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Foraging ecology of a large opportunistic predator (adult *Lateolabrax latus*) on a temperate-subtropical rocky shore

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Abstract

Foraging ecology of a large opportunistic predator (adult *Lateolabrax latus*) was investigated through intensive, targeted sampling of the species on an exposed shallow rocky shore of south-western Japan. The abundance of *L. latus* increased in autumn and spring, whilst no individual occurred in summer when water temperatures were $>24^{\circ}\text{C}$. In spring larger sized individuals (>70 cm TL) tended to occur, resulting in a wide range of body sizes. *L. latus* consumed a wide variety of organisms, of which fishes and benthic crustaceans were particularly important. Overall, the relative importance of invertebrates as food increased in spring, which may be related to seasonal fluctuations of macro-algae and algae-associated faunas. The fact that a large number of adult fish was collected at high tide in intertidal areas and their guts contained intertidal organisms suggests that *L. latus* relies on the rocky intertidal habitat as a major foraging ground. This in turn points to the potential importance of large, highly mobile predators such as adult *L. latus* in the food web dynamics of shallow-water (including the intertidal) assemblages.

Keywords: diet, intertidal, piscivore, sea bass, seasonal occurrence, stomach contents

Introduction

Shallow coastal areas are generally characterised by high productivity and provide a large amount of resources to diverse marine organisms. In addition, shallow water habitats including intertidal zones constitute important nursery grounds for larval stages of marine taxa, generally being considered as 'refugia' with lowered risks of predation (e.g. Blaber & Blaber 1980; Kneib 1987; McIvor & Odum 1988, Ruiz, Hines & Posey 1993). Therefore, shallow coastal areas play important ecological functions for different

assemblages of organisms. Whilst migration of fishes into intertidal habitats has been reported under various environmental settings (e.g., Burrows et al. 1994; Rangeley & Kramer 1995; Sheaves 2001; Faria & Almada 2006; Castellanos-Galindo, Krumme & Willis 2010), most studies dealt with juveniles or relatively small fishes and information on large-sized foragers is scarce. Intermittent use of intertidal areas as foraging sites is a potentially important ecological topic that could link subtidal and intertidal ecosystems. Although some previous studies suggested a possibility that migratory foraging may have a significant impact on intertidal communities (e.g. Edwards, Conover &

Sutter 1982; Lubchenco et al. 1984; Castellanos-Galindo, Krumme & Willis 2010), our understanding of such situations is limited. Thus, the present study focused on the temperate sea bass, *Lateolabrax latus*, as one of the potentially important large predators in shallow rocky shore habitats of south-western Japan.

Sea basses of the genus *Lateolabrax* are common coastal fishes that constitute important elements of commercial and recreational fisheries in East Asia including Japan, Korea and China. The blackfin sea bass, *Lateolabrax latus*, is considered to have a relatively limited distribution, mainly occurring on rocky shores of southern Japan, while a congener *L. japonicus* occurs widely in both open and inner coastal areas including estuaries, and occasionally in rivers from northern Japan to southern coasts of the Korean Peninsula (Hatooka 2002).

While a good number of studies have dealt with different ecological aspects of *L. japonicus* (e.g., Mito 1957; Hatanaka & Sekino 1962; Matsumiya, Mitani & Tanaka 1982; Matsumiya, Masumoto & Tanaka 1985; Nip, Ho &

Wong 2003; Islam & Tanaka 2006; Islam, Yamashita & Tanaka 2011), studies on *L. latus* have largely been limited to investigations of their early life stages in surf zones or estuaries and other soft-bottom environments (Fujita et al. 1988; Kinoshita & Fujita 1988; Inoue, Suda & Sano 2005, Yube et al. 2006). The apparent paucity of ecological information on adult *L. latus* is due mainly to the difficulty of specimen collection and observation on exposed rocky shores where adult individuals are known to occur. In order to build a more comprehensive understanding of the ecological roles of a predatory species in shallow coastal waters, it is vital to elucidate their patterns of resource utilisation, particularly at the adult stage when the level and impacts of resource consumption are higher.

The objective of the present study is to quantitatively analyse the foraging ecology of adult *L. latus* on a temperate-subtropical rocky shore. We relied on intensive line-fishing surveys to obtain numerically adequate data on adult individuals.

Materials and Methods

Study site and fish collection

Fish samples were collected within a radius of 3 km of the Amakusa Marine Biological Laboratory, Kyushu University (32°32'N, 130°02'E), located in the north-western corner of the Amakusa-Shimoshima Island, south-western Japan. This area has a variety of shore habitats at the scale of several kilometers with complex and occasionally strong currents at the entrance of the Ariake Bay facing the East China Sea (Tokeshi and Arakaki 2011). The sampling sites were moderately exposed rocky shores with a gentle slope and a tidal amplitude of about 3.5 m: the shores were exposed for a distance of about 80-120 m seaward at the low tide (Fig 1). The substrates were variable and consisted mainly of rocks and boulders with patchy occurrence of seaweeds, especially in winter to spring season. Water temperature was monitored with a data logger (HOBO Water Temp Pro v2, onset) at 7 m depth. Using this record, 3-day mean temperature trends were worked out to determine the annual minimum and the maximum temperature with the period from the former to the latter being defined as the 'rising' period and the opposite as the 'declining' period.

Lateolabrax latus individuals (Fig 1) were collected during daylight hours (including twilight) between January 2000 and March 2007 (except January-February 2006) by line fishing from the shore using artificial lure baits. The

sizes of the artificial lure baits used, 70-140 mm in length, meant that fish individuals targeted were skewed towards larger sizes (i.e. adult stage), as intended in the present study. Fish collection was conducted at least once in three weeks. Collection effort was raised once a fish was captured or some responses (biting/chasing) were obtained and discontinued when there was no sign of fish (with a minimum effort of once in three weeks). Time of capture, total body length (TL, to the nearest 0.5 cm) and body weight (to the nearest 0.1 kg) were recorded.

Gut contents

A total of 112 individuals of *Lateolabrax latus* (i.e. 60% of those captured in April 2004 - March 2007, size range 39.0 - 73.0 cm) were subjected to gut content analysis. Samples were preserved in 10% formalin and gut contents were sorted and identified to broad taxonomic categories. Samples were rinsed in 70% ethanol before being labelled, dried to constant weight at 60°C. Preliminary observation indicated that both ripe and spent gonads were observed in March while no spent gonad was found before March. Fish samples were therefore divided into two groups, "pre-spawning" (October to February, $n = 53$) and "post-spawning" (March to July, $n = 59$) (see Supplementary Information). Mean sizes of fishes for gut contents analyses were not significantly different between the pre-spawning and the post-spawning group (Mann-Whitney U test, $P > 0.05$). The percentage occurrence of each prey item (%O) was

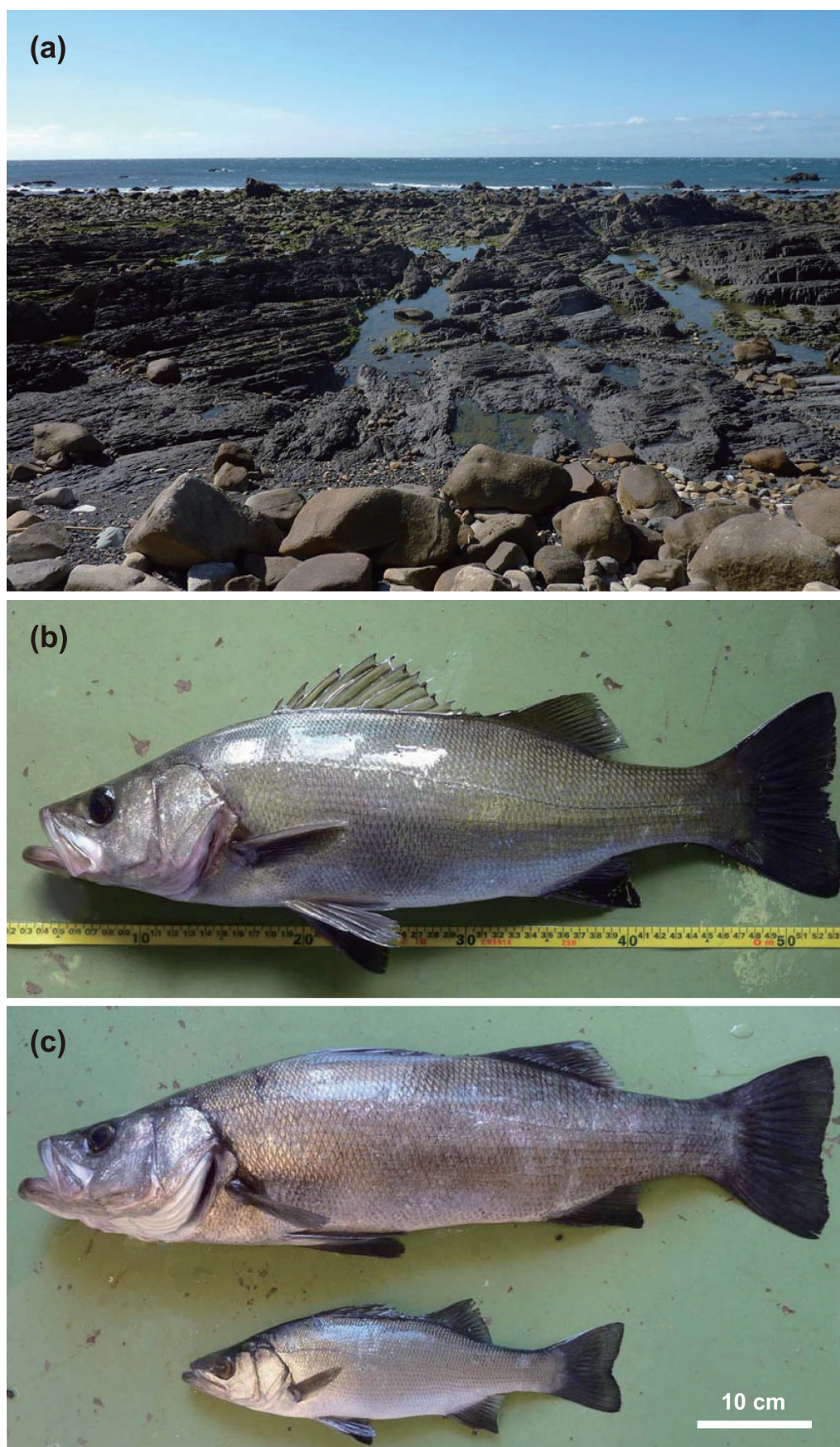


Fig. 1 (a) Study site at low tide: a moderately-exposed shallow rocky shore, (b) *Lateolabrax latus* in the pre-spawning season (November), an individual with 'average' (common) body size (50 cm TL) in this study and (c) samples of a large (upper, 71 cm TL) and a small (lower, 38.5 cm TL) individual of *Lateolabrax latus* in the post-spawning season (April).

calculated as the proportion of the total number of guts (of *L. latus* individuals) containing it, while abundance and dry weight data of prey were used to calculate the mean percentage number (%N) and weight (%W) of each prey item in the guts.

One way ANOSIM and nMDS were then used to identify differences in gut contents between the two sampling seasons based on Bray-Curtis similarities with $\log(x+1)$ transformed data (Clarke & Warwick 2001). Individuals with no or very small quantity (number and weight) of gut contents were excluded from this analysis, resulting in 40 samples each for the pre- and the post-spawning season. Where significant differences were identified, SIMPER (Clarke & Warwick 2001) was used to determine the relative contribution of different prey categories.

Relative importance (RI) of fish (including fish fragments) against invertebrates (benthic crustaceans, other benthic invertebrates and planktonic crustaceans) in the diet was calculated for each individual of *L. latus* in the pre- and post-spawning periods,

$$RI = (V_f - V_i)(V_f + V_i)^{-1}$$

where V_f and V_i are values (number or weight) for fish and invertebrates in a gut, respectively. The index ranged from -1 (consumed invertebrates only) to 1 (consumed fish only) with 0 representing an equitable consumption of two categories. Guts with no or small amounts of prey ($n = 9$ and 3, respectively) were excluded from this analysis.

Results

Fish occurrence

A total of 409 individuals of *Lateolabrax latus* were collected in the course of this study. There were two clear modes of fish occurrence in spring and autumn, while no individual was recorded in the summer season (August to September) (Fig. 2). Body weight measures were obtained for 175 individuals only (80 pre- and 95 post-spawning individuals) because some individuals were released to the field without measuring weight. There was a clear positive relationship between total length and body weight (Supplementary Information, Fig. S1). For simplicity, total body length is referred to as body size in the rest of the text. The body sizes of *L. latus* collected ranged from 30.0 to 83.0 cm TL (Fig. 3). The mean size of fishes collected varied significantly among months (Kruskal-Wallis test, $P < 0.01$); there was a significant difference between the group of March and April and the group of October, November, December and January (and also April and February) (Scheffe's post-hoc test, $P < 0.01$). Variance in body size reached a peak in spring and large individuals exceeding 70.0 cm TL were recorded in spring only.

L. latus individuals were collected both at high and low tidal times (Fig. 4). There was no steep rocky shore in our study area (Fig 1) and we could not approach subtidal

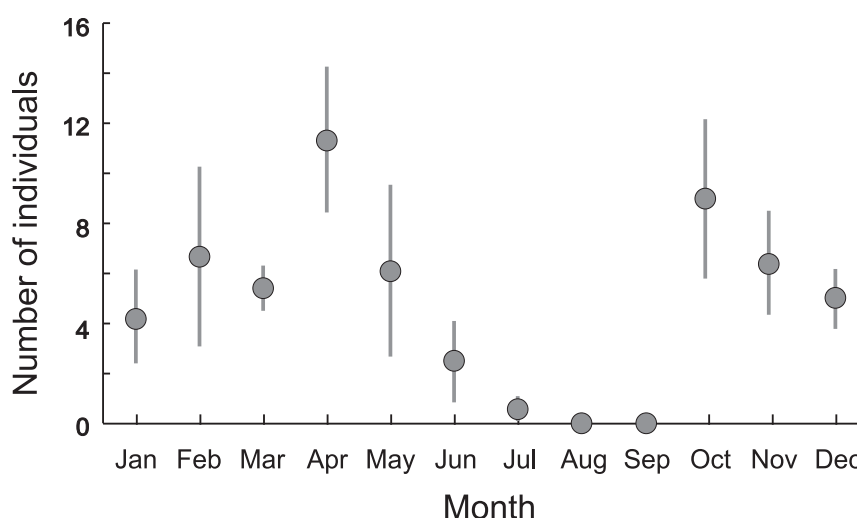


Fig. 2 Seasonal changes in occurrence (mean $\pm$ 1SD) of *Lateolabrax latus*. The values are averaged over the whole study period: 2000-2007.

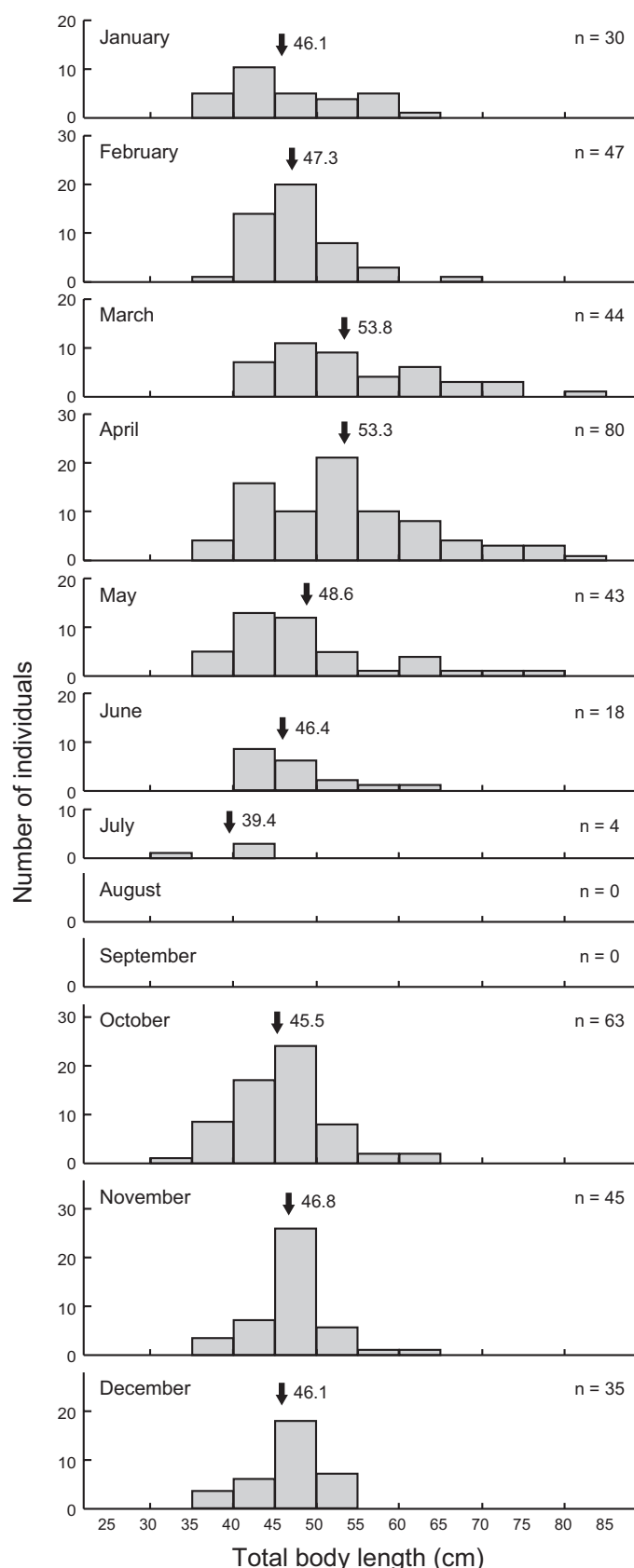


Fig. 3 Size frequency distributions of collected *Lateolabrax latus* are shown in monthly samples. Vertical arrows and numbers beside denote mean total body length.

zones from the shore at high tide. Thus, our record showed that nearly half of all specimens were collected from the intertidal at high tide. Note that, however, the trend in the figure just showed the evidence for utilisation of intertidal zone as feeding ground but not for the probability of temporal occurrence.

There was a clear trend of fish occurrence in relation to water temperatures. While temperatures in the study site were generally $>25^{\circ}\text{C}$ in summer with the maximum of 29.5°C , no *L. latus* individual was observed when water temperature was higher than 24.2°C . Temperatures on the days of capture were significantly higher in the declining period than in rising period (Fig. 5, Kolmogorov-Smirnov test, $P < 0.01$).

Gut contents

A total of 103 out of 112 gut samples contained food material while guts of 8 pre-spawning and 1 post-spawning individuals were empty. Both prey number and weight were significantly greater in the post-spawning season

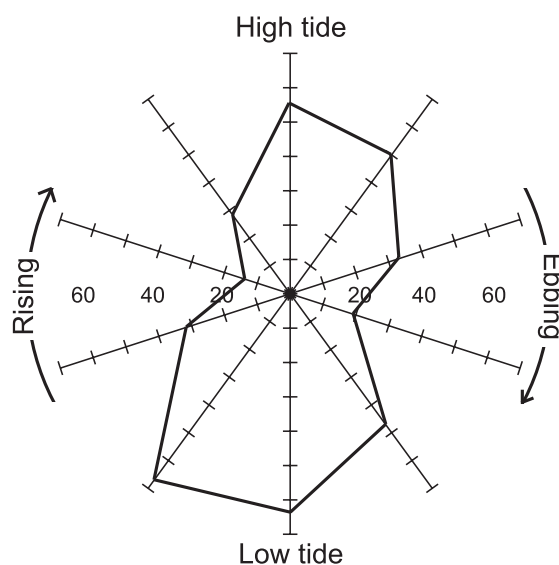


Fig. 4 Number of fish captured during different tidal phases.

Table 1 Prey items in the guts of *Lateolabrax latus* caught in 2004 - 2007. Percentage values of occurrence (%O, proportion of guts containing a prey category out of all guts), number (%N, mean of the proportional number of individuals of a prey category out of all prey) and weight (%W, mean of the proportional weight of a prey category) are given separately for the post- and the pre-spawning season.

Prey categories	%O		%N (mean)		%W (mean)	
	post-	pre-	post-	pre-	post-	pre-
fish	71.2	68.0	22.9	60.6	83.0	89.8
fish fragments	18.6	9.4	1.4	1.7	6.9	0.8
benthic crustaceans	71.2	35.9	53.6	33.4	8.0	6.7
other benthic invertebrates	1.7	1.9	1.0	0.3	0.02	0.01
planktonic crustaceans	6.8	3.8	20.2	0.6	0.1	0.1
nematodes	0	1.9	0	0.3	0	0.001
unidentified tissue	6.8	7.6	0.6	1.4	0.4	0.2
algae	1.7	0	0.2	0	0.001	0
detritus	5.1	7.6	0.2	2	1.6	2.4

(number = 32.7, weight = 4.4 g) than in the pre-spawning season (number = 8.8, weight = 1.9 g, Mann-Whitney U test, $P > 0.05$). The most important prey items throughout the sampling period were fishes (including fish fragments) and benthic crustaceans (Table 1, examples shown in Fig. 6). Prey fishes included mostly pelagic species (e.g., Clupeidae, Engraulidae and Atherinidae) and some demersal species ones (e.g., Blenniidae, Gobiidae, Pomacentridae and Tripterygiidae). Most conspicuous benthic crustaceans were Flabellifera (Cirolanidae and Sphaeromatidae); in addition, Caprellidea, Gammaridea, Alpheus sp. and Nihonotrypaea sp. were also recognised. Parasitic nematodes were also found in the gut samples, but are not discussed any further.

While there was little seasonal difference in the proportion of the number of fish sampled that had fish in their guts, gut samples from the pre-spawning season contained higher proportions of fish by both number and weight, than the post-spawning season samples (Table 1). In the post-spawning season, benthic crustaceans were consumed more frequently and made up a large proportion of items found in guts based on number but not on weight.

One factor ANOSIM indicated that there was a small but significant difference between the two seasons in terms of both the abundance (Global $R = 0.105$, $P = 0.002$) and weight (Global $R = 0.076$, $P = 0.002$) of different prey categories. nMDS showed some segregation of the two

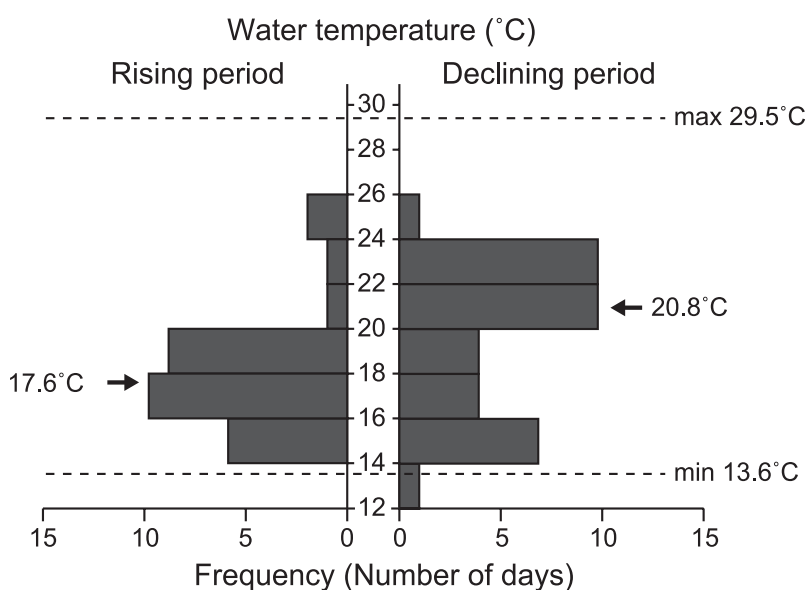


Fig. 5 Number of days on which *Lateolabrax latus* was collected in relation to water temperature. Data are separately shown for the rising (left) and the declining (right) period. An arrow indicates a median value. Broken horizontal lines denote the maximum and the minimum water temperature.



Fig. 6 Examples of gut contents of *Lateolabrax latus*: (a) Atherinidae; (b) Engraulidae; (c) Mugilidae; (d) fishes (Girellidae, etc.) and crustaceans (Flabellifera, Gammaridea, *Nihonotrypaea* sp. etc.); (e) miscellaneous fishes and crustaceans (Decapod, Flabellifera). Open bars in panels represent a 1 cm scale.

seasons in terms of number while the trend was weak in weight (Fig. 7). Further analysis with SIMPER indicated that in terms of both abundance and dry weight the prey categories that contributed most to differences between the seasons were benthic crustaceans (41.2 and 20.8% in number and dry weight, respectively) and fish (39.3 and 62.3%).

Fishes were predominant in the guts of *L. latus* in both pre- and post-spawning seasons (Fig. 8), but their relative importance was significantly lower in the post-spawning than in the pre-spawning season (Mann-Whitney U test, $p < 0.05$, for both numbers and weight). Note that the observed wide scatter of values indicates substantial dietary variation among *L. latus* individuals (except in the pre-spawning season, in terms of weight). There was no significant correlation between total body length and the RI value (Kendal rank correlation coefficient 0.023, $P = 0.7511$).

Discussion

Shallow water habitats constitute important nursery grounds for diverse marine organisms, generally being considered as 'refugia' with lowered risks of predation (e.g. Blaber & Blaber 1980; Kneib 1987; McIvor & Odum 1988, Ruiz, Hines & Posey 1993). On the other hand, evidence supporting the proposition that there is a reduced risk of predation in such habitats is equivocal (Sheaves 2001). Additionally, the effects of predators with high mobility and temporal (e.g. diel, tidal and seasonal) occurrence on intertidal community structure are often overlooked and misinterpreted (Edwards, Conover & Sutter 1982). Our ecological knowledge of such highly mobile, opportunistic predators is limited, especially in the case of large predators, due to the problems of sampling efficiency (e.g. methodological and numerical restrictions). Given such a background, the present study focused on *Lateolabrax latus* as one of the potentially important large opportunistic predators on temperate-subtropical shallow rocky shores of south-western Japan. Information

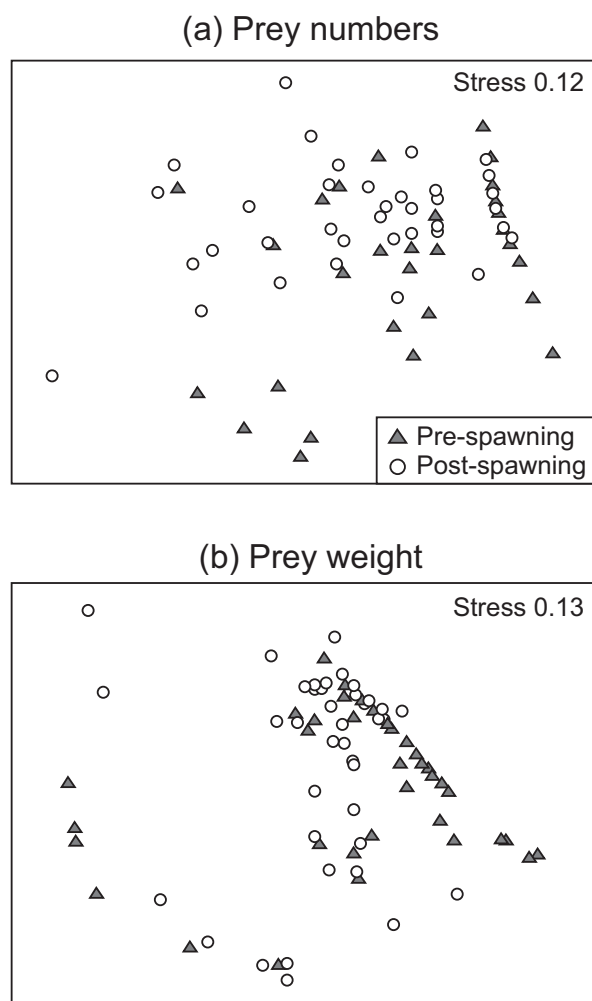


Fig. 7 nMDS plot of gut contents similarity based on (a) prey numbers and (b) weight in the pre-spawning (grey triangles) and the post-spawning (open circles) season of *Lateolabrax latus*.

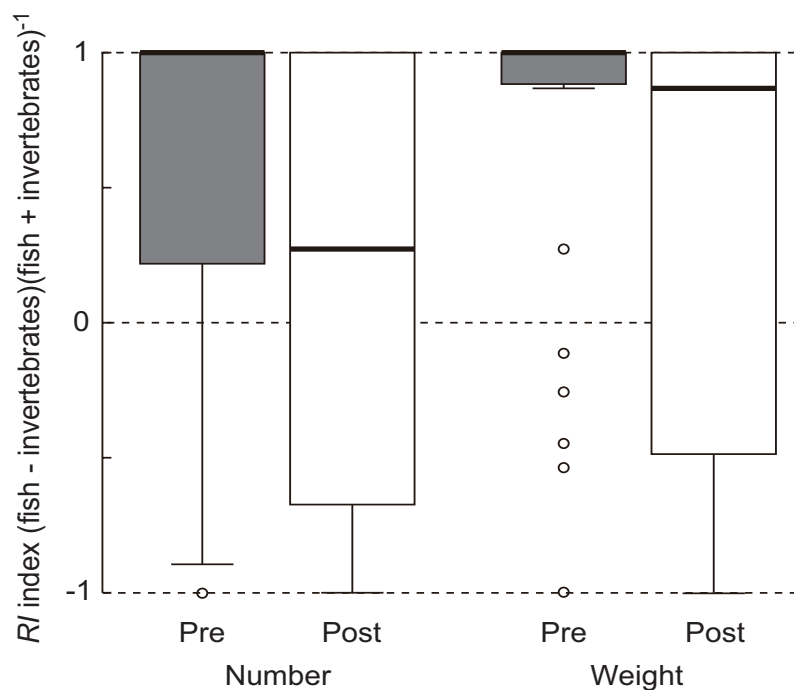


Fig. 8 Values of the relative importance index of fishes against invertebrates in the diet of *Lateolabrax latus*, based on prey numbers (left) and weight (right) in the pre- and the post-spawning season. The approximate 95% confidence range is indicated by the vertical line, the 25-75% range by box height, and the median by the thick horizontal line in each box. Open circles are outliers.

concerning the foraging habits of the species, including its seasonal occurrence in shallow habitats, is considered important as basic ecological knowledge for evaluating the roles of such predators in local communities.

Lateolabrax latus showed clearly seasonal patterns of occurrence on temperate-subtropical shallow rocky shores of the Amakusa-Shimoshima Island, south-western Japan. Two peaks of occurrence were detected in spring and autumn, while no fish was recorded in summer. Such a seasonal pattern with conspicuous absence in summer has also been reported for the early life stages of *L. latus* in different parts of southern Japan (Fujita et al. 1988; Kinoshita & Fujita 1988; Yube et al. 2006). According to these results, seasonal occurrence in shore areas is likely to be related with fluctuations in water temperature. In the present study, adult *L. latus* was observed at temperatures between 13.9 to 24.2°C, concurring with results from previous studies in shallow waters: 12.2–24.0°C (Kinoshita & Fujita 1988) and 11.8–26.6°C (Yube et al. 2006). These suggest that water temperature is possibly a good indicator of the appearance of *L. latus* in shallow waters, not only for larvae and juveniles but also for adult individuals.

It is probable that *L. latus* individuals move to cooler or deeper waters when surface temperature becomes higher than its suitable range. Migration to northern areas is not

plausible, as its geographical distribution is limited to mainly around southern Japan. There is a report that *L. latus* was collected in the freshwater habitat of a river at Tanegashima Island, ~230 km south of our study site, in August: water temperature was 24.5°C at the time of collection (Sakai, Satou & Nakamura 1998). Thus, migration to river is possible under certain circumstances, but is unlikely to be important in our region where there are not enough large rivers to support a large population biomass of this species. We note that fish sizes in our study are much larger than the size (ca. 110 mm standard length) reported from a freshwater habitat. Nevertheless, they may be able to utilise river mouths or surrounding areas with cooler water inflows.

Migration to deeper waters is another possibility but no further scientific data are available to date. According to information gained from commercial fishermen, the species is only occasionally caught by gill nets set up in near shore areas in the same seasons as the present study but not at all by line and net fishing in off-shore and deeper waters throughout the year. Thus, the species probably has a very limited distribution in shallow coastal zones.

Yet another possibility is a shift in feeding time from day to night, thus reducing the probability of capture during day-time sampling. Such a shift in daily foraging time depending on temperatures has been known in salmonids

(Fraser, Metcalfe & Thorpe 1993). Furthermore, there is also a methodological issue as temperature is known to constitute one of the important environmental variables that affect fishing with baited gear (Stoner 2004). Thus, further research on wider regional and temporal scales with different approaches are necessary to clarify the details and mechanistic background of seasonal occurrence of this fish in shallow rocky shore environments.

Our results demonstrated that this species showed slightly different patterns of response to water temperature depending on the period of rising or declining temperature: the occurrence peak during the rising period was lower than those on the declining period. It has been suggested that the behaviour of ectothermal organisms may be affected by the current tendency of temperature change rather than by absolute values on exact time. Therefore, it may make more sense to consider those two periods separately for the prediction of fish occurrence based on water temperatures. In similar vein, trends in short time scale (i.e. tendency in daily temperature fluctuation) could be important for understanding the variation in fish activity and occurrence, especially in shallow waters.

A major peak of occurrence accompanied by increase in body size was observed in spring. While both ripe and spent

gonads were observed in individuals caught in March and April, no spent gonad was found in January and February in the present study. Previous studies on larval occurrence and otolith analysis suggested that spawning occurs in nature from winter to spring (Fujita et al. 1988; Kinoshita & Fujita 1988; Yube et al. 2006). Therefore, seasonal appearance of this species may also be related to reproduction.

It may be conjectured that the two peaks of occurrence represented feeding activity in relation to pre- and post-reproduction. Relative reduction of occurrence in winter was probably due to low feeding activity during the reproductive and/or the coldest season. Another possibility is that *L. latus* might have migrated to its reproduction site(s) elsewhere, thereby resulting in reduced numbers of adults in the study site. Unfortunately, our data do not allow a clear separation of 'actual' disappearance individuals vs 'apparent' disappearance due to low feeding activity. Incorporation of other methods such as direct observation will be needed to clarify this point.

Lateolabrax species have been considered as typical piscivorous fish. Previous studies reported that *L. japonicus* (Hatanaka & Sekino 1962; Nip, Ho & Wong 2003) and *L. latus* (Inoue, Suda & Sano 2005) ontogenetically changed food utilisation towards fish consumption. Furthermore,

early stages of *L. latus* were more piscivorous than those of *L. japonicus* (Fujita et al. 1988). Our analysis also showed that the major food item of adult *L. latus* (390 - 730 mm TL) was fish. On the other hand, it is notable that adult *L. latus* also consumed a variety of other food items, especially relatively small crustaceans; even some squids (3-5 cm dorsal mantle length) were found in the guts in our preliminary observations. A similarly wide range of diet was reported for *L. latus* populations, in particular juveniles (< 73 mm standard length), from the Shimanto estuary (Fujita et al. 1988), the Sanrimatsubara (Inoue, Suda & Sano 2005) and the Uwajima Bay (Yube et al. 2006). According to these studies, juveniles mainly consumed small crustaceans such as copepods, mysids, amphipods, decapods and some fish larvae, with their relative proportions varying depending on study sites and sampling occasions.

Additionally, it was shown in the present study that the relative importance of fish/invertebrates in the diet varied among *L. latus* individuals and between the pre- and the post-spawning period, but was not related to their body size. These suggest that *L. latus* is an opportunistic consumer, but given the high proportion of fish in the diet of larger individuals (i.e. from young adult stage onwards), it is considered primarily a piscivore. However, this dietary pattern may also be explained by a preferential feeding

of abundant or favourable (in terms of sizes) food items in the foraging site. It would be necessary to conduct a more rigorous testing of feeding preference based on the abundance and size frequency distribution of potential prey items in nature (e.g. Tokeshi & Daud 2011).

Most of the consumed benthic crustaceans in the present study are closely associated with seaweeds (e.g., Caprellidea, Gammaridea and Sphaeromatidae) or dwell in nearby substrates (e.g., *Alpheus* sp., *Cirolanidae*, *Nihonotrypaea* sp. and *Sphaeromatidae*). It is notable that their proportions in the diet increased in the post-spawning season, which is probably due to their availability in relation to the phenology of seaweeds and wavy conditions in spring time. Previous studies near our study site have shown that the abundances of seaweeds and associated epifauna peaks in spring and thereafter declines towards summer (Aoki 1988; Edgar & Aoki 1993). A large amount of epifauna is thought to become available when seaweeds are agitated or dislodged from the substrates under strong wave movements in spring. These may constitute easily-available food, even though prey items are of small body size, and the large gape of *L. latus* may be effective in capturing such food in the water column.

This may point to the importance of seaweed-associated organisms as food for adult *L. latus* in the post-

spawning season. It has long been recognised by fishermen and recreational anglers that the feeding activity of the sea bass is enhanced under wave-disturbed conditions. Thus, *L. latus* is considered to rely on turbulent conditions for effective foraging. In addition, *L. latus* consumes a large number of benthic organisms dwelling under and between the stones which would probably come out to the surface or into the water column when disturbed by waves. It is also known that benthic invertebrates, especially crustaceans, tend to be more active during the nocturnal high tide (e.g. De Ruyck, McLachlan & Donn 1991; Saigusa, Okochi & Ikei 2003). In these respects, seasonal and temporal occurrence of *L. latus* in shallow rocky habitats may also be related to the availability of potential food organisms. Water temperature may not only affect directly but also have an indirect effect via the occurrence of prey species.

The fact that a large number of *L. latus* was collected in shallow coastal areas including the intertidal zone at high tide suggests that *L. latus* rely on shallow areas as feeding sites. Indeed, a wide variety of organisms from shallow areas was detected in their gut contents. Interestingly, in addition to benthic invertebrates, some demersal and supposedly intertidal fishes (e.g., *Blenniidae*, *Gobiidae* and

Tripterygiidae) were taken by *L. latus*, while the majority of consumed fishes were pelagic ones (e.g., *Clupeidae*, *Engraulidae* & *Atherinidae*). Effects on community structure of such highly mobile, opportunistic predators are hard to assess, but assuming them to be unimportant may perpetuate oversimplified models of community interactions (Edward, Conover & Sutter 1982).

Thus, it is plausible that the foraging behaviour of *L. latus* may have some influence upon the abundance and distribution of intertidal assemblages (i.e. not only benthic invertebrates but also fishes). The influence of such migratory/transient predators has been demonstrated in different shallow water systems including coral reefs (Hixon & Carr 1997) and estuaries (Sheaves 2001, Baker & Sheaves 2005). In addition, it has been revealed that there are generally more predators with a wide range of body sizes (<ca 100 cm TL) in shallow water environments than previously thought (Baker & Sheaves 2005, 2006; Becker et al. 2011). More intensive research is necessary to clarify the impact of migratory predation upon intertidal and shallow-water prey communities in different environmental settings. Clearly, exposed shallow rocky shores including intertidal areas constitute potentially important feeding sites for large predatory fish such as adult *L. latus*.

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References

- Aoki M (1988) Factors affecting population fluctuations of caprellid amphipods in habiting *Sargassum patens* bed (Preliminary report). Benthos Research 32, 42-49 (In Japanese with English abstract).
- Baker R & Sheaves M (2005) Redefining the piscivore assemblage of shallow estuarine nursery habitats. Marine Ecology Progress Series 291, 197-213.
- Baker R & Sheaves M (2006) Visual surveys reveal high densities of large piscivores in shallow estuarine nurseries. Marine Ecology Progress Series 323, 75-82.
- Becker A, Cowley PD, Whitfield AK, Järnegen J & Næsje TF (2011) Diel fish movements in the littoral zone of a temporarily closed South African estuary. Journal of Experimental Marine Biology and Ecology 406, 63-70.
- Blaber SJM & Blaber TG (1980) Factors affecting the distribution of juvenile estuarine and inshore fish. Journal of Fish Biology 17, 143-162.
- Burrows MT, Gibson RN, Robb L & Comely CA (1994) Temporal movement patterns of juvenile flatfishes and their predators: under water television observations. Journal of Experimental Marine Biology and Ecology 177, 241-268.
- Castellanos-Galindo GA, Krumme U & Willis TJ (2010) Tidal influences on fish distributions on tropical eastern Pacific rocky shores (Colombia). Marine Ecology Progress Series 416, 241-254.
- Clarke KR & Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation (2nd ed). PRIMER-E, Plymouth, UK.
- De Ruyck AMC, McLachlan A & Donn TE (1991) The activity of three intertidal sand beach isopods (Flabellifera: Cirolanidae). Journal of Experimental Marine Biology and Ecology 146: 163-180.
- Edger GJ & Aoki M (1993) Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese Sargassum. Oecologia 95,122-133.
- Edwards DC, Conover DO & Sutter III F (1982) Mobile predators and the structure of marine intertidal communities. Ecology 63, 1175-1180.
- Faria C & Almada VC (2006) Patterns of spatial distribution and behaviour of fish on a rocky intertidal platform at high tide. Marine Ecology Progress Series 316, 155-164.
- Fraser NHC, Metcalfe NB & Thorpe JE (1993) Temperature-dependent switch between diurnal and nocturnal foraging in salmon. Proceedings of the Royal Society, London, B 252, 135-139.
- Fujita S, Kinoshita I, Takahashi I & Azuma K (1988) Seasonal occurrence and food habits of larvae and juveniles of two temperate basses in the Shimanto Estuary, Japan. Japanese Journal of Ichthyology 35, 365-370.
- Hatanaka M & Sekino K (1962) Ecological studies on the Japanese sea-bass, *Lateolabrax japonicus* – I. Feeding habit. Bulletin of the Japanese Society for the Science of Fish 28 851-856 (In Japanese with English abstract)
- Hatooka K (2002) Moronidae. In: T Nakabo (ed) p 683. Fishes of Japan with Pictorial Keys to the Species (English ed), Tokai University Press, Tokyo.
- Hixon MA & Carr MH (1997) Synergistic predation, density dependence, and population regulation in marine fish. Science 277, 946-949.
- Inoue T, Suda Y & Sano M (2005) Food habits of fishes in the surf zone of a sandy beach at Sanrimatsubara, Fukuoka Prefecture, Japan. Ichthyological Research 52, 9-14.
- Islam MS & Tanaka M (2006) Ontogenetic dietary shift of Japanese sea bass during larva-juvenile transition in Ariake Bay. Marine Ecology Progress Series 323, 305-310.
- Islam MS, Yamashita Y & Tanaka M (2011) A review on the early life history and ecology of Japanese sea bass and implication for recruitment. Environmental Biology of Fishes 91, 389-405.
- Kinoshita I & Fujita S (1988) Larvae and juveniles of temperate bass, *Lateolabrax latius* occurring in the surf zones of Tosa Bay, Japan. Japanese Journal of Ichthyology 34, 468-475.

- Kneib RT (1987) Predation risk and use of intertidal habitats by young fishes and shrimp. *Ecology* 68, 379-386.
- Lubchenco L, Menge BA, Garrity SD, Lubchenco PJ, Ashkenas LR, Gaines SD, Emlet R, Lucas J & Strauss S (1984) Structure, persistence and role of consumers in a tropical rocky intertidal community (Taboguilla Island, Bay of Panama). *Journal of Experimental Marine Biology and Ecology* 78, 23-73.
- McIvor CC & Odum WE (1988) Food, predation risk, and microhabitat selection in a marsh fish assemblage. *Ecology* 69, 1341-1351.
- Matsumiya Y, Mitani T & Tanaka M (1982) Changes in distribution pattern and condition coefficient of the juvenile Japanese sea bass with the Chikugo River ascending. *Bulletin of the Japanese Society for the Science of Fish* 48, 129-138.
- Matsumiya Y, Masumoto H & Tanaka M (1985) Ecology of ascending larval and early juvenile Japanese sea bass in the Chikugo estuary. *Bulletin of the Japanese Society for the Science of Fish* 51, 1955-1961.
- Mito S (1957) On the egg development and larvae of a Japanese sea bass, *Lateolabrax japonicus* (Cuvier). *Science Bulletin Faculty of Agriculture, Kyushu University* 16, 115-124 (In Japanese with English abstract).
- Nip THM, Ho WY & Wong CK (2003) Feeding ecology of larval and juvenile black seabream (*Acanthopagrus schlegelii*) and Japanese seaperch (*Lateolabrax japonicus*) in Tolo Harbour, Hong Kong. *Environmental Biology of Fishes* 66, 197-209.
- Rangeley RW & Kramer DL (1995) Tidal effects on habitat selection and aggregation by juvenile pollock *Pollachius virens* in the rocky intertidal zone. *Marine Ecology Progress Series* 126, 19-29.
- Ruiz GM, Hines AH & Posey MH (1993) Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. *Marine Ecology Progress Series* 99, 1-16.
- Saigusa M, Okochi T & Ikei S (2003) Nocturnal occurrence, and synchrony with tidal and lunar cycles, in the invertebrate assemblage of a subtropical estuary. *Acta Oecologica* 24, S191-S204.
- Sakai H, Satou M & Nakamura M (1998) A record of the temperate bass, *Lateolabrax latius*, from a freshwater habitat of Tanegashima Island, Japan. *Japanese Journal of Ichthyology* 45, 107-109 (In Japanese with English abstract).
- Sheaves M (2001) Are there really few piscivorous fishes in shallow estuarine habitats? *Marine Ecology Progress Series* 222, 279-290.
- Stoner AW (2004) Effects of environmental variables on fish feeding ecology: implications for the performance of baited fishing gear and stock assessment. *Journal of Fish Biology* 65, 1445-1471.
- Tokeshi M & Arakaki S (2011) Habitat complexity in aquatic systems: fractals and beyond. *Hydrobiologia* 685, 27-47.
- Tokeshi M & Daud JRP (2011) Feeding electivity in *Acanthaster planci*: a null model analysis. *Coral Reefs* 30, 227-235.
- Yube Y, Iseki T, Hibino M, Mizuno K, Nakayama K & Tanaka M (2006) Daily age and food habits of *Lateolabrax latius* larvae and juveniles occurring in the innermost shallow waters of Uwajima Bay, Japan. *Fisheries Science* 72, 1236-1249.



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There is a paucity of information on large mobile predators in shallow marine environments. While the influence of selectivity in sampling cannot be assessed in this study, nevertheless the basic data are considered of value.

Supplementary Information

“Foraging ecology of a large opportunistic predator (adult *Lateolabrax latus*) on a temperate-subtropical rocky shore”

by

Arakaki S, Hutchinson N and Tokeshi M

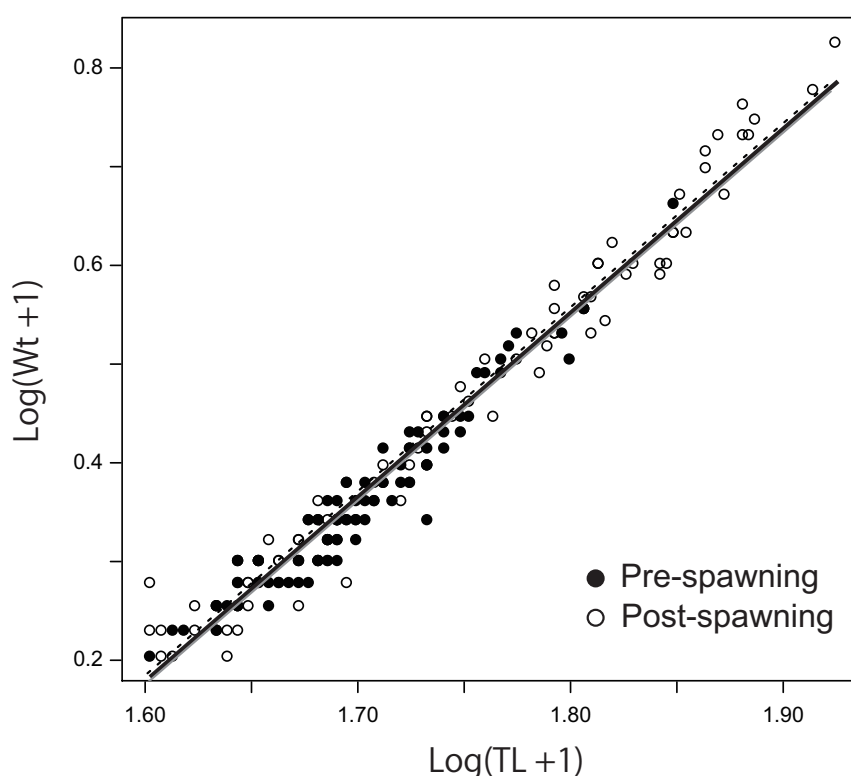


Fig. S1 Relationship between total body length (TL) and body weight (Wt) on the logarithmic scale. There was a significant positive relationship (filled and open circles with dark line: $\text{Log}(Wt) = -2.83 + 1.88 \cdot \text{Log}(TL)$, $r^2 = 0.97$, $P < 0.01$). The generalised liner model (GLM) and ANCOVA were performed to examine differences in the relationship between reproductive seasons. In the case of GLM, the best model (according to the smallest AIC value, -777.6) included reproductive season as an explanatory variable (i.e. seasonal differences were detectable). Estimated lines are: (pre-spawning) filled circles with grey line, $\text{Log}(Wt) = -2.80 + 1.86 \cdot \text{Log}(TL)$; (post-spawning) open circles with dotted line, $\text{Log}(Wt) = -2.81 + 1.86 \cdot \text{Log}(TL)$. ANCOVA also revealed significant difference between seasons: post-spawning individuals were slightly heavier than pre-spawning ones ($P < 0.022$). Regression lines were essentially very similar, although the seasonal differences were statistically significant at $P = 0.05$. On balance, we believe more data are needed to discuss further the TL-Wt relationship.

A note on data handling in this study:

The present study demonstrated that the foraging pattern of *L. latus* varied temporally and among individuals, though the mechanistic background of variation is uncertain at this stage. In relation to the analysis of temporal change in diet, the system of time categorization used can be important. In *L. latus*, spawning is expected from winter to spring, which basically coincides with the period of change in water temperature trends (declining to rising). Therefore, time categorization based on (i) spawning periods and (ii) temperature trends are essentially equivalent (i.e. pre-spawning = the declining period, post-spawning = the rising period). There were only 8 cases (out of all 112) that did not match these. We also conducted the analyses based on water temperature categories, which showed the same pattern as for the spawning period categories. Water temperature may have some influence on the behaviour of the species including spawning and foraging, directly and indirectly. If so, temperature rather than calendar month may be more appropriate a measure for evaluating changes in foraging patterns. However, the relationship between water temperature and spawning of the species is still not clear. In the present study, we focused on the 'potential' influence of spawning on the fish's foraging pattern; hence our preference for the categorization based on spawning seasons. Apart from water temperature and spawning seasons, there are possibly other criteria usable for time series categorization.

In addition to above, time resolution is also an important aspect for evaluating the patterns and their causes. In the present study, the observed data were separated into and compared between two groups (i.e. pre- and post-spawning) only. Ideally, a larger number of temporal divisions should be employed if sufficient numbers of samples are available. These points await further research.

