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Ontogenetic shift in susceptibility to predators in juvenile northern abalone, *Haliotis kamtschatkana*

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ABSTRACT

Predation has been suggested as a major cause of juvenile mortality in benthic marine invertebrates. However, the extent to which juveniles are susceptible to predators is unknown for most species, and it remains unclear to what extent ontogenetic shifts in susceptibility to predators are common among marine invertebrates. This study examined the northern abalone *Haliotis kamtschatkana*, a species listed as threatened in British Columbia, Canada. Our goals were to characterize the diversity and abundance of species that prey on juvenile abalone and determine if abalone experience an ontogenetic shift in susceptibility to predators. Juvenile *H. kamtschatkana* were found to be susceptible to a broad variety of predators: 14 of the 37 potential predator species to which we offered juvenile abalone (≤28 mm shell length (SL)) consumed at least one juvenile abalone. Four of those species (three crabs and one seastar) consumed ≥10% of the juvenile abalone that were offered in the laboratory. These species were present at field sites where abalone are found, indicating that they have the potential to be significant predators of juvenile *H. kamtschatkana* in the wild. The most abundant predators were small crabs, especially *Lophopanopeus bellus* (black-clawed crabs) and *Scyra acutifrons* (sharp-nosed crabs). Juvenile *H. kamtschatkana* also experienced a pronounced ontogenetic shift in susceptibility to predators. The risk of predation for juvenile *H. kamtschatkana* decreased rapidly with increasing body size, especially over the 12–13 mm SL size range. Susceptibility remained low beyond 13 mm SL, indicating relatively low and unchanging levels of predation risk once the individual reaches this size. Although abalone are susceptible to several species during the first 1–2 years of life, predator effects on juvenile abalone abundance and microhabitat use may largely be attributable to the influence of only 1 or 2 predator species that can only kill abalone <13 mm SL.
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1. Introduction

In benthic marine invertebrates, mortality during juvenile life is high, often exceeding 90% (Gosselin and Qian, 1997). Juvenile mortality influences the number of individuals that survive to reproduce, the size and distribution of populations, as well as community structure (Sih et al., 1985; Gosselin and Qian, 1997; Moran, 1999; Osman and Whitlatch, 2004). Predation, competition, physiological stress, biological and physical disturbances, and delayed metamorphosis all contribute to mortality in juvenile invertebrates (Spight, 1976; Rumrill, 1990; Gosselin and Qian, 1997; Hunt and Scheibling, 1997; Moran, 1999). Of these, predation is the best documented mortality factor (Gosselin and Qian, 1997; Hunt and Scheibling, 1997).

Ontogenetic shifts in susceptibility to predators occur in part because the juveniles progressively grow larger and develop more resistant protective structures such as shells, carapace or tegument, and because predators with feeding structures that are effective at handling small juveniles are less efficient at handling large juveniles (Rumrill, 1990; Gosselin and Qian, 1997; Osman and Whitlatch, 2004). A partial refuge from predators may therefore be reached if juveniles grow large enough to exceed the handling capabilities of predators that specifically feed on small juveniles (Gosselin, 1997). As they grow, however, juveniles may then become susceptible to a different set of predators (Hunt and Scheibling, 1997; Osman and Whitlatch, 2004). Ontogenetic shifts in distribution in benthic invertebrates, from cryptic microhabitats during the early juvenile stage to exposed microhabitats later in life, have therefore been proposed as an adaptation to minimize exposure to juvenile mortality factors, especially predation (Hines and Pearse, 1982; Peterson, 1982; Gosselin, 1997). Predators specifically consuming juvenile invertebrates may therefore play an important role in structuring the abundance and distribution of invertebrate populations. However, while ontogenetic shifts in susceptibility to predators have been

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reported for some marine invertebrates, it is not clear how common such shifts might be.

Knowledge of the role of predation as a cause of juvenile mortality and of ontogenetic shifts in susceptibility to predators can be particularly useful for understanding the population dynamics of a given species, and for managing species that are threatened or commercially harvested. For instance, several species of abalone (marine gastropods in the genus *Haliotis*) have declined substantially in abundance since the 1970s, in some cases by as much as 99% (National Marine Fisheries Service, 2006). The initial dramatic declines in most abalone species were primarily due to overharvesting. However, populations of some species have failed to recover despite the closure of all harvesting. In the case of the northern abalone (*H. kamtschatkana*), populations of this species continued to decline after the closure of all harvesting and the species is now listed as "threatened" by the Committee on the Status of Endangered Wildlife in Canada (Campbell, 2000; Lessard et al., 2004). Small juvenile abalone can experience substantially higher mortality rates than larger juveniles and adults (Kojima, 1995; Shepherd, 1998). In addition, small juveniles of some abalone species can be killed by a variety of predators (Shepherd and Breen, 1992), but the role of juvenile mortality as a factor in the ontogenetic shift in mortality rates or in the poor recovery of abalone populations is largely unknown. The ontogeny of vulnerability to predators is unknown in most abalone species, and in some species, such as *H. kamtschatkana*, even the identity of the predators of juvenile abalone remains unknown.

We therefore set out to examine the susceptibility of juvenile *Haliotis kamtschatkana* to predators. Little is known about the predators that attack *H. kamtschatkana* during juvenile life (first 3 years) (Sloan and Breen, 1988; Campbell, 2000). Predators known to feed upon juveniles of other species of abalone include gastropods (Shepherd and Breen, 1992), polychaete worms (Naylor and McShane, 1997), anemones (Shepherd, 1998), wrasses (Shepherd et al., 2000), crabs, seastars and lobsters (Schiel and Welden, 1987). In addition, adult *H. kamtschatkana* are killed by several predators, including sea otters (*Enhyra lutris*), crabs (*Cancer productus*), octopuses (*Octopus dolfleini*), seastars (*Pycnopodia helianthoides*) (Emmett and Jamieson, 1988; Sloan and Breen, 1988; Campbell, 2000; Watson, 2000), and fish such as wolf-eels (*Anarrhichthys ocellatus*) and cabezon (*Scorpaenichthys marmoratus*) (Emmett and Jamieson, 1988). Juvenile *H. kamtschatkana* may therefore also be susceptible to a broad set of predators. The specific goals of this study were therefore to (1) identify the predators of juvenile *H. kamtschatkana*, (2) determine the abundance and size-structure of predator populations in the field, and (3) determine if juvenile *H. kamtschatkana* experience a shift in susceptibility to predators during juvenile life.

2. Methods

2.1. Study sites and organism

This study took place in Barkley Sound, located on the West Coast of Vancouver Island, British Columbia, Canada. Field work was carried out at 3 sites (Fig. 1): Eagle Bay (48°50.252′ N, 125°08.670′ W), Brady's Rock (48°49.940′ N, 125°09.021′ W), and Bamfield Harbour entrance (48°50.561′ N, 125°07.995′ W) all of which supported wild abalone. All laboratory work was carried out at the Bamfield Marine Sciences Centre (BMSC). Abalone used in this study were obtained from the Bamfield Huu-Ay-Aht Community Abalone Project (BHCAP) hatchery located in Bamfield, and all broodstock used by the hatchery to produce juveniles originate from Barkley Sound. The abalone size classes used in these experiments, all within a ≈3 – 28 mm shell length (SL) size range, were selected to cover a broad range of juvenile sizes, but were also constrained by availability from the BHCAP hatchery at the time of experimentation. The selected size classes were based on abalone year classes spawned in the hatchery and were common size ranges that would be available to predators in the field.

2.2. Potential predators

To determine which of the species that coexist with *Haliotis kamtschatkana* in the field might prey on juvenile abalone, we set out to collect specimens of all animal species present at field sites where *H. kamtschatkana* is found and which might be capable of killing juvenile abalone ≤28 mm SL. We therefore collected 37 species of potential predators from Eagle Bay and Brady's Rock and brought these to the laboratory. Potential predators were identified to genus and species using identification keys by Hart (1973), Lamb and Edgell (1986), Jensen (1995), Kozloff (1996), Harbo (1999), and by Lamb and Hanby (2005). Crabs, snails, sea urchins and worms were hand picked by SCUBA divers. Fish were captured underwater in dip nets by SCUBA divers, in beach seines, or using hook and line fishing. All SCUBA diving collections occurred at depths of 5–15 m. Whenever possible, at least 4 individuals of each species of potential predator were tested. Some species, however, were uncommon in the field, in which cases fewer than 4 individuals were obtained for testing. Four fish species, *Enophrys bison* (buffalo sculpin), *Scorpaenichthys marmoratus* (cabezon), *Ophiodon elongates* (lingcod), and *Anarrhichthys ocellatus* (wolf-eel), were not obtained for use in the laboratory trials as they were rarely observed in the field and difficult to capture by SCUBA diving, beach seining or fishing.

Crab size was measured at the widest part of the carapace. Hermit crabs were weighed with their shells (total wet weight) as they could

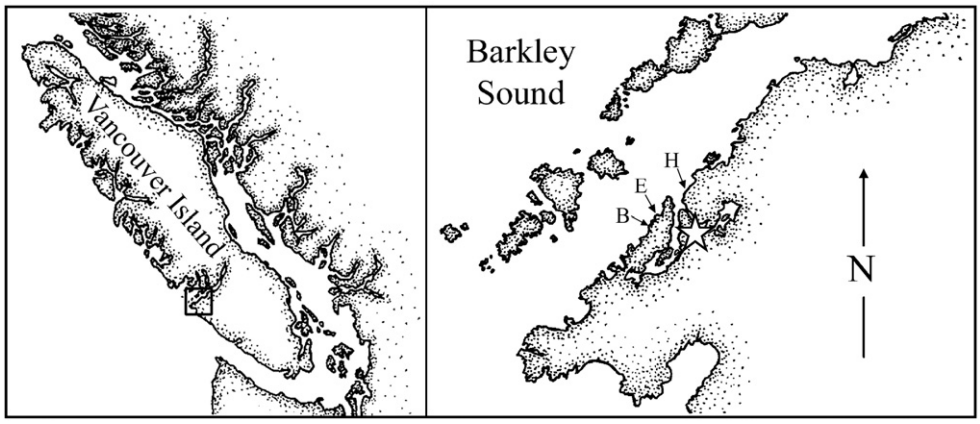

Fig. 1. Map of Barkley Sound, British Columbia, Canada. Bamfield Marine Sciences Centre is represented by the star symbol. The 3 field sites, Brady's Rock, Eagle Bay and Bamfield Harbour entrance, are represented in the figure by B, E, and H respectively. Map modified from Gosselin and Chia (1995).

not be removed from the shells without causing damage; total wet weight is not an ideal measure of hermit crab size, it is used here only as an indicator of hermit crab body size. We measured the diameter of the central disk of sea stars and the test diameter of sea urchins. Fish size was determined by measuring the distance from snout to caudal fork. Snails were measured from the apex of their shell to the most anterior tip of the aperture. Worms were measured from the anterior tip of the body to the posterior point.

Each collected animal was placed in a plastic cage, with four rectangular windows covered by a 600 μm mesh screen. Three sizes of plastic containers were used: 16×16×3 cm, 34×22×17 cm, and 33×33×8 cm. The cage size used for any given predator was chosen based on the size of the animal being tested, to ensure the predator had sufficient space to move about. Fish species were tested either in one of the two larger sized plastic containers or in an open seawater tank (117×119×36 cm). Potential predators were held in these containers with flowing seawater without food for 72 h after collection to acclimate to their new surroundings prior to feeding trials. Each cage then received 3 abalone <5 mm SL, 2 abalone 5–10 mm SL, 2 abalone 10–15 mm SL, and one abalone 15 – 25 mm SL; cages received more individuals of the smaller size classes to compensate for their smaller size and thus reduced likelihood of being encountered by the potential predators. The abalone were examined again after 24, 48 and 72 h for evidence of predation.

2.3. Population abundance and size-structure of predators in the field

Field surveys were carried out in the summer of 2005 to determine the population abundance and size structure of the species that were most likely to pose a substantial threat as predators of juvenile *Haliotis kamtschatkana,* based on the above predation experiment. Time constraints limited our ability to survey all species that might on occasion kill a juvenile *H. kamtschatkana*; we therefore surveyed predator species that had consumed on average 10% or more of juvenile *H. kamtschatkana* in the above potential predator experiments. The cut-off level of 10%, which corresponds to an average of less than 1 juvenile consumed per individual predator, allowed us to focus our efforts on the predators likely to consume enough juvenile abalone to have a significant influence on the population dynamics of the abalone in the wild. Thus, 6 predator species were surveyed: *Lophopanopeus bellus* (black-clawed crab), *Scyra acutifrons* (sharp-nosed crab), *Cancer productus* (red rock crab), *Pycnopodia helianthoides* (sunflower star), *Amphissa columbiana* (wrinkled Amphissa) and *Rhacochilus vacca* (pile perch). Transect surveys were carried out by SCUBA divers on two separate occasions at each of the 3 field sites (Eagle Bay, Brady's Rock and Bamfield Harbour entrance). During each survey, a transect line was set out along the bottom at depths of 7–10 m. Sampling took place within 1 m^2 quadrats placed at 2 m intervals along the transect line. Rocks were overturned to search for predators. Predators found were measured using plastic callipers to an accuracy of 0.1 mm. Once a predator was measured and recorded, it was placed approximately 0.5 m outside the sampling quadrat to avoid sampling the individual more than once. A total of 13 quadrats were sampled at each site: 5 quadrats were sampled at each site during a first sampling period (22 May – 2 June) and 8 quadrats were sampled at each site on a second sampling period (4 – 22 June). In addition, during the transect surveys all *R. vacca* observed to come within 1 m of the transect line were recorded.

2.4. Relationship between predator size and prey size

To determine the relationship between predator size and the sizes of juvenile abalone they could consume, we collected specimens of 5 of the 6 species that killed ≥10% of juvenile abalone in the first experiment. These predators were collected from Eagle Bay and Brady's Rock from 15 May - 1 July 2005 and brought to the laboratory. *Rhacochilus vacca* (pile perch) were not obtained for these laboratory trials as they were rarely observed at the field sites in 2004 and were not found at the field sites in 2005. For this experiment, we used the following size range of each predator: *Lophopanopeus bellus,* 8–26 mm carapace width (CW); *Scyra acutifrons*, 8–32 mm CW; *Cancer productus,* 65–101 mm CW; *Pycnopodia helianthoides,* 13–53 mm central disk diameter (CD); *Amphissa columbiana,* 10–16 mm SL. These represent the broadest ranges of sizes that could be found at the field sites from May to July that summer. These animals were brought back to the laboratory, placed in separate cages and held without food for 72 h to acclimate prior to experimentation. The abalone size classes offered to these predators were: 10–12 mm SL, 15–19 mm SL, 21–24 mm SL, and 25–28 mm SL. Juvenile abalone <10 mm SL were not used in these experiments as they were not available from the hatchery at the time. After the 72 h acclimation period, 3 abalone from the smallest size class were added to each cage. The number of consumed abalone was recorded after 48 h. If a predator ate at least one abalone from a size class, the predator was then offered the next larger abalone size class. If an individual predator did not consume any abalone of a given size class, the predator was again offered 3 other abalone of the same size class. If this second time the predator still did not succeed in consuming an abalone of that size class, feeding trials for that individual predator were considered complete and the range of size classes consumed was recorded. Incomplete attacks (i.e. partly chipped or cracked abalone shells) were not recorded as successful predation. When a crab moulted during a trial, the trial was terminated and a new individual was tested.

2.5. Ontogeny of susceptibility to predators

A predation susceptibility index, as defined by Gosselin (1997), was calculated to determine how susceptibility to predators in the field changes as juvenile abalone grow. The index value for a given abalone size represents the density, at the given site, of juvenile abalone predators that would feed on an abalone of this size. To determine the index value for a given abalone size, first the size-range of *Lophopanopeus bellus* capable of killing juvenile abalone of this size was established from the above abalone size feeding trials. Second, field densities (number of individuals m^{-2}) of *L. bellus* within this size range were determined using size-frequency data obtained from the field surveys. The two steps were then repeated for *Scyra acutifrons*, *Cancer productus* and *Pycnopodia helianthoides*. Since our prey selection experiments indicated *Amphissa columbiana* do not to pose an important threat to healthy juvenile *H. kamtschatkana*, this species was not included in the predation susceptibility index calculations. The resulting densities (number of individuals m^{-2}) of the 4 predators were totalled, resulting in the index value for that given abalone size. The predation susceptibility index is thus an indicator of the risk of predation for juvenile *Haliotis kamtschatkana* of a given size at a given field site.

3. Results

3.1. Potential predators

Thirty-seven potential predator species were tested to determine if they would eat juvenile *Haliotis kamtschatkana*. Of these, 14 species consumed at least one juvenile abalone in the trials (Table 1). Seven species successfully attacked on average 10% or more of the juvenile abalone that were offered: the crabs *Cancer productus*, *Lophopanopeus bellus, Scyra acutifrons,* and *Pelia tumida*, the seastar *Pycnopodia helianthoides,* the snail *Amphissa columbiana*, and the fish *Rhacochilus vacca. Cancer productus* consumed an average of 67% of the juvenile abalone available to them, the highest proportion consumed by any predator species in our experiments. *Cancer productus* left behind only fragments of juvenile abalone shells or sometimes no traces at

Table 1
Potential predators of juvenile *Haliotis kamtschatkana*

Potential predator species	Predator size range tested	n	Abalone sizes offered (mm SL)	Average % of abalone that died
Controls	No Predator	63	1–25	1.9±0.1
Annelida				
Polychaeta				
Halosydna brevisetosa	22–40 mm AP	4	1–20	0±0
Platyhelminthes				
Turbellaria				
Pseudostylochus ostreophagus	28 mm AP	1	1–20	0
Mollusca				
Gastropoda				
Prosobranchia				
Neogastropoda				
Muricidae				
Ceratostoma foliatum	6.14–11.6 g	4	1–20	0±0
Columbellidae				
Amphissa columbiana	11–16 mm SL	6	1–25	15.0±0.1
Arthropoda				
Crustacea				
Decapoda				
Cancridae				
Cancer productus	58–95 mm CW	3	1–25	67.0±0.4
Majidae				
Scyra acutifrons	16–30 mm CW	6	1–25	22.0±0.4
Mimulus foliates	22 mm CW	1	1–25	0
Paguridae				
Pagurus hemphilli	1.75–10.37 g	5	1–25	0±0
Pagurus caurinus	0.995 g	1	1–15	0
Paguristes turgidus	Not recorded	1	1–20	0
Pisidae				
Pelia tumida	16 mm CW	1	1–20	43.0
Porcellanidae				
Pachycheles rudis	10–17 mm CW	4	1–25	0±0
Petrolisthes eriomerus	10 mm CW	2	1–15	0±0
Xanthidae				
Lophopanopeus bellus	10–25 mm CW	9	1–25	35.0±0.3
Echinodemata				
Asteroidea				
Forcipulatida				
Asteriidae				
Evasterias troschelii	11–24 mm CD	4	1–20	8.0±0.1
Orthasterias koehleri	5–35 mm CD	6	1–25	4.0±0.1
Pycnopodia helianthoides	6–31 mm CD	4	1–20	32.0±0.4
Spinulosida				
Solasteridae				
Crossaster papposus	47–55 mm CD	2	1–25	0±0
Solaster dawsoni	21–60 mm CD	4	1–25	5.0±0.1
Solaster stimpsoni	43–55 mm CD	2	1–25	0±0
Valvatida				
Asteropseidae				
Dermasterias imbricate	36–50 mm CD	5	1–25	5.0±0.1
Echinoidea				
Echinoida				
Strongylocentrotidae				
Strongylocentrotus droebachiensis	63–55 mm TD	3	9–16	0±0
Strongylocentrotus franciscanus	85–125 mm TD	13	6–25	0±0
Strongylocentrotus purpuratus	60–65 mm TD	3	7–16	0±0
Chordata				
Osteichthyes				
Teleostei				
Perciformes				
Embiotocidae				
Rhacochilus vacca	65–82 mm SF	5	1–25	17.0±0.2
Embiotoca lateralis	70–100 mm SF	3	1–25	8.0±0.2
Cymatogaster aggregate	45–95 mm SF	5	1–25	2.0±0.1
Micrometras frenatus	65–90 mm SF	6	1–25	2.0±0.1
Gobiidae				
Coryphopterus nicholsi	5–65 mm SF	3	1–5	0±0
Scorpaeniformes				
Cottidae				
Artedius fenestralis	85 mm SF	1	1–25	0
Asemichthys taylori	50–65 mm SF	2	1–5	0±0
Leptocottus armatus	150–190 mm SF	2	1–25	0±0
Oligocottus maculosus	42–50 mm SF	4	1–5	0±0
Hexagrammidae				
Hexagrammos decagrammus	200–250 mm SF	2	7–21	0±0
Hexagrammos stelleri	70–115 mm SF	2	1–25	0±0

Table 1 (*continued*)

Potential predator species	Predator size range tested	n	Abalone sizes offered (mm SL)	Average % of abalone that died
Scorpaeniformes				
Scorpaenidae				
Scorpaenichthys marmoratus	90 mm SF	1	1–25	0
Sebastes melanops	200 mm SF	1	7–25	0

Abbreviations in the table are as follows: AP = anterior to posterior, CW = carapace width, CD = central disk diameter, SF = standard fork length measured from snout to caudal fork, TD = test diameter, SL = shell length, n = number of replicate cages, each with one predator (except controls). In the controls, 7 out of 387 juvenile abalone died during the experiment.

all, and *L. bellus* and *S. acutifrons* left small abalone shell fragments or shells chipped near the whorl. One *P. tumida* (dwarf teardrop crab) consumed 43% of the juvenile abalone. This, however, was the only specimen of *P. tumida* we found in the field over the 2 years of this study; given the very low abundance in the field, this species was not investigated in further experiments. When attacking juvenile abalone, *Pycnopodia helianthoides* consumed the abalone tissue and left behind clean intact shells. *Amphissa columbiana* produced 1 or 2 holes approximately 1 mm in diameter in the soft tissues of the abalone they attacked; they did not drill the shell nor did they consume the entire abalone.

Seven other predator species consumed 1–9% of the abalone offered: *Dermasterias imbricata*, *Evasterias troscheli*, *Orthasterias koehleri*, *Solaster dawsoni*, *Cymatogaster aggregata*, *Embiotica lateralis,* and *Micrometras frenatus.* Abalone that had been preyed upon by the fish *C. aggregata, E. lateralis* and *M. frenatus* had damaged shells or were crushed into many fragments. *C. aggregata* and *M. frenatus,* as well as *Rhacochilus vacca*, only consumed juvenile abalone smaller than 10 mm SL.

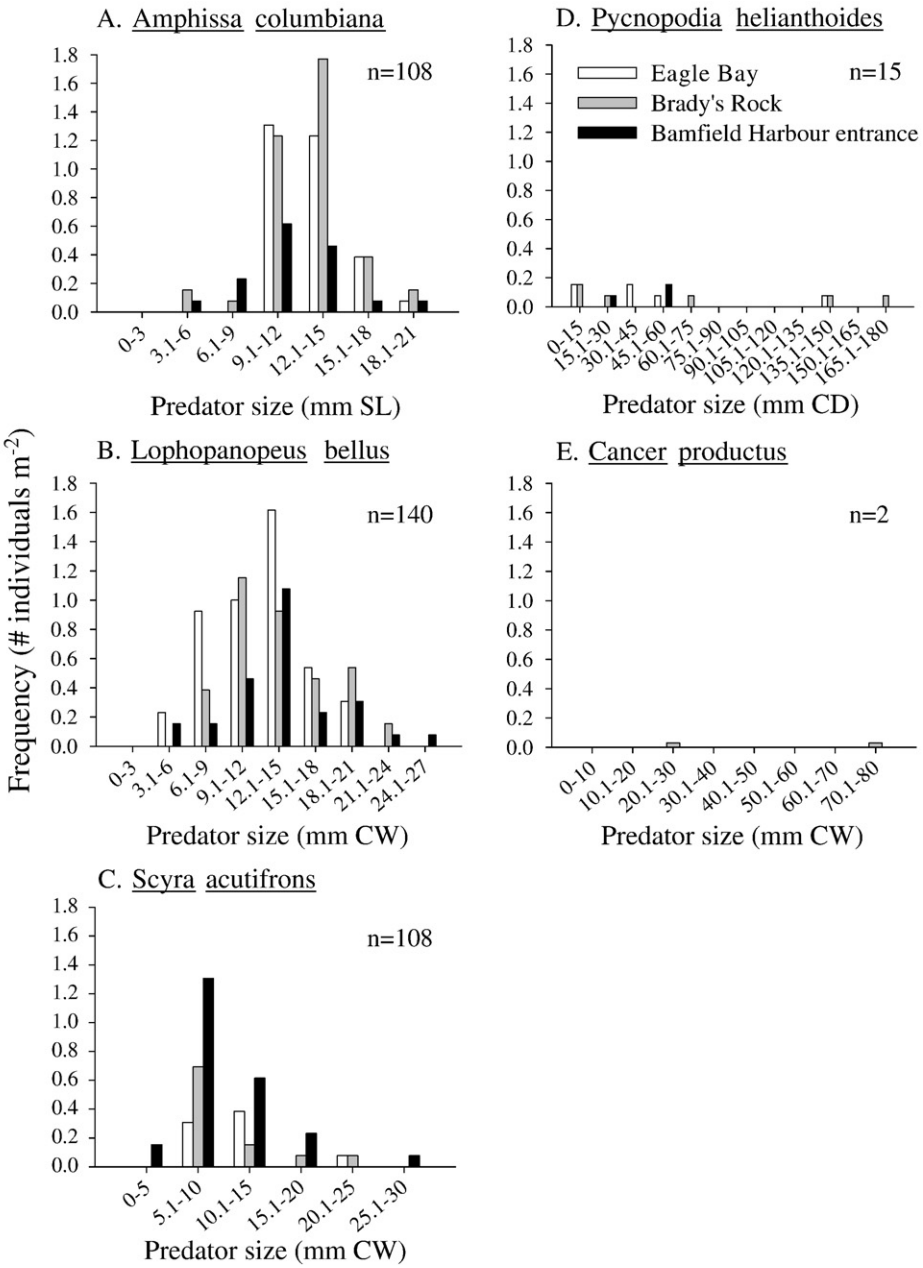

Fig. 2. Size frequency distributions of predators of juvenile *Haliotis kamtschatkana* in the field. (A) *Amphissa columbiana.* (B) *Lophopanopeus bellus*. (C) *Scyra acutifrons.* (D) *Pycnopodia helianthoides.* (E) *Cancer productus*. Note: CW = carapace width, SL = shell length, CD = central disk diameter.

Table 2
Comparison of size frequency distributions among the 3 field sites using two-sample Kolmogorov-Smirnov tests; n represents the number of size categories into which predators were separated

	Z	*P*	n
Amphissa columbiana			
Eagle Bay vs Brady's Rock	0.286	0.919	7
Eagle Bay vs Bamfield Harbour entrance	0.286	0.919	7
Brady's Rock vs Bamfield Harbour entrance	0.286	0.919	7
Lophopanopeus bellus			
Eagle Bay vs Brady's Rock	0.111	1.000	9
Eagle Bay vs Bamfield Harbour entrance	0.333	0.662	9
Brady's Rock vs Bamfield Harbour entrance	0.333	0.662	9
Scyra acutifrons			
Eagle Bay vs Brady's Rock	0.167	1.000	6
Eagle Bay vs Bamfield Harbour entrance	0.333	0.778	6
Brady's Rock vs Bamfield Harbour entrance	0.333	0.778	6
Pycnopodia helianthoides			
Eagle Bay vs Brady's Rock	0.083	1.000	12
Eagle Bay vs Bamfield Harbour entrance	0.167	0.985	12
Brady's Rock vs Bamfield Harbour entrance	0.250	0.769	12

3.2. Population abundance and size-structure of predators in the field

Of the 6 predator species that were surveyed, only 3 species were common at the field sites (Fig. 2). Total population densities of *Amphissa columbiana*, *Lophopanopeus bellus*, and *Scyra acutifrons* at the field sites ranged from 2.9 – 4.5 individuals m^{-2}, 2.5 – 4.6 individuals m^{-2}, and 1.0 – 2.4 individuals m^{-2}, respectively. *Scyra acutifrons*, however, were often in crevices, and crevices were present in ≈60% of the area surveyed at Brady's Rock and Bamfield Harbour entrance, and ≈40% of the Eagle Bay site. Although all such crevices were inspected as closely as possible during our surveys, the cryptic behaviour of this species may have resulted in an under-estimation of their abundance. Densities of *Pycnopodia helianthoides* (0.2 – 0.5 ind. m^{-2}) and *Cancer productus* (0.0 – 0.1 ind. m^{-2}) were low at all 3 field sites. Only two *C. productus* (25 mm CW and 75 mm CW) were found at Brady's Rock, buried in sand; none were found at the 2 other field sites during our surveys. The size-frequency distributions of these predators did not differ significantly among the 3 field sites (Table 2). Finally, *Rhacochilus vacca* (pile perch) were not observed at any of the field sites during these surveys.

3.3. Relationship between predator size and prey size

In addition to data on the abundance and size-structure of predator populations, the relationships between predator size and the size of the largest juvenile abalone that was consumed were needed to calculate the predation susceptibility index for juvenile *Haliotis kamtschatkana*. This experiment allowed us to identify the range of predator sizes that could feed on a given size class of juvenile *H. kamtschatkana*. *Rhacochilus vacca* were not included in size vulnerability experiments as this species was not found in the field that summer. Of the 20 *Amphissa columbiana* tested in this experiment, none ate any abalone. All individuals of the other 4 predator species tested in this experiment consumed the smallest abalone size classes offered but differed in the largest size class they could kill. Where appropriate, the relationship between predator size and the largest abalone size the given predator could consume was determined by linear regression analysis; only predators that consumed abalone were included in the regressions.

Lophopanopeus bellus smaller than 20 mm CW consumed juvenile abalone size classes up to 12 mm SL; one large *L. bellus* measuring 26 mm CW was able to eat slightly larger abalone (Fig. 3A). Each *Cancer productus* used in this experiment consumed all sizes of

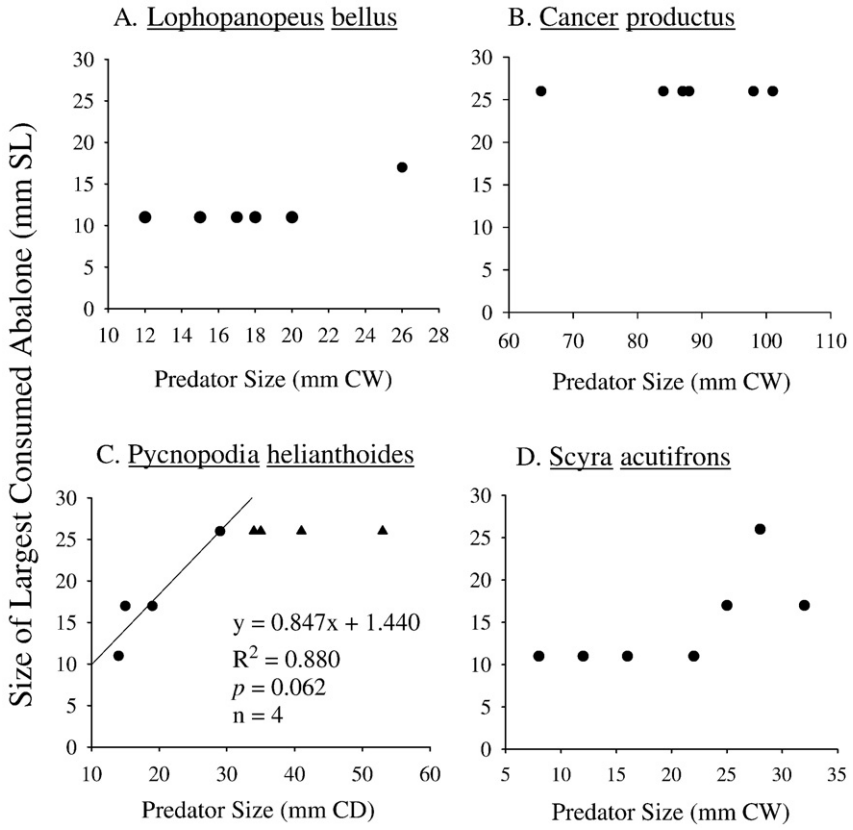

Fig. 3. Relationship between predator size and the average size of the largest juvenile *H. kamtschatkana* size consumed. Note: CW = carapace width, CD = central disk diameter. Triangle symbols in (D) represent values that were not used to calculate the regression (see text).

abalone offered (Fig. 3B). Among *Pycnopodia helianthoides* ≤29 mm CD, the size of the largest abalone consumed increased linearly with seastar size (Fig. 3C), whereas all *P. helianthoides* ≥29 mm CD consumed the full range of abalone sizes that were offered. All *Scyra acutifrons* smaller than 22 mm CW consumed abalone size classes up to 10–12 mm SL; for *S. acutifrons* ≥22 mm CW, however, the size of the largest abalone killed increased with crab size (Fig. 3D).

3.4. Ontogeny of susceptibility to predators

The predation susceptibility index (PSI) value for a given abalone size represents the total density (individuals m^{-2}) of juvenile abalone predators (*Lophopanopeus bellus, Scyra acutifrons, Cancer productus* and *Pycnopodia helianthoides*) that would feed on an abalone of the given size at the given site. Based on the feeding trials, we considered all *L. bellus* ≤20 mm CW to be able to consume abalone up to 12 mm SL, and all *L. bellus* >20 mm CW to consume abalone up to 19 mm SL. All sizes of *C. productus* present at the field sites were considered to be able to consume the full range of abalone sizes up to 28 mm SL. For *P. helianthoides*, the largest abalone size that would be consumed by seastars <29 mm CD was determined by the regression equation between largest abalone consumed and seastar size (Fig. 3C); all *P. helianthoides* ≥29 mm CD were considered to consume the full range of abalone sizes up to 28 mm SL. Finally, all *S. acutifrons* ≤22 mm CW were considered to consume juvenile abalone sizes up to, but not exceeding, 12 mm SL; *S. acutifrons* 23 – 27 mm CW were considered to consume abalone up to 19 mm SL, and *S. acutifrons* ≥28 mm CW were considered to consume the full range of abalone size up to 28 mm SL.

The PSI decreased dramatically over the 10–15 mm SL size range at all 3 field sites (Fig. 4A). Only slight differences were apparent among field sites, the PSI for abalone ≤13 mm SL being highest at the Eagle Bay site and slightly lower at the Brady's Rock and Bamfield Harbour entrance sites. At all sites, the density of predators capable of killing abalone ≤13 mm SL was ≈6 predators per m^{-2}; this value decreased to ≈0.5 predators m^{-2} for juvenile abalone ≥13 mm SL, decreasing very slightly from that point on up to 28 mm SL.

PSI calculations were then repeated without data from *L. bellus*, the most abundant predator in the field at all 3 sites, to distinguish the contribution of *L. bellus*, relative to the other 3 predators, to the PSI for juvenile *H. kamtschatkana*. Excluding *L. bellus* from the calculations resulted in a noticeably lower PSI for all sizes of juvenile abalone at all 3 sites, but a distinct drop in the PSI over the 12 – 13 mm SL size range was still apparent (Fig. 4B).

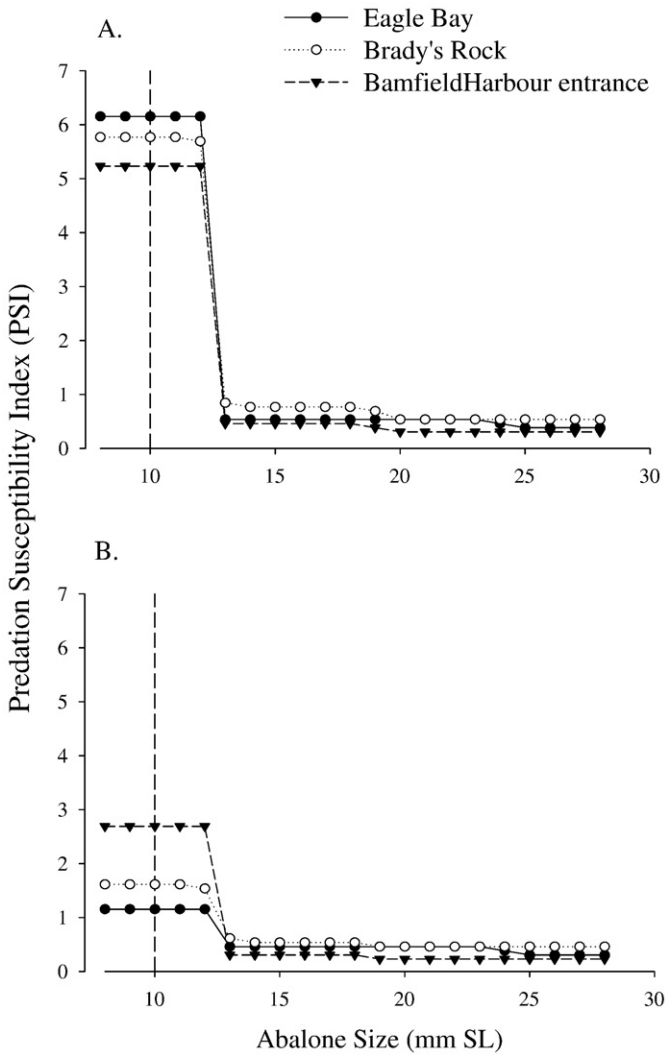

Fig. 4. Predation susceptibility index (PSI) for juvenile *Haliotis kamtschatkana* at 3 field sites in Barkley Sound, B.C. The predation susceptibility index consists of the total density (number of individuals m^{-2}) of all juvenile abalone predators (*Lophopanopeus bellus, Scyra acutifrons, Cancer productus* and *Pycnopodia helianthoides*). (A) represents the ontogenetic change in PSI including all four juvenile abalone predator species, and (B) represents the ontogenetic change in PSI excluding *L. bellus*. Index values were calculated for every 1 mm shell length increment. The dashed line at 10 mm represents the smallest size of abalone that was tested in the laboratory with the four predators; PSI values for abalone <10 mm SL are extrapolations.

4. Discussion

4.1. Predators of juvenile Haliotis kamtschatkana

Juvenile *Haliotis kamtschatkana* can be killed by several species of fish and invertebrate predators, but only a small number of predators, mostly decapod crustaceans, appear to constitute significant threats. Of the 37 species of potential predators tested, 14 consumed juvenile *Haliotis kamtschatkana* ≤28 mm SL. Seven of these consumed at least 10% of juvenile abalone: *Lophopanopeus bellus, Scyra acutifrons, Cancer productus, Pycnopodia helianthoides, Amphissa columbiana, Rhacochilus vacca* and *Pelia tumida*.

Lophopanopeus bellus and *Scyra acutifrons* readily killed and consumed small juvenile abalone in our experiments, but these crab species do not appear to grow large enough in this area to kill *H. kamtschatkana* larger than 28 mm SL; these two species would therefore prey exclusively on juvenile abalone. However, *C. productus* and *P. helianthoides* prey on juvenile and adult *H. kamtschatkana* (Campbell, 2000; Emmett and Jamieson, 1988, this study) and therefore constitute threats to *H. kamtschatkana* through most or possibly all of benthic life in this species.

Amphissa columbiana was the only gastropod to attack juvenile *H. kamtschatkana*, consuming small amounts of the tissues of some abalone in the first feeding experiment. However, in the second set of feeding experiments, examining the relationship between predator size and prey size, *A. columbiana* did not consume any abalone. Other gastropod species, including neogastropod species in the genera *Nassarius, Buccinum, Kelletia*, and *Pleuroploca,* have been reported to prey on abalone species such as *Haliotis rubra* and *Haliotis scalaris* in Australia (Shepherd, 1973). In a review of the causes of natural abalone mortality, Shepherd and Breen (1992) reported that weakened, stressed or aged abalone comprise the majority of reported cases of all gastropod predation where the gastropod inserts its proboscis into the abalone soft tissues, which is what we observed with *A. columbiana*. *Amphissa columbiana* are scavengers and will attack carcasses releasing body fluids (Lamb and Hanby, 2005). It therefore seems likely that those abalone attacked in the first experiment by *A. columbiana* were already unhealthy. Consequently, although *A. columbiana* are abundant in the field, they may not pose a threat to healthy juvenile *H. kamtschatkana*. *Rhacochilus vacca*, on the other

hand, will readily consume juvenile abalone, but this fish species was rarely observed in areas where *H. kamtschatkana* are found and thus may not play an important role as predators of juvenile abalone. However, fishes in the wrasse family (Shepherd, 1998) as well as rays and small sharks (Shepherd and Breen 1992) are known to be predators of juvenile *H. laevigata* and *H. scalaris* in Australia. Therefore, other fish species not tested in the present study might also prey upon juvenile *H. kamtschatkana*. Finally, one *Pelia tumida* consumed 43% of the juvenile abalone offered. This, however, was the only *P. tumida* we found in the field, precluding replication of the feeding trials with this crab species. Individuals of this species might therefore willingly prey on juvenile abalone, but due to their near absence at our field sites it would not have been a significant predator of juvenile abalone.

Our findings from the laboratory feeding experiments, combined with the data on predator abundance in the field, suggest decapod crustaceans constitute the most important group of predators of juvenile *H. kamtschatkana*. Decapod crustaceans are often major predators of small juvenile invertebrates because these crustaceans often have high abundances, broad vertical distributions (e.g. intertidal and subtidal), high mobility, the ability to crush protective structures (Seed and Hughes, 1995; Gosselin and Qian, 1997; Yamada and Boulding, 1998; Schenk and Wainwright, 2001), and need to obtain large quantities of food (Juanes, 1992; Gosselin and Qian, 1997). Among the species identified in the present study as most likely to constitute substantial threats to juvenile *H. kamtschatkana*, *Lophopanopeus bellus* was the most abundant at all 3 field sites. These cryptic crabs are found under rocks and among gravel (Kozloff, 1996; Harbo, 1999), substrates inhabited by juvenile abalone (Mortimor et al., 2003). Often when rocks were overturned, *L. bellus* were seen quickly moving to find new shelter. These motile predators can move rapidly to attack juvenile *H. kamtschatkana* in the field (personal observations). *Scyra acutifrons* was the second most abundant predator in our surveys; this crab is also commonly found between and underneath rocks (Jensen, 1995; Harbo, 1999). For both of these crab species, all individuals found in our field surveys were ≤30 mm CW, and most were ≤20 mm CW. Only the largest individuals of these 2 species could kill juvenile *H. kamtschatkana* ≥13 mm SL, and those larger size classes of these crab species were rare in the field. As a result, *L. bellus* and *S. acutifrons* would mostly be a threat to juvenile *H. kamtschatkana* <13 mm SL. *Cancer productus* also readily killed and consumed juvenile abalone, but they were either absent or in very low densities at all 3 study sites, and therefore may constitute a modest threat to juvenile *H. kamtschatkana*.

Pycnopodia helianthoides were present at all 3 field sites, but in low densities. Of those present, 33 – 50% were ≤30 mm CD; this portion of *P. helianthoides* populations can only kill juvenile *H. kamtschatkana* ≤28 mm SL and are therefore not a threat to abalone that have grown beyond 28 mm SL. In addition, *P. helianthoides* will feed on juvenile abalone, but they are generalist feeders that would prefer sea urchins and bivalves as prey (Shivji et al., 1983). *Pycnopodia helianthoides* may therefore also be a relatively modest threat to juvenile *H. kamtschatkana*.

4.2. Ontogenetic shift in susceptibility to predators

Predation susceptibility index values for all 3 field sites show a sharp decrease in risk of predation for juvenile *Haliotis kamtschatkana* with increasing body size. Juveniles ≥13 mm SL were at a considerably lower risk of predation than smaller sized abalone. Index values changed very little beyond 13 mm SL, indicating relatively low and unchanging levels of predation risk after the individual has reached this size. In the hatchery, *H. kamtschatkana* takes 1–2 years to reach a size of 12–13 mm SL (D. Renfrew, personal communication); assuming comparable growth rates in the field, *H. kamtschatkana* would require at least one year to complete this shift and escape the early period of high predation risk. In comparison, the susceptibility of the intertidal snail *Nucella ostrina* to juvenile predators decreases to low levels after only ≈3–4 months, at a size of 7 mm SL (Gosselin, 1997).

This ontogenetic shift in risk of predation in juvenile *H. kamtschatkana* is largely due to changes in susceptibility to *Lophopanopeus bellus* and *Scyra acutifrons* as the abalone grow. The most common size classes of these 2 crab species at all 3 field sites were unable to kill abalone >12 mm SL. Juvenile *H. kamtschatkana* <12 mm SL were most at risk of predation from *L. bellus* due to the high abundance of this crab species in the field. This is particularly apparent when densities of *L. bellus* are removed from the calculations of the PSI; the ontogenetic shift in susceptibility to predators is still apparent, but is considerably reduced (Fig. 4B). Finally, 3 fish species that consumed abalone (*Raccochilus vacca, Cymatogaster aggregata*, and *Micrometras frenatus*) only consumed abalone <10 mm SL in the first experiment. These predators were not included in the PSI calculations due to low abundance at the field sites or low attack rates in the laboratory, and thus are likely to be only occasional predators of *H. kamtschatkana*. Nevertheless, any predation from these species would likely cause the ontogenetic shift to be even more pronounced than shown in Fig. 4B.

The ontogenetic shift in susceptibility to predators in *H. kamtschatkana* is consistent with available information on microhabitat use by this species. Sloan and Breen (1988) reported that juvenile *H. kamtschatkana* <10 mm SL are highly cryptic, whereas juveniles ≈10 to 70 mm SL have a weak tendency for cryptic habitats, a finding supported by our personal observations in the field. This cryptic distribution of small juveniles would no doubt reduce the likelihood of being killed by predators during the early period of high susceptibility. Similarly, juvenile red abalone, *H. rufescens*, remain relatively cryptic under boulders until 1–2 cm SL and then move into open crevices (Hines and Pearse, 1982). Juvenile *H. laevigata* also remain hidden under boulders in the wild until they reach approximately 2.5 years of age; *H. laevigata* juveniles then move into more exposed crevice locations (Shepherd, 1998). The correspondence between the shifts in predation risk and microhabitat use in *H. kamtschatkana* suggest predation risk during juvenile life is a substantial selective pressure and that juvenile predators may be an important cause of mortality.

4.3. Implications for the persistence and enhancement of Haliotis kamtschatkana populations

The findings of this study are of significance for abalone populations in the wild. *Haliotis kamtschatkana* are found in waters from Japan to Northern Mexico at depths ranging from lower intertidal to 35 m (Lamb and Hanby, 2005). The potential predators identified in the present study overlap in geographical range with *H. kamtschatkana* (Lamb and Hanby, 2005). The present findings are therefore likely to apply to much of the range of *H. kamtschatkana*. Predator species composition may nevertheless differ in certain regions, particularly in warmer southern regions (e.g. California and Northern Mexico).

Although predation is not the only factor influencing the persistence and health of wild abalone populations (Sloan and Breen, 1988; Campbell, 2000; Watson, 2000; Griffiths, 2006), our findings nevertheless identify predators as an important feature of the environment to be considered when determining conservation strategies for wild abalone populations. The abundance and population size-structure of species that prey on juvenile abalone during the first 1–2 years of life could have a determining influence on the overall abundance of abalone. For example, sites with the highest densities of small predatory crustaceans, such as *Lophopanopeus bellus* and *Scyra acutifrons*, are likely to be poor recruitment sites for *H. kamtschatkana*.

Efforts to help wild abalone populations recover will benefit from an understanding of the timing of ontogenetic shifts in susceptibility to juvenile predators. This information can help assess the value of

conservation strategies such as the identification of field sites most favourable to abalone recruitment, the removal of specific predators from field sites at the time of recruitment, the provision of artificial shelters in the field to protect juvenile abalone until they reach the size at which predation risk shifts, or the determination of the size at which hatchery-reared juvenile abalone should be outplanted to maximise survival.

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References

Campbell, A., 2000. Review of northern abalone, *Haliotis kamtschatkana*, stock status in British Columbia. In: Campbell, A. (Ed.), In workshop on rebuilding abalone stocks in British Columbia. Can. Spec. Publ. Fish. Aquat. Sci., vol. 130, pp. 41–50.

Emmett, B., Jamieson, D., 1988. An experimental abalone transplant project in Barkley Sound, British Columbia. Fish. Bull. 87, 95–104.

Gosselin, L.A., 1997. An ecological transition during juvenile life in a marine snail. Mar. Ecol. Prog. Ser. 157, 185–194.

Gosselin, L.A., Chia, F.S., 1995. Characterizing temperate rocky shores from the perspective of an early juvenile snail: the main threats to survival of newly hatched Nucella emaginata. Mar. Biol. 122, 625–635.

Gosselin, L.A., Qian, P.Y., 1997. Juvenile mortality in benthic marine invertebrates. Mar. Ecol. Prog. Ser. 146, 265–282.

Griffiths, A.M., 2006. Investigations into mortality in juvenile *Haliotis kamtschatkana* (northern abalone) and factors that affect outplanting. MS dissertation, University of Victoria, British Columbia, Canada.

Harbo, R.M., 1999. Whelks to whales. Coastal marine life of Oregon, Washington, British Columbia and Alaska. Harbour Publishing, British Columbia, Canada.

Hart, J.L., 1973. Pacific fishes of Canada. Fish. Res. Board. Can. Bull. 180.

Hines, A.H., Pearse, J.S., 1982. Abalones, shells, and sea otters: dynamics of prey populations in central California. Ecology 1547–1560.

Hunt, H.L., Scheibling, R.E., 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Mar. Ecol. Prog. Ser. 155, 269–301.

Jensen, G.C., 1995. Pacific coast crabs and shrimps. Sea challengers, Monterey California.

Juanes, F., 1992. Why do decapod crustaceans prefer small-sized molluscan prey? Mar. Ecol. Prog. Ser. 87, 239–249.

Kojima, H., 1995. Evaluation of abalone stock enhancement through the release of hatchery-reared seeds. Mar. Fresh. Ecol. 46, 689–695.

Kozloff, E.N., 1996. Marine invertebrates of the Pacific Northwest. University of Washington Press.

Lamb, A., Hanby, B.P., 2005. Marine life of the Pacific Northwest. A photographic encyclopedia of invertebrates, seaweeds and selected fishes. Harbour Publishing, British Columbia, Canada.

Lamb, A., Edgell, P., 1986. Coastal fishes of the Pacific Northwest. Harbour Publishing, British Columbia, Canada.

Lessard, J., Brouwer, D., Mortimor, J.P., 2004. Survey of northern abalone, *Haliotis kamtschatkana,* populations in Southeast Barkley Sound, British Columbia, October 2002. Can. Spec. Publ. Fish. Aquat. Sci. 2685.

Moran, A.L., 1999. Size and performance of juvenile marine invertebrates: potential contrasts between intertidal and subtidal benthic habitats. Am. Zool. 39, 304–312.

Mortimor, J.P., Henderson, C.R., Elliott, G.R.D., 2003. Night and day surveys of a northern abalone (*Haliotis kamtschatkana*) population in Eagle Bay, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 2482.

National Marine Fisheries Service, 2006. White Abalone Recovery Plan *(Haliotis sorenseni*), DRAFT. National Marine Fisheries Service, Long Beach, CA.

Naylor, J.R., McShane, P.E., 1997. Predation by polychaete worms on larval and post-settlement abalone *Haliotis iris* (Mollusca:Gastropoda). J. Exp. Mar. Biol. Ecol. 214, 283–290.

Osman, R.W., Whitlatch, R.B., 2004. The control of the development of a marine benthic community by predation on recruits. J. Exp. Mar. Biol. Ecol. 311, 117–145.

Peterson, C.H., 1982. Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. Mar. Biol. 66, 159–170.

Rumrill, S.S., 1990. Natural mortality of marine invertebrate larvae. Ophelia 32 (1–2), 163–198.

Schenk, S.C., Wainwright, P.C., 2001. Dimorphism and the functional basis of claw strength in six brachyuran crabs. J. Zool. Soc. London. 225, 105–119.

Schiel, D.R., Welden, B.C., 1987. Responses to predators of cultured and wild red abalone, *Haliotis rufescens,* in laboratory experiments. Aquaculture 60, 173–188.

Seed, R., Hughes, R.N., 1995. Criteria for prey size-selection in molluscivorous crabs with contrasting claw morphologies. J. Exp. Mar. Biol. Ecol. 193, 177–195.

Shepherd, S.A., 1973. Studies on southern Australian abalone (genus *Haliotis*) ecology of five sympatric species. Australian J. Mar. Freshw. Res. 24, 217–257.

Shepherd, S.A., 1998. Studies on southern Australian abalone (genus *Haliotis*) XIX: long-term juvenile mortality dynamics. J. Shellfish. Res. 17 (3), 813–825.

Shepherd, S.A., Breen, P.A., 1992. Mortality in abalone: its estimation, variability and causes. In: Shepherd, SA, Tegner, MJ, Guzman del Proo, SA (Eds.), Abalone of the world; biology, fisheries and culture, pp. 276–304. Oxford, UK.

Shepherd, S.A., Preece, P.A., White, R.W.G., 2000. Tired nature's sweet restorer? Ecology of abalone (*Haliotis spp*.) stock enhancement in Australia. *In* Workshop on rebuilding abalone stocks in British Columbia. Edited by A. Campbell. Can. Spec. Publ. Fish. Aquat. Sci. 85–95.

Shivji, M., Parker, D., Hartwick, B., Smith, M.J., Sloan, N.A., 1983. Feeding and distribution study of the sunflower sea star *Pycnopodia helianthoides* (Brant 1835). Science 37 (2), 133–140.

Sih, A., Crowley, P., McPeek, M., Peetranka, J., Strohmeier, K., 1985. Predation, competition and prey communities: a review of field experiments. Ann. Rev. Ecol. Syst. 16, 269–311.

Sloan, N.A., Breen, P.A., 1988. Northern abalone, *Haliotis kamtschatkana* in British Columbia: fisheries and synopsis of life history information. Can. Spec. Pub. Fish. Aquat. Sci. 103, 6–10.

Spight, T.M., 1976. Ecology of hatching size for marine snails. Oecologia 24, 283–294.

Watson, J., 2000. The effects of sea otters (*Enhydra lutris*) on abalone (*Haliotis spp.*) populations. In: Campbell, A. (Ed.), In workshop on rebuilding abalone stocks in British Columbia. Can. Spec. Publ. Fish. Aquat. Sci., vol. 130, pp. 123–132.

Yamada, S.B., Boulding, E.G., 1998. Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. J. Exp. Mar. Biol. Ecol 220, 191–211.