925:4 (four specimens; Napier Harbour, North Island, New Zealand).
- Graham 1938:408 (in part; may include more than one species; abundant; mostly outside Otago Harbour, South Island, New Zealand; maximum total length 30 inches).
- Graham 1939:365 (in part; may include more than one species; notes on size at maturity; mature adults absent, but juveniles common year-round in Otago Harbour).
- Phillipps 1948:129 (in part; may include more than one species; taken in small numbers, Rona Bay, Wellington Harbour, North Island, New Zealand).
- Graham 1953:206 (in part; may include more than one species; life-history summary; relative abundance and commercial importance off Otago, South Island, New Zealand; feeding behavior, diet; predators).
- Graham 1956:206 (in part; may include more than one species; life-history summary; relative abundance and commercial importance off Otago, South Island, New Zealand; feeding behavior, diet; predators).
- Parrott 1960:115 (common in New Zealand waters; diet; spawning; common names; size; inhabits sand substrata).
- Doogue & Moreland 1961:218 (in part; may include more than one species; distribution North and South islands, New Zealand; common names; food qualities).
- Doogue & Moreland 1964:218 (in part; may include more than one species; distribution North and South islands, New Zealand; common names; food qualities).
- Moreland 1963:22 (illustration; ecological notes; shallow-water species to 40 fathoms; diet; size).
- Graham 1963:168 (common, desirable commercial species on North Otago shelf).
- Ralph & Yaldwyn 1965:82 (uncommon in Otago Harbour).
- Powell 1966:242 (size; edibility).
- Heath & Moreland 1967:32 (inshore to 100 feet; geographic distribution; diet; common names).
- Tong & Elder 1968:65 (relative abundance, <10% of 141 trawls in Bay of Plenty, North Island, New Zealand).
- Manikiam 1969:126 (in part, includes more than one species; common names; size; distribution around New Zealand including Chatham Islands; food qualities; brief comment on commercial importance).
- Webb 1972:580 (in part; may include more than one species; occurrence in deeper parts of Avon–Heathcote estuary, east coast of South Island; abundance, distribution; year-class estimate).

- Hewitt & Hine 1972:92 (checklist, parasite fauna of *P. novaezeelandiae*).
- James 1972:345 (size information; depth 2–124 m, more abundant between 5–40 m; endemic throughout New Zealand waters, including Chatham Islands; individuals larger and more abundant in southern part of range).
- Webb 1973a:53 (in part; may include more than one species; egg sizes at different maturity stages; both sexes mature at end of year two and at ca. 220 mm; adults migrate out of estuary in winter for spawning on shelf; juveniles use estuary as nursery area and adults as feeding ground; Avon–Heathcote estuary, east coast, South Island).
- Webb 1973b:228 (in part; may include more than one species; feeding biology, Avon–Heathcote estuary, east coast, South Island; diets of 121 specimens included crustaceans, mollusks, polychaetes, sea anemones).
- Webb 1973c:301 (in part; may include more than one species; parasites of *P. novaezeelandiae* inhabiting Avon–Heathcote estuary, east coast, South Island).
- Robertson 1973:417 (in part; may include more than one species; description of eggs, yolk-sac larvae; spawning season winter-spring (July–October); eggs difficult to distinguish from those of *P. tenuis*).
- Ryan 1974:133 (occasional visitor, Lake Ellesmere, Canterbury).
- Robertson 1975:8 (in part; may include more than one species; description of planktonic eggs; brief comment on spawning seasonality).
- Kilner & Akroyd 1978:49 (infrequently captured in low abundance, Ahuriri Estuary, Napier).
- Roper 1979:136 (in part; may include data from *Peltorhampus* n. sp. Munroe; Blueskin Bay, South Island; juvenile and adult densities, distribution; ecology; size to 500 mm; ontogenetic series of juveniles figured).
- Frentzos 1980:150 (difficult to distinguish larvae from those of *P. latus*; description of prejuvenile; photo of late larvae (12.8); meristic features of adults; Wellington Harbour).
- Healy 1980:121 (seasonal occurrence in Pauatahanui Inlet, southwest coast of North Island; juveniles common and moderately abundant mainly during warmer months on sandy bottoms and in less turbid waters of Pauatahanui Inlet; adults move into inlets with incoming tide; species apparently absent from Porirua Inlet, which has muddy bottom, more turbid waters, and higher pollution levels).
- Roper 1981:753 (description of superficial neuromasts).
- Roper & Jillett 1981:2 (larvae rare in inlets and shallow coastal waters; larvae common in coastal waters off Otago coast; juveniles and adults common in Blueskin Bay; juveniles (5–49 mm TL) not found in inlets; adults only in Blueskin Bay, not inlets).
- Crossland 1981:46 (rarely observed in Hauraki Gulf).
- Ayling & Cox 1982:312 (ecological notes; to about 100 m; maximum size ca. 450 mm TL; New Zealand, most commonly around South Island).
- Doogue & Moreland 1982:227 (distribution North and South islands; common names; ecology; food qualities).
- Paul *et al.* 1983:15 (widespread distribution in New Zealand in shallow waters  $\leq 50$  m; low abundance in trawls off west coast of North Island; not taken in Tasman Bay).
- Paulin & Stewart 1985:57 (widespread in coastal waters; depth range 0–200 m; modest commercial importance).
- Paul 1986:141 (widespread around New Zealand, more abundant in southern parts of range; inhabits broad bays, sheltered inshore waters to 100 m and sometimes deeper; growth rates; spawning seasonality; diet; commercial importance in some inshore fisheries; food fish).
- Livingston 1987a:776 (morphological specializations related to feeding; description of taste buds, free neuromasts, mouth, jaws, teeth and feeding behavior; nocturnal feeding; diet).
- Livingston 1987b: (feeding and diets of adults (150–450 mm TL) in Wellington Harbour; feeds nocturnally on benthic infauna and epifauna; diverse diets including 18 different prey types with dominant items being polychaetes, crustaceans, ophiuroids; slight seasonality in diet composition).
- Powell 1993:60 (brief colour description with black & white illustration; size to 600 mm (TL?); occurs in estuaries and in deeper water on continental shelf; esteemed food fish).
- Armitage *et al.* 1994:110 (summary of life-history information; endemic to New Zealand; caught to 100 m; most abundant and caught year-round in trawl fishery off South Island; minor commercial importance).
- Colman 1994:34 (New Zealand, more common around South Island; commercial species, especially in coastal trawl fisheries).
- Francis 1996:69 (behavioral observations on swimming, feeding, escape response; spawning seasonality).
- Dolphin 1997:142 (winter-spring spawners; brief description of eggs, early life-history stages; off east coast Southern New Zealand).
- Paulin 1996:13 (size; distribution; listed among quota management species).
- Paul & Heath 1997 (no pagination; species account 89) (ecological notes; fishery information).

Anderson *et al.* 1998:218 (in part, may include data for two other species; geographic and bathymetric distributions around New Zealand based on research trawl data).

Paulin 1998:19 (distribution; biological notes; esteemed food fish).

Parsons 1999:121 (in part, data combined with that for other species of *Peltorhamphus*; spawning seasonality and distribution of eggs, larvae; off Otago coast and Blueskin Bay).

Beentjes & Stevenson 2000:7 (off east coast of South Island; main species targeted by inshore trawl fisheries; catch rates higher in summer versus winter; shallow-water species on inner shelf; depth range 10–50 m, preferred depth 41 m).

Hurst *et al.* 2000:27 (adult and juvenile distributions; spawning seasonality; estuarine use by juveniles; juvenile abundance Auckland harbour).

Paul 2000:141 (ecological notes; fishery information).

Beentjes *et al.* 2002:206 (common and abundant species in trawl fishery; higher catch rate in summer versus winter; bathymetric distribution; member of shallow-water demersal species group inhabiting 10–50 m; preferred depth 41 m; inner continental shelf, east coast of South Island, New Zealand).

Francis *et al.* 2002:218 (member of inshore demersal fish assemblages of New Zealand; estimated preferred depth 20 m; present in nearly 3% (540 of 19232) of trawl catches).

Kendrick & Francis 2002:703 (in part; catches may have contained *P. latus*; component of fish assemblage, Hauraki Gulf; predominant occurrence on shallow, soft mud bottoms).

Beentjes 2003:4 (constitutes large proportion of total flatfish catch (16%); main fishing areas west coast of South Island, Otago, and Canterbury Bight).

Stevenson 2004:9 (low biomass in trawl survey off west coast, South Island; most fish 200–360 mm TL, fewer to 500 mm TL; length-weight relationship for fish 200–480 mm; collected between 27–49 m).

Hirt-Chabbert 2006:120 (bathymetric distribution 0–100 m on inner continental shelf; brief ecological notes).

Stevenson 2006:9 (low biomass in trawl survey off west coast, South Island; length-weight relationship for fish 200–480 mm; collected between 26–47 m; length frequency information partitioned by sex).

Banks *et al.* 2007:132 (brief notes on spawning seasonality and location; size, weight; caught year-round mainly by trawling off South Island's West Coast, also off Otago and Southland).

Francis *et al.* 2011:1333 (rarely collected in beach seine survey of fishes in New Zealand estuaries).

McMillan *et al.* 2011:277 (endemic to New Zealand, more common around South Island; to 550 mm TL; 0–100 m; demersal, including bays and estuaries).

Francis 2012:247 (behavioral observations on swimming, feeding, escape response; comments on spawning seasonality).

Beentjes & MacGibbon 2013:14 (age, growth rate, longevity; seasonal migrations; commercial catches; length at maturity; spawning seasonality; size in commercial catches; depth range; depth of capture in commercial fisheries; biomass estimate).

MacGibbon & Stevenson 2013:18 (low abundance in inshore trawl survey, West Coast of South Island, NZ; depth range 24–64 m; length-weight relationship for fishes 200–480 mm).

Mockett 2013:1 (population connectivity Otago and Southland; diet analysis using stomach contents and stable isotopes; age-growth estimates; von Bertalanffy growth models; sex ratios; morphological comparisons between populations).

Morrison *et al.* 2014a:84 (fisheries information; brief summary of life-history information).

Munroe 2015b:1696 (common names; size to 525 mm SL; biology, endemic to New Zealand, including Chatham Islands; habitat information briefly summarized).

New Zealand Ministry for Primary Industries 2017:292 (part of combined flounder catch; important fishing areas off West Coast of South Island, Otago, Southland and Canterbury Bight; historical fisheries data; landings by area; select biological parameters; length-weight formula; CPUE and stock trends).

New Zealand Seafood Industry Council 2018 (endemic to New Zealand; size in fishery catches usually 250–350 mm; reaching 400 mm; more common around South Island; occurs to 100 m; spawns in shallow water from July–September).

Anglade & Randhawa 2018:187 (parasite survey; insights into ecological role of *P. novaezeelandiae* in parasite transmission off Otago, New Zealand).

McMillan *et al.* 2019:250 (size to 550 mm TL; New Zealand endemic; widespread, more common around South Island; demersal, including shallow bays and estuaries to 100 m).

**APPENDIX 2. Biological, ecological and fisheries references for *Peltorhamphus tenuis*, with annotated comments.  
Complete references listed in Literature cited section.**

- Robertson 1973:417 (description of unfertilized eggs stripped from female; one ripe female captured in July in Otago region; eggs collected in field samples similar to, and difficult to distinguish from, those of *P. novaezeelandiae*).
- Robertson 1975:8 (description of planktonic eggs; eggs occasionally in neritic waters of South Island during winter and spring).
- Robertson 1980:50 (eggs stripped from ripe female; Otago coast; eggs cannot be differentiated from those of *P. novaezeelandiae*; field collection of eggs likely composite samples of more than one species of *Peltorhamphus*).
- Roper 1979:136 (Blueskin Bay, South Island; juvenile and adult densities, distribution; to 190 mm SL; figures of juveniles at various sizes).
- Roper & Jillett 1981:4 (68 juveniles and adults, Blueskin Bay, South Island; peak density in summer; size-depth relationship for juvenile and adult fish; smaller fishes inshore, larger fishes offshore; neither juveniles nor adults found in inlets).
- Crossland 1981:46 (not recorded from Hauraki Gulf, northeast New Zealand).
- Paul *et al.* 1983:15 (uncommon species; widespread in New Zealand waters, but with localized distribution; one specimen taken at 40 m in trawl study off west coast of North Island).
- Paul 1986:141 (less common species compared with congeners; probably winter spawner with larvae and juveniles close to shore).
- Livingston 1987b:281 (collected in Wellington Harbour).
- Cooper *et al.* 1990:152 (listed among prey items in diets of Fiordland Crested Penguin; Jackson Bay and Martins Bay, South Island, New Zealand).
- Colman 1994:34 (briefly mentioned; small size; no commercial value; common in bays and harbours).
- Dolphin 1997:197 (reference describing eggs listed in appendix).
- Anderson *et al.* 1998:219 (occurrence in research trawls conducted in New Zealand waters; infrequently captured off North vs. South Island; not at Chatham Islands; captured mostly at depths of 30 m or less).
- Paul 2000:141 (less common species compared with congeners; black & white illustration; probably winter spawner with larvae and juveniles close to shore).
- Beentjes *et al.* 2002:205 (listed, member of demersal fish species assemblage east coast South Island).
- McMillan *et al.* 2011:277 (briefly mentioned; size < 200 mm TL).
- Munroe 2015b:1697 (brief summaries of biology, distribution and habitat).

**APPENDIX 3. Biological, ecological and fisheries references for *Peltorhamphus latus*, with annotated comments.  
Complete references listed in Literature cited section.**

- Ryan 1974:133 (suspected occurrence in Lake Ellesmere when spit opens and connection to Pacific Ocean restored).
- Roper 1979:136 (in part; may include data from *Peltorhamphus n. sp.* Munroe 2015b; Blueskin Bay, South Island; juvenile and adult densities, estuarine distribution; ecology; to 180 mm TL; figures of juveniles of various sizes and adult).
- Frentzos 1980:150 (larvae difficult to distinguish from those of *P. novaezeelandiae*; description of prejuvenile; photos of late-stage larvae 8.3–11.1 mm SL; Wellington Harbour).
- Healy 1980:121 (widely distributed species resident in Pauatahanui–Porirua inlets to submaturity; fish 50–130 mm, estimated ages I–IV; occurring year-round, lower abundance in winter).
- Roper & Jillett 1981:4 (in part; may include data from *Peltorhamphus n. sp.* Munroe 2015b; spawning seasonality in Otago Harbour and Blueskin Bay, South Island; larvae common in Otago Harbour in late winter–early summer; peak settlement during summer; juveniles and adults common in Otago Harbour and Blueskin Bay; peak density of juveniles in summer; juveniles inhabit wide depth range including shallow-water inlets; juvenile abundance declined in winter; adults inhabit Blueskin Bay, not inlets).
- Crossland 1982:42 (distribution, abundance of larvae off northeast New Zealand; peak spawning in mid-spring; spawning season in northern New Zealand prolonged, at least October–February).
- Paul *et al.* 1983:15 (common in inshore waters around New Zealand; low to moderate abundance in shallow-water trawls off west coast of North Island, especially Tasman Bay, Golden Bay, outside of Kawhia Harbour and Manakau Harbour).
- Roper 1986:709 (seasonal occurrence and abundance of larvae; Whangateu Harbour, North Island).
- Colman 1994:34 (brief mention; small size; no commercial value; common in bays and harbours).

Dolphin 1997:197 (listed in appendix; summary list of references describing eggs, larvae).

Anderson *et al.* 1998: distribution map (distribution in New Zealand exclusive economic zone based on trawls conducted by research vessels; widespread off both islands; shallow-water species).

Keith 1998:95 (description of two larvae from Wellington Harbour; colour photograph of 11.0 mm TL larvae).

Parsons 1999:121 (in part; data combined with that for other species; spawning seasonality and distribution of eggs, larvae; off Otago coast and Blueskin Bay).

Kendrick & Francis 2002:703 (in part; catches may have contained *P. novaezeelandiae*; component of fish assemblage, Hauraki Gulf; predominant occurrence on shallow, soft mud bottoms).

Beentjes *et al.* 2002:205 (listed in table; member of demersal fish assemblage east coast of South Island; not captured in summer surveys).

Morrison *et al.* 2002:797 (common species on mud flat in Manukau Harbour, North Island; diurnal and tidal variation in occurrence and abundance in seine and trawl collections; captured mostly juveniles; higher abundance in night versus day collections).

Stevenson 2004:67 (rarely captured in trawl survey, West Coast of South Island; 22–27 m).

Francis *et al.* 2005:424 (common species in estuaries, northern North Island; fourth most frequently caught, and fifth most abundant species taken by beach seines).

Stevenson 2006:65 (rarely captured in trawl survey, West Coast of South Island; 20–33 m).

Taylor & Morrison 2008:209 (infrequent occurrence in scallop dredge samples on sand habitat; Omaha Bay, northeastern New Zealand).

Francis *et al.* 2011:1332 (common, abundant species in New Zealand estuaries; one of top two most frequently occurring demersal fishes; captured at 50% of 679 beach sites located in 83% of 69 New Zealand harbours on North and South islands; 5024 individuals, mostly juveniles, captured, constituting 2.4% of 223,000 fish collected).

Francis 2012:246 (sand, mud substrata; estuaries and inner continental shelf to 55 m).

Lowe 2013:24 (local distribution, abundance, habitat use, and diets; Pahurehure Inlet, Manukau Harbour, northern New Zealand; dominant member of fish assemblage inhabiting intertidal sand and mud flats, and bank and channel habitats in mid- to lower estuary).

MacGibbon & Stevenson 2013:113 (rarely captured in inshore trawl survey, West Coast South Island; 33 m).

Morrison *et al.* 2014a:85 (brief mention; very common in estuaries).

Morrison *et al.* 2014b:23 (presence, abundance in seagrass meadows and other inshore habitats on both islands; trophic ecology; ontogenetic changes in diets).

Munroe 2015b:1695 (size to 150 mm SL; females slightly larger than males; brief summaries of biology, distribution and habitat; New Zealand, Norfolk Island record erroneous).

Munroe 2016:1 (IUCN Red List Assessment; Least Concern; summary of life history and ecological information; evaluation of conservation status).