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Morphological differences in the scapula-coracoid of seawater and freshwater fish

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Abstract. Pectoral fins are important structures that generally reflect the lifestyles of fish species, owing to their involvement in fish movement, and the skeletal scaffold of pectoral fins includes both the scapula and coracoid. However, only a few studies have compared the morphology of pectoral skeletons from different species. Accordingly, the present study analyzed the scapula-coracoid morphology of 102 species of seawater and freshwater from 12 orders and 45 families. The species were collected and divided into four groups, based on their habitat: seawater benthic (group 1), seawater pelagic (group 2), freshwater benthic (group 3), and freshwater pelagic (group 4). Based on the difference between groups 1 and 2, it was clear that the coracoids of pelagic species were longer than those of benthic species, thereby indicating a morphological difference between the scapula-coracoid of fish species from different habitats. Furthermore, the three-dimensional scapula-coracoid aspects and coracoids were deeper and shorter, respectively, in the freshwater species (groups 3 and 4) than in the seawater species (groups 1 and 2). Together, these results support the hypothesis that pectoral fin morphology reflects the lifestyle of the fish species. In addition, the present study also examined the relationship between the body length and scapula-coracoid length of 12 fish species and found that scapula-coracoid length increases with body length. However, the slopes of the regression lines for the seawater and freshwater species were significantly different (ANCOVA, $p < 0.01$), which suggests that seawater and freshwater fish species possess different skeleton growth rates.

Keywords: scapula, coracoid, pectoral fin, the fish in the fish

1. Introduction

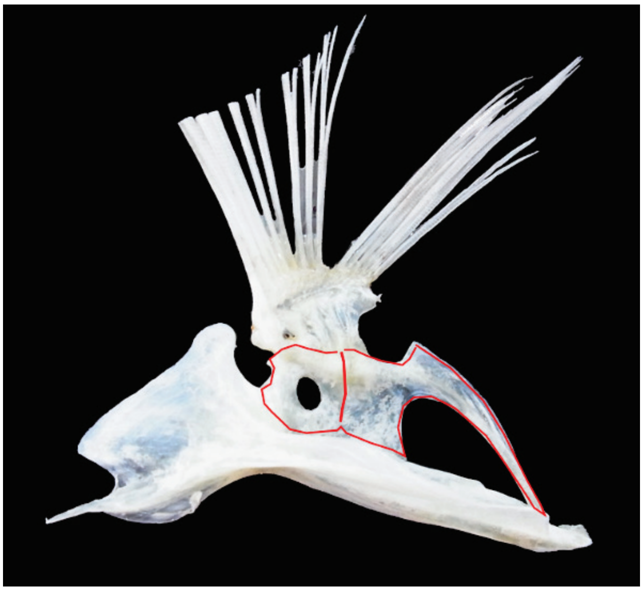

Figure 1. Skeletal structure of a *Pagrus major* pectoral fin, including the scapula (a) and coracoid (b), which are framed in red.

The scapula (Figure 1. a) and coracoid (Figure 1. b) are components of the pectoral fin skeleton in fish and are commonly called "the fish in the fish" in Japan, owing to their fish-like shape (Shimamoto, 2006).

The morphology of fish species reflects their lifestyle. For example, *Thunnus* species, which are famous for migratory ability, have fusiform body shapes, whereas benthic species, like *Paralichthys* species, possess flat bodies. These morphological characteristics affect swimming cost (e.g., Lighthill, 1969; Reis and Pawson, 1999). Similarly, the pectoral fin structure also reflects species lifestyle. By monitoring pectoral fin movement patterns, the difference of the driving force of each fish species were found (reviewed by Drucker *et al*., 2005). Thorsen and Westneat (2005) revealed the musculoskeletal diversity of pectoral fins in 12 species. Therefore, it is important to study the skeletal morphology of fish species with different lifestyles, such as *Thunnus* and *Paralichthys* species. However, few studies have examined the relationship between pectoral fin shape and life-style or between body and scapula-coracoid size. Accordingly, the present study compared the morphology of scapula-coracoids from various fish species and investigated both the relationship between skeletal morphology and lifestyles and that between body and scapula-coracoid size.

2. Materials and Methods

2. 1. Fish sampling and scapula-coracoid measurement

Seawater and freshwater fish species were collected using a fishing rod at Wakasa Bay (Fukui Prefecture, Japan) or at the Ado River or a fishing pond (Shiga Prefecture, Japan), respectively, from 1999 to 2005. Each fish was classified, measured, and boiled to remove its scapula-coracoid. The scapula-coracoids were then washed in fresh water, dried 24 h, and measured for the following parameters: TL, total length of the scapula-coracoid; HL, length of the scapula; BL, length of the coracoid; HH, height of the scapula; BH, height of the coracoid; and LL, diagonal distance between the upper- and lowermost points of the coracoid (Figure 2). The values for HL, HH, BL, BH, and LL were standardized using TL. Each of the parameters was analyzed using Spearman's rank-order correlation.

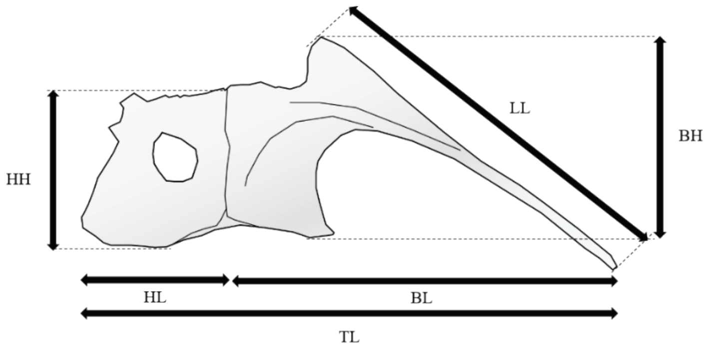

Figure 2. Scapula-coracoid measurements.

2. 2. Morphological categorization of scapula-coracoids

The habitats of the fish species could be roughly categorized into two types: bottom and surface (i.e., benthic and pelagic areas). Therefore, species that live on or near the sea bottom were defined as benthic (Dictionary of Zoology, 1999), and the others were defined as pelagic. Following these definitions, the collected species were divided into four groups: seawater benthic (group 1), seawater pelagic (group 2), freshwater benthic (group 3), and freshwater pelagic (group 4). To examine the relationship between habitat and scapula-coracoid shape, the scapula-coracoid measurements of the four groups were compared. Because the scapula-coracoid of *Pagrus major* (Figure 3) is the most familiar example of "the fish in the fish" in Japan, it was used as the standard shape to which the other scapula-coracoids were compared.

Figure 3. Scapula-coracoid of *Pagrus major*.

2. 3. Relative scapula-coracoid growth

Only the species represented by >3 specimens were included in this analysis: eight seawater species (*P. major, Acanthopagrus schlegelii, Rhyncopelate oxyrhynchus, Sillago japonica, Sebastes pachycephalus, Epinephelus akaara, Seriola quinqueradiata,* and *Seriola dumerili*) and four freshwater species (*Oncorhynchus mykiss, Salmo trutta, Salvelinus* sp., and *Oncorhynchus masou*). The relationship between fish body size and TL within species was investigated using Spearman's rank-order correlation, and differences between this relationship in seawater and freshwater species was investigated using analysis of covariance (ANCOVA), with TL as the objective variable, fish body size as the explanatory variable, and species (seawater or freshwater) as the covariate. The analysis was performed using R ver. 3.1.3.

3. Results

3. 1. Categorization of scapula-coracoid by morphological characteristics

A total of 102 seawater and freshwater fish species from 12 orders and 45 families were collected (Supplement 1). The freshwater species primarily belonged to the Salmonidae. The scapula-coracoids of the seawater benthic species (Figure 4; group 1) were flat or round, and the scapula-coracoids of deep-sea benthic species, such as *Myoxocephalus polyacanthocephalus*, *Beryx splendens*, *Scombrops boops*, showed specific forms. Meanwhile, the seawater pelagic species (group 2) possessed relatively long coracoids. Both the freshwater benthic species (group 3), which only included *Pseudogobio esocinus*, and the freshwater pelagic species possessed deeper three-dimensional aspects and shorter coracoids, when compared to those of the seawater species (groups 1 and 2).

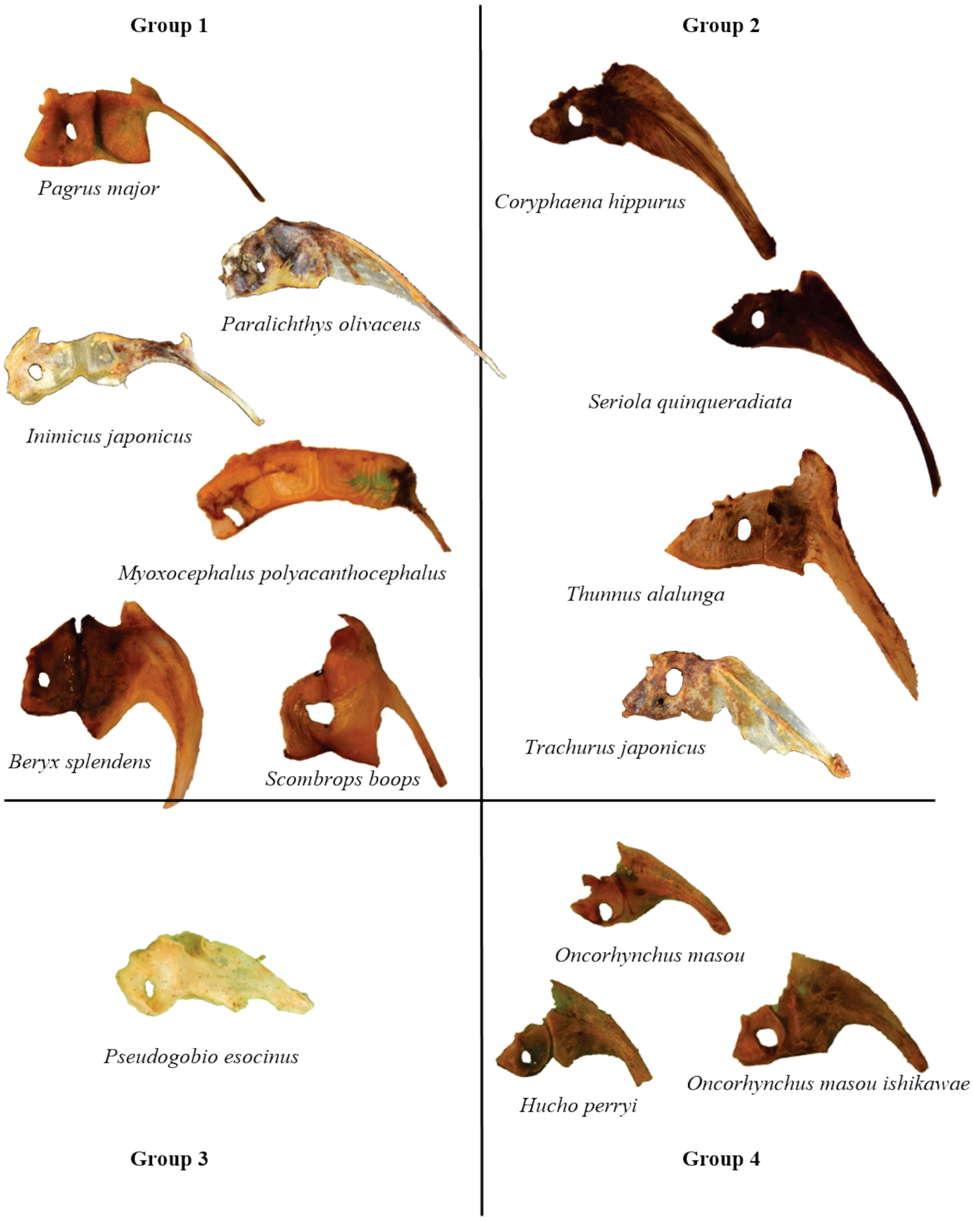

Figure 4. Scapula-coracoids of a subset of the collected species, separated by habitat: group 1, ocean bottom; group 2, ocean surface; group 3, river bottom; and group 4, river surface (all grouped species were shown in Supplement 1).

Figure 5 shows the relationships between the relative values of HL and BL, HH and BH, and HL and LL. There were some positive or negative linear relationships in individual panels. Relative HL of group 1, 2 become smaller when relative BL become bigger (Figure 5a, $p < 0.05$). On the other hands, relative HH of group 1, 2 indicated positive relationships with relative BH (Figure 5b, $p < 0.05$). In the relationships between the relative HL and relative LL, HL of group 1 become smaller in relation to LL whereas HL of group 2 become bigger according to their LL (Figure 5c, $p < 0.05$). Group 4 indicated only negative relationships when comparing HL with BL (Figure 5a, $p < 0.05$).

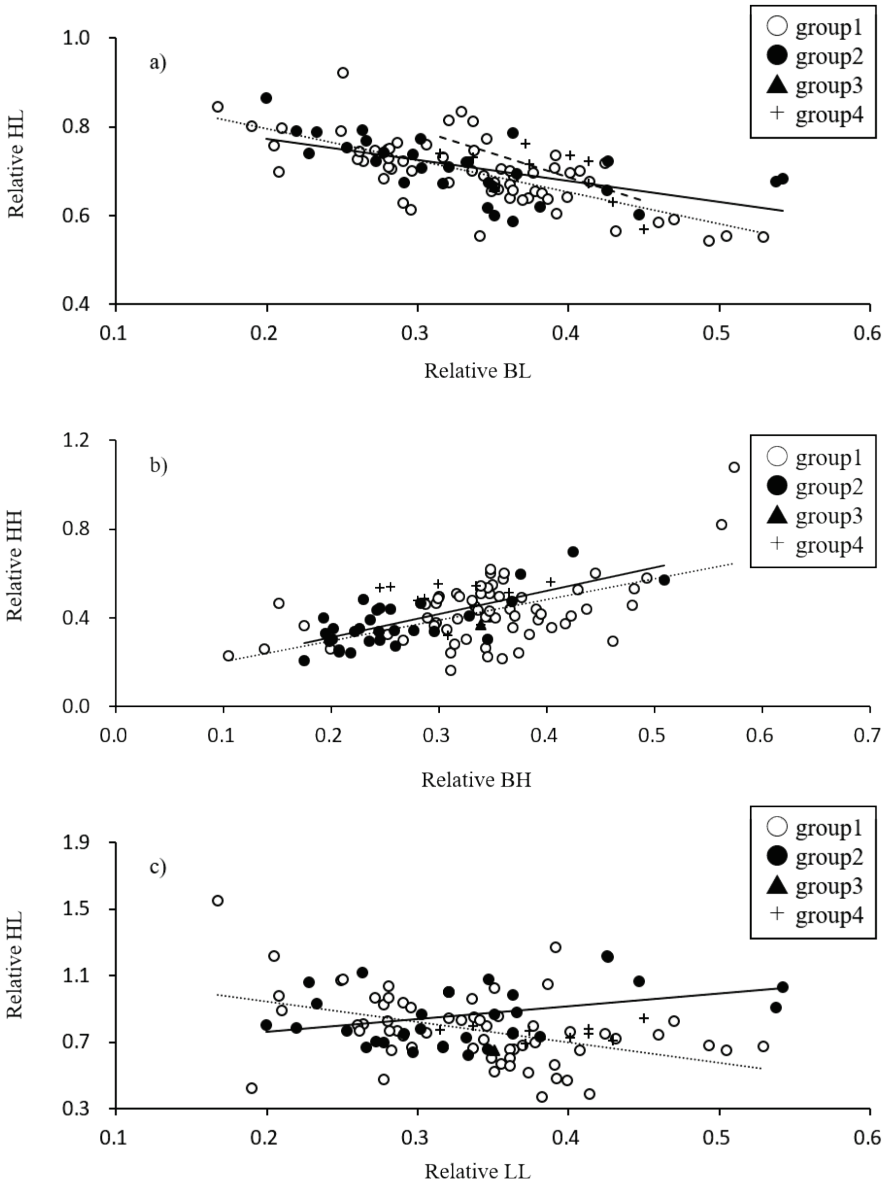

Figure 5. Relationships among relative HL, BL, HH, BH, HL, and LL. Relative HL and BL (a), relative HH and BH (b), and relative HL and LL (c) were shown respectively. The dotted lines indicate the regression lines of group 1, the solid lines indicate the regression lines of group 2, and the dashed lines indicate the regression lines of group 4. HL, length of the scapula; BL, length of the coracoid; HH, height of the scapula; BH, height of the coracoid; and LL, diagonal distance between the upper- and lowermost points of the coracoid.

3. 2. Relative growth of the scapula-coracoid

The relationships between body size and scapula-coracoid size were examined in 12 species (*P. major, A. schlegelii, R. oxyrhynchus, S. japonica, S. pachycephalus, E. akaara, S. quinqueradiata, S. dumerili*, *O. mykiss, S. trutta, Salvelinus* sp., and *O. masou*). The scapula-coracoid sizes were positively correlated with body size ($p < 0.05$) in six of the 12 species (*E. akaara*, *S. quinqueradiata*, *A. schlegelii*, *S. pachycephalus*, *P. major*, and *O. mykiss*) but not in the others (also see Figure 6), and the regression slope of the seawater fish was significantly different from that of the freshwater fish ($p < 0.01$, Figure 7).

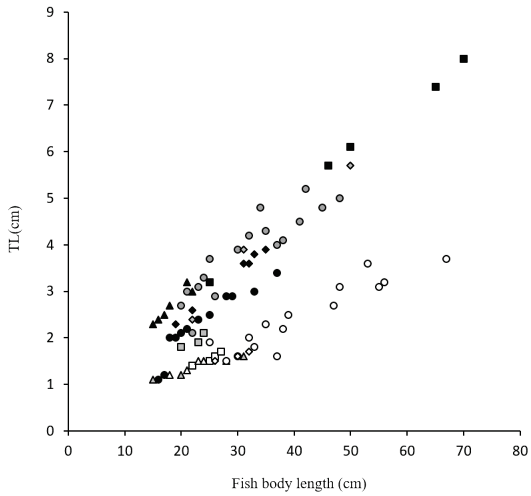

Figure 6. Relationships between the body and scapula-coracoid lengths of eight seawater species (black- and gray-filled symbols) and four freshwater species (open symbols). ●: *Epinephelus akaara* (n = 12), ■: *Seriola quinqueradiata* (n = 5), ◆: *Acanthopagrus schlegelii* (n = 7), ▲: *Sebastes pachycephalus* (n = 6), ●: *Pagrus major* (n = 17), ■: *Rhyncopelate oxyrhynchus* (n = 3), ◆: *Seriola dumerili* (n = 3), ▲: *Sillago japonica* (n = 4), ○: *Oncorhynchus mykiss* (n = 15), □: *Salmo trutta* (n = 4), ◇: *Salvelinus* (n = 3), and △: *Oncorhynchus masou* (n = 4).

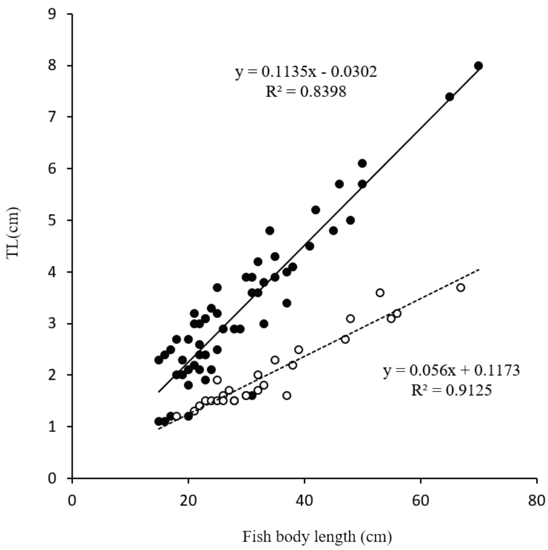

Figure 7. Relationships between the body and scapula-coracoid lengths of eight seawater species (filled circles) and four freshwater species (open circles). The solid and dashed lines represent the regression lines of the seawater and freshwater species, respectively.

4. Discussion

The present study demonstrates that species lifestyle (i.e., habitat) influences scapula-coracoid morphology and that the relationship between body and scapula-coracoid size differs between seawater and freshwater species. The species in group 1, which included the standard type, used their pectoral fins for crawling, hovering during feeding, performing complex maneuvers, and competing with the others during mating season. Group 1 also included deep-sea species that are adapted to specific environment like high pressure and low temperature. Therefore, the deep-sea species in group 1 could possess unique lifestyles that affected the shape of their skeletons. In contrast, group 2, which primarily included migratory species that mainly use their pectoral fins for maneuvering, possessed relatively long coracoids, thereby suggesting that relatively long coracoids allow the use of pectoral fins for instantaneous force maneuvers. The coracoids of group 3, which only included a single species, were relatively short, when compared to those of seawater pelagic species (group 2). Therefore, the results of the present study suggest that the morphological characteristics of the coracoid, not the scapula, reflect species habitat.

The form of scapula-coracoid could affect the swimming velocity. Group 4, which primarily included salmonids, exhibited a more three-dimensional form than the seawater groups (1 and 2). Taylor and Foote (1991) reported that the anadromous sockeye salmon *Oncorhynchus nerka* swims at greater velocities and possesses more vertebrae than the non-anadromous kokanee. The authors suggested that the difference in vertebrae number could influence swimming performance. The present study assumed that the riverine environment was more severe than the oceanic environments in regards to velocity. Therefore, the greater three-dimensional forms of group 4 could increase the species' swimming performance. Additionally, as indicated in Figure 5, the relationship between relative HL and BL exhibited an opposite trend, when compared to the relationship between relative HH and BH. Furthermore, the relationship between relative HL and LL for group 1 differed from that for group 2, a trend that has also been observed among different-sized individuals of the same species (Murase, unpublished data). Therefore, this phenomenon may indicate that the scapula and coracoid perform different roles in different-sized individuals.

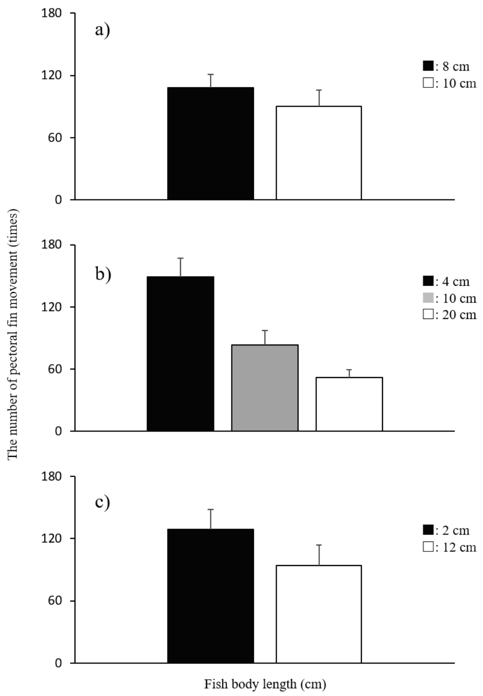

Figure 8. Number of pectoral fin movements per minute for two seawater species: a) *Pagrus major*, b) *Oplegnathus fasciatus*) and one freshwater species: c) *Carassius auratus*. Values and error bars represent means ± standard error. Each species was bred separately in an aquarium (60 cm W × 30 cm D × 40 cm H). The number of pectoral fin movements within one minute was counted for each fish by visual observation (n = 7).

The difference in the relationship between body size and scapula-coracoid morphology for the seawater and freshwater fish indicated that the growth rates of the seawater and freshwater fish differed (Figure 7). Differences in habitat space or the ratio of energy distribution might explain this difference. The function of pectoral fins changes according to growth stage. Pectoral fins are primarily used for feeding or escaping predators during early life; however, their function becomes more complex as individuals mature. For example, some species use their pectoral fins during courtship or for protecting their eggs. Regarding the pectoral fin movement of different-sized individuals, the number of fin movements decreased in relation to body size (Figure 8), which indicated that swimming velocity might increase in relation to body size. Whether the changes in pectoral fin use with maturity affect the morphology of the scapula-coracoid is an interesting question. However, almost all the samples used in the present studies were adults, and as such, it is difficult to answer this question. Because the present studies investigated only 10 freshwater species compared to 92 seawater species, it would be necessary to study more freshwater species for establishing the morphological differences between seawater and freshwater fish species.

5. Acknowledgements

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Supplement 1. Sampled species.

order	family	species	groups
Perciformes	Sparidae	*Pagrus major*	1
		Evynnis tumifrons	1
		Acanthopagrus schlegelii	1
	Carangidae	*Trachurus japonicus*	2
		Uraspis helvola	2
		Decapterus muroadsi	2
		Caranx sexfasciatus	2
		Carangoides equula	2
		Pseudocaranx dentex	2
		Alectis ciliaris	2
		Seriola lalandi	2
		Seriola dumerili	2
		Seriola quinqueradiata	2
		Decapterus maruadsi	2
	Branchiostegidae	*Branchiostegus japonicus*	1
		Branchiostegus albus	1
	Haemulidae	*Parapristipoma trilineatum*	1
		Plectorhinchus cinctus	1
		Hopalogenys sennin	1
	Oplegnathidae	*Oplegnathus fasciatus*	1
		Oplegnathus punctatus	1
	Nemipteridae	*Nemipterus virgatus*	1
	Centrolophidae	*Hyperoglyphe japonica*	1
		Psenopsis anomala	1
	Embiotocidae	*Ditrema temmincki temmincki*	1
		Neoditrema ransonneti	1
	Sphyraenidae	*Sphyraena pinguis*	1
	Sillaginidae	*Sillago japonica*	1
	Priacanthidae	*Cookeolus japonicus*	1
		Priacanthus macracanthus	1

Supplement 1 (continued). Sampled species.

order	family	species	groups
Perciformes	Scombridae	*Euthynnus affinis*	2
		Thunnus orientalis	2
		Katsuwonus pelamis	2
		Sarda orientalis	2
		Scomber japonicus	2
		Scomber australasicus	2
		Thunnus alalunga	2
	Lateolabracidae	*Lateolabrax japonicus*	1
	Pomacentridae	*Chromis notata*	1
		Abudefduf vaigiensis	1
	Cheilodactylidae	*Cheilodactylus zonatus*	1
	Trichiuridae	*Trichiurus lepturus*	1
	Serranidae	*Epinephelus awoara*	1
		Epinephelus akaara	1
	Trichodontidae	*Arctoscopus japonicus*	1
	Lutjanidae	*Lutjanus ophuysenii*	1
		Lutjanus stellatus	1
		Lethrinus semicinctus	1
		Lethrinus atkinsoni	1
		Lethrinus microdon	1
	Labridae	*Pseudolabrus sieboldi*	1
		Pteragogus aurigarius	1
		Halichoeres poecilopterus	1
		Semicossyphus reticulatus	1
	Girellidae	*Girella punctata*	1
	Scombropidae	*Scombrops boops*	1
	Leiognathidae	*Nuchequula nuchalis*	1
	Coryphaenidae	*Coryphaena hippurus*	2
	Pomacanthidae	*Chaetodontoplus septentrionalis*	1
	Gadidae	*Gadus macrocephalus*	1

Supplement 1 (continued). Sampled species.

order	family	species	groups
Perciformes	Terapontidae	*Rhyncopelate Oxyhynchus*	1
	Gerreidae	*Gerres equulus*	1
Scorpaeniformes	Hexagrammidae	*Hexagrammos agrammus*	1
		Pleurogrammus monopterygius	1
		Pleurogrammus azonus	1
		Hexagrammos otakii	1
	Scorpaenidae	*Sebastiscus marmoratus*	1
		Sebastes ventricosus	1
		Sebastes thompsoni	1
		Sebastes hubbsi	1
		Sebastes vulpes	1
		Sebastes schlegelii	1
		Sebastes pachycephalus	1
		Inimicus japonicus	1
	Triglidae	*Chelidonichthys spinosus*	1
	Cottidae	*Myoxocephalus polyacanthocephalus*	1
	Agonidae	*Podothecus sachi*	1
Pleuronectiformes	Pleuronectidae	*Hippoglossoides dubius*	1
		Glyptocephalus stelleri	1
		Tanakius kitaharai	1
		Pleuronichthys cornutus	1
		Kareius bicoloratus	1
	Paralichthyidae	*Paralichthys olivaceus*	1
Beryciformes	Berycidae	*Beryx splendens*	1
Clupeiformes	Clupeidae	*Etrumeus teres*	2
Beloniformes	Hemiramphidae	*Hyporhamphus sajori*	2
	Exocoetidae	*Cypselurus agoo agoo*	2
		Cypselurus pinnatibarbatus japonicus	2
Zeiformes	Zeidae	*Zeus faber*	1
Tetraodontiformes	Monacanthidae	*Stephanolepis cirrhifer*	1
		Thamnaconus modestus	1
		Aluterus monoceros	1
Mugiliformes	Mugilidae	*Mugil cephalus*	2

Supplement 1 (continued). Sampled species.

order	family	species	groups
Osmeriformes	Osmeridae	*Plecoglossus altivelis*	4
Salmoniformes	Salmonidae	*Oncorhynchus keta*	4
		Oncorhynchus masou ishikawae	4
		Salvelinus	4
		Oncorhynchus masou	4
		Oncorhynchus mykiss	4
		Salmo trutta	4
		Hucho perryi	4
Cypriniformes	Cyprinidae	*Pseudogobio esocinus*	3