# LIFE HISTORY OF BANGGAI CARDINALFISH, *PTERAPOGON KAUDERNI* (ACTINOPTERYGII: PERCIFORMES: APOGONIDAE), FROM BANGGAI ISLANDS AND PALU BAY, SULAWESI, INDONESIA

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**Background.** The paternal mouthbrooding Banggai cardinalfish, *Pterapogon kauderni* Koumans 1933, has an exceptionally restricted endemic range for a marine fish, is traded internationally as a marine ornamental and listed as *endangered* in the IUCN Red List. This paper aims to contribute to the body of knowledge regarding the biology of this species, based on studies on the endemic population in the Banggai Archipelago and the introduced population in Palu Bay, Central Sulawesi Province, Indonesia.

**Materials and methods.** Length frequency data collected over the period 2004–2012 ($n = 23\ 230$) were analysed using the ELEFAN approach (FiSAT software). A length–weight relation was derived from measurements of 1002 individuals from the Banggai Archipelago. Specimens from the Palu Bay population were used to study reproductive parameters ($n = 80$), morphometric relations ($n = 54$) and feeding habits ($n = 30$).

**Results.** The ELEFAN analysis suggested an annual recruitment peak (September to December) and VBGF parameter estimates of $L_\infty = 7.1$ cm (SL), $K = 0.74$ year$^{-1}$ and $t_0 = -0.11$ year, suggesting first maturity at 1 year, and longevity of 3–5 years. Total mortality ($Z$) and natural mortality ($M$) estimates of 4.4 year$^{-1}$ and 2.2 year$^{-1}$ yielded fishing mortality $F = 2.2$ year$^{-1}$ and exploitation rate $E = 0.5$. Length–weight relation parameters were: $a = 0.18$; $b = 2.15$. There was no significant morphological difference between sexes. Gonad maturation began at 2.9–3.5 cm SL, all specimens $\geq 4.2$ cm SL were sexually mature. Mean observed fecundity (59, $n = 21$) and number of eggs brooded by males (59, $n = 17$) were similar. Observed sex ratio was 1.67 males per female. Gut content indicated an omnivorous, predominantly carnivorous diet. Copepods and decapod larvae were the most abundant components in adult (SL $\geq 4.2$ cm) and sub-adult (SL $\leq 4.2$ cm) diets respectively. Adult diet appeared to be more varied. No empty guts were observed.

**Conclusion.** This study provides data for a major reassessment of *Pterapogon kauderni* life history parameters in FishBase, the global database of fishes. *P. kauderni* spawning is associated with the lunar cycle; the seasonal recruitment peak is probably related to improved reproductive success during the calm season. With strong indications of a decline in the endemic population due to habitat degradation and loss (independent of fishing pressure), current exploitation levels may be unsustainable. Research is required to further refine life-history parameters (e.g. sex ratio) and elucidate issues such as fasting in brooding male Banggai cardinalfish and ontogenetic differences in diet.

**Keywords:** growth, mortality, length-frequency, ELEFAN, length–weight relation, maturity, reproduction, diet and feeding habits

## INTRODUCTION

The Banggai cardinalfish, *Pterapogon kauderni* Koumans, 1933, is a small and visually attractive shallow-water reef fish, popular in the marine aquarium trade. The known endemic distribution is extremely limited for a marine fish, with ±30 km$^2$ of habitat spread over around 32 small islands within an area of ±5500 km$^2$ (Vagelli 2008). Introduced populations have become established along

several trade routes, including at least two sites in Palu Bay (Moore and Ndobe 2007). The Banggai cardinalfish is a paternal mouth-brooder with direct development and without pelagic dispersal phase, as the larvae, on release, swiftly seek refuge in nearby substrate (Vagelli 1999). Post-release, Banggai cardinalfish maintain a sedentary lifestyle with high site fidelity (Kolm et al. 2005).

Considered at risk of extinction in the wild due to over-exploitation for the marine aquarium trade (Lunn and Moreau 2004) and habitat degradation (Moore et al. 2011, 2012), international concern has led to listing of the Banggai cardinalfish as endangered in the IUCN (International Union for the Conservation of Nature) Red List (Allen and Donaldson 2007). While a number of studies have been published on various aspects of *Pterapogon kauderni* biology and ecology, literature on specific Banggai cardinalfish life-history traits, both in its endemic distribution area and for the introduced populations, remains limited, as reflected by the paucity of life history data in FishBase (Froese and Pauly 2013). This paper presents data on life-history parameters of *P. kauderni* including growth, mortality, reproduction, and diet, based on research carried out over 8 years (2004–2012) in the Banggai Archipelago and in Palu Bay, Central Sulawesi Province, Indonesia. This information will contribute to the knowledge base for conservation management of the species.

## MATERIALS AND METHODS

**Sampling.** Banggai cardinalfish, *Pterapogon kauderni*, specimens were captured at Bone Baru, Banggai Island and in Palu Bay (Fig. 1) using a '*cang*'-style mobile fyke net, such as used in the ornamental fishery[*]. The dates and coordinates for each site as well as the number of fish captured, post-capture treatment, and use in this study are given in Table 1, and the habitats defined as follows:

- Coral reef (CR): coral reef area near the reef crest or upper slope;
- Reef flat (RF): flat or slightly sloping areas shoreward from the reef crest, substrate dominated by coral or dead coral and rubble;
- Seagrass (SG): areas shoreward from the reef crest, substrate usually predominantly sandy with visually obvious seagrass cover, some coral and/or rubble;
- Mangrove (MG): between the prop roots of *Rhizophora* sp., mainly below the low-tide line.

Length-frequency data were also obtained from belt transect surveys (transect size 20 m × 5 m = 100 m², census of fish within transect) carried out over the period 2004–2012. The number of fish, month, and year are shown in Table 1. The sea surface temperature (SST) and other environmental parameters at the sampling sites are given in Table 2.

**Growth and mortality.** The available length frequency data were regrouped into 6 mm classes (0–5.9; 6–11.9, etc., with class mid-lengths [ML] at 3, 9, etc.; see Table 3), then analysed using the FISAT II software (Gayanilo et al. 2005) to obtain estimates of the parameters of the von

Bertalanffy Growth Function (VBGF), of the form

$$L_t = L_\infty \cdot (1 - e^{-K(t - t_0)}) \qquad [1]$$

where: $L_\infty$ is the mean length the fish would attain is they were to live indefinitely, $K$ (time$^{-1}$) is the rate at which $L_\infty$ is approached, and $t_0$ the predicted 'age' at a length (or weight) of zero (Pauly 1984). Specifically, $L_\infty$ was estimated from a Wetherall Plot (Wetherall 1986) as implemented in FiSAT II, $K$ was estimated by its 'scanning for K routine', and $t_0$ was estimated by solving equation [1] for a size at known age, once $L_\infty$ and $K$ had been estimated (see below). Note also that longevity ($t_{max}$), if it is assumed to be the age at which fish reach 95% of $L_\infty$, can be approximated by $t_{max} \approx 3 \cdot K^{-1}$ (Pauly 1984).

Comparisons between pairs of $L_\infty$ and $K$ estimates were performed using an index of growth performance (ø') defined by the formula proposed by Pauly (1983, 2010):

$$ø' = \log(K) + 2 \cdot \log(L_\infty) \qquad [2]$$

Natural mortality ($M$) was estimated from the empirical equation (Pauly 1980):

$$\log(M) = -0.0066 - 0.279 \cdot \log(L_\infty) + 0.6543 \cdot \log(K) + 0.4634 \cdot \log(T) \qquad [3]$$

where: $L_\infty$ is expressed in cm, $K$ is in year$^{-1}$, and $T$ is the mean water temperature, in °C.

Total mortality ($Z$) was then estimated using a length-converted catch curve (Pauly and Ingles 1981), thus allowing fishing mortality (from $Z - M = F$) and exploitation rate (from $E = F \cdot Z^{-1}$) to be estimated as well.

**Length–weight relation and other morphometrics.** The parameters 'a' and 'b' of a length–weight relation of the form

$$W = a \cdot L^b \qquad [4]$$

where: $W$ is the wet weight in g and $L$ is the standard length (SL) in cm, were determined from the analysis of 1002 Banggai cardinalfish specimens collected from Bone Baru in the Banggai Archipelago. The length ($L$) of each specimen was measured to the nearest millimetre (mm). The specimens were then weighed to the nearest 0.1 g, and the weights averaged within each mm length class. A linear regression was then fitted to the log-transformed variables, i.e., $L$ and the corresponding (mean) weights, which leads to an equation of the form

$$\log(W) = \log(a) + b \cdot \log(L) \qquad [5]$$

Fifty four specimens from Kadongo in Palu Bay were measured to the nearest mm to relate their standard length to a number of other morphometric features (Fig. 2). The ratios of each measurement to standard length were then calculated, and averaged for females ($n = 27$), males ($n = 27$) and for the entire sample ($n = 54$). The ratios for females and males were compared using one-way analysis of variance (ANOVA). Linear regression was performed for the ratio of total length to standard length (TL · SL$^{-1}$).

**Reproductive biology.** Each specimen ($n = 80$) was dissected and the gonad removed and weighed. The gonadosomatic index (GSI) was calculated from

$$GSI = W_g \cdot W^{-1} \qquad [6]$$

where: $W_g$ is the gonad weight and $W$ is the total body weight. Eggs were counted in both females (in developing egg masses) and males (in their buccal cavities). In juvenile specimens, where sex was not visually apparent, his-

tological preparations were made and examined under a binocular microscope (4 × 20 magnification). The eggs contained in the egg sacs were clearly visible beside mature and maturing ovaries; this yielded fecundity (number of eggs in female specimens). This was complemented by effective fertility (number of eggs brooded by males), size at first maturity and sex ratio (number of males × number of females$^{-1}$) of the sample.

**Feeding habits.** Specimens from the Palu Bay population used in the feeding study ($n = 30$) were measured and weighted (see above), and their gut tract was then removed and assessed as to its fullness, which ranged from very full to near empty (there were no empty guts).

Each gut tract was then weighed (to the nearest 0.01 g), and the gut contents separated using 70% alcohol (4 drops) and prepared for examination under a (4 × 10 magnification) binocular microscope. Food item identification was based mainly on Sachlan (1972).

**RESULTS**

**Environmental parameters.** All specimens of *Pterapogon kauderni* were collected from shallow (maximum 6 m) coastal waters, mainly embayments or lagoons or other habitats sheltered from strong wave action (e.g., mangrove stands). Environmental parameter values at the sites where *P. kauderni* samples were collected are given in Table 2.
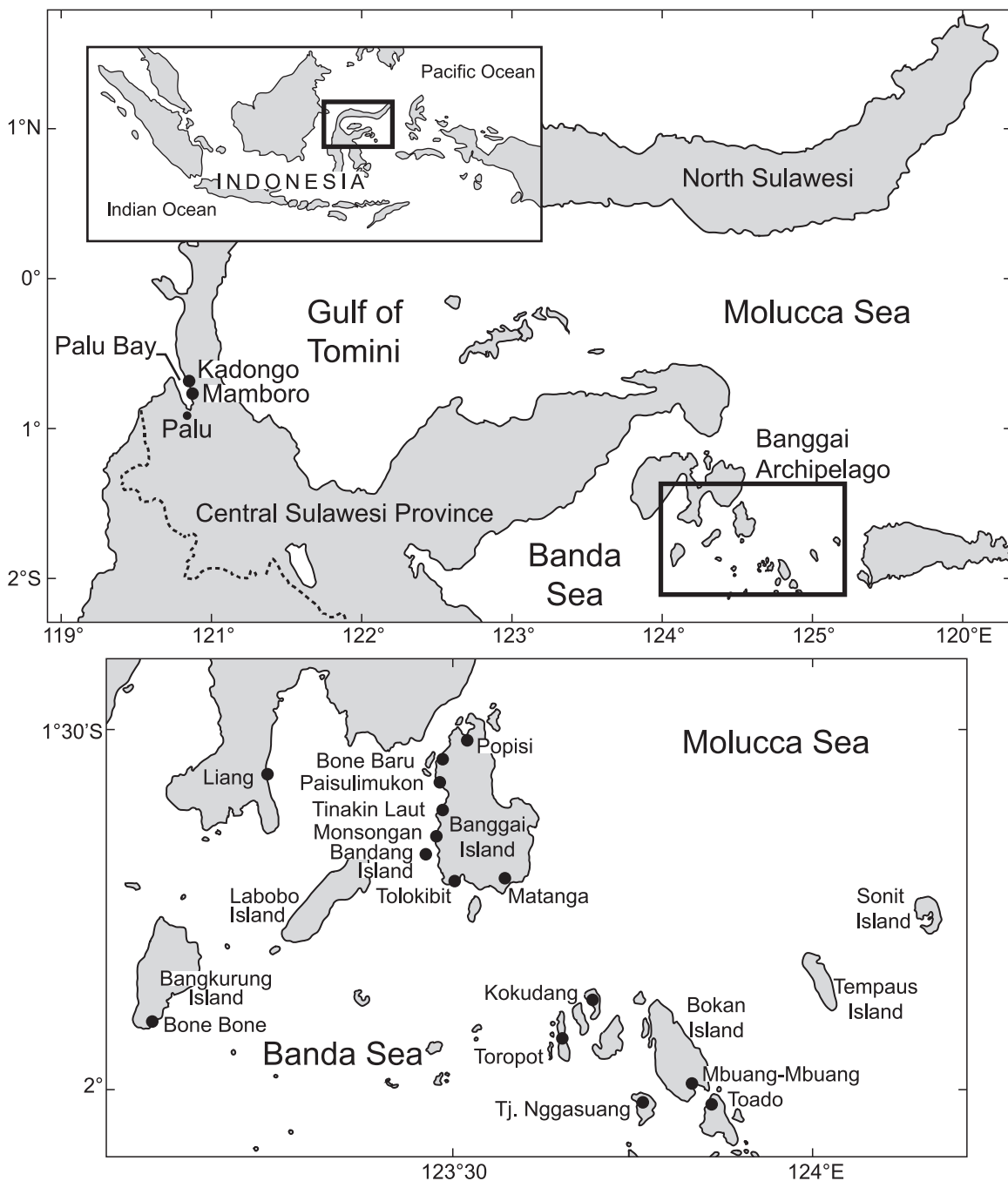


**Fig. 1.** Map of Central Sulawesi, showing the locations of the sampling sites mentioned in the text and tables of this contribution

The observed water temperature range was 26–31ºC. Despite a preponderance of readings of 29ºC, the average temperature in *P. kauderni* habitat is probably 28ºC, given that temperatures are lower at night, when few samples were taken. Salinity was in the PSS 29–35 range at all sites and in all seasons where measurements were taken. **Growth and mortality.** The largest specimen found in this study also seems to be the largest specimen of *Pterapogon kauderni* reported to date. This specimen, a female, provided a value of $L_{max} = 6.6$ cm (SL) and 8.6 cm (TL), and a weight of 11.3 g.

The analysis of the length-frequency data in Table 3 yielded $SL_\infty = 7.1$ cm (or $TL_\infty = 10.7$ cm; Table 4) and

$K = 0.74$ year$^{-1}$ (Fig. 3). Given these parameter values, solving the VBGF [equation 1] for a length of 4 cm at 1 year (taken to be the mean length and age at first maturity respectively, see below) yields an estimated $t_0 \approx -0.11$. Thus, the growth in SL of *P. kauderni* can be described by

$$L_t = 7.1 \cdot (1 - \exp^{-(0.74(t + 0.11))}) \qquad [7]$$

which implies a longevity of 3–5 years.

Total mortality $Z$ was 4.4 year$^{-1}$ (Fig. 4). Subtracting $M$, estimated for a temperature of 28ºC as 2.2 year$^{-1}$, yields an estimate of $F$ as 2.2 year$^{-1}$ and an $E$ of 0.5.

**Length–weight relation and other morphometrics.** The 1002 Banggai cardinalfish, *Pterapogon kauderni*, in this study ranged from 1 cm to 6 cm. The 48 log-transformed

**Table 1**

Details on samples of Banggai cardinalfish, *Pterapogon kauderni*,
collected from 2008 to 2011 in Central Sulawesi

| Date [D/M/Y] (time) | Sampling site | Latitude/ Longitude | Fish sampled | Field treatment | Primary use |
|---|---|---|---|---|---|
| 29/10/08 (1000–1300) | Mamboro (Palu Bay) | 0°47′51″S 119°52′14″ E | 30 | Preserved in 70% alcohol | Diet study |
| 12/05/09 24/05/09 17/07/09 31/07/09 (0900–1200) | Kadongo (Palu Bay) | 0°44′51″S 119°51′21″E | 20 20 20 20 | Preserved in 70% alcohol | Reproductive biology |
| 26/12/11 (1500–1700) | Bone Baru | 1°31′53″S 123°29′35″E | 1003 | Fixed in formalin (4% for 24 h) then preserved in 70% alcohol | Growth parameters |

**Table 2**

Environmental parameters at Banggai cardinalfish, *Pterapogon kauderni*,
sample collection sites (Central Sulawesi)

| Site | Month/ Year | Time of day [GMT + 8] | SST [ºC] | Depth [m] | Salinity [psu] | Habitat/ Ecosystem |
|---|---|---|---|---|---|---|
| Popisi | | 0800 | 28 | 0.5–1.5 | 34 | CR, RF, SG |
| Bone Baru | | 0700 1500 | 28 29 | 0.5–3 | 32 | CR, RF, SG |
| Paisulimukon | | 1100 | 29 | 0.5–3 | 34 | CR |
| Tinakin Laut | 12/2011 | 0830 | 28 | 1–2 | 33–34 | RF, SG |
| Monsongan | | 1130 | 29 | 1–2 | 34 | RF, SG |
| Tolokibit | | 1100 | 29 | 1–2 | 30–32 | RF, SG |
| Matanga | | 1300 | 29 | 1–2 m | 31–32 | RF, SG |
| Tinakin Laut | 04/2007 | 0830–1730 | 30–31 | 0.5–3 | 32–35 | CR, RF, SG |
| Tanjung Nggasuang | | 1000 | 29 | 1–3 | 33 | Lagoon |
| Kokudang | | 0830 | 29 | 1–3 | 34 | CR, RF, SG |
| Toropot | | 1230 | 29 | 1–2 | — | SG |
| Mbuang-Mbuang | 06/2012 | 1200 | 29 | 1–2 | — | SG, sand |
| Toado | | 1000 | 29 | 1–2 | 33 | MG, RF |
| Bone Bone | | 0930 | 29 | 0.5–3 | — | RF, SG, sand |
| P. Bandang | | 1040 | 28 | 0.5–6 | — | CR, RF, SG |
| Mamboro | 11/2006 10/2008 | Monitoring (24 h) | 26–31 | 0.5–4 | 29–34 | CR, SG |
| Kadongo | 05/2009 07/2009 | 1030 | 29 | 1–3 | 32 | CR, RF, SG |

GMT = Greenwich mean time, SST = sea surface temperature, CR = coral reef, RF = reef flat, SG = seagrass, MG = mangrove.

data pairs used for the analysis are shown in Fig. 5, along with the linear regression $\log(W) = 2.151 \cdot \log(SL) - 0.744$ ($r = 0.993$), from which the relation $W = 0.18 \cdot L^{2.15}$ can be derived. Thus, the growth in (wet) weight of *P. kauderni* can be described by

$$W_t = 12.2 \cdot (1 - \exp^{-(0.74(t+0.11))})^{2.15} \qquad [8]$$

Figure 6 illustrates the growth in length and weight of *P. kauderni* as inferred from the data presented so far.

Morphometric parameters and weight of the specimens measured in this study are given in Table 4 for females and males. Differences between males and females in average values of the ratios calculated were not significant ($F < F_{crit, \alpha = 0.05} = 4.03$), except for the mouth gape (MG) to standard length ratio ($F = 7.52 > F_{crit, \alpha = 0.01} = 7.15$; $P = 0.0083$). There was no significant difference between the TL $\cdot$ SL$^{-1}$ ratio for males and females

**Table 3**

Standard length-frequency data of Banggai cardinalfish, *Pterapogon kauderni*, sampled in the Banggai Archipelago over the period of 2004–2012 based on 6-mm size classes

| ML | 2004 | | 2006 | | 2007 | | | 2009 | 2011 | | 2012 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| [mm] | Oct | Nov | Nov | Dec | Apr | Jul | Oct | Sep | Sep | Dec | Jun |
| 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9 | 14 | 9 | 77 | 21 | 76 | 72 | 75 | 13 | 84 | 542 | 685 |
| 15 | 17 | 10 | 141 | 194 | 161 | 59 | 101 | 21 | 89 | 581 | 989 |
| 21 | 12 | 8 | 151 | 177 | 355 | 84 | 112 | 86 | 98 | 1301 | 2586 |
| 27 | 11 | 7 | 109 | 96 | 291 | 70 | 89 | 69 | 91 | 1213 | 1874 |
| 33 | 9 | 6 | 39 | 46 | 153 | 67 | 78 | 36 | 79 | 409 | 1325 |
| 39 | 7 | 8 | 48 | 35 | 118 | 114 | 69 | 49 | 98 | 533 | 577 |
| 45 | 9 | 17 | 94 | 84 | 296 | 129 | 64 | 84 | 39 | 567 | 1174 |
| 51 | 13 | 19 | 135 | 91 | 248 | 147 | 125 | 91 | 40 | 396 | 2173 |
| 57 | 3 | 7 | 25 | 10 | 57 | 9 | 39 | 5 | 6 | 38 | 165 |
| 63 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 6 |
| Total | 95 | 91 | 819 | 754 | 1756 | 751 | 752 | 454 | 624 | 5580 | 11554 |

ML = class mid- length ($n = 23230$).
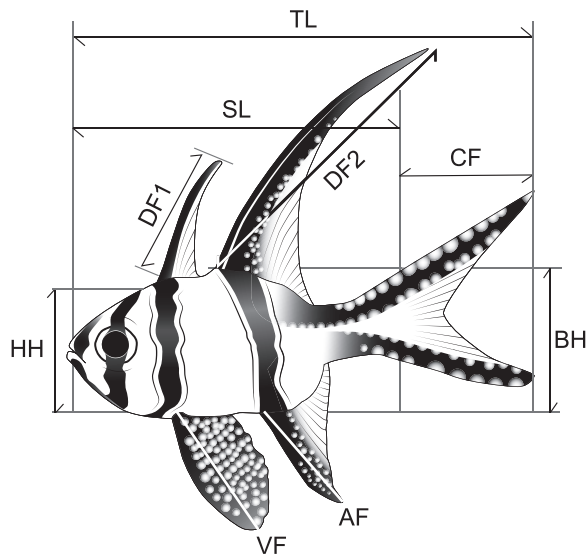




**Fig. 2.** Schematic representation of a specimen of Banggai cardinalfish, *Pterapogon kauderni*, illustrating where measurements were taken; TL = total length; SL = standard length; HH = head height; BH = body height; CF = caudal fin length; DF1 = anterior dorsal fin length; DF2 = posterior dorsal fin length; VF = ventral fin length; AF = anal fin length; PL = pectoral fin length (not shown) and MG = mouth gape (not shown)
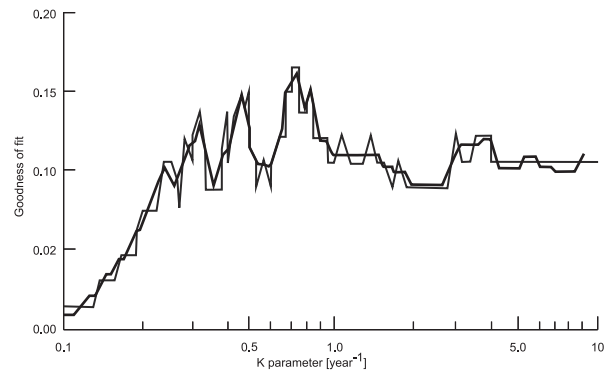
**Fig. 3.** Output of the ELEFAN software routine scanning for the optimal estimates of *K* for Banggai cardinalfish, *Pterapogon kauderni*, given SL$_\infty$ = 7.1 cm and the length-frequency data in Table 3; The best estimate of *K* = 0.74 year$^{-1}$, corresponding to a longevity of 3–5 years

($F = 0.007 < F_{\text{crit}, \alpha = 0.05} = 4.03$). The mean value of the ratio of TL to SL ± SD expressed in percentage points was ≈ 150 ± 12 and linear regression of TL versus SL yielded a slope ± SE of 1.5 ± 0.1 with an $r^2$ of 0.99 ($n = 54$). The mean aspect ratio (standard length divided by body height) ± SE was 2.07 ± 0.02 for the total sample ($N = 54$) and was not significantly correlated with length ($r^2 = 0.001$) or sex ($F = 1.01 < F_{\text{crit}, \alpha = 0.05} = 4.03$).

**Reproductive biology.** A synopsis of the data on female *Pterapogon kauderni* gonad development is shown in Table 5 ($n = 30$). The (single) gonad shape and size was similar in male and female *P. kauderni*, varying in colour (paler in males) and texture (granulose in females). Developing masses encased in an egg envelope were present in most adult female specimens. Mature male and female *P. kauderni* gonads photographed during this study are shown in Fig. 7.

Effective fertility based on numbers of eggs or larvae brooded by male specimens (13 specimens collected from Bone Baru and 4 brooding males collected at Kadongo) ranged from 45 to 99 eggs, with a mean value ± SE of 59 ± 2.7 eggs or larvae. Several other males captured during the length/weight study were also brooding however the eggs or larvae were released on capture and could not be recovered for counting. The smallest of these had an SL of 4.2 cm.

A regression of fecundity and fertility against body size (SL or *W*) showed no significant trend ($P > 0.05$, $r^2 < 0.1$), and thus fecundity in adult *P. kauderni* can be summarized by their mean fecundity ± SE (58 ± 4 eggs per female). The similarity between fertility estimates based on numbers of eggs in female gonads and eggs/larvae brooded by male *P. kauderni* indicates that few (if any) eggs are lost in the process of fertilisation and transfer to the male buccal pouch. The sex ratio of the (random) sample ($n = 80$) was 1.67, i.e., heavily biased towards males.

Table 6 shows the percentages of occurrence of various stages of gonad development in male *P. kauderni*. Male gonad development began at SL ≈ 3 cm and all male
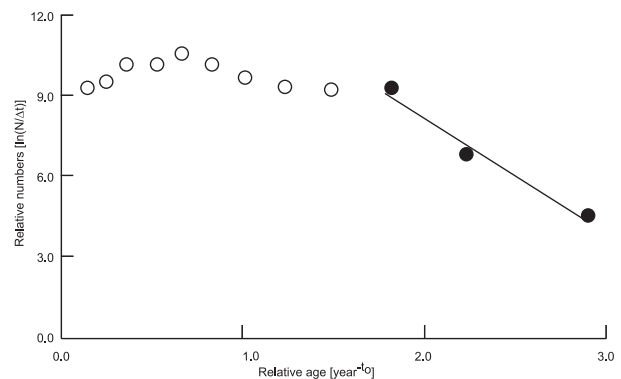


**Fig. 4.** Length-converted catch curve for Banggai cardinalfish, *Pterapogon kauderni*, as used to estimate $Z = 4.4$ year$^{-1}$ from the 3 largest length classes

**Table 4**

Standard length (SL), weight (*W*) and 13 morphometric ratios (expressed as percentages) for 27 male and 27 female Banggai cardinalfish, *Pterapogon kauderni*, and significance levels of a one-way analysis of variance (ANOVA) for male (♂) versus female (♀) specimens

| Parameter | Adult Male *P. kauderni* ($n = 27$; SL: 4.3–5.4 cm) | | | Adult Female *P. kauderni* ($n = 27$; SL: 4.1–5.7 cm) | | | ANOVA ♂–♀ |
|---|---|---|---|---|---|---|---|
| | Average | SD | SE | Average | SD | SE | |
| SL [cm] | 4.86 | 0.33 | 0.06 | 4.87 | 0.43 | 0.08 | ns |
| *W* [g] | 4.89 | 1.23 | 0.24 | 4.78 | 1.34 | 0.26 | ns[c] |
| TL · SL$^{-1}$ [%] | 150.43 | 12.38 | 2.38 | 150.17 | 10.50 | 2.02 | ns |
| DF1 · SL$^{-1}$ [%] | 36.03 | 6.14 | 1.18 | 33.84 | 5.18 | 1.00 | ns |
| DF2 · SL$^{-1}$ [%] | 74.23 | 15.25 | 2.94 | 66.85 | 18.09 | 3.48 | ns |
| PF · SL$^{-1}$ [%] | 26.49 | 6.18 | 1.19 | 25.10 | 3.55 | 0.68 | ns |
| VF · SL$^{-1}$ [%] | 45.34 | 4.65 | 0.90 | 44.30 | 3.88 | 0.75 | ns |
| AF · SL$^{-1}$ [%] | 38.59 | 6.38 | 1.23 | 38.41 | 6.91 | 1.33 | ns |
| CF · SL$^{-1}$ [%] | 49.73 | 7.26 | 1.40 | 46.84 | 6.27 | 1.21 | ns |
| HH · SL$^{-1}$ [%] | 37.13 | 6.78 | 1.30 | 37.19 | 4.87 | 0.94 | ns |
| MG · SL$^{-1}$ [%] | 27.89 | 2.77 | 0.53 | 25.51 | 3.58 | 0.69 | vs |
| TL · BH$^{-1}$ [%][a] | 3.06 | 0.29 | 0.06 | 3.14 | 0.28 | 0.05 | ns |
| SL · BH$^{-1}$ [%][b] | 2.04 | 0.19 | 0.04 | 2.09 | 0.16 | 0.03 | ns |
| MG · SL$^{-1}$  range | 22.73%–32.65% | | | 19.51%–33.33 % | | | |

SD = standard deviation; SE = standard error; ns = not significant ($F < F_{\text{crit}, \alpha = 0.05} = 4.03$); vs = very significant ($F = 7.52 > F_{\text{crit}, \alpha = 0.01} = 7.15$; $P = 0.00835 < 0.01$; $n$ = number of fish measured; TL = total length; SL = standard length; DF1 = anterior dorsal fin; DF2 = posterior dorsal fin; PF = pectoral fin; AF = anal fin; CF = caudal fin; HH = head height; MG = mouth gape; BH = body height; [a] average aspect ratio for TL ($n = 54$) = 3.10 (SD = 0.28; SE = 0.04); [b] average aspect ratio for SL ($n = 54$) = 2.07 (SD = 0.18; SE = 0.02); [c] ANOVA male vs. female for SL$^3$ · $W^{-1}$ was also not significant.

specimens with a SL of 4 cm or above were either reproductively active (brooding and/or spent) or appeared physically capable of reproduction. Female gonad development was less well documented, due to sample size (Table 5). However, both female specimens in the SL 3.1–3.5 cm size class had gonads in the early stages of development, and all female *P. kauderni* over 4 cm SL ($n = 28$) were either currently producing egg masses ($n = 24$), including the smallest female over 4 cm SL (4.1 cm SL), or appeared to have recently spawned ($n = 4$). Overall, this suggests that mean length at first maturity of male and female *P. kauderni* is about 4 cm SL, as assumed above for the estimation of $t_0$.

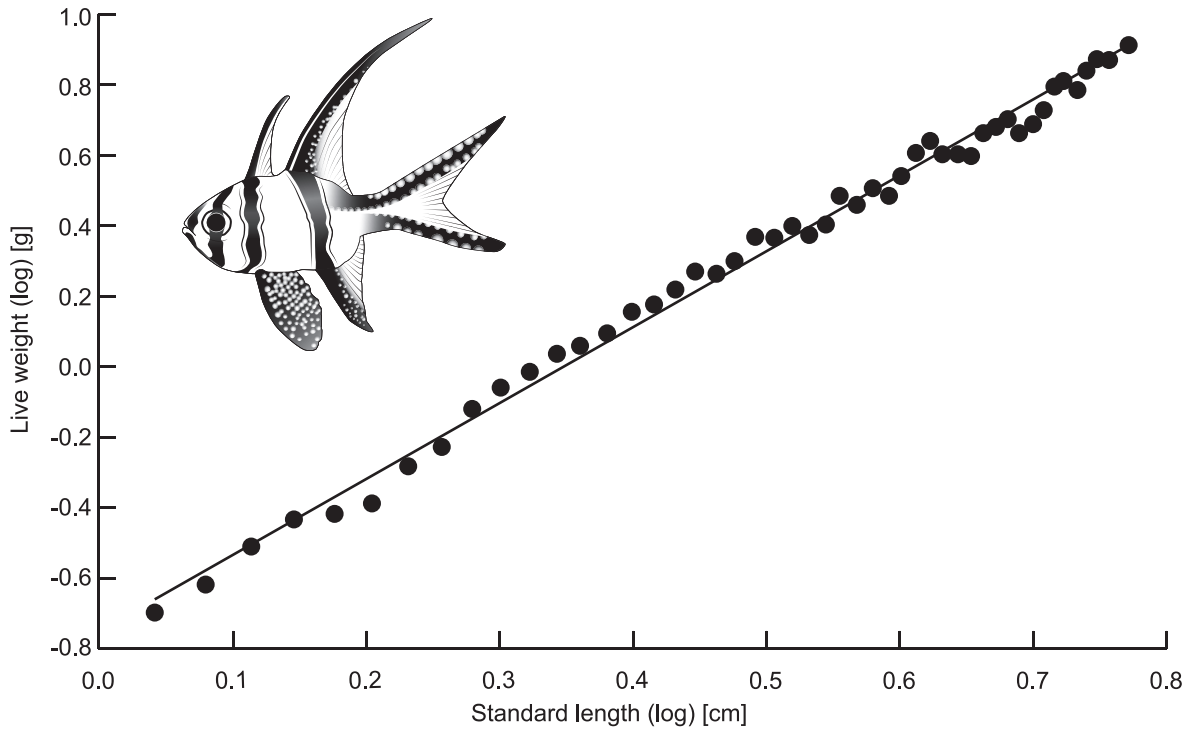**Feeding habits.** Quantitative gut content data for the sub-



**Fig. 5.** Data points and log transformed length–weight relation in Banggai cardinalfish, *Pterapogon kauderni*, i.e., $\log(W) = -0.744 + 2.151 \cdot (\log L)$, with $r^2 = 0.993$; $n = 1002$; Standard error SE of slope = 0.025
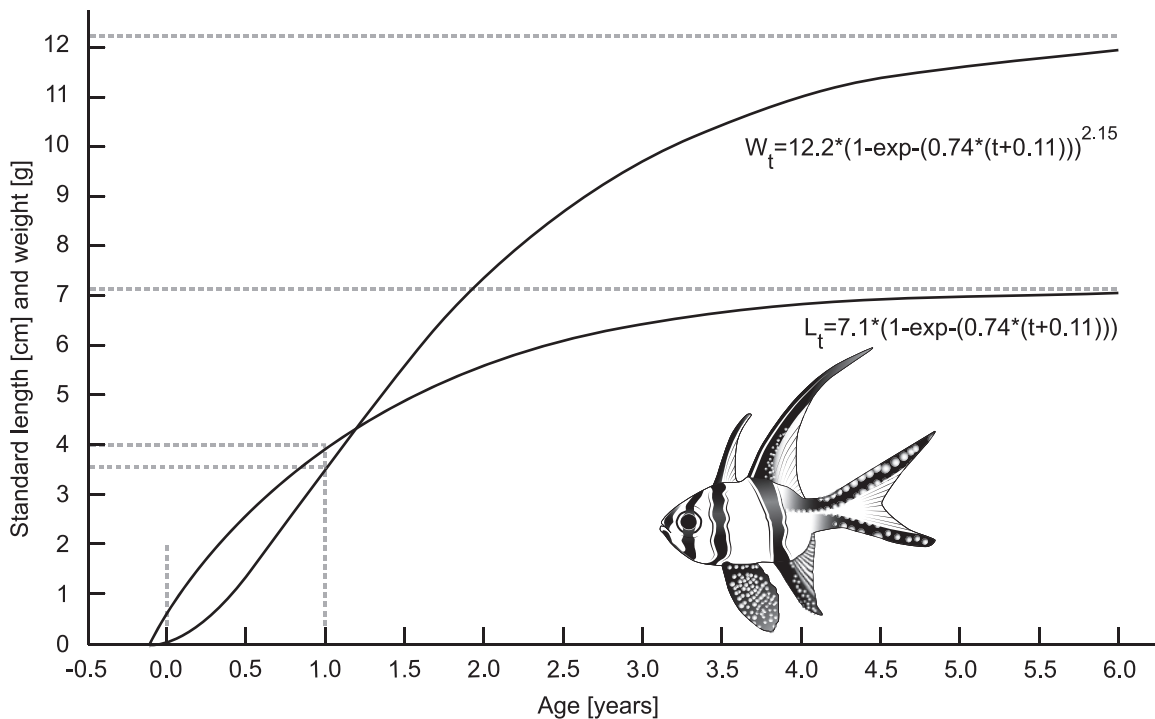


**Fig. 6.** Estimated mean growth curves in length and weight of Banggai cardinalfish, *Pterapogon kauderni*

adult (SL < 4.2cm, $n = 9$) and adult (SL $\geq$ 4.2 cm, $n = 21$) specimens are shown in Tables 7 and 8. Trophic level could not be calculated due to the lack of volume/weight data and the substantial proportion of unidentified items.

**DISCUSSION**

**Environmental parameters.** Water quality parameters were within normal limits for tropical marine fishes and coral reef ecosystems. The observed salinity (PSS 29–35)

was within the range for which growth and survival of *Pterapogon kauderni* juveniles reared in captivity was acceptable but higher than the value (PSS 27) for which growth and survival were highest (Madinawati et al. 2009). **Growth, mortality, and life cycle.** The estimated asymptotic length of 7.1 cm (SL) is higher than the longest fish recorded by the authors i.e., 6.6 cm, in Palu Bay, but appears reasonable for this species. Overall, the growth parameters and *M* that were estimated here suggest that

**Table 5**

Gonad development and fecundity of female Banggai cardinalfish, *Pterapogon kauderni*,
in Palu Bay ($n = 30$)

| Moon phase (date) | Sample no. | SL [cm] | W [g] | Fecundity | $W_g$ [g] | GSI |
|---|---|---|---|---|---|---|
| Full Moon (12 May) | 1 | 4.50 | 3.66 | 57 | 0.23 | 0.05 |
| | 2 | 4.50 | 4.03 | 92 | 0.32 | 0.07 |
| | 3 | 4.60 | 3.45 | 49 | 0.27 | 0.06 |
| | 4 | 4.70 | 4.45 | 51 | 0.28 | 0.06 |
| | 5 | 4.80 | 4.40 | — | 0.01 | 0.00 |
| | 6 | 5.00 | 5.40 | 50 | 0.40 | 0.08 |
| | 7 | 5.30 | 5.52 | — | 0.04 | 0.01 |
| | 8 | 5.60 | 6.68 | 77 | 0.64 | 0.11 |
| | Mean | 4.88 | 4.70 | 62.67 | 0.27 | 0.06 |
| Dark Moon (24 May) | 9 | 4.10 | 3.84 | 30 | 0.01 | 0.00 |
| | 10 | 5.40 | 6.83 | 53 | 0.06 | 0.01 |
| | 11 | 5.40 | 5.98 | 60 | 0.06 | 0.01 |
| | 12 | 5.40 | 6.78 | 50 | 0.19 | 0.04 |
| | 13 | 6.60 | 11.30 | 85 | 0.27 | 0.04 |
| | Mean | 6.36 | 7.89 | 68.13 | 0.17 | 0.03 |
| Waxing (17 July) | 14 | 3.30 | 2.08 | — | 0.03 | 0.01 |
| | 15 | 3.40 | 2.13 | — | 0.02 | 0.01 |
| | 16 | 4.50 | 4.94 | — | 0.08 | 0.02 |
| | 17 | 4.50 | 5.16 | 45 | 0.09 | 0.02 |
| | 18 | 4.60 | 4.37 | 46 | 0.08 | 0.02 |
| | 19 | 4.60 | 5.54 | — | 0.09 | 0.02 |
| | 20 | 4.90 | 5.39 | 60 | 0.14 | 0.03 |
| | 21 | 5.40 | 6.14 | 19 | 0.09 | 0.02 |
| | 22 | 5.70 | 7.73 | 86 | 0.19 | 0.03 |
| | Mean | 4.54 | 4.83 | 51.20 | 0.09 | 0.02 |
| Waning (31 July) | 23 | 5.20 | 3.13 | 64 | 0.29 | 0.06 |
| | 24 | 5.00 | 4.95 | 42 | 0.09 | 0.02 |
| | 25 | 4.90 | 3.25 | 39 | 0.11 | 0.02 |
| | 26 | 4.20 | 3.75 | 102 | 0.28 | 0.07 |
| | 27 | 4.40 | 2.92 | 28 | 0.09 | 0.02 |
| | 28 | 4.70 | 4.23 | 50 | 0.07 | 0.01 |
| | 29 | 4.80 | 3.52 | 55 | 0.13 | 0.03 |
| | 30 | 4.90 | 3.93 | 64 | 0.16 | 0.03 |
| | Mean | 4.76 | 3.71 | 55.50 | 0.15 | 0.03 |
| Overall mean | | 5.04 | 5.11 | 58.87 | 0.17 | 0.03 |

SL = standard length; $W$ = whole body weight; $W_g$ = gonad weight; GSI = gonadosomatic index = $W_g \cdot W^{-1}$.
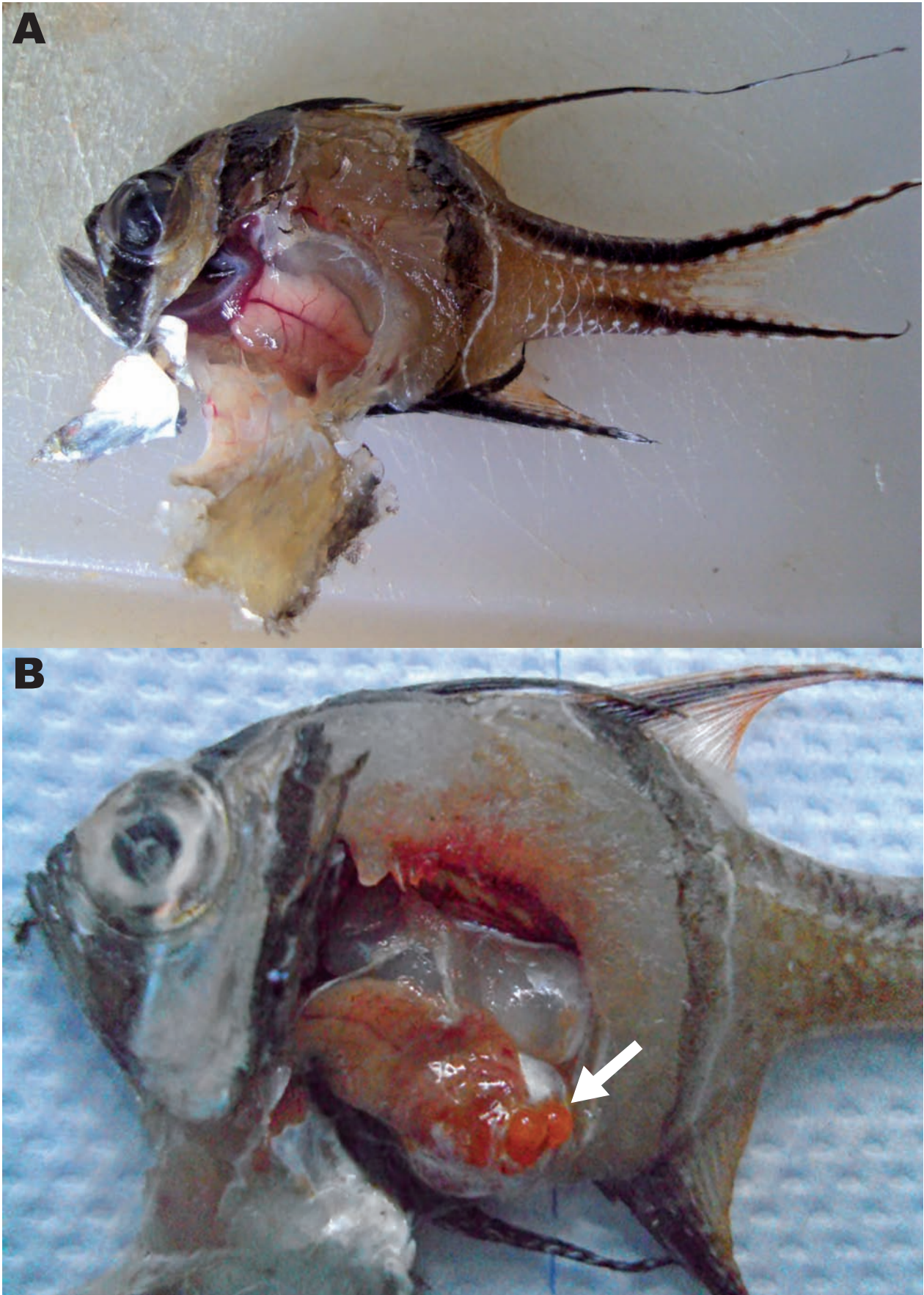
**Fig. 7.** Mature (single) gonads of male (**A**) and female (**B**) Banggai cardinalfish, *Pterapogon kauderni*, the white arrow indicates a developing egg mass

Banggai cardinalfish, *Pterapogon kauderni*, has a longevity of 3–5 years, and that first maturity is reached in a year, at a size of about 4 cm SL (Table 6, Fig. 7).

There are few estimates of growth parameters in cardinalfishes (Family Apogonidae) with which to compare our results. FishBase (Froese and Pauly 2013) provides growth parameters for only 5 'stocks' in 2 apogonid species, *Apogon imberbis* (L.) and *A. lineatus* Temminck et Schlegel, 1842 (Table 9). However, the mean value of ø' (see Equation 2) that can be calculated from these 5 $L_\infty/K$ pairs (ø' = 1.911) matches almost exactly the values of ø' = 1.928 computed from the growth parameters estimated for *P. kauderni* (Table 9) and hence our growth curves are compatible with what little is known of the growth of cardinalfishes.

Spawning occurs throughout the year, but may be more intensive around September–October. This being the calm season in most of the Banggai Archipelago, *P. kauderni* appears to behave as predicted by the 'triad hypothesis' of Bakun (1996), as modified by Pauly and Navaluna (1983), which states that fish reproduction, in monsoon-dominated tropical areas, peaks in the lulls between the monsoons. Abesamis and Russ (2010) report a similar pattern for reef fish in the Philippines, with "peaks in density and species richness of recruits during the [...] periods of the year when temperatures were highest and [...] winds were weak". This pattern would explain why recruits have been more commonly observed during field expeditions in October–December (for example during the collection of much of the data used in this analysis) compared expeditions in the early part of the year such as that reported by Vagelli and Erdmann (2002).

This pattern would also suggest that a cohort of *P. kauderni* hatched in October would reach first maturi-

**Table 6**

Male Banggai cardinalfish, *Pterapogon kauderni*, gonad development in Palu Bay (*n* = 50), with bold percentage values for each size class highlighting the relation between size (standard length) and maturation stage

| SL [cm] | Gonad development stage | | | | | *n* |
| | Undeveloped | Developing | Well developed | Mature | Spent | |
|---|---|---|---|---|---|---|
| 2.1–2.5 | **100** | 0.0 | 0.0 | 0.0 | 0.0 | 1 |
| 2.6–3.0 | **75.0** | 0.0 | 25.0 | 0.0 | 0.0 | 4 |
| 3.1–3.5 | **66.7** | **16.7** | 0.0 | 16.7 | 0.0 | 6 |
| 3.6–4.0 | 0.0 | **70.0** | **20.0** | 10.0 | 0.0 | 10 |
| 4.1–4.5 | 0.0 | 0.0 | **12.5** | **62.5** | 25.0 | 8 |
| 4.6–5.0 | 0.0 | 0.0 | 6.7 | **60.0** | **33.3** | 15 |
| 5.1–5.5 | 0.0 | 0.0 | 0.0 | **66.7** | **33.3** | 6 |

Values shown are the percentage of the age-class sample in each gonad development stage SL = standard length; $W_g$ = gonad weight [g]; *n* = number of specimens in each size class; Undeveloped = ($W_g < 0.2$ g); Developing = ($W_g \geq 0.2$ g); Well developed = ($W_g \geq 0.3$ g); Mature = ($W_g \geq 0.5$ g).

**Table 7**

Food items identified in the guts of sub-adult and adult Banggai cardinalfish, *Pterapogon kauderni*

| Food item | Total No. of occurrences | Percentage of guts | | | Approximate trophic level |
| | | Sub-adult | Adult | Overall | |
|---|---|---|---|---|---|
| Copepods | 120 | 66.7 | 47.6 | 53.3 | 2.2–3.2[a] |
| Cypris nauplii | 105 | 88.9 | 23.8 | 46.7 | 2.2–2.6[b] |
| *Conochilus volvox* | 90 | 44.4 | 52.4 | 50.0 | 2[a] |
| *Planktothrix agardhii* | 70 | 11.1 | 33.3 | 26.7 | 1[a] |
| *Enteromorpha* spp. | 45 | 11.1 | 19.0 | 16.7 | 1[a] |
| *Nitzschia* spp. | 25 | 11.1 | 9.5 | 10.0 | 1[a] |
| *Asterionella* spp. | 25 | 0 | 19.0 | 13.3 | 1[a] |
| *Euglena* spp. | 25 | 0 | 23.8 | 16.7 | 1[a] |
| *Allogromia* spp. | 20 | 0 | 9.5 | 6.7 | ≈ 2 |
| *Diadema* spp. | 20 | 11.1 | 14.3 | 13.3 | 2.4[b] |
| *Desmidium baileyi* | 5 | 0 | 4.8 | 3.3 | 1[a] |
| Unidentified matter | 105 | 55.6 | 57.1 | 56.7 | — |

Sub-adult = (SL < 4.2cm, *n* = 9); adult = (SL ≥ 4.2cm, *n* = 21); [a] Anonymous (2008); [b] Pauly and Christensen (1995).

ty in September of the following year (see also Fig. 6), notwithstanding suggestions that *P. kauderni* reaches first maturity in about 9 months (Vagelli 1999). Indeed, a 9-month lag between hatching and first maturity is hard to conceive for fishes living in the wild, as it would cause successive cohorts to be out of phase with recurrent annual events every 3 out of 4 years.

There are strong indications from the most recent surveys (December 2011 and June 2012, Ndobe et al. unpublished[*]) that most *P. kauderni* populations in the Banggai Archipelago are declining due to habitat degradation and loss, added to the strong fishing pressure quantified here. Monitoring and management of the fishery as well as addressing habitat loss and degradation (especially the loss of microhabitat, see Moore et al. 2012) are crucial to ensure the conservation of *P. kauderni*, which is at risk of extinction.

**Length–weight relation, other morphometrics and reproductive biology.** Growth of *Pterapogon kauderni* exhibits a negative allometry ($b < 3$). The equation $W = 0.18 \cdot L^{2.15}$ obtained for *P. kauderni* is close to the value predicted by the empirical equation for short and deep bodied fish in Froese (2006): $\log a = -1.358 \cdot b + 2.322$. A regression using data from 216 mainly juvenile or subadult specimens from Kadongo in Palu Bay (Moore, unpublished data) yielded a value of $b = 2.32$, which is also strongly allometric negative and close to the predicted value from Froese (2006).

The morphological data also confirm the results of Vagelli and Volpedo (2004) that there is no significant external morphological difference between male and female *P. kauderni*. The only parameter with a statistically significant difference between male and female *P. kauderni* was the mouthgape (MG/SL) ratio. Despite the high confidence level (99%) yielded by the ANOVA, the range of values for adult male *P. kauderni* was contained within the range for adult female specimens. The high level of overlap and individual variability in MG/SL values preclude the use of this characteristic for sex determination.

However, subtle sexual dimorphism may be masked by the relatively high variance associated with fin measurements in *P. kauderni*, itself due to the fact that these fins are extremely vulnerable to damage, especially the caudal and dorsal ones. Indeed fin damage is the main reason for rejection of market-sized specimens by buyers in the ornamental fish trade at the lowest (fishermen) trading level, and the reason why standard-, rather than total length is the reference length throughout this study.

The sex ratio of the sample, of 1.67 males for every female, confirmed Vagelli and Volpedo (2004) who, while finding no significant difference in sex ratio, also had a sample in which the number of males exceeded that of females. A greater number of males would potentially improve reproductive capacity at population level: while female *P. kauderni* are capable of producing eggs on a monthly basis, male *P. kauderni* require a period to recuperate after brooding for almost a month, or in the words of Kolm (2002): "females produce eggs faster than males can 'process' them".

Because of the pair-forming inherent in *P. kauderni* spawning, sexual maturity does not guarantee participation in reproductive activity. The gonad development data coupled with field observations suggest that reproductive success in *P. kauderni* may tend to be delayed relative to physical sexual maturity (gonad development), especially in males whose gonad development appears to take place at a smaller size/earlier age than brooding. Kolm (2001) reports that *P. kauderni* females seem to have a preference

**Table 8**

Food items and food types in the guts of individual groups/classes of Banggai cardinalfish, *Pterapogon kauderni*

| Group/class | No. of food items per gut | No. of food types per gut |
|---|---|---|
| Sub-Adult | 18.3 ± 8.8 | 3.0 ± 1.0 |
| Adult | 22.4 ± 12.3 | 3.1 ± 1.1 |
| Overall | 21.8 ± 11.3 | 3.1 ± 0.99 |
| Brooding males | 30.0 ± 14.1 | 3.5 ± 0.7 |

Values are mean ± standard deviation; sub-adult = (SL < 4.2 cm, $n = 9$); adult = (SL ≥ 4.2cm, $n = 21$).

**Table 9**

Growth parameter comparison in three species of cardinalfishes (see text)

| Species (sex) | TL$_\infty$ [cm] | $K$ [year$^{-1}$] | ø' | Location; Source |
|---|---|---|---|---|
| *Apogon lineatus* (F) | 8.5 | 1.23 | 1.949 | Off Niigata Prefecture; Kume et al. (2003) |
| *Apogon lineatus* (M) | 9.5 | 0.50 | 1.654 | |
| *Apogon lineatus* (F) | 8.7 | 1.12 | 1.928 | Tokyo Bay; Kume et al. (2003) |
| *Apogon lineatus* (M) | 11.9 | 0.37 | 1.719 | |
| *Apogon imberbis* (both) | 15.0 | 0.90 | 2.306 | Mediterranean; Pauly (1978)* |
| Mean | — | — | 1.911 | — |
| *Pterapogon kauderni* (M, F) | 10.7 | 0.74 | 1.928 | Central Sulawesi; this study |

* based on data in Garnaud (1962); TL$_\infty$ = total asymptotic length; K = rate at which asymptotic length is approached in the VBGF (Von Bertalanffy Growth Function); ø' = index of growth performance in terms of total length (TL) = $\log(K) + 2 \cdot \log(TL_\infty)$.

for (and produce larger eggs for) larger males. Both Vagelli (1999) and Kolm (2001) report that female *P. kauderni* are active in the courtship process, both in attracting and selecting a mate. This is likely to mean that in a situation where there are sufficient males, smaller males may have to wait (and grow) before mating, even if they are adults in terms of their gonad development.

Spawning does not guarantee reproductive success, as it is not uncommon for male *P. kauderni* to fail to brood to term. In addition, many factors affect recruit survival (Moore et al. 2012, Moore et al. unpublished*). These include the availability of microhabitat, especially sea anemones and *Diadema* sp. sea urchins, and the prevalence of predation, including cannibalism (observed both in the wild and in captivity, Moore et al. 2012). Recruit and juvenile survival seems to correlate negatively with adult *P. kauderni* density (Moore et al. unpublished*), most likely due to increased levels of cannibalism. Sea anemones (an effective refuge against cannibalism) and sea urchins are being exploited at an unprecedented rate due to recent (over the last 3–6 years) changes in human consumption patterns and their decline seems to have caused sharp declines in the *P. kauderni* population, including at unfished sites, wherever these key microhabitats have been substantially reduced (Moore et al. 2011, 2012, Moore et al. unpublished*).

In view of the complexity of these issues, the biological parameters related to reproductive output (e.g., fecundity/fertility and spawning frequency) are not sufficient to estimate the true resilience or the ability of the species to withstand exploitation. It should be remembered that with no pelagic dispersal stage, sedentary habit and depth-restricted habitat, populations lost through whatever set of circumstances are unlikely to ever recover/return naturally. A population on an island off Liang which had been reduced to 13 individuals by 2004 has not recovered and was locally extinct at this site in June 2012 (Ndobe et al. unpublished**). The high level of genetic population structure over distances as short as 2–5 km (Hoffman et al. 2005, Vagelli et al. 2009) mean that local extinctions can result in the total loss of entire genetic strains and make re-stocking a controversial issue (Ndobe et al. 2012).

**Feeding habits.** None of the specimens observed had an empty stomach; two brooding males had stomachs that were half full and full, which appears to be incompatible with the assumption (Vagelli 1999) that male *Pterapogon kauderni* fast while brooding the eggs (around 20 days) and larvae (around 9 days). This phenomenon requires further research; however, this should be based on specimens of opportunity, as the sacrifice of large numbers of brooding males could have a significant impact on the population of this endangered species.

The results in Tables 7 and 8 are consistent with the findings of Vagelli and Erdmann (2002), who, based on gut content analysis of *P. kauderni* collected in the Banggai Archipelago, stated that "*P. kauderni* is a generalist planktivore–carnivore [whose diet includes] representatives from the benthic and neustonic communities",

and compatible with the estimated trophic level of *P. kauderni* ± SE of 3.3 ± 0.41 currently indicated in FishBase (Froese and Pauly 2013). However a surprisingly large number of phytoplankton food items were also observed in the gut tracts of adults, though such items were rare in the gut tracts of sub-adults (Tables 7 and 8).

While crustaceans dominated gut content in terms of volume and number of items in both sub-adult and adult *P. kauderni*, decapods (cypris stage larvae) were more important in sub-adult gut content and copepods in adult gut content. Adult *P. kauderni* in Palu Bay appeared to feed on a wider variety of food items than sub-adults (Tables 7 and 8), but this could be an artefact of sample size (21 as opposed to 9 individuals).

Though several taxa recorded by Vagelli and Erdmann (2002) in gut samples from the *P. kauderni* endemic region (Banggai Archipelago) were not observed during this study, one taxon reported here, apparently for the first time in the diet of *P. kauderni,* is a sea urchin, most likely the long-spined sea-urchin *Diadema setosum*. In the Banggai Archipelago, sea urchins are abundant and groups of *Diadema setosum* provide the most common microhabitat or refuge for *P. kauderni,* though it has also been observed associated with other urchins of the Family Diadematidae, in particular *Echinothrix* sp. (Moore et al. 2012).

At the Mamboro site (Palu Bay), where *P. kauderni* was introduced, sea urchins (including *Diadema* sp.) are rare. It would therefore be reasonable to assume that the fact they were eaten by over 13% of the *P. kauderni* sample could indicate a positive preference. However the natural abundance of *Diadema setosum* and other members of the Diadematidae in the Banggai Archipelago would indicate that this predation, if it does indeed occur there, does not seriously affect the sea urchin population under natural conditions.

The condition of the items recorded as "unidentified matter" in Tables 7 and 8 was such that these items could not be precisely identified with the resources available. However, in almost all cases small fragments including small fish bones (mostly broken) were visible. While not quantifiable, these observations indicate that small fish do form part of the *P. kauderni* diet, confirming observations of predation of new recruits by adult *P. kauderni* immediately or shortly after release both in captivity and in the wild (Moore et al. 2012). Detailed bone studies and/or genetic (DNA) studies on the gut content of *P. kauderni* (preferably specimens of opportunity) could no doubt further elucidate the incidence of piscivory including cannibalism in the species. Such a study would also contribute to an informed evaluation of the trophic level of *P. kauderni,* and, in general, to the further definition of its niche.

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** See footnote on page 247.

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